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# A Model For Assessing The Likelihood Of Self-Sustaining Populations Resulting From Commercial Production Of Triploid Suminoe Oysters (Crassostrea Ariakensis) In Chesapeake Bay

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**Abstract**—Culture of a non-native species, such as the Suminoe oyster (*Crassostrea ariakensis*), could offset the harvest of the declining native eastern oyster (*Crassostrea virginica*) fishery in Chesapeake Bay. Because of possible ecological impacts from introducing a fertile non-native species, introduction of sterile triploid oysters has been proposed. However, recent data show that a small percentage of triploid individuals progressively revert toward diploidy, introducing the possibility that Suminoe oysters might establish self-sustaining populations. To assess the risk of Suminoe oyster populations becoming established in Chesapeake Bay, a demographic population model was developed. Parameters modeled were salinity, stocking density, reversion rate, reproductive potential, natural and harvest-induced mortality, growth rates, and effects of various management strategies, including harvest strategies. The probability of a Suminoe oyster population becoming self-sustaining decreased in the model when oysters are grown at low salinity sites, certainty of harvest is high, minimum shell length-at-harvest is small, and stocking density is low. From the results of the model, we suggest adopting the proposed management strategies shown by the model to decrease the probability of a Suminoe oyster population becoming self-sustaining. Policy makers and fishery managers can use the model to predict potential outcomes of policy decisions, supporting the ability to make science-based policy decisions about the proposed introduction of triploid Suminoe oysters into the Chesapeake Bay.

# A model for assessing the likelihood of self-sustaining populations resulting from commercial production of triploid Suminoe oysters (*Crassostrea ariakensis*) in Chesapeake Bay

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The native eastern oyster (*Crassostrea virginica*) population in Chesapeake Bay has declined because of habitat degradation, over-harvest, and disease- and parasite-mediated mortality. Efforts to restore the eastern oyster population in Maryland and Virginia have been hindered by persistent diseases and habitat degradation (Mann et al., 1991; Gottlieb and Schweighofer, 1996). Recent restoration efforts have included intensified reef building programs. In addition to restoring the native oyster, discussions about introducing non-native disease- and parasite-resistant oyster species into the Chesapeake Bay have gone forward since the early 1990s (Mann et al., 1991; Lipton et al., 1992; Gottlieb and Schweighofer, 1996; Hallerman et al., 2002).

In 1997, in-water testing of non-native oyster species (sterile triploids) began in Virginia, first with the Pacific oyster (*Crassostrea gigas*), then with the Suminoe oyster (*Crassostrea ariakensis*) (Calvo et al., 1999; Calvo et al., 2001). Field studies with Pacific oysters showed poor performance under Chesapeake Bay conditions (Calvo et al., 1999). However, field studies with Suminoe oysters demonstrated disease resistance and rapid growth, and indi-

viduals reached minimum harvest shell length of about 77 mm in approximately one year (Calvo et al., 2001). These results, and subsequent small-scale trials by industry, evoked strong interest in the commercial culture of Suminoe oysters to supplement the eastern oyster fishery.

Ideally, aquaculture with 100% triploid oysters would pose no risk of establishment of a self-sustaining oyster population (Guo and Allen, 1994a). However, a number of factors make the use of triploids imperfect. For example, recent data have shown that a small percentage of triploid oysters progressively revert toward diploidy with age (Calvo et al., 2001; Zhou, 2002). Reversion of triploids leads to mosaicism in which individuals comprise both diploid and triploid cells. Mosaics themselves are innocuous unless the re-establishment of diploid cells leads to recovered reproductive capability, which could in turn lead to the establishment of a self-sustaining Suminoe oyster population. We define this hazard, "reproductively effective reversion," as the process of yielding mosaics with recovered reproductive capability. Reproductively effective reversion introduces the possibility that triploid Suminoe

oysters planted for aquaculture could become a self-sustaining population of diploid Suminoe oysters and introduce numerous unknown ecological consequences.

Another hazard associated with deployment of triploid Suminoe oysters is the possibility that nontriploids might be stocked inadvertently because of failure to detect them in a mixed batch of triploid and diploid individuals. Although technology to produce "100%" triploids is now available, as practiced on Pacific oyster (Guo and Allen, 1994b; Guo et al., 1996), the reliability of the approach for producing "100%" triploids in Suminoe oyster is yet undetermined. Diploids may enter the population from several sources: chromosomal nondisjunction in tetraploid males producing haploid gametes, low level hermaphrodism in diploid females yielding self-fertilized embryos, and cross-contamination between diploid and triploid cultures (cf. Guo and Allen, 1997). Typically, flow cytometry has been used to determine the presence or absence of diploid cells (Allen, 1983). Flow cytometry has the sensitivity to detect one diploid among a thousand triploid oysters (Allen and Bushek, 1992); thus, the detection threshold is 0.001 with current technology. Should the (nonzero) frequency of diploids be greater than zero but less than one in a thousand, then the batch would be certified 100% triploid. This failure to detect diploid individuals in a mixed batch poses a hazard for stocking other fertile diploid oysters in that batch into culture systems.

Before substantial commercial introduction of triploid Suminoe oysters into the Chesapeake Bay, any environmental hazards of reproduction associated with a range of management scenarios should be assessed. Hazards are defined as undesirable outcomes from an activity (Hallerman and Kapuscinski, 1995). Stocking triploid Suminoe oysters produces two hazards in this model: the inadvertent stocking of diploids and the reproductively effective reversion of triploids. These two hazards may lead to the establishment of a self-sustained Suminoe oyster population and the probability of this occurring is defined as a risk. Risk assessment is the process of 1) identifying hazards posed by management actions, such as deployment of triploid Suminoe oysters, 2) quantifying the associated risks of hazards being realized (Hallerman and Kapuscinski, 1995), such as the population becoming self-sustaining, and 3) evaluating the consequences of the hazards. Quantitative models often are used to assess risk (Lackey, 1994). Building upon data collected on growth, mortality, and reproductively effective reversion for Suminoe oysters, we have developed a quantitative model to estimate the risk associated with large-scale deployment of triploid Suminoe oysters under a range of management scenarios. The model predicts the likelihood of out-planted triploid Suminoe oysters giving rise to a self-sustaining population at a given site in the Chesapeake Bay given user-specified stocking, reproductively
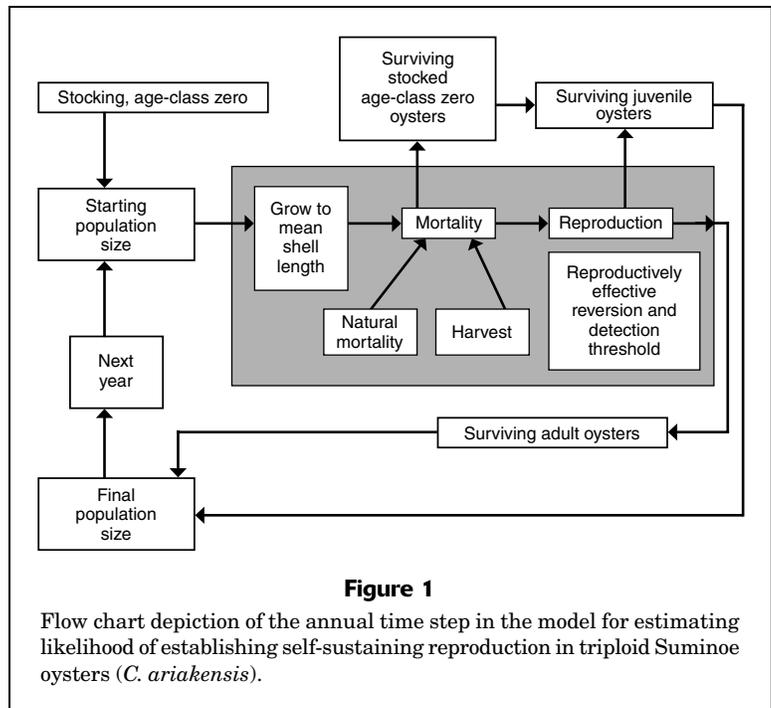


**Figure 1**

Flow chart depiction of the annual time step in the model for estimating likelihood of establishing self-sustaining reproduction in triploid Suminoe oysters (*C. ariakensis*).

effective reversion, reproduction, growth, and mortality rates (both natural and harvest), as well as user-specified management options.

## Methods

### Overview of model

A quantitative population model of the Suminoe oyster was developed to evaluate the consequences of hazards associated with introducing triploid Suminoe oysters under a range of environmental conditions and management strategies. The model includes set demographic parameters (length-fecundity, oyster density-fertilization efficiency, and salinity-fecundity relationships) and user-specified variables (reproduction, growth, and natural and harvest mortality rates). It includes options for varying stocking rates, harvest rates, and other management actions. Because little is known about Suminoe oyster reproduction, we assumed that Suminoe oysters would behave like the congeneric eastern oysters in Chesapeake Bay; hence, an eastern oyster fecundity model (Mann and Evans, 1998) was used to estimate fecundity of Suminoe oysters. The model assumes that the Suminoe oyster population is closed, i.e. that natural immigration and emigration do not occur. The model is age-structured, and a yearly time step is used. The state variable tracked through time is population size. Intrinsic population growth rate is exponential and without density dependence. The final output of the model is the predicted population size of Suminoe oyster assuming specified demographic parameters and environmental and management variables. The model was programmed in Visual Basic (Microsoft Corp., Redmond, WA).

## Modeling approach

In each annual time step for age classes one through six, growth occurs to the mean shell length of the age class, then natural mortality and harvest are imposed, and then reproduction occurs (Fig. 1). Because Suminoe oysters grow quickly in autumn (Cahn, 1950), the annual time step begins in September. Harvest occurs from October to April. Natural mortality occurs at the greatest rates during the summer months. Because an annual time step is being used, the model is designed so that natural mortality and harvest are imposed simultaneously. Reproduction occurs during the summer months. The model simulates reproduction for fertile individuals in all mature age classes. The final population size for a particular age class after natural mortality and harvest becomes the starting value for population size for the next age class in the next time step. All individuals stocked each year are age-class zero individuals. The starting population size for age-class one in the next time step is equal to the sum of all individuals less than one-year old produced by all age classes, plus the number of individuals stocked.

## Model variables, parameters, and equations

The initial conditions for the model are determined by the user's choice of specific values for several variables (Tables 1 and 2). The key abiotic variable driving population growth is salinity, because fecundity is highly dependent upon salinity (Mann and Evans, 1998). Biotic variables of the model include mean shell length for each age class, mortality (natural and harvest) for each age class, disease prevalence, total mortality of oysters less than one year old, oyster population density, sex ratio for each age class, and reproductively effective reversion rate for each age class (Table 1). Other variable inputs are stocking rates, harvest regulations, and management strategies.

Stochasticity is programed into the model to incorporate both the uncertainty involved in estimating variable values and environmental variation. Some variables are regarded as stochastic variables because they vary around some mean value from year to year, whereas other variables (such as salinity and sex ratio of the population for each age class) are deterministic in the model because they fluctuate over a longer period of time in the absence of a catastrophe (Kennedy et al., 1996). Stochasticity affects shell length, natural mortality, and reproductively effective reversion rates at each age, and the degree of variance is set by the user as a constant for each year. At each time step, a mean shell length, mortality rate, and reproductively effective reversion rate for each age class is randomly drawn from a log normal distribution around a mean with an associated variance.

We assume that the mean shell length of each age class at the current time step does not affect the mean length of the age class at a subsequent time step, because of large, highly variable growth rates per year (Calvo et al., 2001). Default mean shell length for each age-class values were obtained from Cahn (1950). The user may, of course, specify other mean shell lengths. Growth affects the potential for

**Table 1**
Definitions of model parameters and variables.

| Symbol | Parameter and variable definition |
| --- | --- |
| $A$ | Area (square meters) |
| $C$ | Certainty in obtaining the desired harvest rate ($0 \leq C \leq 1$) |
| $D_{t,i}$ | Oyster density (number of oysters per m$^2$) at time $t$ for age-class $i$ |
| $F_{t,i}$ | Total fecundity (number of eggs) at time $t$ for age-class $i$ |
| $Fd$ | Effect of disease on fecundity ($0 \leq Fd \leq 1$) |
| $Ff_{t,i}$ | Fertilization efficiency at time $t$ for age-class $i$ ($0 \leq Ff_{t,i} \leq 1$) |
| $Fq_i$ | Effect of sex ratio on fecundity for age-class $i$ ($0 \leq Fq_i \leq 1$) |
| $Frevert_{t,i}$ | Total fecundity (number of eggs) of reverted triploid oysters at time $t$ for age-class $i$ |
| $Fs$ | Effect of salinity on fecundity ($0 \leq Fs \leq 1$) |
| $Ftotal_t$ | Modified total number of offspring produced at time $t$ for all age classes |
| $H_i$ | Harvest mortality for age-class $i$ |
| $i$ | Age class |
| $K_t$ | Number of stocked oysters at time $t$ |
| $L_{t,i}$ | Mean shell length (mm) at time $t$ for age-class $i$ |
| $Lmort$ | Daily larval mortality rate until settlement |
| $M_{t,i}$ | Natural mortality at time $t$ for age-class $i$ |
| $N_{t,i}$ | Population size (number of oysters) at time $t$ for age-class $i$ |
| $Ntotal_t$ | Total population size (number of oysters) for all age classes at time $t$ |
| $P_{met}$ | Probability of successful metamorphis ($0 \leq P_{met} \leq 1$) |
| $R_{t,i}$ | Reproductively effective reversion rate at time $t$ for age-class $i$ ($0 \leq R_{t,i} \leq 1$) |
| $T_{t,i}$ | Detection threshold at time $t$ for age-class $i$ ($0 \leq T_{t,i} \leq 1$) |
| $S$ | Salinity (ppt) |
| $t$ | Time (years) |

recruitment through the effect of shell length on fecundity in Equation 1 below.

An equation for individual size-specific fecundity presented by Mann and Evans (1998) was multiplied by the numbers and mean sizes of females in each mature age class in order to estimate total fecundity for a diploid population:

$$F_{t,i} = 39.06 \times [0.000423 \times L_{t,i}^{1.17475}]^{2.36} \times N_{t,i}, \tag{1}$$

where $F_{t,i}$ = total fecundity (number of eggs produced) at time $t$ for age-class $i$ greater than one;

**Table 2**
Default values and age-class default values set in the model.

| Variable | Default value |
|---|---|
| $A$ (square meters) | 220 |
| $C$ | 0.9 |
| Extra timesteps without stocking (years) | 20 |
| $Fd$ | 1.0 |
| $H_t$ | 1.0 |
| Iterations | 350 |
| $K_t$ | 10000 |
| Minimum shell length-at-harvest (mm) | 76.6 |
| $S$ (ppt) | 15 |
| $t$ (years) | 50 |

| Variable | Age-class default values | | | | | | |
|---|---|---|---|---|---|---|---|
| | $i = 0$ | $i = 1$ | $i = 2$ | $i = 3$ | $i = 4$ | $i = 5$ | $i = 6$ |
| $Fq_i$ [1] | | 0.28 | 0.66 | 0.8 | 0.9 | 0.95 | 0.95 |
| $L_{t,i}$ (mm) [2] | | 54.5 | 96.9 | 124.2 | 151.5 | 178.7 | 196.9 |
| $M_{t,i}$ [3] | 0.98 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 |
| $R_{t,i}$ [3] | | 0 | 0 | 0.049 | 0.009 | 0.014 | 0.019 |
| $T_{t,i}$ [3] | | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 |
| Variance of $L_{t,i}$ (mm) [3] | | 5 | 10 | 10 | 10 | 10 | 10 |
| Variance of $M_{t,i}$ [3] | | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 |
| Variance of $R_{t,i}$ [3] | | 0.0005 | 0.0005 | 0.0005 | 0.005 | 0.005 | 0.005 |

[1] (Yingya et al., 1992).

[2] (Cahn, 1950).

[3] (Calvo et al., 2001).

$L_{t,i}$ = mean shell length (mm) at time $t$ for age-class $i$ greater than one; and

$N_{t,i}$ = population size (number of diploid oysters) at time $t$ for age-class $i$ greater than one.

We recognize that growth forms in oysters are fluid, and that fecundity may be more closely related to weight than to length. However, available growth data for *C. ariakensis* described length-at-age, and therefore we modified Mann and Evans' (1998) fecundity equation to use length as the independent variable.

Equation 1 is used when determining the number of eggs produced by diploid oysters that survived from the previous year. Equation 1 must be modified to determine the number of eggs produced by triploid oysters undergoing reproductively effective reversion. The reproductively effective reversion rate comprises two reproduction-related processes, nondetection of diploids ($T_{t,i}$) and reproductively effective reversion ($R_{t,i}$) of triploids. First, diploid individuals may enter the population through a failure to detect them at frequencies lower than 0.001 in mixed batches with triploids. We make the ecologically conservative assumption that diploid individuals will enter the first age class at the detection threshold of 0.001. After age-class 2, reproductively effective reversion is the percentage of

the population that reverts from triploidy to mosaicism (i.e. contains both triploid and diploid gamete cells) and therefore has the potential to reproduce. We conservatively assume that reverted triploids will have full reproductive capabilities, even though this has not yet been observed (Allen, unpubl. data). Default values for reproductively effective reversion were obtained from Calvo et al. (2001). The Mann and Evans (1998) fecundity model was modified to include reproductively effective reversion in the following way:

$$Frevert_{t,i} = 39.06 \times [0.000423 \times L_{t,i}^{1.17475}]^{2.36} \times N_{t,i} \times (R_{t,i} + T_{t,i}), \quad (2)$$

where $Frevert_{t,i}$ = total fecundity (number of eggs produced) for reverted triploid oysters at time $t$ for age-class $i$ greater than one;

$R_{t,i}$ = reproductively effective reversion rate at time $t$ for age-class $i$ greater than one; and

$T_{t,i}$ = diploid detection threshold at time $t$ for age-class $i$ greater than one.

The variable $Fs$ is the effect of salinity on fecundity obtained by using the mean salinity value for the area in Chesapeake Bay where a particular population of Suminoe

oysters is located. The value of $Fs$ ranges from zero (meaning zero fecundity) to one (meaning no effect of salinity on fecundity). For the eastern oyster, when salinity is below 8.0 ppt, $Fs$ is equal to zero, thereby making fecundity zero (Mann and Evans, 1998). When salinity is between 8.0 ppt and 13.5 ppt, there is a positive relationship between salinity and fecundity as described below:

$$Fs = \frac{(S-8)}{5.5}, \qquad (3)$$

where $Fs$ = the effect of salinity on fecundity; and
$S$ = salinity (ppt) between 8 ppt and 13.5 ppt.

When salinity is greater than 13.5 ppt, $Fs$ is equal to one denoting no effect of salinity on fecundity. When salinity is greater than 35 ppt, $Fs$ is equal to zero, making fecundity equal to zero (Mann and Evans, 1998). Low or no fertility at high salinity is apparently the case for *C. ariakensis* as well (Langdon and Robinson, 1996).

The variable for disease prevalence, $F_d$, has a value between 1.0 (no mortality from disease) and 0.0 (all oyster spat die from disease). Recent field studies have suggested that the Suminoe oyster is resistant to diseases on the east coast of North America (Calvo et al., 2001); therefore, the default value of $Fd$ was set at one. Nevertheless, we retained this variable in the model to account for future data sets or other diseases so that the user can select $F_d$ based on the prevalence of disease in the area to be modeled.

Oyster density is determined from the area over which the population occurs. Density affects gamete fertilization efficiency such that more dense oyster deployments (farms, reefs, etc.) exhibit an increased fertilization rate. Levitan (1991) reported the influence of body size and population density on fertilization success and reproductive output, and his equation was rewritten by Mann and Evans (1998) as

$$Ff_{t,i} = 0.0049 \times D_{t,i}^{0.72}, \qquad (4)$$

where $Ff_{t,i}$ = fertilization efficiency at time $t$ for age-class $i$ greater than one ranging from zero (meaning zero fertilization) to one (meaning all gametes become fertilized); and
$D_{t,i}$ = oyster density (number of oysters per square meter) at time $t$ for age-class $i$ greater than one.

For diploid oysters, oyster density is equal to the number of oysters in the population divided by the area (m²). However, the density value for Equation 4 will differ with triploid populations because not all oysters may be able to reproduce; thus we modified the density equation to reflect the density of only undetected diploids and reverted triploids:

$$D_{t,i} = \frac{N_{t,i} \times (R_{t,i} + T_{t,i})}{A}, \qquad (5)$$

where $A$ = area (square meters).

The variable for sex ratio, $Fq_i$, of females to males in the population per age class is a value from 0.0 to 1.0 (Mann and Evans, 1998). $Fq_i$ modifies fecundity so that population size in Equations 1 and 2 comprised females only. The ratios of female-to-male Suminoe oysters at ages 1, 2, 3, and 4 are 0.28, 0.66, 1.00, and 1.00, respectively (Yingya et al., 1992).

Hence, total number of offspring produced per each age class at each time step modified with the previous variables (Mann and Evans, 1998) is as follows:

$$Ftotal_t = \sum (Frevert_{t,i} \times Fs \times Fq_i \times Fd \times Ff_{t,i}), \qquad (6)$$

where $Ftotal_t$ = modified total number of offspring produced at time $t$ summed across all age classes.

The number of recruits obtained from the model that survive to the next time step, thereby becoming age class one, depends on the total number of offspring produced from reverted oysters in older age classes, daily mortality rate (ranging from 0.07 to 0.1) until settlement (21 days after fertilization) (Mann and Evans, 1998), the probability of successful completion of metamorphosis (0.25) (Mann and Evans, 1998), and total mortality for settled oysters less than one year old (Thorson, 1966). Hence, the number of individuals that will survive to enter age-class one at the next time step is given by the equation below:

$$N_{t,0} = K_t + \left(Ftotal_t \times \left(Pmet \times (1 - Lmort)^{21} \times (1 - M_0)\right)\right), \qquad (7)$$

where $K_t$ = the number of oyster spat stocked at time $t$;
$Pmet$ = probability of successful completion of metamorphosis;
$Lmort$ = daily larval mortality rate until settlement at 21 days; and
$M_0$ = total mortality rate for settled oysters less then one year old.

The mortality variables in the model for adult oysters are natural mortality and harvest mortality. Natural mortality determines the proportion of oysters in each age class of the population from nonharvest causes each year. Default natural mortality rates were taken from Calvo et al. (2001) (Table 2). Stochastic values of these variables are chosen from a log normal distribution of the variance around the mean mortality rate for each age class of the population. Harvest-mediated mortality in the population was imposed by randomly selecting individuals for harvest in the age classes whose mean shell length is greater than the set minimum shell length-at-harvest. The harvest rate was a percentage of the population removed from the total population each year.

Certainty of harvest is defined as how certain we are that harvest occurs at a desired harvest rate. This variable in the model captures the effects of different harvest strategies. For example, if oysters are contained in wire cages, the certainty of obtaining a given harvest rate could be 100%. However, for oysters planted on the bottom, the

certainty in obtaining a 100% harvest rate would be lower.

Population size for the current year is determined from the previous year's population size, harvest rate, natural mortality, and certainty in obtaining the desired harvest rate. Thus, the next year's starting population for the next age class greater than one is

$$N_{t+1,i+1} = N_{t,i} \times e^{-((H_i \times C) + M_{t,i})}, \qquad (8)$$

where $H_i$ = harvest rate for age-class $i$ greater than one;
$C$ = certainty in obtaining the desired harvest rate; and
$M_{t,i}$ = natural mortality rate at time $t$ for age-class $i$ greater than one.

Total population size is determined by the summation of all individuals across all age classes:

$$Ntotal_t = \sum N_{t,i}, \qquad (9)$$

where $Ntotal_t$ = the total population size at time $t$ for all age classes.

## Model simulations and output

The model provides two options for output to the user. The first option shows results of one run of the simulation model. The output is a graph showing population size over time. The other output option shows the distribution of outcomes resulting from running the same scenario (i.e. the same input parameter and variable values) a set number of times. This output option shows the probability of the population becoming self-sustaining given the specified set of input conditions and yields probability profiles for risk assessment (Rosenburg and Restrepo, 1994). Probabilities range from 0%, meaning there is a zero probability of a population becoming self-sustaining given a set of input conditions, to 100%, meaning that this outcome will occur every time under the given set of input conditions.

Self-sustainability of a population is tested by running the simulation for a specified number of years with stocking, and then continuing to calculate population size for a specified number of additional years without stocking. Should the population size become zero, then the population is supported solely by stocking. However, should population size prove greater than the number stocked in earlier years, then the population is self-sustaining. The default setting for the simulation is to continue running the simulation twenty years without stocking, reflecting a maximum longevity of 20 years for Suminoe oyster (Cahn, 1950).

To understand the effects of changes in key variables on model predictions, we performed a sensitivity analysis.
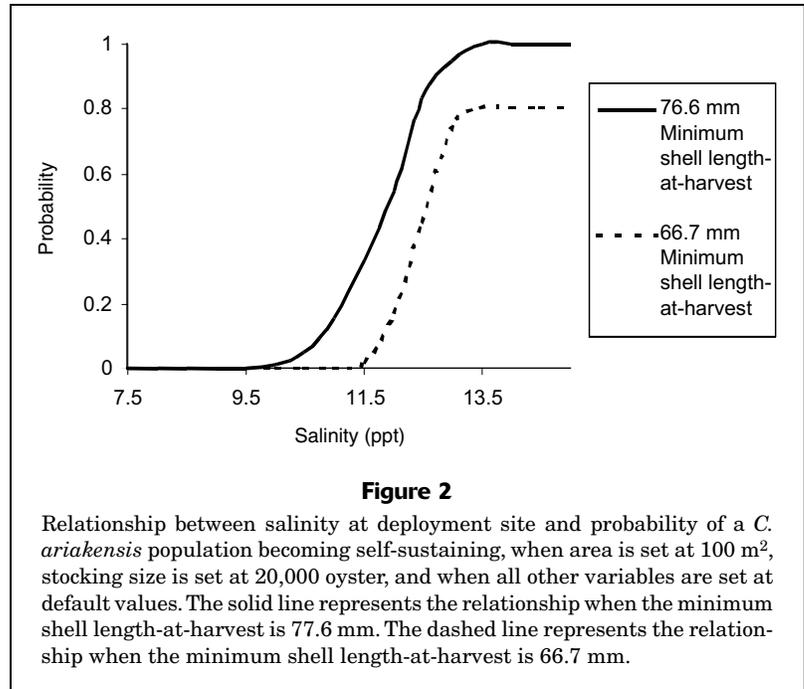


**Figure 2**
Relationship between salinity at deployment site and probability of a *C. ariakensis* population becoming self-sustaining, when area is set at 100 m$^2$, stocking size is set at 20,000 oyster, and when all other variables are set at default values. The solid line represents the relationship when the minimum shell length-at-harvest is 77.6 mm. The dashed line represents the relationship when the minimum shell length-at-harvest is 66.7 mm.

A first set of model runs changed the value of only one variable at a time, while keeping all other variables constant at default values. The variables that were changed were salinity, certainty of obtaining the desired harvest rate, minimum shell length-at-harvest, and stocking density. The second set of model runs was similar to the first, except changes were made to the values of two variables at a time while all other variables remained constant at default values. Salinity was varied from 8.5 ppt to 13.5 ppt. Certainty of obtaining the desired harvest rate was varied from 0.5 to 1.0. Minimum shell length-at-harvest was varied from 60 mm to 100 mm. To determine stocking density, the number of oysters stocked was varied from 100 to 1,000,000 oysters, but the area was set at 300 m$^2$.

All simulation results reported below were obtained by using default values for all variables (Table 2), unless noted otherwise.

## Results

Effects of four major variables on the probability of a Suminoe oyster population becoming self-sustaining were examined by using the simulation model. These variables were salinity, certainty of obtaining the desired harvest rate, minimum shell length-at-harvest, and stocking density.

### Salinity

Salinity between 8 ppt and 13.5 ppt affected the likelihood of developing self-sustaining populations because when salinity decreases, fecundity decreases (Fig. 2). However, this trend can be altered or masked by the effects of other variables on the probability of a population becoming self-

sustaining. For example, when minimum shell length-at-harvest was lowered from 76.7 mm to 66.7 mm, oysters could be grown in higher salinity areas without increasing the probability of the population becoming self-sustaining (Fig. 2). By harvesting the oysters sooner, there is decreased likelihood of reproductively effective reversion.

### Certainty in harvest rate

As the certainty of obtaining the desired harvest rate increased, the probability of the population becoming self-sustaining decreased (Fig. 3). For example, if oysters were grown on the bottom, inability to reliably recapture all individuals is such that the certainty of obtaining the
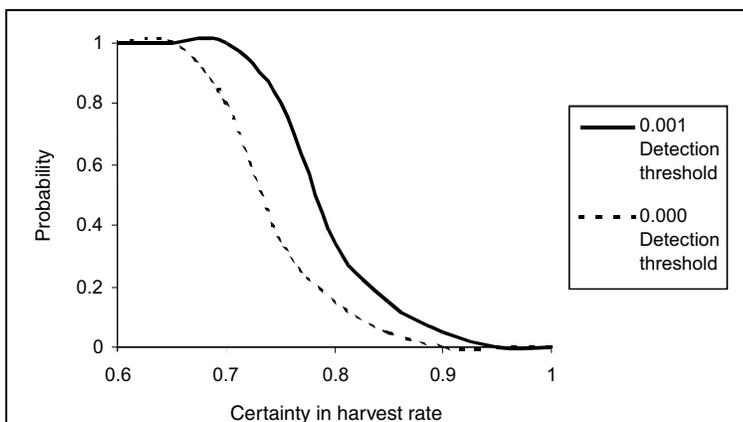


**Figure 3**

Relationship between the certainty in obtaining a specified harvest rate and probability of a *C. ariakensis* population becoming self-sustaining, when area is 300 m² and all other variables are set at default values. The solid line represents the relationship when the detection threshold for diploids is 0.001. The dashed line represents the relationship when the detection threshold for diploids is 0.000.
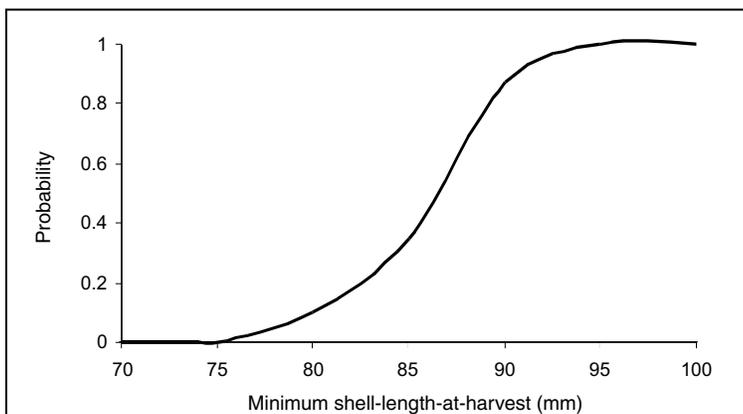


**Figure 4**

Relationship between minimum shell length-at-harvest (mm) and probability of a *C. ariakensis* population becoming self-sustaining, keeping all other variables at default values.

desired harvest rate would be lower than if cages were used. Lower certainty of harvest would increase the likelihood of reproductively effective reversion among older individuals remaining on site, thereby increasing probabilities of both reproduction and the development of a self-sustaining population. In contrast, if oysters were kept in confinements such as wire cages, the certainty in obtaining the desired harvest rate would be high. As a result, this would decrease the likelihood of reproductively competent individuals remaining on site and giving rise to a self-sustaining population.

We also examined the relationship between certainty in obtaining the desired harvest rate and probability of a population becoming self-sustaining when the diploid detection threshold was zero, meaning 100% triploids were stocked (Fig. 3). This procedure distinguished between the effects of the technical problem of detection from the biological problem of reversion. It modeled the ideal scenario where flow cytometry detected any and all diploids in a batch but still allowed reproductively effective reversion to occur in age classes greater than two. When the detection threshold was set at zero and as certainty in obtaining the desired harvest rate increased, the probability of a population of triploid oysters becoming self-sustaining was decreased in relation to a detection threshold of 0.001. For example, when the detection threshold is 0.001 and certainty of harvest is set at 0.75, the probability of the population becoming self-sustaining is 0.082. In contrast, when the detection threshold is 0.000 and certainty of harvest is set at 0.75, the probability of the population becoming self-sustaining is 0.006.

### Minimum shell-length-at-harvest

As the minimum shell-length-at-harvest was increased, the probability of the population becoming self-sustaining increased (Fig. 4). Increased probability of self-sustainability is due to the probability of reproductively effective reversion increasing the longer oysters are in the water, and the number of offspring produced by undetected diploids becoming higher.

### Stocking density

With a 0.001 threshold for detecting diploids in triploid batches, and certainty of harvest of 0.9, the probability of the population becoming self-sustaining increased with increased stocking density (Fig. 5). Increased probability of self-sustainability is due to an increase in gamete fertilization efficiency as density increases (Mann and Evans, 1998). In contrast, when the diploid detection threshold was decreased to 0.000, meaning that all oyster spat stocked were indeed triploid, and certainty of harvest

was maintained at the default value of 0.9, higher stocking densities barely increased the probability of the population becoming self-sustaining (Fig. 5). Absence of reproduction from undetected diploids, and the lack of reproduction in mosaic (reverted triploid) oysters until age 3, well past harvest size, were the principal determinants of lowered reproductive risk.

### Interaction of stocking density and salinity

At lower salinity sites, changes in stocking density had less of an effect on the likelihood of developing a self-sustaining population than at higher salinities when all other variables were set at default values (Fig. 6). Lower salinity decreases fecundity, which counteracts the increased fertilization efficiency at higher population densities.

### Interaction of stocking density and certainty of harvest

Stocking density could be increased without increasing the risk of a self-sustaining population by increasing certainty of harvest, and keeping all other variables set at the default values (Fig. 7). Increased certainty of harvest decreased the number of oysters remaining in culture that were able to revert and reproduce, countering the increase in fertilization efficiency from increased density.

## Discussion

The introduction of any non-native species into a new environment poses a number of potential ecological hazards. In general, these are related to two root causes: 1) the associated introduction of epibionts, pathogens, or other infectious agents, and 2) ecological disruption from the persistence of the introduced species (i.e. through reproduction, competition, etc.). To a large degree, associated introductions (with the possible exception of viruses) can be eliminated by adherence to codes of practice for proper quarantine and propagation, such as those set by the International Council for the Exploration of the Seas (ICES, 1994). The second risk of ecological disruption is caused by reproduction and subsequent naturalization. To address this hazard, sterile triploids have been proposed as a means to introduce the Suminoe oyster for commercial aquaculture. This model addresses those elements of risk
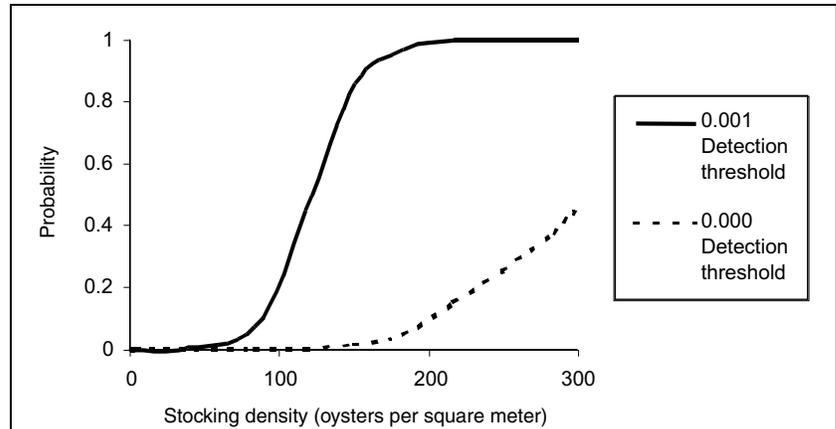


**Figure 5**

Relationship between stocking density and probability of a *C. ariakensis* population becoming self-sustaining, keeping all other variables at default values. The solid line represents the relationship when the detection threshold for diploids is 0.001. The dashed line represents the relationship when the detection threshold for diploids is 0.000.
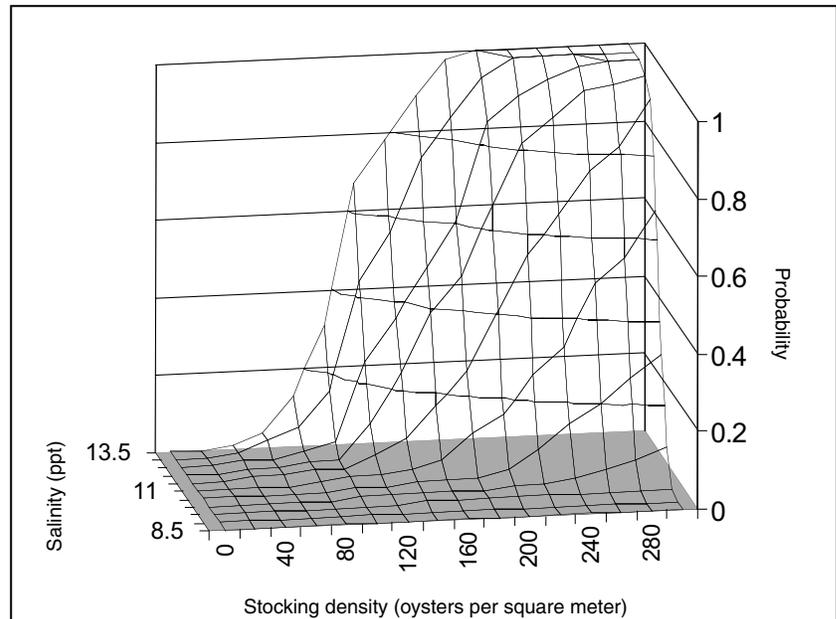


**Figure 6**

Relationship between stocking density, salinity at deployment site, and the probability of a *C. ariakensis* population becoming self-sustaining, keeping all other variables constant at default values and stocking area set at 300 square meters.

associated with reproduction. Risk assessment modeling will enable managers to anticipate which management actions can have the greatest impact on decreasing the likelihood of a self-sustaining population. According to our results, risk reduction strategies include stocking Suminoe oysters in relatively low salinity, growing oysters in

confinements (i.e. floating cages, lantern nets, bags, etc.) to maximize the certainty of achieving harvest, harvesting at the earliest possible (and presumably, economically feasible) opportunity, and maintaining a low population density of stocked oysters.

There are several key factors that affect the model's overall predictive value. First, few of the biological parameters that determine reproductive potential of Suminoe oyster are well known. All key parameters in the reproduction equations of the model were based on eastern oyster data (Mann and Evans, 1998) because of a lack of corresponding information about Suminoe oyster. For example, the parameter values in the equation for the relation-ship of oyster density and fertilization efficiency are not known for Suminoe oysters; therefore those for eastern oysters were used. It is important to deter-mine these parameter values for Suminoe oyster so that the model may more accurately predict the relationship between density and the probability of the population becoming self-sustaining. Also, parameter values relating salinity and fecundity are unknown for Suminoe oyster; therefore eastern oyster parameter values were used. For most oyster species, gametogenesis is decreased or even nonex-istent at lower salinities; however, the exact salinity value at which gametogenesis is decreased or absent may vary among species (Amemiya, 1929; Calabrese and Davis, 1970; Kennedy et al., 1996). The Sumi-noe oyster seems to thrive in estuarine conditions (Huang, 1962; Calvo et al., 2001) and there may be biological parallels to the eastern oyster. However, details about lower reproductive potential in lower salinity waters may be different for Suminoe oysters. In the wild, some populations of Suminoe oyster spawn in early spring in salinity as low as 10 ppt (Zhang and Lou 1956; Huang, 1962); therefore the model may slightly underestimate fe-cundity of Suminoe oyster in low salinity environments.

In this model, we also assumed that any oyster whose gamete cells reverted from triploid to "reproductive" mosaic or diploid recovered full fecundity. However, studies have yet to quantify recovered reproductive function in reverted triploids (Chandler et al., 1999). It is likely that reverted oysters would exhibit lower fecundity than diploid oysters because revertant oysters are mosaic; i.e. they comprise both triploid gamete-producing cells that are unable to produce viable gametes, and also diploid gamete-producing cells that are able to produce viable gametes. Continuing research with triploid Suminoe oyster should help us fill this gap in knowledge; however, until then, we decided that the model should err on the ecologically conservative side with the assumption that all reverted triploids exhibit full reproductive potential.

Despite its limitations, the model clearly points out key areas of concern, as well as highlights areas where more information or improvements in technology could prove critical. For example, advances in techniques for detect-ing very low proportions of diploids could reduce risk of a triploid Suminoe oyster population becoming self-sustain-ing under high stocking rates. Currently, flow cytometry is
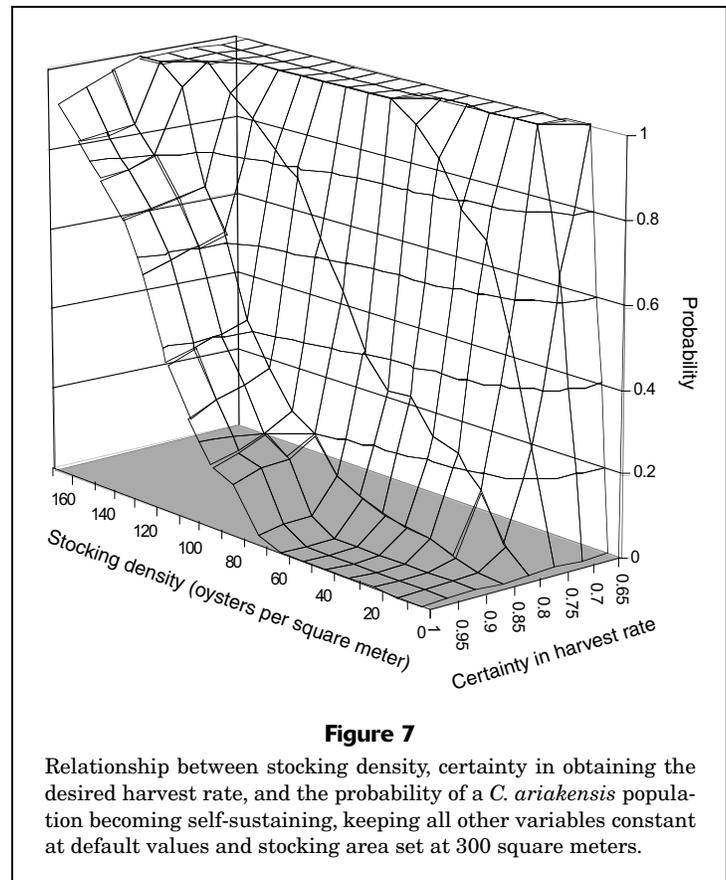


**Figure 7**

Relationship between stocking density, certainty in obtaining the desired harvest rate, and the probability of a *C. ariakensis* popula-tion becoming self-sustaining, keeping all other variables constant at default values and stocking area set at 300 square meters.

used for certifying triploid batches in subsampling larval populations (Allen and Bushek, 1992). Up to hundreds of thousands of larvae can be subsampled from a hatchery-scale larval culture. Cells disaggregated from triploid (and intermingled diploid) larvae then can be assayed. The difficulty lies in detecting extremely low levels of diploid cells within the mix. Improved detection by flow cytometry through repeated sampling techniques could help decrease the probability of stocking diploid individuals, thereby de-creasing the subsequent chance for reproduction. Improved detection would also allow watermen to stock more Sumi-noe oysters in a smaller area.

We developed our own demographic model instead of using existing oyster models, such as the time-dependent, energy flow eastern oyster model (Hofmann et al., 1992; Dekshenieks et al., 1993; Hofmann et al., 1994; Powell et al., 1994; Powell et al., 1995; Dekshenieks et al., 1996; Pow-ell et al., 1996; Ford et al., 1999) for various reasons. First, there were only two years of growth, mortality, and rever-sion rate data available for Suminoe oysters in the Chesa-peake Bay (Calvo et al., 2001) and very little information in the literature about the Suminoe oyster in general. Hence, we decided that a demographics-based population dynam-ics model that tracked population size over time would be the most defensible method for achieving the objective of estimating the probability of a population becoming self-sustaining. Although the time-dependent energy flow model also tracks population size over time, all calcula-

tions are done in terms of energy, which then is converted into population size. Because the available Suminoe oyster data were demographic instead of bioenergetic, we felt a demographic population dynamics model made defensible use of available information. Additionally, the equations of the time-dependent energy flow model included parameters such as filtration rates, respiration, assimilation, and reproduction efficiency. These parameters have yet to be determined for the Suminoe oyster.

The scope of our model could be easily expanded to investigate more detailed scenarios and outputs. Economic aspects could be modeled to examine cost and profit and loss relationships for commercial production of triploid Suminoe oyster under various assumptions. In addition, the model could be adapted to a monthly instead of yearly time step, allowing managers to examine effects of stocking at different times of the year. The model could be made more spatially explicit, allowing managers to examine the probability of a population becoming self-sustaining over a larger area encompassing multiple deployment sites. Physical processes of water flow may have important effects on oyster recruitment. In our model, we assumed that water flow mimicked that in the James River, Virginia, as described in Mann and Evans (1998). Hence, our model is most appropriate for ecosystems where, as in the James River, larvae remain in the approximate area of their production. Clearly, this would not be the case at all sites. In sites where advection of larvae into or out of the area is at issue, one or more terms would have to be added to the model to account for such movement. Additional work is needed to assess a wider range of management options and potential risks.

## Acknowledgments

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