

Environmental change in the coastal environment: challenges for the selection and propagation of filter feeding species in aquaculture, stock enhancement and environmental rehabilitation.

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Abstract Selection of species for aquaculture, fishery stock enhancement and environmental rehabilitation or restoration in the coastal zone requires consideration of the fact that species have evolved over geological time whereas changes in the coastal environment have occurred predominantly over recent historical time, often with the largest changes occurring within the past decades of human activity. The evolutionary issue is particularly noted with filter feeding molluscs, where extant species supporting both major natural fisheries and aquaculture have ancient lineages and evolved in environments that may have differed considerably from the locally turbid, nutrient enriched, disturbed (through watershed change and local activity) waters in which they now survive. We cannot presume that native species are strongly selected to survive in the environments in which they currently reside. Neither can we presume that they will be successful candidates for aquaculture, fishery stock enhancement, environmental rehabilitation (the restoration of ecological services in community structure), or environmental restoration (restoration of native community structure with associated ecological services). Watershed and coastal use impacts have, over recent human history, altered community structure in coastal waters, and diminished the ability of surviving community members to perform the ecological services that are one end product of their evolution. A challenge is therefore presented to students of intensive species culture, extensive fishery enhancement, and ecological rehabilitation or restoration: how to best use the tools of husbandry in concert with large and small scale environmental manipulation to promote progress in the designated area of interest? Ecological rehabilitation or restoration centered on cornerstone filter feeding species must employ local environmental rehabilitation, but this will only be successful if it is accompanied by a wider commitment to watershed management protocols that protect all life history stages, including the delicate early stages. A numerical argument for this approach, based on Paulik life history models, will be presented. Intensive aquaculture, by comparison, may be able to progress in marginal environments where delicate early life history stages are cultured in controlled situations, thus limiting mortality, before transfer to open systems. Fishery enhancement resides between these options, where a dual role of supplementing local reproduction is balanced against increased exploitation of commercial product.

Key words: bivalve molluscs, aquaculture, stock enhancement, environmental rehabilitation

Selection of species for aquaculture, fishery stock enhancement and environmental rehabilitation or restoration in the coastal zone requires consideration of the fact that species have evolved over geological time whereas changes in the coastal environment have occurred predominantly over recent historical time, often with the largest changes occurring within the past decades of human activity. A history of the traits driving selection of aquaculture species is given by Mann (1984a), and emphasizes the roles of species low in the food chain with physiologically tolerant adult stages and reproductive cycles that are easily subject to control and manipulation. Filter feeding bivalve molluscs fit these requirements.

The evolutionary time frame is particularly important with filter feeding molluscs, where extant species supporting both major natural fisheries and aquaculture have ancient lineages and evolved in environments that may have differed considerably from the locally turbid, nutrient enriched, disturbed (through watershed change and local activity) waters in which they now survive. This grouping includes extant oysters, mussels and clam species of commercial interest, especially those under active aquaculture. Oysters are a notably primitive form, exemplified by the loss of the second adductor to the monomyarian form. They have survived by migrating over geological time into geologically ephemeral estuarine environments, being served in this purpose by their complex life history employing pelagic larval forms. Recent commentaries on the evolution of the larval form summarized in McEdward (1995) and Hall and Wake (1999) emphasize why the combination of these "dual" evolutionary paths of the adult and larval forms in response to stage specific selection pressures has left the "primitive" bivalves so well equipped to respond to rapid (in the evolutionary time frame) changes in local environments that would typically lead to local extinction. Oyster populations in the Chesapeake Bay provide an excellent example of successful invasion in geologically ephemeral environments. The current

bay is a product of 8,000 years of Holocene sea level rise (Haven and Whitcomb, 1983; Hargis 1999). Recent fossil deposits including oyster shells can be found many kilometers offshore of the current shoreline in depths corresponding to earlier sea level stanzas. These illustrate both the changing environment with sea level rise over recent geological time and the accompanying "migration" of the oyster populations.

Substantial changes have occurred in both the watershed biology and physical environment of the Chesapeake Bay since the arrival of European colonists. The past four centuries have been marked by deforestation for agriculture, urban development on the shoreline of the bay or its tributaries, and increasing, and mostly uncontrolled exploitation of the fishery resources for much of the period. The human population in the Chesapeake Bay watershed has reached approximately 15 million with projected growth rates at double the national average for the next twenty years. The record of watershed change is abundant from both direct public records and indirect evidence from sources such as pollen records of land use change. Extensive records of recent and current land use patterns are available from the U.S. Environmental Protection Agency world wide web site at <http://www.chesapeakebay.net/bayprogram> with summary information changes in land use practices such as no till farming and shoreline buffer zones designed to reduce non point source sediment and nutrient runoff into the bay. In addition, changes in the bay and tributary morphologies have resulted from river dredging and shoreline development. Fundamental changes in the biology of the aquatic system have been caused by over fishing and critical environmental degradation. Failure to return shell to the bottom after oyster harvest has resulted in once significant three dimensional reef structure being reduced to patchy monolayers of substrate for extant oyster populations with accompanying change in both the complexity of the associated communities and the ecological services they provide (compare data from Baylor 1894 with

Luckenbach, Mann and Wesson 1999). This rapid, in an evolutionary time frame, change in local environment has clear implications for changes in community structure in the local community (Mann, 2001). We cannot presume that target species are strongly selected to survive in the environments in which they currently reside, as opposed to those in which they evolved. Neither can we presume that they will be successful candidates for aquaculture, fishery stock enhancement, environmental rehabilitation (the restoration of ecological services in community structure), or environmental restoration (restoration of native community structure with associated ecological services) in these rapidly changing environments. Indeed, this realization has been a driving force for the use of non-native species in both intensive aquaculture and fishery enhancement in recent decades (see Mann 1979, 1984b; Rosenfield and Mann, 1992).

A challenge is presented to students of intensive species culture, extensive fishery enhancement, and ecological rehabilitation or restoration: how to best use the tools of husbandry in concert with large and small scale environmental manipulation to promote progress in the designated area of interest? Ecological rehabilitation or restoration centered on cornerstone filter feeding species must employ local environmental rehabilitation, but this will only be successful if it is accompanied by a wider commitment to watershed management protocols that protect all life history stages, including the delicate early stages. The cost-benefits of each component of this restoration or rehabilitation strategy on the performance of a target species in culture or as a fishery are of direct interest. Can specific management actions be targeted at improving the response of the most susceptible life history stages to specific stresses? A numerical approach to this question is offered by consideration of Paulik life history models.

Paulik (1973) provide a useful conceptual tool for quantitative descriptions of the stock - recruit relationship in commercially exploited

marine fish species. Examples are discussed in Rothschild (1986). The graphical presentation of the concept, the Paulik diagram, consists of a four-quadrant plot. Quadrant 1, proceeding in a clockwise direction, is the desired stock-recruitment function. It is constructed from the end product of the other three quadrants. The second quadrant relates stock size to egg production and thus incorporates absolute number of fertile individuals, demographics through size specific fecundity, and the integrated effect of environment and prior feeding history on fecundity. The third quadrant relates egg production to larval production and incorporates spawning synchrony, spawning behavior where applicable, and density dependent fertilization success. The fourth quadrant describes the relationship of larval production to recruitment to the subsequent spawning generation. In fish populations this does not involve a transition from pelagic to attached or sessile benthic form, although a larval to adult metamorphosis is included. Application of Paulik models to benthic invertebrates with complex life histories dictates that this quadrant include larval growth and loss to predation and dispersal to hostile environments, settlement and metamorphosis, and post settlement growth to sexual maturity. Applications of such models to cultured benthic species are somewhat rare, yet the structure provides a useful tool for integrating studies of individual life history stages. Of particular importance in the context of stresses acting on coastal ecosystems is the ability to quantitatively describe the impact of a stress on one life history stage on a separate but subsequent life history stage. In the coastal zone where increasing eutrophication and other pressures can disproportionately impact one life history stage over another in isolated test challenges the utility of this holistic approach is both obvious and powerful.

Mann and Evans (1998) adapted the approach of Paulik (1973) in estimation of oyster, *Crassostrea virginica*, standing stock, larval production and advective loss in relation to

observed recruitment in the James River, Virginia. The present 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 sub-optimal feeding conditions, and (3) varying loss to advection related to estuarine tidal exchange. All three variants are examples of the effect of possible environmental stresses on critical life history stages. Others can be examined by the method described below as appropriate to the location under stress.

Methods

To summarize and simplify Mann and Evans (1998), recruitment to the 25mm size class is estimated from larval supply thus:

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

where:

F_{tot} is total egg production and 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 40mm 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 :

if $S > 13.5$, $F_s = 1.0$

if $S < 13.5$, 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 present 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 present 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} .

$(1 - exch)^{2d}$: Mann and Evans (1998) estimated retention of the larvae within the James River during planktonic development using the three dimensional flow model of Hamrick (1992a, 1992b) to provide source and sink data at scales within the estuary. For the present illustration a simple dilution function 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 $(1 - exch)^{2d}$ 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 2 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 sub-optimal value of 25 days based on assumed reduction of feeding and hence growth in low salinity and/or high turbidity regions.

$(1 - L_{mort})^d$ 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 insures 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 pre-metamorphic 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 critical to successful recruitment (Morales-Alamo and Mann 1990). Consider that a shell layer one-cm thick covering one-sq. m of bottom has a volume of 10L. For the current illustration a premise is adopted that a shell layer a minimum of one cm thick is required to offer a suitable substrate. P_{sub} is estimated thus:

$$\begin{aligned} &\text{if shell volume} > 10L \text{ m}^{-2}, P_{sub} = 1.0 \\ &\text{if shell volume} < 10L \text{ m}^{-2}, \\ &P_{sub} = 0.1 \times \text{Shell Vol. (in liters)} \end{aligned}$$

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 employed.

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 present application the value is set at 0.20.

Recruitment 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:

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

$(1 - J_{mort})^{dp}$ modifies this estimator for post settlement mortality and growth rates, both of which are known to be size dependent (Roegner and 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 % over a 28 days 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 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 pre-metamorphosis larvae to 25 mm size class, including a P_{met} value of 0.20 is 99.84 %, or a proportional survival of 0.0016.

Demographics for a virtual population were generated from a data set describing Horse Head Reef in the upper James River for the period 1993-1996 (National Oceanic Atmospheric Administration Chesapeake Bay Stock Assessment funds to R. Mann and J. Wesson, Virginia Marine Resources Commission). 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 5m size classes) was converted to an age frequency demographic using an a modified Von Bertalanffy plot with growth oscillation corresponding to seasonal change in growth rate (Evans and Mann, unpublished data based on field data from Horse Head reef in the James River, Virginia, by Mann and Morales). This takes the form:

$$\begin{aligned} L_t &= L_{inf} (1 - e^{-A(t-t_0)}), \\ \text{where: } A &= C \sin(2(t - t_s) / 2), \end{aligned}$$

$$\text{and } B = C \sin(2(t_o - t_s) / (2 \quad))$$

The parameters are: L_t is the length at time t , L_{inf} is asymptotic length set at 120mm based on field observations, K is the growth constant, t_o is age at which length is zero, C is the amplitude of the growth oscillation, and t_s is the starting point of the oscillation with respect to $t = 0$. 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 L_1 , L_2 , and so on. The rearranged function is:

$$L_2 = L_{inf} (1 - (1 - L_1/L_{inf}) e^{A' - B'})$$

$$\text{where } A' = C \sin(2(t_1 - t_s) / (2 \quad)),$$

$$\text{and } B' = C \sin(2(t_2 - t_s) / (2 \quad))$$

The parameters were estimated as follows:

$$K = 0.204, t_o = 0.36, \text{ and } t_s = 0.608.$$

The virtual population demography is illustrated as population A in Fig. 1A, together with a series of subsequent populations (B-E inclusive) generated by gradually increasing age specific mortality (illustrated as cumulative mortality in Fig. 1B) specifically 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 population has the 25mm size class, here considered the young of the year recruits or zero class, set at 100 oyster m^{-2} . This corresponds to the end point of the above "recruitment to the benthos" estimator. In all simulations, which are run as a sequential spreadsheet in Microsoft Excel the barometer for successful recruitment of a subsequent generation is attaining a 25mm size density of 100 oyster m^{-2} .

Results

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 Fig. 1C - 1H. Although these are just a subset of the many

options that can be run with the simulations they illustrate the following important points: Under low tidal exchange and optimum larval development the recruitment values are very high even with high larval mortality rates (Fig. 1C). Consider, however, that the employed scenario uses many optimal conditions including no reduction in fecundity attributable to salinity, no shell limitation and only modest competition for substrate. This is very much an optimal scenario.

- (a) Increasing larval duration by only 4 days reduces recruitment considerably (Fig. 1D).
- (b) Increasing tidal loss to 20% drives all recruitment values below the critical 100 m^{-2} even with everything else at optimum (Fig. 1E).
- (c) Reducing fecundity by 25% as a proxy for impact of disease and/or salinity has a proportional effect (Fig. 1F).
- (d) 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 (Fig. 1G, 1H).

These examples underscore the very non-linear response of recruitment to various combinations of tidal *exchange*, reduced fecundity, and larval duration as we move away from an optimal combination. They also illustrate that even the most stable population structure, A in Fig. 1A, to produce marginal recruitment even with shell and competition (P_{sub} and P_{foul}) optimized and with no consideration of greater impact of post settlement mortality. In a large number of slightly less than optimal scenarios even a population with increased mortality under sustained disease pressure - E in Fig. 1A - are prone to inadequate recruitment.

Discussion

These limited simulations underscore the need for holistic approaches to restoration or response to multiple stresses. Approaches that focus on only optimizing one life history stage

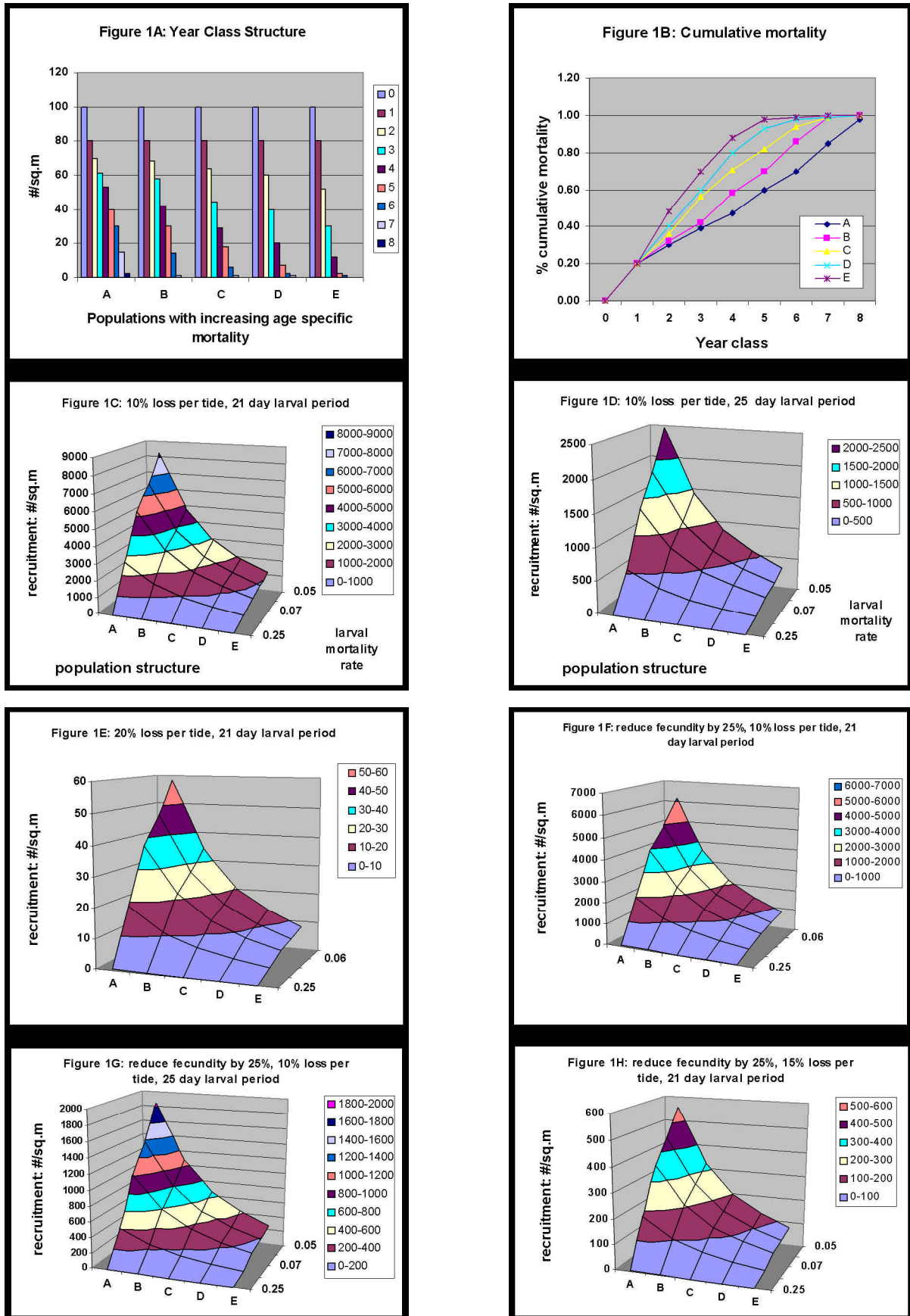


Fig. 1. Virtual oyster population year class structure (1A) and cumulative mortality (1B). Estimated recruitment (1C-1H) is shown under a variety of tidal loss, larval duration, and reduced fecundity scenarios

response may be strongly compromised. For example, even moderate disease tolerance alone will not be effective under sustained disease pressure, and restoration based only on this improved trait will fail. 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 1995, Hall and 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 limitations in the velar structure and the clear selective pressure over time for larval forms that recruit in optimal rather than sub-optimal 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, drive the need

for focused research to address these deficiencies. Without quantitative descriptors of the response of each life history stage to the local stresses, their subsequent holistic synthesis in a practical model, and employment of sensitivity analyses, the options for adaptive management of long term, often very costly restoration efforts, are limited, indeed sobering and probably doomed to failure. Intensive aquaculture, by comparison, may be able to progress in marginal environments where delicate early life history stages are cultured in controlled situations, thus limiting mortality, before transfer to open systems. Fishery enhancement resides between these options, where a dual role of supplementing local reproduction is balanced against increased exploitation of commercial product.

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