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APPLICATION OF A GENE-BASED POPULATION DYNAMICS MODEL TO THE OPTIMAL EGG SIZE PROBLEM: WHY DO BIVALVE PLANKTOTROPHIC EGGS VARY IN SIZE?

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ABSTRACT   The presumption is that egg quality influences larval survival and that egg size influences egg quality. Thus, larger eggs should be favored by selection. Counterweighing the tendency for egg size to increase is the number of eggs that can be produced if egg size remains small. We examine how egg size and egg number counterbalance in *Crassostrea* oysters, resulting in an average egg size near 50 μm. Simulations imposing a diversity of ranges in larval survivorship—from little advantage for large eggs relative to small eggs to a great advantage—yield some anticipated outcomes in which genotypes generating larger eggs are favored. In other simulations, however, genotypes generating smaller eggs became increasingly common. In these cases, egg size declines, as does the likelihood of survival of individual larvae: the antithesis of expectation. Few simulations identify preferred egg sizes near the size typically observed, suggesting that, under most field conditions, a selective advantage exists for smaller or larger eggs than those typically spawned. However, the extremes in egg size are rarely advantageous. Most simulations resolve an optimal intermediate egg size. Thus, observed egg size is a balance between the chanciness of larval survival enhanced by the production of a larger number of eggs and the genetically predisposed, but environmentally modulated, individual probability of larval survival that is a function of egg size, with environment determining the optimal size. The 50-μm size observed likely represents the median outcome of a range of larval survivorship probabilities, each selecting for relatively larger or smaller eggs, imposed stochastically over multiple generations. In this scenario, each year the population is pulled toward smaller or larger egg sizes, but in the next year the impetus is independent of the previous year. Reduced generation time, by disease or fishing, modifies the extent, but not the direction of trend. Thus, environmental stochasticity retains preeminence in stabilizing a balance between the probabilities of survival modulated by egg number and by egg size. The influence of shortened generation time—by disease, for example—is unlikely to be manifest in a modification in egg size and hence egg number.

KEY WORDS: planktotrophy, oyster, egg size, fecundity, larval survival, fitness, environmental variability, food quality, natural selection

INTRODUCTION

Reproductive potential can be expressed by the spawning of a relatively few large eggs or the spawning of relatively many small eggs. The end members of this distribution distinguish lecithotrophy from planktotrophy (e.g., Shuto 1974, Strathmann 1977, Strathmann 1986, Pearse et al. 1987). The presumption is that egg quality influences larval survival and that egg size influences egg quality (Gallager et al. 1986, Wilson et al. 1996, Utting & Millican 1997, Podolsky 2001, Laptikhovsky 2006). Thus, larger eggs should be favored by selection, all else being equal. However, within the planktotrophs are a relatively wide range of egg sizes (e.g., McEdward & Morgan 2001). The eggs of the hard clam *Mercenaria mercenaria* are consistently larger than the eggs of the eastern oyster *Crassostrea virginica*, for example (e.g., Gallager & Mann 1986, Gallager et al. 1986, Lee & Heffernan 1991, His et al. 2000, Bochenek et al. 2001, Powell et al. 2002). Moran (2004) observed a wide range of egg sizes among arcid species. Cardoso et al. (2007) document latitudinal variation in *Crassostrea gigas* egg size. Nevertheless, modeling of larval survival consistently demonstrates increased survival from larger eggs for oyster (Bochenek et al. 2001, Powell et al. 2002, Hofmann et al. 2004, Powell et al. 2004) and hard clam (our unpubl. data) larvae. Whether this outcome is characteristic of Bivalvia is unknown, but Moran (2004), for example, infers the same for arcids. Presumably, then, in cases

when larval performance is substantively influenced by egg quality or when increased egg size begets shorter planktonic life spans, selection favors larger eggs. However, a wide range in relative survivabilities occurs in these models, depending on the range of physiological capabilities in the cohort and the range of environments to which they are exposed. Thus, the relationship between egg size and larval survival is likely strongly modulated by both genotype and environmental conditions.

Counterweighing the tendency for egg size to increase is the number of eggs that can be produced if egg size remains small (e.g., Huner & Lindqvist 1991, Marshall & Keough 2003; for a terrestrial example, see Brown (2003)). If the energy available for reproduction is constant, a given energy allotment may give rise to a few large eggs or many small eggs. Egg volume being the primary scaler of egg number ordains that a small reduction in egg size (diameter) generates a large increase in egg number, enough that the sheer number of small eggs may sufficiently outweigh their tendency to give rise to larvae with inherently lower survival.

The dichotomous and antithetical outcomes of planktotrophy and lecithotrophy have received some attention in modeling studies, with the two diametric end members being favored outcomes relative to intermediate states (e.g., Vance 1973, Smith & Fretwell 1974, Levitan 2000). However, observation shows that intermediate egg sizes occur, at least within supraspecific taxa (e.g., Huner & Lindqvist 1991, McEdward & Morgan 2001, Marko & Moran 2002, Laptikhovsky 2006), suggesting that egg size is more modulatory than expressed by the end-member

options. Some models have identified conditions favoring intermediate states (e.g., Christians 2000, Levitan 2000). Complex relationships between offspring number, maternal investment, and survival can exist (e.g., Lloyd 1987, Sargent et al. 1987, Winkler & Wallin 1987, Wilson et al. 2009). Even within species, some studies have revealed a range of egg sizes at spawning (e.g., Gallager & Mann 1986, Hadfield & Strathmann 1996, Wilson et al. 1996, Bertram & Strathmann 1998, Fan & Dai 1999, Mashiko & Numachi 2000, Miles et al. 2007, Marroquin-Mora & Rice 2008). Presumably, some more sensitive interweaving of environmental and genotypic variation permits intermediate egg sizes to express the delicate balance between increases in egg quality and increases in egg number on larval, and perhaps juvenile, survival.

A practical example is the oyster (*C. virginica*), in which larger eggs of higher quality survive better (e.g., Gallager & Mann 1986; see also Powell et al. 2004). In these animals, maternal investment is likely a simple function of the gamete fraction of total body weight at spawning, not egg size per se, and the cost of reproduction in terms of increased female mortality is likely small (but see a possible exception for the larger investment by *C. gigas* (Tran et al. 2008, Li et al. 2009), a species with a gamete fraction at spawning near 50% (Héral & Deslous-Paoli 1983, Kang et al. 2003, Ngo et al. 2006)). Furthermore, time to hatch is a small fraction of the time from spawning to set (Stafford 1913), so that the duration and travails of larval life are a principal modulator of larval survival (e.g., Rumrill 1990; but see Johnson & Shanks 2003). Models demonstrate the preferred outcome of selection toward larger eggs, all else being equal (Bochenek et al. 2001, Powell et al. 2002, Hofmann et al. 2004, Powell et al. 2004); yet, oyster eggs remain small (e.g., *C. virginica* eggs average about 50 μm (Stafford 1913, Quayle 1988, Arakawa 1990, Wintermyer & Cooper 2003; but see Valdez-Ramirez et al. 2002, Cardoso et al. 2007, and Castaños et al. 2009 for a range of egg sizes), suggesting that egg number is a substantive counterweight to egg quality in determining preferred genotypes, at least in species of *Crassostrea* characterized by low effective population size (Hedgecock et al. 1992, Hedgecock 1994). However, models also emphasize the possibly large range in larval survival generated by variation in egg size under a range of realistic planktonic conditions, suggesting that modulators of larval life span may exert an inordinate influence on preferred egg size.

Here, we use a gene-based population dynamics model configured for *Crassostrea* oysters to examine how egg size and egg number counterbalance, resulting in the expression of a characteristic range of egg sizes. We specifically examine the interaction of variations in egg quality, expressed by variations in egg size, with the influence of egg number, both permitting, in independent fashion, an increased likelihood that some larvae will survive the vagaries of larval life. We suspect from previous modeling exercises that some planktonic conditions, such as minimal food supply, limit the lower range of egg sizes capable of giving rise to successful larvae (e.g., Powell et al. 2002). For simplicity, we exclude such harsh conditions and focus on more benign scenarios capable of giving rise to successful larvae over a relatively wide range of egg sizes. We then examine the influence of certain population characteristics on the outcome of selection for egg size. Among these are effective population size, which can be low in species such as oysters (Hedgecock et al. 1992, Hedgecock 1994); generation time, which has declined during modern times

as a result of disease in *Crassostrea virginica* (Mann & Powell 2007, Powell et al. 2011); variations in fecundity originating from variations in environment or food supply (e.g., Cox & Mann 1992, van der Meer et al. 2003, Chávez-Villalba et al. 2003); and a more knife-edge process of mortality exemplified by fishing (Powell et al. 2005).

THE MODEL: DYPOGEN (DYNAMIC POPULATION GENETICS ENGINE)

Model Structure and Flow

The Dynamic Population Genetics Engine (DyPoGen) is a numerical model that simulates genetic structure and population dynamics configured, in this case, for *Crassostrea* oysters (e.g., Harry 1985, Lawrence 1995) such as *C. gigas* and *C. virginica*. The model simulates a population composed of multiple cohorts, each composed of multiple individuals. However, the age, sex, and genotype of each individual is stored independently. The genetic structure of each individual is defined in terms of 10 pairs of chromosomes (Wang et al. 1999, Wang et al. 2005), each with 4 genes, each with 2 alleles. Thus, the animal is configured with 40 genes and 80 alleles, and the genotypes permitted at each locus are *AA*, *AB*, and *BB*. In the text that follows, model parameters are shown in `typewriter` font whereas variables are shown in *italics*.

The population evolves as follows. An initial population numbering `NewAnimals` is created with a random genetic structure. Cohorts are tracked by generation, not by calendar age, because the model permits multiple spawnings within 1 y, as occurs in southern climes (Ingle 1951, Hayes & Menzel 1981, Hofmann et al. 1994). For simplicity, simulations supporting this study were run under the assumption of one spawning season per year, a reproductive pattern typical of northern climes (Stauber 1950, Kennedy & Krantz 1982, Barber et al. 1991). Each year, the age of all individuals is incremented by one, after which adult mortality occurs at an age-dependent rate, and some individuals change functional sex, as explained later. Then reproduction occurs. Gametes are formed through meiosis with each set of haploid chromosomes obtained as a random draw from the parental genotype. Recombination occurs by the random choice of a location for each chromosome pair for each parent and the genetic information is crossed over at this point. The fate of each offspring is controlled by random larval mortality at a rate set to permit establishment of a relatively stable population.

Many of the processes in the model depend on a random draw. Unless otherwise indicated, a number is drawn from a uniform distribution with a range from 0–1. These uniform deviates (*R*) are obtained from the pseudorandom generator function `ran3` described by Press et al. (1986). Repeat simulations using different sequences of random numbers returned results with only modest variations in scale and trend in initial trials. Consequently, results are provided only for single simulations for each set of parameter values.

The model can be thought of as the marriage of 3 components: a postsettlement population dynamics submodel with parameterizations for growth, mortality, and reproduction; a larval submodel with parameterizations for larval mortality; and a genetics submodel that describes each animal in terms of its genotype and that interprets genotype in terms of fitness that then influences the larval and postsettlement submodels through a genotype–phenotype interface.

Postsettlement Population Dynamics

Sex Determination

Oysters are protandrous (Kennedy 1983, Morton 1990, Guo et al. 1998). Gender is specified by a recessive protandrous allele (P) and a dominant male allele (M) according to Guo et al. (1998). Animals can be protandrous (PP) or permanently male (PM). The homozygous male animal (MM) does not occur, because no matings can generate this genotype.

At every generation, a protandrous male is given the chance to convert to a functional female. A conversion probability was obtained from empirical data from Delaware Bay (our unpubl. data) using age–length relationships recorded by Kraeuter et al. (2007). This probability is calculated as

$$P = min\left(1., \left(\frac{\texttt{SexChange0} + \texttt{SexChange1}}{1 - \texttt{SexChange2} - \texttt{SexChange1} \times \log(age)}\right)\right), \tag{1}$$

where age is the age of the animal. To keep the denominator positive, age is limited by

$$age = min(age, \exp[1 - \texttt{SexChange2}/(\texttt{SexChange1}))). \tag{2}$$

Because of the age dependence of the sex change probability, all long-lived protandrous individuals eventually become functional females.

Reproduction

In the simulations presented here, the fraction of parents reproducing each mating season (`FracParents`) is based on estimates of effective population number for oysters (Hedgecock et al. 1992, Hedgecock 1994). This parameter is used to determine the number of parental pairs each mating season as

$$\begin{aligned} nParents = max(&0.5 \times \texttt{FracParents} \\ &\times LastAnimal, \texttt{minParent}), \end{aligned} \tag{3}$$

where $LastAnimal$ is the count of adult animals in the population. At least some parents, defined as `minParents`, are allowed to reproduce, thus guaranteeing some, albeit low, level of reproduction if abundance becomes low.

Parental pairs are drawn randomly, without replacement, from a list of all animals. Each pair potentially produces a number of offspring, controlled by `MaxOffspring`, having a genetic structure chosen from the parent's genes. However, oyster fecundity varies with size (Choi et al. 1993, Hofmann et al. 1994, Kobayashi et al. 1997). Consequently, the number of offspring is affected by parental age through a weight-based von Bertalanffy process (Fabens 1965, Vakily 1992, Mancera & Mendo 1996, Jensen 1997) to relate size and fecundity to age:

$$W = W_\infty\left(1 - e^{-k\left(age - age_\circ\right)}\right)^2, \tag{4}$$

where the exponent comes from the relationship between weight and length in oysters. For oysters, weight scales more nearly to the square of the length than the more typical cube (Yoo & Yoo 1973, Powell & Stanton 1985, Powell unpubl. data). The von Bertalanffy parameters [$k = 0.4$, $W_\infty = 4.32\,g$ ($L_\infty = 120$ mm), $age_\circ = 0.32$ y] were representative of $C.\ virginica$ near the center of its latitudinal range: literature values cover a relatively wide range (e.g., Rothschild et al. 1994, Arizpa 1996, Mancera & Mendo 1996, Mann & Evans 2004, Kraeuter et al. 2007).

Eq. (4) is applied to fecundity by assuming that oyster spawn is a standard fraction of biomass (Choi et al. 1993, Hofmann et al. 1994). Hence, the fecundity equivalent of W_∞, `MaxOffspring`, is scaled to animal size by the von Bertalanffy correction factor, $AgeFactor$, defined as

$$AgeFactor = \left(1 - e^{-k\left(age - age_\circ\right)}\right)^2. \tag{5}$$

$AgeFactor$ is the same for males and females; however, the partner producing the fewest gametes determines total fecundity. The number of eggs produced is

$$nOff = 1 + fix(AgeFactorF \times \texttt{MaxOffspring}); \tag{6}$$

the number of sperm produced is

$$nOffM = 1 + fix\left(AgeFactorM \times \texttt{MaxOffspring} \times 2^{11}\right). \tag{7}$$

The size dependency of fecundity in most matings is dependent on the female because the number of sperm per gram gamete is substantially larger than the number of eggs (compare Dong (2005) and Gallager and Mann (1986)). The assumption is made that fertilization is never sperm limited (Powell et al. 2011), although below-optimal sperm-to-egg ratios occasionally occur (e.g., Song et al. 2009; see also Vogel et al. 1982).

Adult Mortality

Although juvenile mortality is high in bivalves (Thorson 1966, Powell et al. 1984, Osman et al. 1989, Ólafsson et al. 1994, García-Esquivel et al. 2001, Powell et al. 2009a), this portion of mortality was subsumed into larval mortality because the genetics of the postsettlement component of the model are influenced only by processes acting on sexually mature animals.

The natural mortality rate for most oyster species is unknown. Age-dependent mortality is an inherent attribute of those species impacted by Dermo or MSX disease (Hofmann et al. 1995, Powell et al. 1996) or exploited by humans, and is characteristic of some other bivalves such as hard clams, $Mercenaria\ mercenaria$ (Hofmann et al. 2006, Kraeuter et al. 2008). Whether mortality in oyster populations existing prior to the onset of disease or human exploitation was age dependent is unknown. However, the mismatch in life expectancy in $C.\ virginica$ based on observed adult mortality rates prior to disease onset of 10–13% per year (Powell et al. 2008, Powell et al. 2009a) inferred from an assumption of constant mortality (e.g., Hoenig 1983) and the few pertinent direct estimates of adult age frequency (e.g., Harding et al. 2008) supports such a formulation in this species, because the former would predict the observation of older animals than is observed.

Thus, an age-dependent adult mortality rate was defined as

$$P = 0.5\left[1 + \tanh\left(\frac{age - \texttt{AvgAgeMort}}{\texttt{AvgSpreadMort}}\right)\right], \tag{8}$$

where P is the probability of death, `AvgAgeMort` is the average age of mortality (P is 0.5 at this age) and `AvgSpreadMort` controls how rapidly the mortality approaches 1. The two sexes were equivalently parameterized for these simulations.

If fishing occurs, an age is derived from the specified von Bertalanffy relationship based on a knife-edge length defining the market-size animal. If the animal is large enough, then a random draw based on a specified fishing mortality rate determines whether it is removed by the fishery.

Larval Mortality

Larval mortality is applied at a time immediately after reproduction. Larval survival is controlled by an estimated population reproductive capacity that depends on `MaxOffspring`, *nParents* (the number of parental pairs), and *LastAnimal*. The estimated reproductive capacity, standardized to the number of individuals, is

$$ReprPerAdult = \frac{\texttt{MaxOffspring} \times nParents}{4 \times LastAnimal}, \qquad (9)$$

where the factor of 4 includes the average of the uniform random deviates (0.5) and the fact that the number of offspring per parent is one half the number of offspring per female.

The probability of a larva surviving is

$$LarvalSurv = (0.5 + 1.5R)\frac{\texttt{CarryCapacity}}{4 \times ReprPerAdult \times LastAnimal}, \qquad (10)$$

where `CarryCapacity` is a desired number of animals in the population. This relationship incorporates a logistic process in which average recruitment per adult declines as population abundance increases with respect to the environmental carrying capacity. A compensatory relationship between broodstock and recruitment has been identified in a number of molluscan stocks (e.g., Hancock 1973, Peterson & Summerson 1992, McGarvey et al. 1993, Kraeuter et al. 2005), including oysters (Powell et al. 2009b).

The probability of death for each larva is calculated as

$$P = 1 - LarvalSurv. \qquad (11)$$

For a random draw, if $R < P$, then the larva dies. If the larva recruits to the population, it is given an identifying number, a birth date, and an age of 0. All oysters that are protandrous begin life as male. Hence, all recruits are male. However, some recruits convert to female prior to first spawning, as appears to be the case in the field (Dinamani 1974, Kennedy 1983, Paniagua-Chávez & de Acosta-Ruiz 1995, Lango-Reynoso et al. 2006).

Definition of Fitness

Ultimately, fitness of any potential parent is established by the number of progeny that live to reproduce. Because the fraction of the population successfully spawning is small, many recruits fail to spawn successfully before they die. Discounting the probabilistic aspects of the model, the factors that control the number of progeny that reproduce are the number of progeny, a function of egg size (and probabilistic factors controlling adult lifespan and the ages of successful reproduction), and the probability of larval survival, a function of egg size (and probabilistic factors determined by population abundance). For simplicity, we will use adjectival modifiers to the term "fitness" to refer to 3 subsets of this overall process. The term "larval fitness" is applied to the probability of an individual larva surviving to recruit to the adult population. The term "adult fitness" is applied to the genetic complement of any adult female controlling the number and size of eggs spawned. The term "allele fitness" is applied to the contribution of any individual locus to "adult fitness."

Implementation of Allele Fitness and Adult Fitness

The genotype for a locus can be *AA*, *AB*, or *BB*. The relative contribution to adult fitness of these combinations is provided by the array `PhysioFuncWeight`. If the genotype is *AA*, *AB*, or *BB*, the allele fitness is the first, second, or third, respectively, weight in `PhysioFuncWeight`. For example, if heterozygosity at a locus is thought to be beneficial and homozygosity is not, then the `PhysioFuncWeight` would be (0, 1, 0): the allele fitness for the heterozygote would contribute a value of 1 to the calculation of adult fitness whereas the allele fitness for the homozygotes would contribute nothing. In most simulations reported here, the allele fitnesses specify additive dominance of the *A* allele (1., 0.5, 0.), but we also investigate the case of overdominance.

Each location on a chromosome pair is assigned a set of allele fitnesses through an index in array `PhysioFuncClass`. Thus, one locus may show dominance and another may show overdominance, for example. The array `FitnessClass` then determines which of the loci influence adult fitness. An entry of 0 in this array indicates that the particular locus has no effect. The sex gene is an example. In the simulations reported here, the first 1 or 2 genes on each chromosome are specified to influence adult fitness. The remaining loci, with the exception of the sex gene, are subject to chance alone and, thus, change in frequency in the population solely through drift.

Consequently, the adult fitness, *AdultFitness*, for any individual is set as follows. The entry for each gene in `FitnessClass` identifies whether the gene contributes to fitness, the entry in `PhysioFuncClass` identifies which set of allele fitnesses to use for these genes, and the allele fitness in `PhysioFuncWeight` for the genotype for each gene gives the value contributed to fitness by each allele pair. After accumulating values of allele fitness for all loci contributing to adult fitness, the total is divided by the number of contributing genes, so that *AdultFitness* for each animal falls between 0 and 1. For most simulations, an adult fitness of 0 is associated with an animal having solely *BB* genotypes at the loci designated to contribute to the determination of egg size; conversely, an adult fitness of 1 is associated with an animal having solely *AA* genotypes. For overdominance, the animal heterozygous at all designated loci has *AdultFitness* = 1, and animals homozygous at all designated loci have *AdultFitness* = 0.

Genotype–Phenotype Interface

Egg size is determined for each adult female by linear interpolation between a specified range of egg sizes, 37–73 μm in this study, using the value for adult fitness, *AdultFitness*, which varies between 0 and 1. The number of eggs produced, determined from animal size and *MaxOffspring* in eq. (6), is adjusted using the value of *EggSize* determined from adult fitness so that more smaller and fewer bigger eggs are produced. Specifically,

$$nOff = nOff \left(\frac{MeanEggSize}{EggSize}\right)^3, \qquad (12)$$

where *MeanEggSize* is the average of the minimum and maximum values of egg size associated, respectively, with values of *AdultFitness* of 0 and 1. Eq. (12) expresses an assumption of constant gonadal volume. This assumption interprets the observation that gonadal volume in oysters and most other invertebrates is already a significant fraction of total body mass

(e.g., Powell & Stanton 1985, Christians 2000, Cardoso et al. 2007, Herreras et al. 2007), so increase in gonadal volume per se is an unlikely response to selection favoring increased egg production (but see Cardoso et al. 2007). Gonadal volume is variable between females in bivalves, including oysters (Choi et al. 1993, Kang et al. 2003, Park et al. 2003). We do not consider this source of variability because the range in gonadal volume is much less than 2, whereas the range in egg number varies by a factor of 10 over a representative range of egg sizes. We do not consider the case in which environment may increase or decrease egg size and gonadal volume simultaneously (e.g., Bertram & Strathmann 1998, Hendriks et al. 2003). Thus, egg number declines proportional to an increase in individual egg volume.

Each larva produced has its own fitness value described by *LarvFitness* and calculated as the mean of the allele fitnesses as described for *AdultFitness*. The value of *LarvFitness* affects larval survival. A survival range, established on input, provides a minimum and maximum value corresponding to values of 0 and 1, respectively, for *LarvFitness*. A survival probability *PSurv* for each value of *LarvFitness* is obtained by linear interpolation. The death probability (eq. (10)) is modified as

$$P = 1 - (LarvalSurv \times Psurv), \tag{13}$$

and a random draw determines the fate of the larvae. If $R < P$, then the larva dies.

Thus, an adult fitness value calculated for the animal is translated into an egg size by linear interpolation between a specified range of egg sizes based on *AdultFitness* that varies from 0–1, and this determines the number of eggs produced within the constraints permitted by the animal's size. Each larva produced has a probability of survival modulated by *LarvFitness* obtained by linear interpolation within a specified range of survival probabilities. This establishes the interface between genotype (the adult fitness value), phenotype (egg size), and selection (probability of larval survival).

SIMULATION CONSTRAINTS AND STATISTICS

Genotype–Phenotype Relationship and Selection

Selection is defined in terms of the relationship between a larval fitness value of an individual and the probability of death. Ultimately, this is determined from individual egg size. The overall fitness of any parent is determined by the lifetime fecundity of the progeny. This is influenced both by the number of eggs produced by the parent and the genotypes of the offspring, both of which are determined by egg size.

Two relationships must be defined: egg size relative to egg number and egg size relative to the probability of larval survival. Levitan (2000) addressed the importance of scaling the influence of egg size proportionally to egg volume. We assume that egg volume is a linear scalar of egg quality, although both nonlinearity and high variability are reported for planktotrophs (e.g., McEdward & Morgan 2001). Our implementation based on oyster physiology is consistent with Levitan's (2000) approach. Thus, the relationship of egg size and egg number is established by eq. (12), the implications of which are shown in Figure 1. Note that the number of eggs rises rapidly and nonlinearly with ever smaller egg sizes based on the assumption of the constant gamete fraction propounded earlier. Egg size was decreed to range from 37–73 µm. This range encompasses the range of oyster egg sizes in
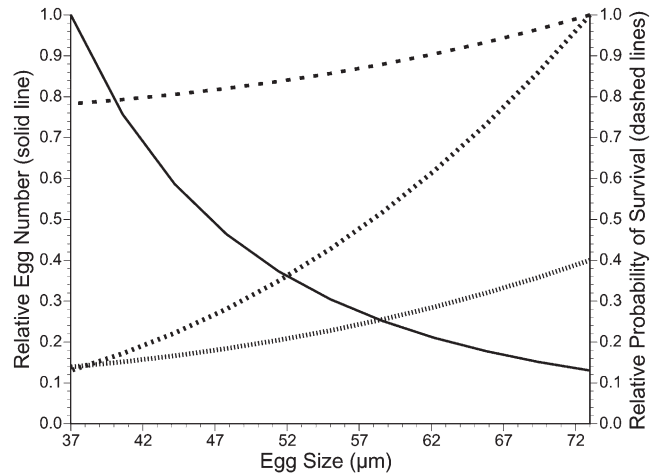

Figure 1. The relationship between egg size, graphed as the diameter, and relative egg number (solid line) or larval survival probability (3 dotted lines). Y-axis values represent relative differences, not absolute values. Three examples of the relationship between egg size and larval survival are shown, taken from a much wider range of relationships investigated (Table 1).

the literature exclusive of the large eggs characteristic of brooding ostreids (Gallager & Mann 1986, Fournier 1992, Ernande et al. 2004, Cardoso et al. 2007) and much of the higher range of egg sizes observed for *Mercenaria mercenaria* (Gallager & Mann 1986, Lee & Heffernan 1991, His et al. 2000). The lower value is also consistent with the analysis of Bochenek et al. (2001), which suggested that egg sizes much less than 40 µm were inherently unviable for oysters, having insufficient stored lipid to initiate larval life.

The relationship between egg size and the probability of larval survival is determined from egg size and a specified range of survival probabilities. Three such options, representative of the suite of options in Table 1, are shown in Figure 1. Note that

TABLE 1.

The ranges of larval survival used in the simulations discussed in the text as a function of egg size.

Simulation	Egg Size Range (µm)	37.0	73.0
1	Survival Probability	0.00	0.25
2	Survival Probability	0.20	0.30
3	Survival Probability	0.15	0.35
4	Survival Probability	0.10	0.40
5	Survival Probability	0.00	0.50
6	Survival Probability	0.40	0.60
7	Survival Probability	0.30	0.70
8	Survival Probability	0.20	0.80
9	Survival Probability	0.00	1.00
10	Survival Probability	0.30	0.90
11	Survival Probability	0.50	0.75
12	Survival Probability	0.40	0.90
13	Survival Probability	0.70	0.80
14	Survival Probability	0.65	0.85
15	Survival Probability	0.60	0.90
16	Survival Probability	0.50	1.00
17	Survival Probability	0.85	0.90
18	Survival Probability	0.75	1.00

The range of egg sizes was set between 37.0 µm and 73.0 µm.

each specifies a nonlinear relationship between egg diameter and larval survival probability, with disproportionately increasing survival at larger egg sizes. However, the range in survivals varies over the allowed range of egg sizes among the 3. These parameterizations are obtained as inferences from the modeling results of Bochenek et al. (2001), Powell et al. (2002, 2004), and Hofmann et al. (2004), which proffer the following conclusions. First, larger eggs tend to be associated with higher survivorships when food quantity or food quality poses a limitation on larval performance. Second, in most of these simulations, as in experimental results (e.g., Gallager et al. 1986), survivorship is nonlinearly related to egg diameter. Third, modal outcomes, cases in which intermediate egg sizes give rise to larvae with higher survival probability than do larger egg sizes, are very rare—that is, larvae from ever larger eggs remain ever more likely to survive. Fourth, the influence of food quantity and food quality, and the timing of changes in food quantity and food quality relative to a larva's birth day, reveal a nearly infinite range of larval survival probabilities as a function of egg size. Thus, in some cases, small eggs and large eggs have nearly equivalent high survival (e.g., top curve in Fig. 1). In other cases, both survive poorly (e.g., bottom curve in Fig. 1). In others, the range of survivals is larger (e.g., middle curve in Fig. 1). It is this plethora of outcomes that is central to the current study, because these differential outcomes interact with the nonlinear relationship of egg number and egg size in often profoundly different ways (Fig. 1). As a consequence, we investigated a wide range in the range of larval survivorship (Table 1). In extrema, the widest range of larval survivorships varied survival probability from 0–1 and the narrowest range of survival probability encompassed a range of ≤0.1, such as 0.2–0.3 or 0.85–0.90.

Note that the formulations depicted in Figure 1 carry the inherent assumption that smaller eggs give rise to larvae requiring a longer planktonic life span. Because larval mortality is assumed to be a first-order process (e.g., Dekshenieks et al. 1997, Ellien et al. 2004), a longer larval life span results in a lower probability of survival (e.g., Levitan 2000, Pfeiffer-Hoyt & McManus 2005, Przeslewski & Webb 2009). The degree to which the influence of original egg size continually exerts an influence on larval life span, relative to, for example, variations in food availability to the feeding larva or the daily predation rate, is likely to be highly variable, and is not well documented experimentally (Hendriks et al. 2003, Johnson & Shanks 2003, Pernet et al. 2005). Our simulations effectively assume, by varying the range of survivorships, that some cohorts are much more influenced by original egg size (e.g., middle curve in Fig. 1) than others (e.g., top and bottom curves in Fig. 1), as we anticipate is, indeed, the case. We recognize the potential importance of fertilization success (sensu Levitan 2006), but note that the aggregative lifestyle of oysters results in a strong tendency for neighboring males and females to be very near each other, and we further note the inference from data on population sex ratios that the ratio of females to males is modulated to retain sperm-to-egg ratios in dense populations at near optimal levels (Powell unpubl. data). Finally, compromised fertilization success would likely further penalize smaller eggs, thereby increasing the range of larval survivorship, as might be approximated by the wider ranges of range values investigated (Table 1). In passing, we note that larval survival is not necessarily routinely related to postmetamorphic success, an underlying assumption of our analysis (e.g., Osman et al. 1989, Ólafsson et al. 1994, Marshall & Keough 2004).

Constraints on Model Parameterization

Some basic assumptions were made initially to limit the range of simulations used for investigation. The first dealt with the distribution of genes determining egg size among the 10 chromosome pairs. Simulations were run with genes determining egg size distributed as 1 or 2 per chromosome evenly distributed among the chromosomes. The distribution and number of genes affecting egg size in oysters is unknown. Fecundity-related traits such as egg size have been shown to respond relatively rapidly to selection in studies of a number of species (e.g., fish (Einum & Fleming 2002), oysters (Ernande et al. 2004), and serpulid worms (Miles et al. 2007); see also Mousseau and Roff (1987)), but this observation does not much constrain the choice of distribution of genes among chromosomes. Hence, we investigate two relatively simple configurations.

The second assumption dealt with the relative allele fitness given the dominant and recessive homozygote and the heterozygote. Once again, although a number of studies have addressed heterozygosity in bivalves (e.g., Hawkins et al. 1994, Hummel et al. 1995, del Rio-Portilla & Beaumont 2001), little basis for choice exists for this study. And again, we investigate relatively simple configurations in which the advantageous allele's importance is proportional to its presence for the case of dominance and in which the heterozygote is maximally advantaged in the case of overdominance.

Last, we choose, as the base case, the oyster as it likely evolved through prehistoric time. This is an animal with low effective population size and long generation time. Galtsoff (1964) maintained *C. virginica* for 9 y, considerably beyond the conservative estimates provided by Comfort (1957) and Custer and Doms (1990), but consistent with estimates for fossil species (Kirby 2000) and recent estimates reported in Berrigan et al. (1991). Such long life spans rarely occur today, because oyster diseases and fishing both limit generation time in most environments relative to prehistoric times (Harding & Mann 2006, Harding et al. 2008, Powell et al. 2009a, Mann et al. 2009).

Simulation Constraints

Preliminary simulations indicated that simulations of 200 generations in length were adequate to reveal how selection influenced the final frequency of egg sizes among the members of the population. This number of generations falls within the range of other models of selection (e.g., Strand et al. 2002, Agrawal & Otto 2006) and, in most cases, established a stable final egg size. Carrying capacity was set so that population abundance remained high enough that genetic drift rarely resulted in the loss of neutral alleles during a 200-y time period. The genetic structure of the initial population, set at a specified abundance, was constructed by random draw. Thus A and B alleles were equally possible, and the average initial adult fitness for all animals fell at a value of 0.55, which corresponds to a mean egg size, *MeanEggSize* in eq. (12), of 55 μm. Miscellaneous parameterizations include SexChange0 = 0.0, SexChange1 = 0.335, and SexChange2 = 0.1178. Parameterizations varying by simulation are summarized in Tables 1 and 2.

Statistics

Generation time was calculated after Felsenstein (1971) with one modification. We defined all *FF* males as immature females and all *FF* females as senescent males. Then, mean generation time *T* is

Parameterizations defining model configurations for examples provided in the text and figures.

Simulation Series	No. of Fitness Genes/ Chromosome	Relative Fitness of AA:AB:BB	Carrying Capacity Scale CarryCapacity	Fraction Parents FracParents	Generation Time AvgAgeMort	Generation Time AvgSpreadMort	No. of Offspring (million) MaxOffspring
Base case	1	1:.5.0	50,000	0.0005	12	7	1
Increased abundance	1	1:.5.0	500,000	0.0005	12	7	1
Increased fecundity	1	1:.5.0	50,000	0.0005	12	7	5
Double gene	2	1:.5.0	50,000	0.0005	12	7	1
High Ne	1	1:.5.0	50,000	0.005	12	7	1
Low Ne	1	1:.5.0	50,000	0.00005	12	7	1
Overdominance	1	0:.1:0	50,000	0.0005	12	7	1
Long generation time	1	1:.5.0	300,000	0.0005	12	7	1
Intermediate generation time	1	1:.5.0	300,000	0.0005	5	3	1
Short generation time	1	1:.5.0	300,000	0.0005	2	1	1
Fishing	1	1:.5.0	50,000	0.0005	12	7	1

Ne, effective population size.

$$T = \sum_{i=0}^{n} l_{i,g} \, b_{i,g} i, \qquad (15)$$

where i is animal age in years and n is the maximum age achieved by animals in the cohort, with 1 cohort per year implicit. The probability of survival to age i for animals in any given cohort g, $l_{i,g}$, is defined as

$$l_{i,g} = \frac{N_{i,g}}{N_{0,g}}, \qquad (16)$$

where N_0 is the initial number of animals in the cohort and N_i is the number of individuals surviving at age i. The number of offspring per female of age i and cohort g, $b_{i,g}$, is defined as

$$b_{i,g} = \frac{O_{i,g}}{N_{i,g}}, \qquad (17)$$

where O is the number of recruited offspring produced by animals of age i in cohort g.

RESULTS

Base Case Series

A series of base cases, covering a range of survivorships relative to egg size (Fig. 2), reveals that a wide range of survivorships—that is, larger eggs surviving much better than smaller eggs—routinely results in preferred egg sizes from 55–66 µm. These are relatively large egg sizes in comparison with the beginning spectrum of 37–73 µm, and relatively large, although not extraordinary (Valdez-Ramirez et al. 2002), in comparison with typically observed oyster egg sizes. As the range of larval survivorship decreases, preferred egg size declines, regardless of the absolute values of larval survivorship bounding the distribution. In all cases, a sufficiently small range of survivorships can be found that yields eggs in the range 41–45 µm. This is a range of egg sizes that is smaller than the egg sizes typically observed in *Crassostrea* oysters (but see Castaños et al. (2009)).

Several case histories demonstrate the origin of these results. A range of larval survivorships from 0.2–0.8 results in a stable egg size of 59 µm (Fig. 3) from an initial population with a mean egg size of 55 µm. Population fitness, expressed by the average of the individual adult fitnesses, rose more or less monotonically over 200 generations (Fig. 4, Simulation 8). During this time, population abundance remained relatively constant (Fig. 5,
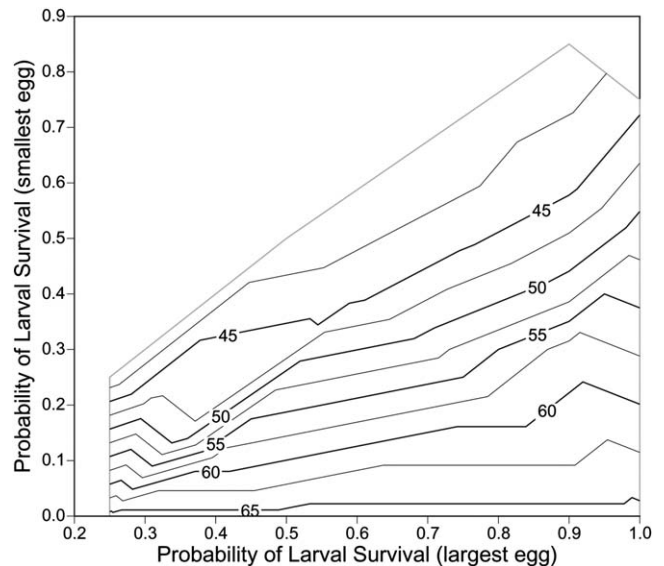

Figure 2. The results of the base case series of simulations defined in Table 2 using the ranges of larval survivorship described in Table 1. Each simulation was run for 200 generations. Plotted are the modal egg sizes obtained with ranges of larval survival defined by the y-axis (lowest probability of larval survival associated with the smallest egg) and the x-axis (highest probability of larval survival associated with the largest egg). For example, an egg size at $y = 0.3$ and $x = 0.5$ is the expected outcome for the case when the probability of larval survival ranged from 0.3–0.5 over the 37–73-µm egg size range. Contours are egg diameter measured in micrometers.
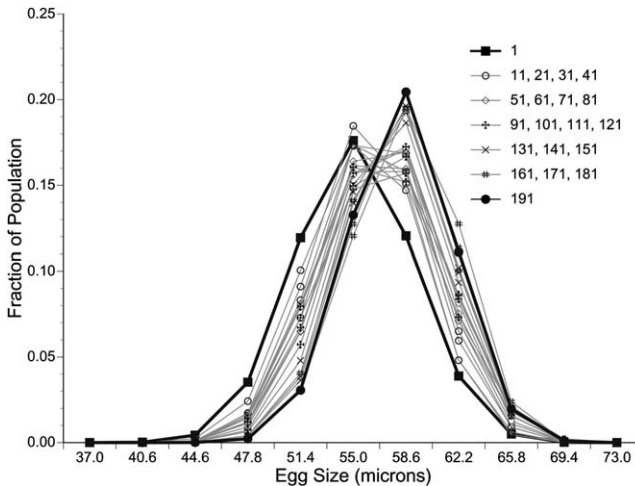
Figure 3. The time series of egg size frequencies over 200 generations for base case simulation 8 (Tables 1 and 2) in which the range in the probability of larval survival was varied from 0.2–0.8 for egg sizes of 37–73 μm.

Simulation 8); no alleles were lost, and average age at death varied around 7 y.

A comparative simulation with a restricted, but high, survivorship range of 0.5–0.75 shows a slowly increasing population (Fig. 5, Simulation 11). In this simulation, egg size declines steadily over 200 generations to a value of 44 μm (Fig. 6). Population fitness declines steadily (Fig. 4, Simulation 11). A contrasting expanded range of larval survivorship of 0–1, the maximum allowed, yields a steadily increasing egg size over 200 generations, culminating in an average egg size of 66 μm (Fig. 7, top). Population fitness increases more or less monotonically over the 200 generations (Fig. 5, Simulation 9).

Sensitivity to Model Parameterization

We increased population abundance for a selection of simulations depicted in Figure 2 by a factor of 10 (Table 2). Trends in egg size with egg survivorship remained unchanged.

Simulations in Figure 2 were conducted under the proviso that 1 gene on each chromosome was involved in determining fitness. A selection of simulations from Figure 2 conducted with egg size determined by 2 genes on each chromosome (Table 2)
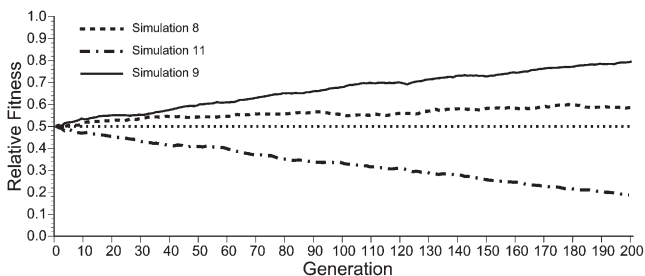

Figure 4. The time series of population fitness over 200 generations for base case simulation 8 (Tables 1 and 2, Fig. 3) in which the range in the probability of larval survival was varied from 0.2–0.8 from an egg size of 37–73 μm, base case simulation 11 (Tables 1 and 2, Fig. 6) in which the range in the probability of larval survival was varied from 0.50–0.75, and base case simulation 9 (Tables 1 and 2, Fig. 7) in which the range in the probability of larval survival was varied from 0.0–1.0.

showed that trends were predictable, but extreme outcomes were muted. Thus, the simulation with larval survivorship ranging from 0.2–0.8 that generated an intermediate preferred egg size was unaffected by this change. In contrast, the simulation with the wider range of larval survivorship of 0–1 resulted in a lesser preferred egg size of 62 μm than 66 μm (Fig. 7, bottom). A reduced range of larval survivorship generated the observed mild decrease in final egg size of 51 μm compared with 44 μm (Fig. 8, bottom). Thus, additional genes did not substantively change the overall pattern of the outcome shown in Figure 2, but did restrain the extreme outcomes to a more moderate range of egg sizes.

We increased the number of offspring per parent by a factor of 5. Increased fecundity varied simulation outcome very little.

We varied the fraction of the population successfully reproducing by a factor of 100 (Figs. 9 and 10 vs. Fig. 2). Once again, the influence of survivorship on preferred egg size did not change materially over this large range of effective population sizes.

Last, we compared the dominance case in which the AA, AB, and BB genotypes were given allele fitnesses of 1, 0.5, and 0, respectively, with a case of heterozygote advantage. We chose the extreme condition of 0 for AA and BB, and 1 for AB. Results in Figure 11 show a substantive change in outcome compared with Figure 2, with the majority of impact associated with larval survivorship ranges that tend to generate large eggs. In this case, eggs larger than 55 μm failed to occur as preferred egg sizes in any simulation. A limited range of larval survivorship returned the predictable transition to smaller preferred egg sizes, but only for cases in which the overall probability of larval survivorship was relatively low. This result, of course, is anticipated from the constraint imposed by the relative allele fitnesses that would require that the best population fitness achieved be about 0.5 under the constraint that maximum probability of survival remain associated with an adult fitness value of 1. This is, of course, an arbitrary constraint.

Thus, simulation results were robust to manipulations of a number of standard measures of population dynamics, including population abundance, effective population size, and fecundity; modified moderately by variations in the number of genes conferring fitness; and modified substantively by the relative importance of heterozygosity in fitness and, by inference, the degree to which relative gene fitness varies from the simple dominance case of 1 for AA, 0.5 for AB, and 0 for BB.

The Influence of Average Life Span

We varied average life span from about 7 y (a 10-y female generation time), to approximately 4 y (a 6-y generation time), and to about 3 y (a 5-y generation time; Fig. 12). A reduction in generation time reduced population abundance, as anticipated (Powell et al. 2011) (Fig. 12, bottom); however, previous sensitivity analyses show that population abundance does not materially influence the outcome of these simulations. The decline in average age from about 7 y to 4 y does not materially change the relationship between preferred egg size and the range of larval survivorship. A comparison of Figures 13 and 14 shows that egg size declined by a very modest amount with a reduction in average age in the population, although the difference is by no means substantive. Note, however, that the area represented by the largest and smallest eggs in Figure 14 is somewhat expanded relative to the original long-generation-time case (Fig. 13). Thus,
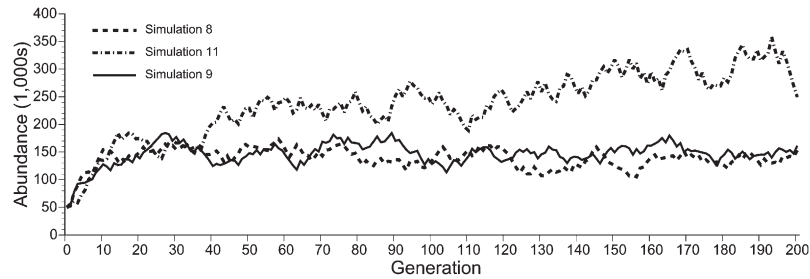
Figure 5. Population abundance for base case simulation 8 (Fig. 3, Tables 1 and 2) (probability of larval survival varied from 0.2–0.8 for an egg size of 37–73 μm), base case simulation 11 (Fig. 6, Tables 1 and 2) (probability of larval survival varied from 0.50–0.75), and base case simulation 9 (Fig. 7, Tables 1 and 2) (probability of larval survival varied from 0.0–1.0) over 200 generations.

extreme outcomes are somewhat more likely to occur at the shorter generation time.

A further reduction of average age, brought about by an increase in adult mortality, to about 3 y, dramatically changes the outcome (Fig. 15). Now the range of larval survivorships that yield intermediate egg sizes is materially reduced. Extreme outcomes, in which egg size is much increased or decreased, occur over a much larger subset of the range of larval survivorships investigated. Thus, extreme outcomes are considerably more likely to occur with much-shortened generation times. One exception exists. The preferred egg size at small ranges of larval survivorship for which larval survivorship is overall low (the lower left quadrant of 15) are somewhat larger than heretofore seen at longer generation times (Figs. 13 and 14).

The Influence of Fishing

Fishing is a knife-edge change in adult mortality rate. In Delaware Bay, the fishery takes oysters 2.5 inches and larger (Powell et al. 2005). Fishing mortality rates have been estimated to cover a wide range in oyster fisheries (Rothschild et al. 1994, Jordan et al. 2002, Jordan & Coakley 2004). Estimates in Delaware Bay range up to about 25% of the stock per year over the time series (Powell et al. 2008), but harvest levels exceeding about 7% per year clearly resulted in overfishing of the resource (Powell et al. 2008, Powell et al. 2009a, Powell et al.

2009b). Estimates of natural mortality during years little affected by oyster diseases (MSX and Dermo (Ford & Tripp 1996)) are about 10% per year (Powell et al. 2009a). This yields a crude estimate of an overfishing threshold of 10% per year (e.g., Vetter 1987), a value consistent with time series analyses (Powell et al. 2009b). Thus, we examined fishing mortality rates of 10% per year and 25% per year.
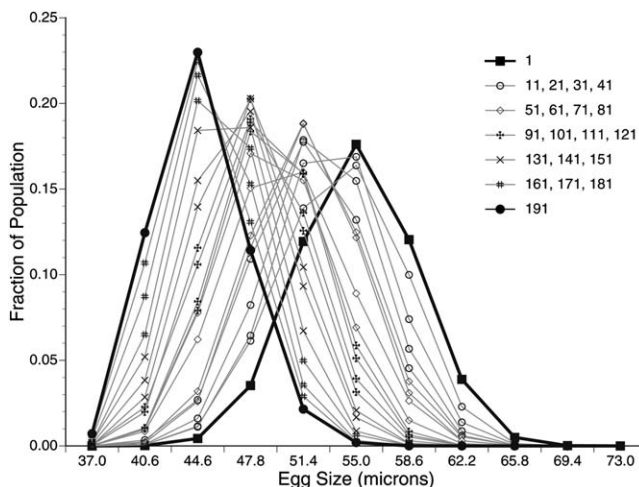

Figure 6. The time series of egg size frequencies over 200 generations for simulation 11 (Tables 1 and 2) in which the range in the probability of larval survival was varied from 0.50–0.75 for a egg sizes of 37–73 μm.
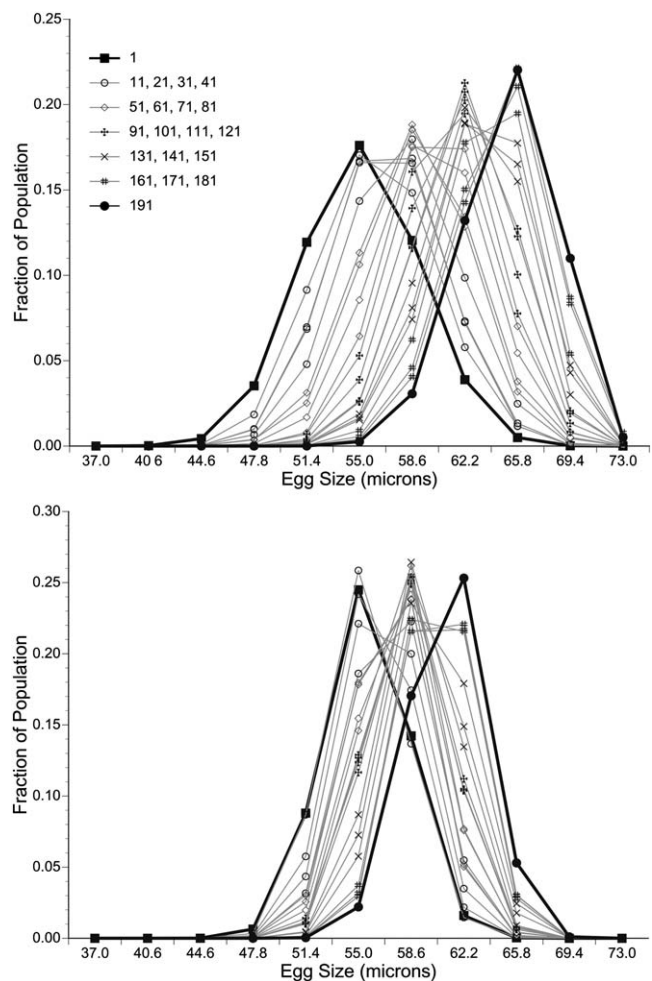
Figure 7. Time series of egg size frequencies over 200 generations for base case simulation 9 (Tables 1 and 2) in which the range in the probability of larval survival was varied from 0.0–1.0 from an egg size of 37–73 μm. (Top) Egg size was determined by 1 gene on each chromosome. (Bottom) Egg size was determined by 2 genes on each chromosome.

Figure 9. The results of a series of simulations defined in Table 2 using the ranges of larval survivorship described in Table 1, in which the fraction of the population reproducing was increased by a factor of 10, equivalent to an increase in effective population size. Each simulation was run for 200 generations. Plotted are the modal egg sizes obtained with ranges of larval survival defined by the y-axis (lowest probability of larval survival associated with the smallest egg) and the x-axis (highest probability of larval survival associated with the largest egg). For example, an egg size at $y = 0.3$ and $x = 0.5$ is the expected outcome for the case in which the probability of larval survival ranged from 0.3–0.5 over the 37–73-μm egg size range. Contours are egg diameter measured in micrometers.
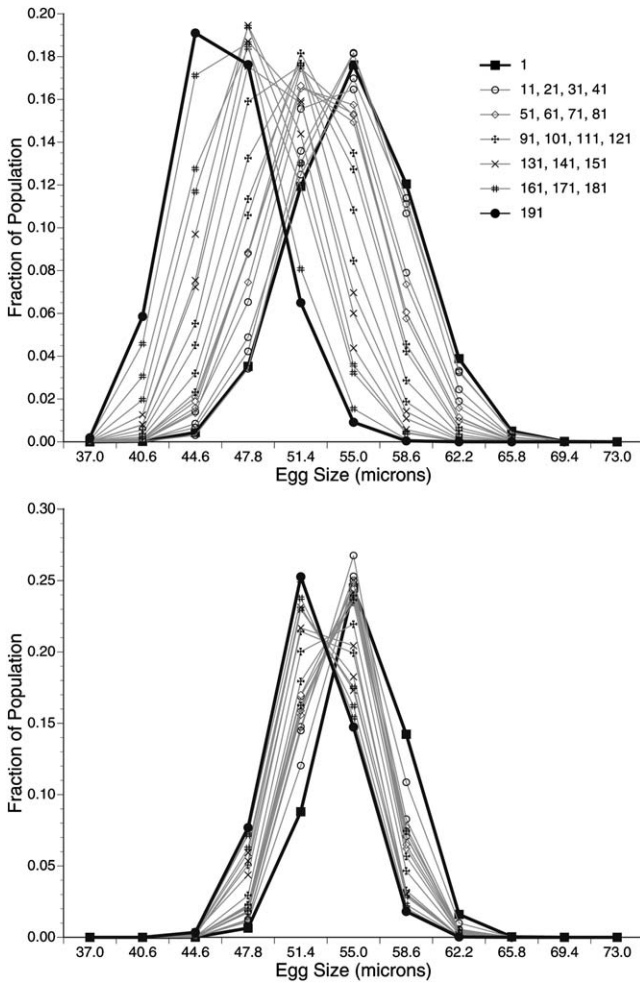
Figure 8. Time series of egg size frequencies over 200 generations for base case simulation 6 (Tables 1 and 2) in which the range in the probability of larval survival was varied from 0.4–0.6 from an egg size of 37–73 μm. (Top) Egg size was determined by 1 gene on each chromosome. (Bottom) Egg size was determined by 2 genes on each chromosome.

The addition of fishing at a removal rate of 25% of the fishable (≥2.5 inches) stock yearly substantially reduces population abundance (Fig. 16) and generation time. Generation time is reduced to a level consistent with the cases of intermediate generation time summarized in Figures 12 and 14. Outcomes are similar. Trends in egg size established without fishing are fostered and accelerated by reduced generation time (Figs. 17 and 18). Cases in which rapid selection for larger or smaller egg sizes in the unfished population occur result in further increases or reductions in egg size (Figs. 17 and 18). Cases for which moderate changes in egg size are observed in the unfished population show limited additional shifts in egg size (Figs. 17 and 18), suggesting a tendency for increased mortality to counter any modest selective advantage for larger eggs.

The relaxation of fishing to a removal rate of 10% permits an increase in population abundance and a modest increase in generation time (Fig. 16). For cases in which the selection for increased or decreased egg size was profound in the unfished population, the process continued apace after fishing was relaxed to 10% of the stock annually, if an equilibrium egg size had not already been achieved (Figs. 17 and 18). For cases in
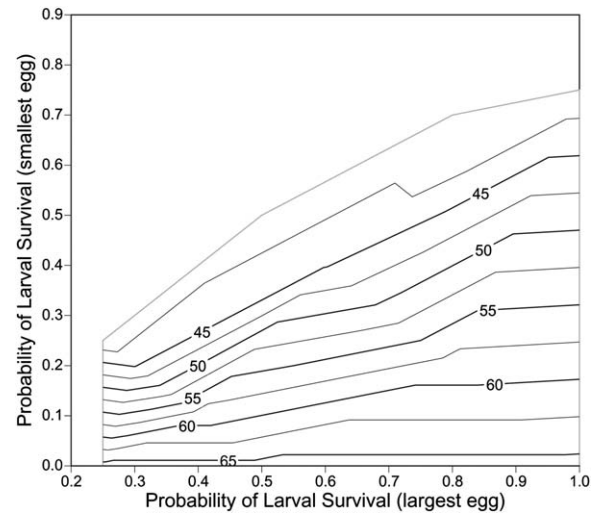
which a moderate change in egg size was observed in the unfished population, for which a moderate counterweight to the selective pressure was imposed by removal of 25% of the stock annually, relaxation of the fishery to 10% permitted, in some cases, the selection process to continue again toward larger egg sizes or, in rare cases, reversed the effect (Figs. 17 and 18). Reversals were exceedingly rare, however.

DISCUSSION

Natural Controls on Egg Size

Bochenek et al. (2001) and Hofmann et al. (2004) showed that packaging of sufficient material to permit any survivorship of larvae in oysters fails at egg sizes smaller than about 40 μm, thus placing a lower limit on oyster egg size. This agrees with empirical data provided by Gallager et al. (1986). However, oyster eggs are routinely 10–15 μm larger than this lower limit (Gallager & Mann 1986, His et al. 2000, Ernande et al. 2004, Cardoso et al. 2007). Why should egg sizes be this large, but no larger? A penalty is imposed by adopting this larger egg size. Volumetrically, the difference equates to a reduction in egg numbers greater than 50% (Fig. 1), a value exceeding the range in gamete fraction for the genus *Crassostrea* (e.g., Héral & Deslous-Paoli 1983, Choi et al. 1993 Choi et al. 1994, Páez-Osuna et al. 1995, Kang et al. 2003, Ngo et al. 2006), and thus potentially of greater importance in determining female lifetime fecundity than any other adaptation. On the other hand, all information on the influence of egg size on survival, both experimental and from simulation, indicates that larger eggs should generate larvae with an increased chance of survival, particularly assuming that egg quality is, in part, a function of
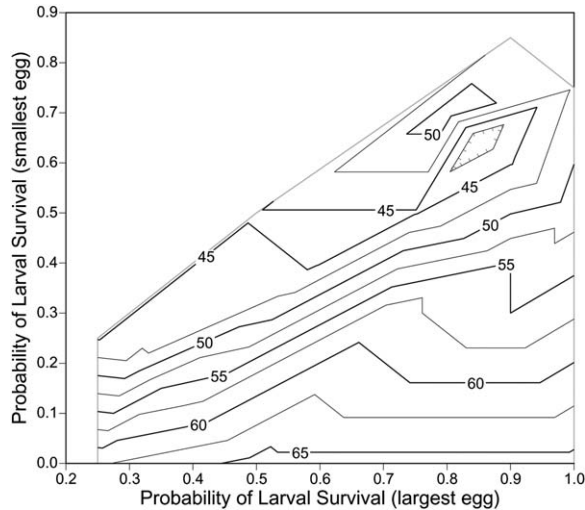
Figure 10. The results of a series of simulations defined in Table 2 using the ranges of larval survivorship described in Table 1, in which the fraction of the population reproducing was decreased by a factor of 10, equivalent to a decrease in effective population size. Each simulation was run for 200 generations. Plotted are the modal egg sizes obtained with ranges of larval survival defined by the y-axis (lowest probability of larval survival associated with the smallest egg) and the x-axis (highest probability of larval survival associated with the largest egg). For example, an egg size at $y = 0.3$ and $x = 0.5$ is the expected outcome for the case in which the probability of larval survival ranged from 0.3–0.5 over the 37–73-μm egg size range. Contours are egg diameter measured in micrometers.
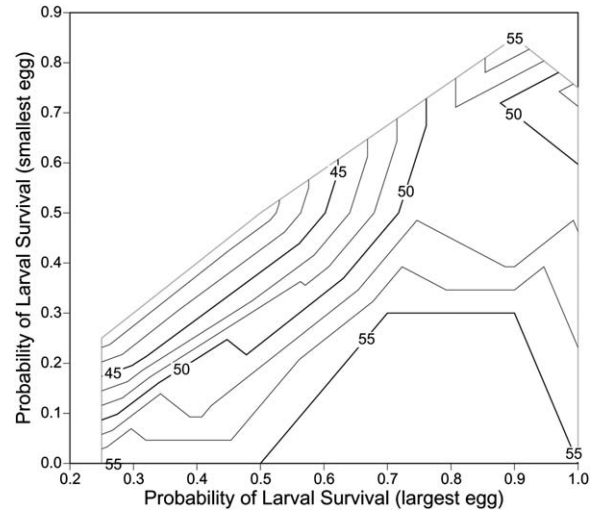
Figure 11. The results of a series of simulations defined in Table 2 using the ranges of larval survivorship described in Table 1, in which the relative fitness of the *AB* genotype was afforded a competitive advantage relative to *AA* or *BB*. Each simulation was run for 200 generations. Plotted are the modal egg sizes obtained with ranges of larval survival defined by the y-axis (lowest probability of larval survival associated with the smallest egg) and the x-axis (highest probability of larval survival associated with the largest egg). For example, an egg size at $y = 0.3$ and $x = 0.5$ is the expected outcome for the case in which the probability of larval survival ranged from 0.3–0.5 over the 37–73-μm egg size range. Contours are egg diameter measured in micrometers.

egg volume (Gallager et al. 1986, Bochenek et al. 2001, Powell et al. 2002, Chávez-Villalba et al. 2003, Hofmann et al. 2004, Powell et al. 2004). This differential in survival should select for increased egg size (e.g., Einum & Fleming 2002, Laptikhovsky 2006). That it has not, at least to the extent that might be anticipated by other bivalves with larger eggs (e.g., *M. mercenaria* (Lee & Heffernan 1991), *Codakia orbicularis* (Alatalo et al. 1984), *Chlamys farreri* (Guo & Luo 2006), *Ostrea puelchana* (Castaños et al. 2005)), suggests a counterweight to the selective advantage of larger, higher quality eggs with enhanced survivorship.

Powell et al. (2004) suggested that an effective counterweight might be the sheer number of smaller eggs that might be produced from the same gonadal volume. Moreover, inherently less successful larvae may produce more successfully reproducing adults than fewer, more successful larvae, particularly if larval survivorship is low. Although little concrete information is known about larval survivorship in oysters, it is generally thought to be low (Rumrill 1990, Dekshenieks et al. 1997, Mann & Evans 1998, Breitburg & Fulford 2006), as evidence of dramatically increased recruitment on clean shell plants would seem to confirm (Haven et al. 1987, Abbe 1988, Bushek et al. 2004).

We simulated a range of larval survivorships and permitted a series of genes to influence egg size. The simulations were based on 2 criteria associated with egg size. First, the number of eggs produced was a function of a constant relationship between animal size and gonadal volume, and the volume of an individual egg (Fig. 1). Thus, as egg volume increased, the number of eggs produced declined, but gonadal volume did not change. Second, the survivorship of an egg from fertilization through metamorphosis was a function of egg volume. Thus, larger eggs generated larvae with a greater inherent chance of survival.

Simulations showed that population genotype was modified over 200 generations in nearly every case. Some cases yielded the anticipated outcome that genotypes generating larger eggs were favorably selected and became more common in the population. In other cases, however, the converse occurred. Genotypes generating smaller eggs became increasingly common in the population, despite a gradient in the probability of survivorship expressed as a function of increasing egg size (Fig. 1). In these cases, the population egg size shifted in such a way that the likelihood of survival for a given larva declined—the antithesis of expectation from individual larval fitness.

What is interesting is how few simulations identify final egg sizes near the center of the range—that is, near the observed egg size of most *Crassostrea* oysters of about 50 μm. Under conditions of environmental constancy, in which the range of larval survivorship relative to egg size is recapitulated year after year, only a relatively few ranges in larval survivorship generate final egg sizes near the center of the range of egg sizes permitted in the simulation (37–73 μm; e.g., Fig. 2). This suggests that, under most field conditions, a selective advantage exists toward smaller or larger egg sizes than those typically spawned, so that the yearly outcome should be to nudge egg sizes larger or smaller. A repetitive series of such "nudgings," over a relatively short passage of years should result in a population spawning eggs distinctly smaller or larger than 50 μm.

The explanation for the dichotomy of outcomes emerging from variation in the range of larval survivorships involves the mechanism by which parental fitness is maximized, typically expressed as the number of progeny surviving over the adult's lifetime or the ratio of reproductive effort to the number of successful offspring (e.g., Smith & Fretwell 1974, Sibley &
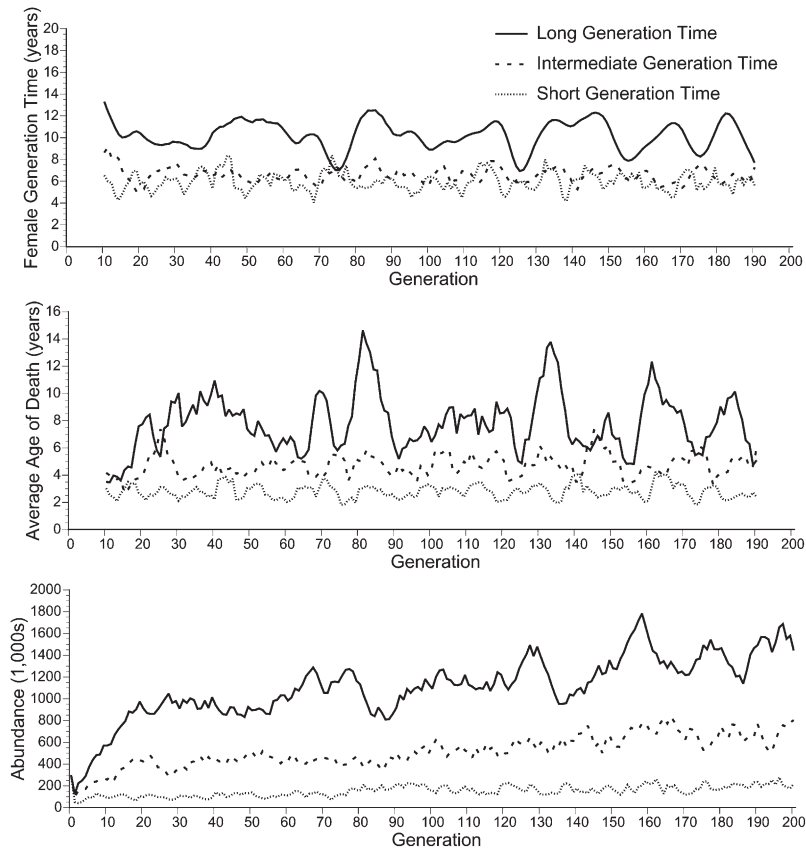
Figure 12. Generation time, average age of death, and population abundance for 3 simulations of case 6 (Table 1) in which the probability of larval survival was varied from 0.4–0.6 for a egg sizes of 37–73 μm. Specifications for the 3 simulations are in Table 2.

Calow 1989, Forbes 1991, Lundberg & Persson 1993). Parental fitness in the context of the number of offspring surviving to the next generation relative to the number of eggs produced is a balance between the increase in the number of larvae that might survive promoted by the production of a larger number of eggs and the genetically determined individual probability of larval survival that we term "larval fitness" and that is a function of egg size. In some cases, survival by chance is more likely than survival of a larva from an inherently more fit egg phenotype. Under this circumstance, egg size declines. In other cases, survival of larvae with more fit phenotypes results in more larvae recruiting than occurs from the chance survival of less fit, but more numerous larvae with phenotypes for small eggs. In these cases, egg size increases.

Sensitivity to Genetic and Population Parameters

One might expect variations in population abundance, inherent fecundity (e.g., gamete fraction), or effective population size to affect the balance between the chanciness of survival and the influence of phenotype on survival. These properties of the population dynamics, however, had little impact on the outcome. In particular, in no case did variation in the properties change the trend toward smaller or larger eggs, and rarely did they modulate the degree of shift in egg size to any degree. Properties of the population dynamics were inconsequential. Had we allowed gonadal volume and egg size to vary in parallel rather than in opposition, a different outcome might have been obtained;

however, variability in gonadal volume is small relative to egg number, so that the relationship between egg number, egg size, and larval success should still have determined overall trends.

The number of genes on each chromosome affecting egg size modulated the outcome of simulations in a predictable way. Multiple genes on a chromosome slowed the rate at which egg size changed over a series of generations. However, in no case did the trend toward smaller or larger eggs vary. Similarly, the difference in relative fitness between dominance and overdominance in which the heterozygote is relatively advantaged or disadvantaged, although profound, did not vary the overall trend, although it substantively constrained the range of outcomes. This ramification is, of course, not surprising, given the assigned allele fitnesses to the AA, AB, and BB genotypes.

Thus, although a variety of modifications in model parameterization modulates the outcome from a minor to a relatively major degree, the controlling influence on the outcome remains dominantly the range of larval survivorship balanced against the number of eggs produced per gonadal volume. In no case are trends in egg size established in the series of base cases reversed by variation in population dynamics, or simple variations in the number of genes affecting fitness or the relative fitness value afforded combinations of the A and B alleles.

Why a 50-μm Egg?

Oyster eggs tend to be about 50 μm in diameter. Few populations vary much from this value, as far as the reports of egg

Figure 13. The results of a series of simulations defined in Table 2 using the ranges of larval survivorship described in Table 1, in which the mortality rate was configured to produce a relatively long generation time. Each simulation was run for 200 generations. Plotted are the modal egg sizes obtained with ranges of larval survival defined by the y-axis (lowest probability of larval survival associated with the smallest egg) and the x-axis (highest probability of larval survival associated with the largest egg). For example, an egg size at $y = 0.3$ and $x = 0.5$ is the expected outcome for the case in which the probability of larval survival ranged from 0.3–0.5 over the 37–73-μm egg size range. Contours are egg diameter measured in micrometers.
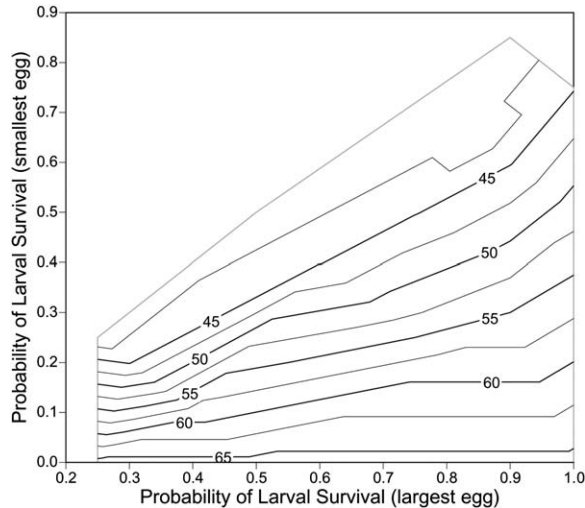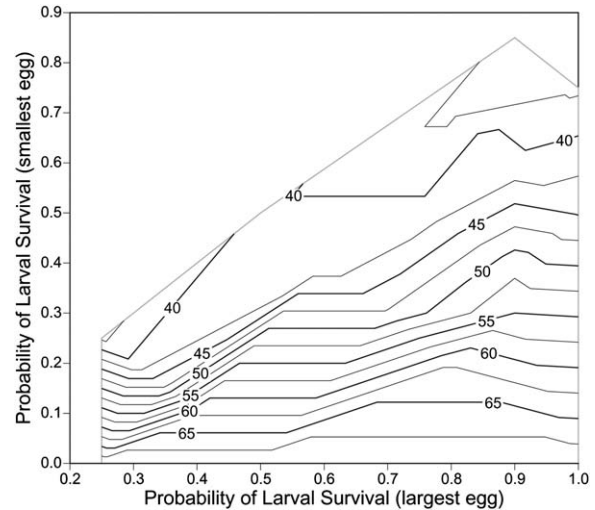
Figure 14. The results of a series of simulations defined in Table 2 using the ranges of larval survivorship described in Table 1, in which the mortality rate was configured to produce an intermediate generation time. Each simulation was run for 200 generations. Plotted are the modal egg sizes obtained with ranges of larval survival defined by the y-axis (lowest probability of larval survival associated with the smallest egg) and the x-axis (highest probability of larval survival associated with the largest egg). For example, an egg size at $y = 0.3$ and $x = 0.5$ is the expected outcome for the case in which the probability of larval survival ranged from 0.3–0.5 over the 37–73-μm egg size range. Contours are egg diameter measured in micrometers.

size permit the inference (see earlier references; but see Cardoso et al. (2007)); however, few comparisons can be made. The suggestion is that variation in egg size is relatively constrained in oysters despite the apparent wide range of impact of varying larval survivorships on egg size (e.g., Gallager et al. 1986).

Two explanations are possible. The first is that the 50-μm outcome represents the favorable balance between a predictable range in larval survivorship and the constraint in total egg production imposed by an invariant gonadal volume. Gonadal volume is relatively constrained within the Bivalvia (e.g., Powell & Stanton 1985). Little is known about the range of larval survivorships, but the influence of temperature, salinity, and turbidity (Dekshenieks et al. 1993, Dekshenieks et al. 1997), plus variations in current velocity (Dekshenieks et al. 1996), is such that a predictably persistent range in larval survivorship over a period of years would seem to have a vanishing low probability.

The alternative is that the 50-μm size represents the median outcome of a range of survivorship probabilities, each selecting for relatively larger or smaller eggs, imposed stochastically over multiple generations. Environmental stochasticity is the norm and is frequently expressed by year-to-year variation in recruitment (e.g., Loosanoff 1966, Keough 1983, Austin et al. 1996, Powell et al. 2008). In this scenario, each year the population is pulled toward smaller or larger egg sizes, but in the next year, by chance, the impetus is independent of the previous year. Over multiple generations, the range of survivorships is such that 50-μm eggs manifest the average of many independent yearly urgings. The dominant influence of environmental stochasticity on reproductive success is well ingrained in population dynamics theory (e.g., Stearns 1976, Forbes 1991). Our results conform to this expectation.

Figure 2 summarizes a series of simulations for animals with a long generation time, arguably the evolutionary condition. The 50-μm trajectory follows a range of moderately variable survivorships relative to egg size. Few extremely narrow and no extremely wide ranges in survivorship foster this outcome. This suggests that environmental conditions are normally such that the fitness of larger eggs is not often expressed overly much. The inference is that environmental conditions routinely include sufficient food resources to enhance the success of larvae from small eggs. This outcome occurs when food quantities are relatively high and/or food qualities provide sufficient lipid that can be stored for metamorphosis (Bochenek et al. 2001, Powell et al. 2002, Powell et al. 2004). Although food quantity frequently may be limiting (Dekshenieks et al. 1993, Dekshenieks et al. 2000), food is typically rich in lipid (Soniat et al. 1984, Hyun et al. 2001, Versar 2002), suggesting that high-quality food may be the norm. Thus, food limitation, often a hypothesis in explaining recruitment dynamics (e.g., Olson & Olson 1989, Ólafsson et al. 1994, Biktashev & Brindley 2004), would appear to be infrequent enough to minimize the adaptive advantage of large eggs, but sufficiently important to minimize the success of the smallest eggs.

Generation Time, Disease, and Fishing

The median egg size resolved after 200 simulated generations is relatively insensitive to a large change in generation time. A decrease in population average age from about 7 y to about 4 y varied the outcome of simulations only moderately. A further reduction to about 3 y or less, however, further modified simulation outcome. In both cases, the result was one of extent,
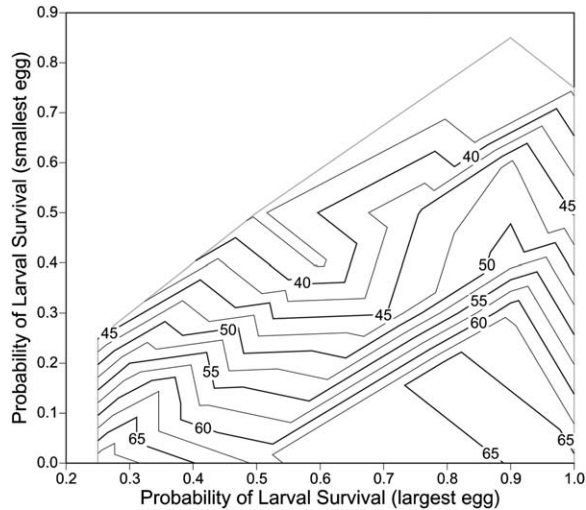
Figure 15. The results of a series of simulations defined in Table 2 using the ranges of larval survivorship described in Table 1, in which the mortality rate was configured to produce a short generation time. Each simulation was run for 200 generations. Plotted are the modal egg sizes obtained with ranges of larval survival defined by the y-axis (lowest probability of larval survival associated with the smallest egg) and the x-axis (highest probability of larval survival associated with the largest egg). For example, an egg size at y = 0.3 and x = 0.5 is the expected outcome for the case in which the probability of larval survival ranged from 0.3–0.5 over the 37–73-μm egg size range. Contours are egg diameter measured in micrometers.

sensitivity to the range of larval survivorship by expressing an increased tendency toward the extremes in egg size.

One notable exception exists to this pattern—namely, the tendency toward larger eggs at low larval survivorship and short generation time. The simulations suggest that, when generation time is sufficiently short and the probability of larval survival over all egg sizes is sufficiently poor, some selective advantage appears for larger egg sizes. Presumably, this indicates a change in the balance between sheer fecundity and egg quality imposed by the necessity for population replacement when adult mortality rates and larval mortality rates are simultaneously high.

Regardless, per previous arguments, environmental stochasticity is likely to retain its preeminence in stabilizing a balance between extremes in egg size, as the dichotomous outcomes are still well ensconced at all simulated generation times. As a consequence, one might anticipate little change in egg size with declining generation time, even with the enhanced tendency toward extreme outcomes observed. Note in Figures 15 and 16, for example, that the sectors encompassing a range of larval survivorship yielding large and small eggs have each expanded relative to the intermediate outcome, not at the expense of each other. Thus, the yearly nudgings have increased in strength, but the likelihood that a span of years will find equally likely outcomes promoting small and large egg size remains.

Dermo and MSX disease have dramatically reduced average life times in *C. virginica*. The degree is poorly documented, because age frequencies for oysters are rare (e.g., Harding et al. 2008). The increase in mortality rate is better documented, however (e.g., Ford & Haskin 1982, Andrews 1988, Burreson & Ragone Calvo 1996, Powell et al. 2008). What is believed to be a plausible predisease mortality rate of 10% per year requires more than 20 y to reduce a cohort to 10% of its original size. We exclude from these calculations the first 1 y of life, during which mortality far exceeds 10%; first-year mortality is about 60% in Delaware Bay (Powell et al. 2009a). Epizootic mortality rates of 25–30% per year reduce a cohort to 10% of its original size in

not direction, of trend. Overall, simulations generating a selective advantage for large eggs resulted in an enhancement of this effect. Simulations generating a selective advantage for small eggs generated an enhancement of that effect. Simulations generating an intermediate outcome, however, became passingly rare. Thus, the conversion of a long-lived animal into an animal with a life span of 2–3 y resulted in a substantially increased

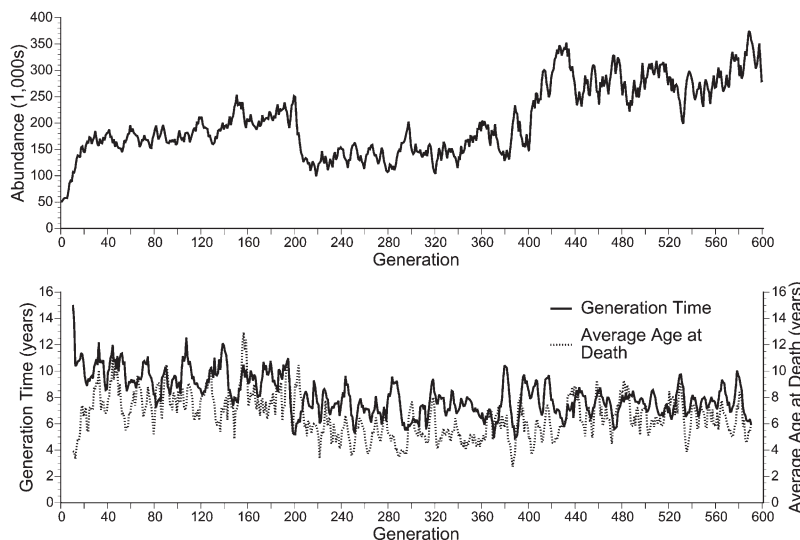**Figure 16. Abundance, generation time, and average age at death for a simulation of case 6 (Tables 1 and 2) in which the probability of larval survival was varied from 0.4–0.6 from an egg size of 37–73 μm. The first 200 generations were run without fishing. From generation 201–400, a fishery removed 25% of the stock ≥63.5 mm. The fishery was relaxed to 10% per year beginning in generation 401.**
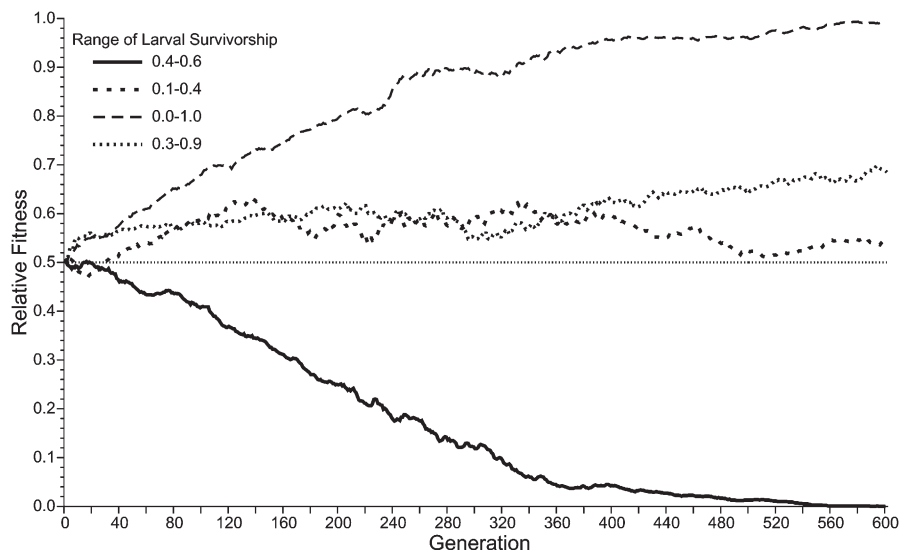
Figure 17. The time series of population fitness over 600 generations for simulations 4, 6, 9, and 10 (Tables 1 and 2). Fitness is defined based on the individual fitness contributions of the genes affecting egg size averaged over the entire population. The population was not fished for the first 200 generations. After that, 25% of the stock $\geq$ 63.5 mm was removed yearly from generations 201–400, and 10% yearly from generations 401–600.

about 9 y. The average age at death for the low-mortality (10% per year) condition is about 9 y, similar to our long life span simulations. For the epizootic case, the average age at death is 4 y, similar to our intermediate life span simulations. This suggests that the tendency toward selection for extreme egg sizes observed at the shortest generation times is unlikely to be expressed in the Dermo-controlled oyster stock as it exists in the Mid-Atlantic Bight today, except under extreme conditions, and such extreme epizootic mortalities are not long-lived.

That fishing can influence reproductive output through genetic selection is well described (Walsh et al. 2006, Sattar et al. 2008), including selection for more smaller eggs (e.g., Huner & Lindqvist 1991). Fishing is merely a mechanism to reduce life span. Simulations support the concept that oysters cannot withstand a fishing level exceeding about 10% per year, and well below this level with Dermo or MSX disease present. In Delaware Bay, a fishery of 10% would raise the mortality rate to about 35% per year under epizootic conditions. This generates an average age for a cohort below 3 y. An indisputable overfishing level of 25% per year for a stock prior to the onset of disease (Powell et al. 2008) would reduce average age to 3.5 y. This level is within the range in which simulations show increased selection favoring extremes in egg size brought about by variations in the yearly range in larval survivorship. Thus, our simulations span the likely range of population dynamics for diseased and undiseased populations, and well-managed and, at least moderately, mismanaged stocks.

Nevertheless, the dichotomous character of selection advantaging large eggs when the range of larval survivorship is large and small eggs when the range of larval survivorship is small remains distinctly manifest. Thus, the preeminence of environmental stochasticity as the paramount factor influencing egg size endures. An expected response to overfishing includes adaptation toward an enhanced capability for population replacement at shorter generation times. Our simulations appear to negate the promise of changes in egg number through smaller

eggs or larval survival through larger eggs. Earlier maturity of females remains the most likely adaptation to any imposition of shortened generation times (Powell unpubl. data), whether by disease, overfishing, or any other factor limiting adult life span.

The origin of the increased selection pressure for extreme outcomes is uncertain. Several options exist. In the first place, reduced generation time reduces the time span over which genotypes are retained in the population simply by continued life of the animals holding them. Thus, as generation time declines, one might expect that disadvantageous genotypes might disappear at an increased rate and the result would be as seen here. Alternatively, reduced generation time, by fishing for example, is accompanied by increased volatility in population abundance (Fig. 16). This is anticipated, as long life spans by their very existence should damp out interannual variations in abundance. Increased volatility in abundance results in some years in which recruitment is much higher than in other years, and one might expect that such years put additional selective pressure on the choice of egg size, whether the force impels a smaller or larger egg size to have the selective advantage. The 2 options very likely both operate in our simulations and can be expected to impute volatility in natural populations under the same pressure of increased mortality and decreased generation time.

CONCLUSIONS

Large eggs auger an increased probability of larval survival. This tendency is well established over a broad range of marine animals (e.g., Gallager et al. 1986, Runsdorp 1994, Marshall et al. 2004). What determines egg size? Our simulations suggest that an optimal egg size exists for any given range in larval survivorships. Our simulations indicate that intermediate egg sizes are optimal over only a narrow range of constant environmental conditions, however. In most cases, egg sizes
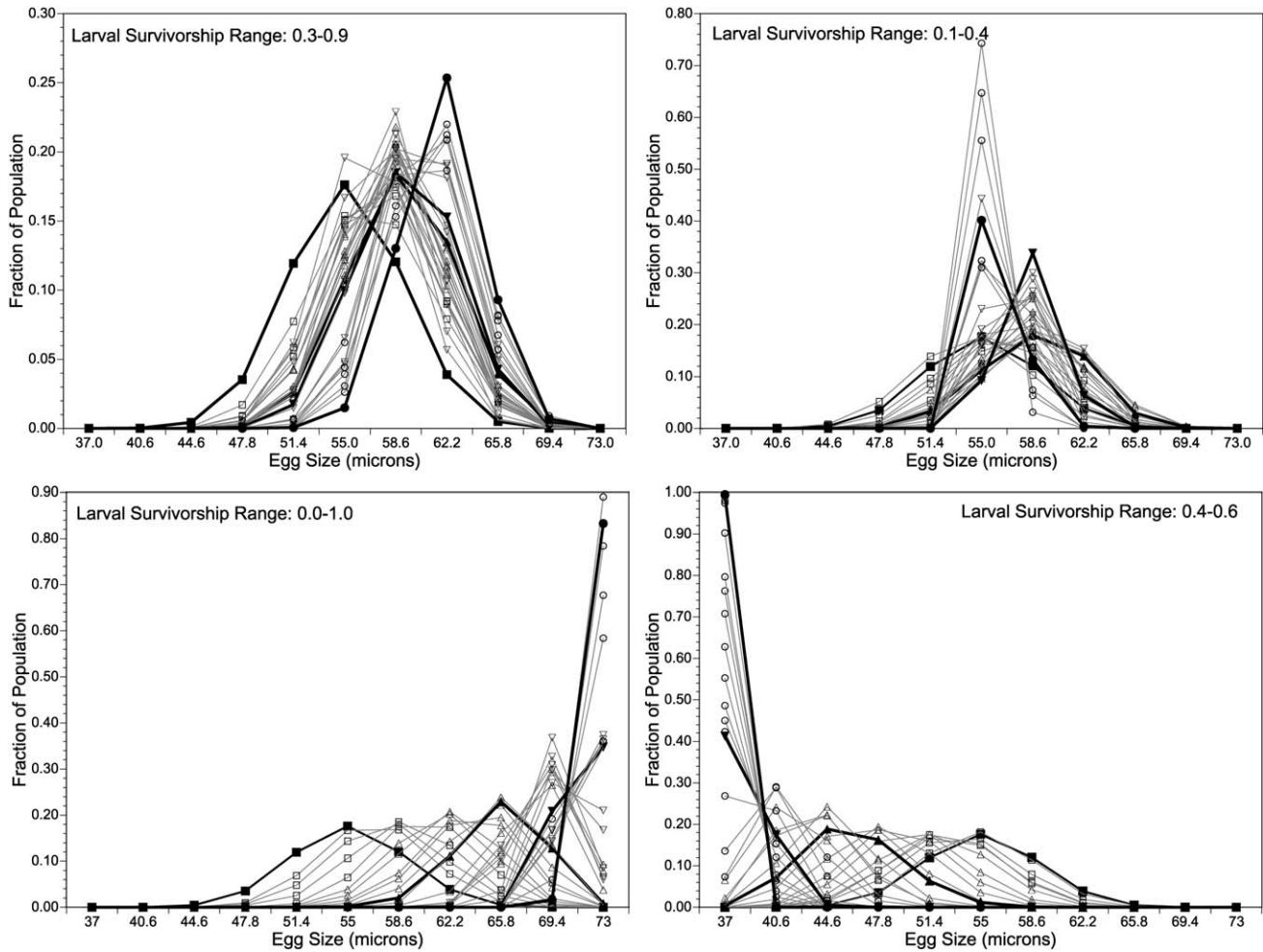
Figure 18. The time series of egg size frequencies over 600 generations for simulations 4, 6, 9, and 10 defined in Table 2 (see also Fig. 17) showing the influence of fishing on egg size. The population was not fished for the first 200 generations. After that, 25% of the stock ≥ 63.5 mm was removed yearly from generations 201–400, and 10% yearly from generations 401–600. Generation 1 is marked by the large solid square symbol; generation 201, the first generation with fishing (25%), is marked by the large solid triangle; generation 401, the first generation with reduced fishing (10%), is marked by the large solid inverted triangle; generation 591, near the end of the simulation, is marked by the large solid circle. Open squares, representative generations for generations 2–100; open triangles, representative generations for generations 101–200 and 202–300; open inverted triangles, representative generations for generation 302–400 and 402–500; open circles, representative generations for generation 501–590. Approximately each 20th generation is plotted.

smaller or larger than the 50-μm egg size typically encountered for *Crassostrea* oysters will be more advantageous, and the differential in egg size between observed and expected is directly related to the range of larval survivorship determined by that environmental regime. This, however, does not necessarily support the extremum hypothesis (e.g., Vance 1973) that imputes preference to the paradigmatic lecithotrophic and planktotrophic conditions with expectations for intermediate outcomes having low probability. The counterweights of egg number and probability of larval survivorship restrain the range of outcomes. However, the range of outcomes would certainly be larger than observed.

However, the environment is not constant. Stochasticity limits the direction of selection for optimal egg size because the optimal egg size favored by selection varies every year. The outcome is the long-term median of the influences of narrowed and expanded ranges of larval survivorship over the range of available egg sizes. This outcome very likely is dominated by the

influence of food concentration and food composition in the plankton (e.g., Dekshenieks et al. 1993, Biktashev & Brindley 2004, Powell et al. 2002, Powell et al. 2004) and the first-order character of daily planktonic mortality that penalizes longer larval life spans (Jackson & Strathmann 1981, Rice et al. 1993), but one should not discount the influence of food supply for early juveniles (e.g., Wikfors et al. 1984, Spencer 1988), particularly when feeding rate is limited by ongoing development of the gills (Baker & Mann 1994, Cannuel & Beninger 2006). The obvious implication is that egg size is an indicator, albeit complex, of environmental conditions, with a narrower range in observed egg sizes indicative of a narrower range of larval survivorships, or a lesser importance of egg quality on overall larval performance. One is left with an interesting query concerning interspecific variation in egg size. Egg sizes average larger for *M. mercenaria*, for example, than for *C. virginica* (e.g., Lee & Heffernan 1991), and the range of egg sizes would also appear to be larger. Our simulations suggest that *M. mercenaria*

larvae experience a wider range in survivorship each year, on average, than larvae of *C. virginica*. Egg size ranges widely over the Bivalvia with the same implications (e.g., Tyler & Young 1999, Marko & Moran 2002, Kang et al. 2004, Castaños et al. 2005, Guo & Luo 2006, Phillips 2007). Data are not yet available to test such a hypothesis.

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