A POPULATION DYNAMIC MODEL ASSESSING OPTIONS FOR MANAGING EASTERN OYSTERS (*Crassostrea virginica*) AND TRIPLOID SUMINOE OYSTERS (*Crassostrea ariakensis*) IN CHESAPEAKE BAY.

by:

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(ABSTRACT)

A demographic population simulation model was developed to examine alternative fishery management strategies and their likely effects on the probability of extirpation of local eastern oyster (*Crassostrea virginica*) populations in the Chesapeake Bay. Management strategies include varying the minimum shell length-at-harvest, harvest rate, and rate and frequency of stocking of oyster seed with respect to varying salinities and oyster population densities. We also examined the rate of disease-mediated mortality that can be tolerated by a viable population.

High density populations at low salinity sites remained viable under a 100% harvest rate and 76.6 minimum shell length-at-harvest due to increased fertilization efficiency in high densities, which increased reproduction. Low density populations at low salinity sites remained viable when harvest rate was set at 0.5 and minimum shell length-at-harvest was set at 85 mm. Neither reducing harvest rate nor minimum shell length-at-harvest produced a viable population at high salinity sites. The effects of disease-mediated mortality were too great for these management options to decrease the probability of extirpation to zero. Supplemental stocking conducted regularly reduced extirpation probabilities to zero and pulse stocking (every five to ten years) did as well, although it required a much larger number of oysters to be stocked. Decreasing disease-mediated mortality rates by 20% in high density populations and by 80% in low density populations reduced the probability of extirpation to zero, suggesting the degree of genetic improvement needed to rebuild eastern oyster populations in the Chesapeake Bay.

Culture of a non-native species, such as the Suminoe oyster (*Crassostrea ariakensis*), could supplement harvest of the declining eastern oyster 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 Suminoe oyster might establish self-sustaining populations. To assess the risk of Suminoe oyster populations becoming established in Chesapeake Bay, a demographic population model was developed. Inputs modeled included: salinity, stocking density, reversion rate, reproductive potential, natural and harvest mortality, growth rates, and effects of various management strategies, including harvest criteria. Results showed decreased probability of a Suminoe oyster population becoming self-sustaining 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. Results of the model suggest management strategies that will 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.

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CHAPTER ONE – INTRODUCTION AND JUSTIFICATION

The eastern oyster (*Crassostrea virginica*) has long been a valued fishery. In colonial times, oyster reefs in the Chesapeake Bay were so vast and abundant that these reefs were marked on nautical charts as nautical hazards (Kennedy et al. 1996); today, however, the eastern oyster population in the Chesapeake Bay is estimated at only 1% of its original abundance (Newell 1985) due to over-harvest, habitat destruction, and disease-mediated mortality (Gottlieb and Schweighofer 1996). The oyster population started to decline in the early 1800s from over-harvest and habitat destruction due to lack of harvest restrictions and dredging (Kennedy and Breisch 1983, Gottlieb and Schweighofer 1996). In the late 1800s and early 1900s, new harvest regulations slowed the decline of the eastern oyster population. These management strategies included requirement for licenses, closed harvest seasons, minimum shell length-at-harvest, and restricted dredging (Kennedy and Breisch 1983). These management strategies might have maintained a viable eastern oyster population. However, natural mortality rates increased to between 40% and 90% per year from the protozoan diseases MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*) in the mid 1900s (Kennedy and Breisch 1983, Burreson 1991, Andrews 1996). Increased natural mortality and continued harvest caused the eastern oyster population and harvest to continue to decline rapidly (Figure 1.1) (Kennedy and Breisch 1983, Burreson 1991). Many oyster reefs were left barren, and localized extirpations occurred throughout the Chesapeake Bay.

Several attempts have been made to decrease the prevalence and effects of Dermo and MSX in eastern oyster populations, including the use of selective breeding and interspecific hybridization with resistant species (Burreson 1991, Allen et al.1993). However, the hybridization attempts failed (Allen et al. 1993), and selective breeding yielded mixed results such as increased MSX resistance at the cost of decreased Dermo resistance (Burreson 1991). Another approach to developing a specific disease-free brood stock used a closed system hatchery for oyster production, but this method proved to be very costly (Krantz 1982).

Both Maryland and Virginia have attempted to restore the eastern oyster population in the Chesapeake Bay through harvest regulations (Mann et al. 1991). These states manage their eastern oyster populations differently (Gottlieb and Schweighofer 1996). Maryland's eastern oyster reefs are managed as public property. These reefs tend to be over-harvested due to lack of incentive for individuals to conserve the population. Maryland uses the "put-and-take" approach to try to maintain its population by planting shell in good spat-set areas and then moving the spat to growth and harvest areas (Gottlieb and Schweighofer 1996, Krantz and Jordan 1996). This program costs Maryland approximately 2.8 million dollars per year (Gottlieb and Schweighofer 1996). Also, Maryland is considering management activities that will artificially re-create oyster reefs. However, the cost to re-create eastern oyster reefs is estimated to be 7.2 to 24 million dollars, and research has not yet evaluated the feasibility of re-creating reefs (Gottlieb and Schweighofer 1996).

In contrast, private individuals and industrial operations manage Virginia's eastern oyster populations. This management approach encourages Virginia's watermen to conserve their private eastern oyster stock so that they will sustain harvest in future years. Virginia requires that watermen throw back shells to provide a hard substrate for spat to settle (McHugh 1984).

Proposed management strategies to increase harvest include culture of oysters in low salinity waters, increasing minimum shell length-at-harvest, and stocking specific disease-free seed (Krantz and Jordan 1996). It is not known whether these actions would minimize or reverse the continued declined of eastern oysters.

Another proposal for increasing oyster harvest is to introduce a non-native oyster species, such as the Suminoe oyster (*Crassostrea ariakensis*), to supplement the eastern oyster fishery. The Suminoe oyster is resistant to both MSX and Dermo (Calvo et al. 2001). Because of possible ecological impacts from introducing a fertile non-native species, introduction of only triploid (and presumably sterile) oysters has been proposed. However, recent data show that a small percentage of triploid oysters progressively revert toward diploidy. This reversion introduces the possibility of reproduction by the Suminoe oyster, thereby creating a self-sustaining population, posing the risk of competition with the eastern oyster population.

Simulation Models as Management Tools

The use of simulation models could support evaluation of possible management strategies (Lackey 1994). In this context, a demographic population model could be developed to examine different management strategies and their effects on eastern oyster populations. Management strategies include varying minimum shell length-at-harvest, varying harvest rate, and stocking additional seed. Simulation results from the model could indicate what management strategies will decrease the probability of local extirpation while continuing harvest for oyster populations of different densities at different salinity sites.

Before a decision to initialize commercial production of triploid Suminoe oysters into Chesapeake Bay can be reached, the associated environmental risks must be assessed. One approach is to develop a quantitative model to estimate the risk involved with the large-scale deployment of triploid Suminoe oysters. The possible hazards involved with introducing Suminoe oysters are: reversion of triploid to diploid individuals, thereby creating a fertile state; reproduction by Suminoe oysters; larval recruitment creating a self-sustaining Suminoe oyster population; competition between the Suminoe oyster and native eastern oyster; and introduction of parasites and pathogens. A model can be developed to predict the risks associated with introducing the Suminoe oyster as either triploids or reverting triploids into the Chesapeake Bay. Policy makers and fishery managers could use the model to predict the potential outcomes of policy decisions, supporting science-based policy decisions about the proposed introduction of the Suminoe oyster into the Chesapeake Bay.

Biology and Ecology of Eastern and Suminoe Oysters

Both Suminoe and eastern oysters are in the family *Ostreidae* and the genus *Crassostrea*. A synonymous Latin name for the Suminoe oyster is *Crassostrea rivularis* (Kennedy et al. 1996). The Suminoe oyster is thought to be derived from the *Crassostrea angulata* lineage (Durve 1986). When the Tethys Sea disappeared, joining the Arabian Peninsula with south Eurasia, it is believed that a population of the ancestral *C. angulata* became isolated and differentiated into two species: *C. ariakensis* and *C. gryphoides*. The

Suminoe oyster once was thought to be conspecific with the Pacific oyster (*Crassostrea gigas*), but phlyogenetic research subsequently showed that they are two different species (Buroher et al. 1979b, Torigoe 1981, Littlewood 1994).

Biological information on the Suminoe oyster is scant. The Suminoe oyster is distributed from southern Japan along the southern Chinese coast through southeast Asia to the western coast of India (Tchang and Tse-kang 1956, Rao 1987, Langdon and Robinson 1996, Calvo et al. 2001). The Suminoe oyster also can be found in the Philippines, Taiwan, Thailand, and North Borneo (Yingya et al. 1992).

The natural range of the eastern oyster is from the Gulf of St. Lawrence, Canada, south to the Gulf of Mexico, Panama, and the Caribbean islands (Kennedy et al. 1996). The Eastern oyster also is found on the coast of Brazil and Argentina. *Crassostrea madrasensis*, which is found in India and Pakistan, is considered by some scientists to be the same species as eastern oyster (Ahmed 1971, 1975).

Suminoe oysters are commercially harvested in China, Japan, and India (Cahn 1950, Rao 1987, Quayle and Newkirk 1989, Cai and Lui 1990, Nie 1991). Suminoe oysters have been cultured in Japan since the 19th century (Langdon and Robinson 1996). The Suminoe oyster also is an important aquaculture species in southern China (Langdon and Robinson 1993). Commercial production of Suminoe oysters has occurred in Oregon and Washington state, USA (Langdon and Robinson 1996). Eastern oysters have high commercial value and are produced mostly in eastern North America, but also in many other places around the world (Kennedy et al. 1996).

Suminoe oysters are tolerant of mid-tropical to sub-tropical environments (Calvo et al. 2001). Suminoe oysters may occur at low tide, but usually are found a few hundred meters off-shore. The habitat for Suminoe oysters consists of intertidal hard grounds and muddy creeks in warmwater areas (Rao 1987). Both Suminoe and eastern oysters prefer estuarine environments with low salinity levels (Kennedy et al. 1996, Calvo et al. 2001).

Suminoe and Eastern Oyster Reproduction

Reproduction in oysters is initiated by the release of gametes into the water column (Kennedy et al. 1996). Fertilization takes place by the encounter of sperm and egg gametes in the water column. Within hours, these zygotes proceed through a series of cleavage divisions, through blastula and gastrula stages, and then though trochopore and veliger larval stages. After a few weeks, larvae metamorphose and settle onto a hard substrate, defined as cultch, and cement to it. The larvae, now called spat, grow into juvenile and then into adult oysters.

The major abiotic factors affecting the time of spawning in oysters are water temperature and salinity (Butler 1949, Loosanoff 1953, Cox and Mann 1992). For eastern oysters, the optimum temperature for spawning is 23^0C (range of 18^0C to 25^0C) with less than 8ppt (parts-per-thousand) salinity. Under Chesapeake Bay conditions, eastern oysters spawn from late May to September in Maryland (Kennedy and Krantz 1982) and late June to late September in Virginia (Andrews 1979).

Optimum temperatures for spawning Suminoe oysters are 30^0C to 40^0C (range of 7^0C to 40^0C) with 15-20ppt salinity levels, and no spawning occurred at salinity levels greater than 35ppt (Mann et al. 1991, Langdon and Robinson 1996). In the Pacific Ocean, in Washington State, Suminoe oysters exhibit gonadal proliferation in late April-early May and start spawning in early June (Langdon and Robinson 1996). In the Suminoe oyster's native range in Gharo-Phitti, Pakistan, Suminoe oysters mature sexually in April and spawn during May through November, with the maximum rate of spawning occurring in June (Asif 1980). In China, Suminoe oysters spawn from early April to late June under conditions of high temperature and low salinity (Yingya et al. 1992).

The age at first reproduction for eastern oysters is one to two years of age at 3.0 cm to 4.7 cm shell length (Galtsoff 1930, Gosselin and Qian 1997). Cox and Mann (1992) found that individual female eastern oysters in the Chesapeake Bay area will release 4 to 9 million eggs, and that fecundity is directly related to the body size. Mann and Evans (1998) developed a model to estimate fecundity for eastern oysters residing in the James River, Virginia. The fecundity of an individual oyster was modeled as a function of shell length, because as shell length increases, egg production and fecundity increase (Cox and Mann 1992). Fecundity also was affected by salinity, disease, oyster density, fertilization efficiency, and sex ratio.

Sex ratio in oyster populations affects fertilization success (Kennedy et al. 1996). Because larger individuals are more fecund (Mann and Evans 1998), it is energetically efficient for small oysters to be male, and to switch to female as they grow. Asif (1979) examined 1090 individuals on the Karachi coast, Pakistan to assess the effects of sex reversal in Suminoe oysters. As Suminoe oysters grow, the proportion of males in the population decreased (Table 1.1). Sex reversion in oysters residing in Zhangjiang Bay, China (Yingya et al. 1992), showed similar results (Table 1.2). Eastern oysters also exhibit protandric hermaphroditism; 90% of eastern oysters smaller than 35mm at six weeks post-settlement were male (Andrews 1979). As eastern oysters increased in weight, the proportion of males in the population was decreased (Galtsoff 1964). Also, when there was high environmental and nutritive stress, the proportion of males in the population was increased (Tranter 1958, Bahr and Hillman 1967, Davis and Hillman 1971). There is some question whether this is actually sex reversal in oysters or selective mortality of smaller individuals, since only random population sampling was done in these experiments.

Oysters are broadcast spawners; therefore, the success of reproduction is dependent upon many factors (Kennedy et al. 1996). These factors include larval viability, gamete concentration, predation, oyster density (Mann and Evans 1998), amount of stored energy remaining after metamorphosis (Whtye et al. 1992), and developmental success. Estimates of mortality rates for oyster larvae have been as high as 98.6%, because success is dependent on all of these factors (Thorson 1966, Kennedy et al. 1996). Relatively high Suminoe oyster larvae mortality occurs with high turbidity and salinities greater than 41 ppt (Ahmed et al. 1987). Eastern oyster gamete mortality also occurs through predation. For example, sea anemones (*Diadumene leucolena*) are benthic filter feeders on oyster gametes (MacKenzie 1977, Steinberg and Kennedy 1979).

After fertilization occurs, the developmental success of larvae depends on temperature, salinity, oxygen concentration, and egg quality (Kennedy et al. 1996). The risks of mortality due to predation and disease increase with time spent in the water column (Underwood and Fairweather 1989). Predation of veliger larvae occurs mostly by filter-feeders such as ctenophores, sea anemones, and barnacles (Mackenzie 1977, Purcell et al. 1991).

Settlement of veliger larvae occurs after two to three weeks (Kennedy et al. 1996). The length of time before settlement is dependent upon temperature, food supply, and oxygen concentration (Baker and Mann 1998, Kennedy et al. 1996). Settlement occurs when veliger larvae find appropriate substrate, called cultch, on which to settle. The larvae, now called spat, will cement themselves to the hard cultch permanently. Cultch is chosen by phototactic behavior (Baker 1997, Baker and Mann 1998), chemical signals (Crisp 1967), and surface composition and texture (Kennedy et al. 1996). Osman et al. (1989) reported 70-99% mortality for juvenile eastern oysters one month after settling onto sub-tidal plates. Roegner and Mann (1995) estimated mortality of juvenile eastern oysters at 64-100% and 86-100% seven days and one month, respectively, after settlement on sub-tidal and inter-tidal plates.

Predators on spat include young oyster drills (*Eupleura caudate*, *Thais haemastoma*, and *Urosalpina cincera*) (Carriker 1961, MacKenzie 1981), blue crabs (*Callinectes sapidus*), and mud crabs (*Panopeus herbstii*) (Carriker 1951, McDermott 1960, Krantz and Chamberlin 1978, Bisker and Castagna 1987). Each young oyster drill will feed on 0.13 juvenile eastern oysters per week in June (MacKenzie 1981). This increases to 0.7 in the month of July. Mortality rates imposed by drills on juvenile eastern oysters average 33% from June to August. A maximum predation rate of 21.5 spat per crab per day, with a mud crab density of 13 to 103 crabs per square meter, was found under laboratory conditions (Bisker and Castagna 1987). Blue crab predation rates occur at 16.7 eastern oysters (24.4 mm shell height) per crab per day in Virginia (Bisker and Castagna 1987). Low salinity and temperature levels limit predation by blue crabs.

Reversion and Reproduction in Triploid Oysters

The possible utility of triploid Suminoe oysters in the Chesapeake Bay is reduced by the possibility of progressive reversion to a diploid condition (Calvo et al. 2001). Calvo et al. (2001) examined reversion of triploid Suminoe oysters toward diploidy by deploying 100% triploid individuals. The mean proportions of mosaic individuals (i.e., individuals that had both diploid and triploid cells) observed in populations held at different salinities ranged from 0-16%: 5.0% at low salinity sites (<15ppt), 7.2% at medium salinity sites (15-25ppt), and 3.7% at high salinity sites (>25ppt). The percent of mosaic individuals in the populations increased from 0.5% in June 1998 to 7.4% in August 1999. Mosaic oysters included 10 females, 23 males, 1 hermaphrodite, and 5 undifferentiated individuals in the total population of 1163.

The degree of mosaicism varies among tissue types. Tissues that reverted from triploid to mosaic are hemolymph (21% diploid cells), digestive system (19% diploid cells), adductors muscles (15% diploid cells), heart and gill (9% diploid cells), and gonad (6% diploid cells) (Stan Allen, Virginia Institute of Marine Science, pers. comm. 2000). Reproduction in mosaic oysters is dependent on gondal cells reverting from triploid to diploid. If gamete-producing cells revert, there is the possibility of the oyster creating viable gametes. The relationship between percent mosaic gondal tissue and the number of viable gametes produced is unknown (Stan Allen, Virginia Institute of Marine Science, pers. comm. 2000).

Success of reproduction also may be altered when two oyster species are residing in the same area, such as triploid Suminoe oysters and diploid eastern oysters. Inviable progeny result when hydrization between Suminoe and eastern oysters occurs (Gaffney and Allen 1993). Gametes are lost, decreasing the chance for successful reproduction within the species. The same presumably would happen when triploid oysters release inviable gametes into the water column (Guo and Allen 1994). Triploid oysters cannot themselves reproduce; however, they do produce inviable gametes (Allen and Downing 1990). Survival of fertilized eggs from triploid individuals to settlement is approximately 0.0085% (Guo and Allen 1994). Triploid male oysters are 1000-fold less potent than diploid males, and triploid female oysters are 20 times less fecund than diploid females (Guo and Allen 1994).

Growth

Eastern oyster larvae grow most rapidly at 30^0C to 32.5^0C and at 10 to 27.5 ppt salinity (Davis and Calabrese 1964). Suminoe oyster larvae exhibit most rapid growth at 28^0C regardless of salinity, but optimal salinity for growth is at 20 ppt (Breese and Malouf 1977).

Growth rates of Suminoe and eastern oysters vary with salinity. Suminoe oysters placed in the Chesapeake Bay grew faster at medium (15 to 25 ppt) and high salinity (greater than 25 ppt) than at low salinity (less than 15 ppt) (Calvo et al. 2001). Suminoe oyster growth (starting shell length at 64 mm) was 2.6, 4.9, and 6.2 mm/month for low, medium, and high salinity sites, respectively. These growth rates were significantly different between species at medium and high salinity sites (Calvo et al. 2001). Eastern oyster growth (starting shell length was 60 mm) was not significantly different at low, medium and high salinity sites with rates of 1.1 mm/month, 1.7 mm/month, and 1.0 mm/month, respectively.

Roegner and Mann (1995) showed that there was no correlation between daily growth rates of juvenile eastern oysters and eastern oyster density, suggesting that competition through crowding does not affect oyster growth rates at the densities tested. However, this was a field experiment, and densities were not manipulated by humans to show the effect of differing densities on oyster growth.

Suminoe oysters grew very fast from one to three years of age in Zhanjiang Bay, China (Yingya et al. 1992). After the Suminoe oyster reached age three, where the average shell length was 100 mm, growth slowed. At ages one to four, mean shell length for the Suminoe oyster was 41 mm, 76 mm, 100 mm, and 121 mm, respectively (Yingya et al. 1992).

It usually takes eastern oysters in the Chesapeake Bay three years to reach harvestable size (shell length greater than 76 mm) (Ortega and Sutherland 1992, Moroney and Walker 1999). Oysters could be harvested sooner if they grew to 76 mm in less than three years, which also would decrease the chance of oysters becoming infected with either Dermo or MSX. Two means of manipulating growth that have been assessed experimentally are selective breeding and induction of triploidy.

Mortality

There are five biotic and five abiotic factors that are known to affect bivalve mortality rates. The five biotic factors are disease, predation, competition, developmental complications, and energy depletion. The five abiotic factors are desiccation, temperature, salinity, water motion, and oxygen depletion (Gosselin and Qian 1997, Baker and Mann 1998). Disease and predation generally have the greatest effect on eastern oyster populations (Kennedy et al. 1996).

Diseases are the greatest cause of mortality in the eastern oyster (Gosselin and Qian 1997). The two main diseases affecting eastern oyster populations in the Chesapeake Bay are Dermo and MSX (Kennedy and Breisch 1983, Paynter and Burreson 1991). With both diseases, there is a positive relationship between temperature and salinity and infection rate (Matthiessen et al. 1990, Gottlieb and Schweighofer 1996). Dermo begins multiplying inside the eastern oyster at temperatures exceeding 20°C and causes mortality after one month of infection (Soniat and Kortright 1988, Burreson and Ragone-Calvo 1993, Chu et al. 1996, Andrews 1996). Dermo also inhibits gondal growth, thereby deceasing reproductive capacity (Kennedy and Breisch 1981, Paynter and Burreson 1991). Entering through the gills of the eastern oyster, MSX spreads through the entire body, resulting in death (Kennedy and Breisch 1981). Calvo et al. (2001) found that MSX and Dermo infections resulted in a cumulative mortality of 81% of three-year-old eastern oysters after one and a half years of residence in the Chesapeake Bay.

Triploid Suminoe oysters are more tolerant of Dermo and MSX than eastern oysters (Calvo et al. 2001). Calvo et al. (2001) found that Dermo susceptibility was low in triploid Suminoe oysters, and there was no susceptibility to MSX. Eastern oysters had increased total mortality due to MSX and Dermo as compared to Suminoe oysters (Table 1.3). Triploid eastern oysters also were found to have a lower rate of mortality when infected with MSX (Mattiessen and Davis 1991, 1992). However, these triploid eastern oysters had increased rates of susceptibility to Dermo than diploid oysters.

Attempts have been made to decrease the prevalence and effects of Dermo and MSX on eastern oyster populations. Burreson (1991) showed that eastern oysters selected for increased resistance to MSX had a higher degree of susceptibility to Dermo. These selected lines suffered 99% mortality due to Dermo and failed to reach market size. Non-selected lines exhibited a lower degree of susceptibility to Dermo, decreased mortality (80%), and grew to market size. Determination of whether a genetic trade-off for the two traits occurred in selected lines of oysters, or whether negative effects of inbreeding or genetic drift resulted from the selection process has yet to be determined.

There is only one documented case of disease prevalence in Suminoe oysters. Suminoe oysters imported from the United States in 1994 into France were affected by a *Bonamia* spp. parasite (Cochennec et al. 1998). The parasite caused nine of the one hundred oysters to die. Little is know about the transmission of the parasite or how it affects Suminoe oysters.

Predation is an important source of mortality for adult oysters (Gosselin and Qian 1997). Predation rate increases with increasing temperature and salinity. For adult eastern oysters, the main predatory species include drills (*Eupleura caudate*, *Thais haemastoma*, and *Urosalpina cincera*) (Carriker 1961, MacKenzie 1981), flatworms (*Stylochus ellipticus*) (Loosanoff 1956, Landers and Rhodes 1970, Hofstetter 1977, Chintala and Kennedy 1993), sea anemone (*Diadumene leucolena*) (MacKenzie 1977, Steinberg and Kennedy 1979), oyster toadfish (*Opsanus tau*) and cow-nosed ray (*Rhinoptera bomaris*) (Krantz and Chamberlin 1978), and sponges (*Clinona celata* and *C. truitti*) (Hopkins 1962).

The main predator for Suminoe oysters in Zhangjiang Bay, China is the oyster drill *Thais gradata* (Yingya et al. 1992). *T. gradata* tends to prey upon one year-old oysters at a rate of 7 oysters per drill per square meter. The author did not provide a time frame this predation (i.e., per day, per month, per year).

Role of the Eastern Oyster in the Chesapeake Bay

The eastern oyster population plays an important role in the economy and ecology of the Chesapeake Bay (Kennedy et al. 1996). Economically, eastern oysters have supported an important commercial industry in the Chesapeake Bay region since the 1880s (McHugh 1984), bringing in a great deal of money and creating many jobs (Gottlieb and Schweighofer 1996). Due to the substantial decline of the eastern oyster, unemployment has increased, and there has been a huge monetary loss on the regional economy (Kennedy et al. 1996). For example, in the 1880s New Jersey, Maryland, and Virginia produced 142.5 million pounds of meat, valued at 200 million dollars using 1980s prices (McHugh 1984). However, by 1982 the eastern oyster industry harvested only 54 million pounds of meat valued at 76 million dollars.

Ecologically, eastern oyster reefs are a key component in the ecology of the Chesapeake Bay because they support extensive ecological communities at the base of several food webs (Mann et al. 1991). Eastern oysters consume microplankton, thereby reducing impacts of eutrophication, improving water quality, and helping maintain biological diversity in the Chesapeake Bay (Mann et al. 1991). Before the 1870s, eastern oyster populations filtered the entire volume of water in the Chesapeake Bay in approximately 3.3 days. However in the 1990s, it took approximately 325 days to do the same due to population decline (Mann et al. 1991). Decline in volume filtered by eastern oysters increased amounts of phytoplankton in the water column, which can cause extreme fluctuations in pH and oxygen levels in the water (Gottlieb and Schweighofer 1996). These fluctuations may negatively affect other organisms, such as fishes residing in the Chesapeake Bay (Gottlieb and Schweighofer 1996).

Eastern oyster reefs help maintain a stable ecosystem by providing habitat and a food source for many species (Kennedy et al. 1996). Eastern oysters provide refuges for smaller organisms from extreme environmental conditions and predation. The oyster shell provides a hard substrate for attachment of species such as barnacles, byssate mussels, and suspension feeders, primarily polychaetes (Kennedy et al. 1996). Oyster gametes in the water column provide a food source to mircoheterotrophs and metazoan suspension feeders. Other organisms, such as blue crabs (*Callinectes sapidus*), prey upon adult oysters as a food source (Menzel and Hopkins 1956, Nichy and Menzel 1960).

Exotic Species Introductions

Efforts to restore the eastern oyster population in Maryland and Virginia have either failed or proven too costly to continue (Mann et al. 1991, Gottlieb and Schweighofer 1996). Because of the limited success and cost of these management efforts, resource agencies and commercial operations have proposed introducing a non-native oyster species into the Chesapeake Bay (Mann et al. 1991, Lipton et al. 1992, Gottlieb and Schweighofer 1996).

The primary reason for proposing the introduction of a non-native oyster species is to restore the fishery and its economic benefits. Introduction of a non-native species could increase employment in the marine sector and the flow of money into the economy through harvest and sale of the non-native oyster species. A highly successful introduction also could increase filtration rates in the water column, decrease the amount of suspended sediment, increase the amount of nutrient cycling, and increase available substrate for settlement (Lipton et al. 1992, Gottlieb and Schweighofer 1996).

Commercial introductions of the Suminoe oyster (*Crassostrea ariakensis*) have taken place in Oregon and Washington (Langdon and Robinson 1996). The Suminoe oyster established itself successfully under regional conditions, and is considered to be an excellent alternative species to the introduced Pacific oyster. The Suminoe oyster also is thought to be the prime candidate species to be used in trial introductions into the Chesapeake Bay (Calvo et al. 2001). Thus far, preliminary reports have shown that the Suminoe oyster has high disease resistance and is likely to thrive under Chesapeake Bay conditions (Calvo et al. 2001).

Modeling Oyster Populations

Few investigators have attempted to model oyster populations. Modeling approaches utilized include: time-dependent modeling of energy flow in post-settled oysters (Hofmann et al. 1992, Dekshenieks et al. 1993, Hofmann et al. 1994, Powell et al. 1994, Powell et al. 1995, Dekshenieks et al. 1996, Powell et al. 1996, Kobayashi et al. 1997, Ford et al. 1999), habitat suitability index modeling (Soniat and Brody 1988), loop modeling (Whitlatch and Osman 1994), size-structured fecundity modeling (Mann and Evans 1998), and bioenergetics modeling (Barille et al. 1997).

Time-dependent models of energy flow in oysters have been built for both eastern (Hofmann et al. 1992, Dekshenieks et al. 1993, Hofmann et al. 1994, Powell et al. 1994, Powell et al. 1995, Dekshenieks et al. 1996, Powell et al. 1996, Ford et al. 1999) and Pacific (Kobayashi et al. 1997) oysters. Equations in these models calculate energy flow through processes of growth and reproduction to estimate population size. Simulation runs at different mortality and recruitment rates were executed to examine their effects on population growth (Powell et al. 1994). Variations in seasonality of food concentration and temperature on reproduction were examined (Hofmann et al. 1992). Alterations to the model were made to study the effects of the diseases Dermo (Powell et al. 1996) and MSX (Ford et al. 1999) on population dynamics. A smaller model was added to the original energy flow model to show the impact of the host-parasite relationship (Powell et al. 1996, Ford et al. 1999). The disease model showed energy flow of the parasite as processes of metabolic growth and mortality, enabling the parasite to divide and cause mortality to the host.

A habitat suitability index, HSI, model (Galloway et al. 1999, Roloff and Kernohoan 1999) has been developed for eastern oyster populations in the Gulf of Mexico (Soniat and Brody 1988). The HSI model assessed habitat quality for existing oyster reefs as well as habitat without existing oyster reefs by examining factors such as percent coverage of the Gulf's floor by oyster shells, mean summer salinity level, mean abundance of living oysters, historic mean salinity levels, mean interval between killing floods, mean substrate firmness, mean predator abundance, and mean disease intensity. These factors were assigned a value from 0.0 to 1.0 by Soniat and Brody (1988). The HSI value was estimated from taking the product of the values assigned for the factors. The closer the HSI value is to one for that area, the more optimal is the habitat for oyster production. This type of model does not track demographic factors and their effects on population growth.

Whitlatch and Osman (1994) modeled interspecific ecological interactions of predation and competition in eastern oyster populations using a loop model. The loop model was set up with an interaction matrix and prediction matrix. The interaction matrix showed the relationships of competition and predation between species as a positive (+), negative (-), or no (0) relationship. The prediction matrix, calculated by taking the inverse of the interaction matrix, shows how increasing one variable (row) manipulates the equilibrium abundance of the other variable (column). The prediction matrix shows positive (+), negative (-), or no (0) relationships. This type of model cannot be used to predict population growth rates over time except in terms of positive or negative growth.

Barille et al. (1997) performed bioenergetics modeling on the black pearl oyster (*Pinctada margaritifera*) based on allometric scaling of physiological functions. The scope for growth was measured as a function of energy gained by obtaining food after subtracting the energy lost for maintenance, growth, and reproduction. The model was individual-based, resulting in trajectories for shell, somatic, and gonad tissue in oysters.

Except for the time-dependent energy flow 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, Powell et al. 1996, Ford et al. 1999), these models cannot be used to show the demographics of an oyster population. We developed our own demographic model instead of using the time-dependent, energy flow eastern oyster model for various reasons. First, there were only two years of growth, mortality, and reversion rate data available for Suminoe oysters in the Chesapeake 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 dynamics model that tracked population size over time would be the most defensible method for achieving the objective of estimating the probability of a Suminoe oyster population becoming self-sustaining. Although the time-dependent energy flow model also tracks population size over time, all calculations are done in terms of energy, which then is converted into population size. Since 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, parameter values that have yet to be determined for the Suminoe oyster.

Project Purpose and Objectives

In response to the declining eastern oyster population and the increased interest in introducing a non-native oyster species into the Chesapeake Bay, the Virginia Sea Grant College Consortium funded a project for Virginia Polytechnic Institute and State University to investigate risks associated with the introduction of triploid Suminoe oysters. The main purpose of the project was to develop a demographic population model for both the eastern oyster and triploid Suminoe oyster to examine the impacts of possible management strategies on population size.

The project had three main objectives. The first objective was to develop a demographic population model for both the eastern oyster and triploid Suminoe oyster. The second was to model the likelihood of local eastern oyster populations becoming extirpated under various management scenarios in the Chesapeake Bay. The third objective was to determine the sensitivity of population growth of triploid Suminoe oysters to the reversion rate of triploid to mosaic individuals (having both diploid and triploid cells) under various management scenarios in the Chesapeake Bay through model simulations. The following chapters present the methods and results of these three objectives.

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Table 1.1: The relationship of shell length (cm), from 0.1 cm to 8.9 cm, and proportion of males in a population of 1090 Suminoe oysters (*Crassostrea ariakensis*) on the Karachi coast, Pakistan (Asif 1979).

Size Class (cm)	Sample Size	Proportion of males	95% Confidence limits
0.1 to 0.9	52	0.635	0.75-0.506
1 to 1.9	191	0.592	0.67-0.484
2 to 2.9	124	0.596	0.68-0.51
3 to 3.9	157	0.598	0.675-0.521
4 to 4.9	154	0.532	0.611-0.453
5 to 5.9	180	0.511	0.652-0.37
6 to 6.9	126	0.476	0.564-0.388
7 to 7.9	74	0.432	0.545-0.318
8 to 8.9	32	0.375	0.542-0.208

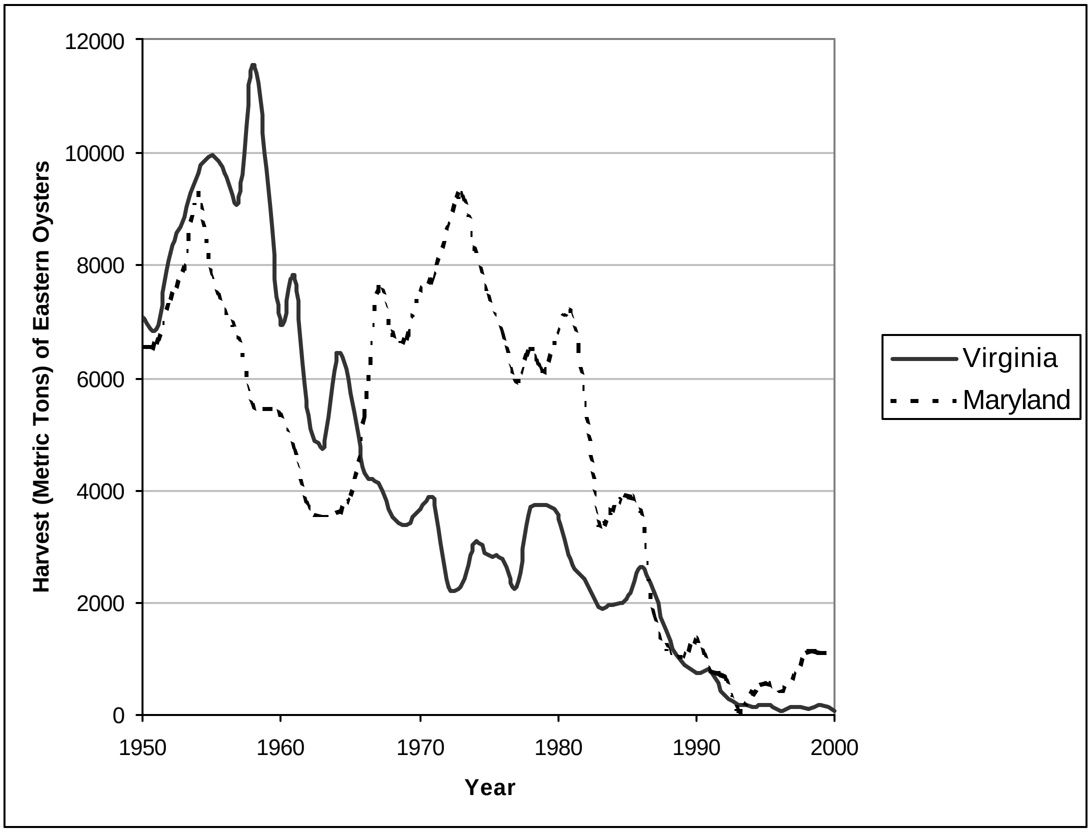
Table 1.2: Numbers of male and female Suminoe oysters (*Crassostrea ariakensis*) ages one to four years in Zhangjiang Bay, China (Yingya et al. 1992).

Sex	Age One	Age Two	Age Three	Age Four
Female	30	43	76	81
Male	108	65	73	79
Female/male	0.28	0.66	1.04	1.03

Table 1.3: Total mortality rates of diploid and triploid eastern oysters (*Crassostrea virginica*) and triploid Suminoe oysters (*Crassostrea ariakensis*) at low, medium, and high salinity sites in the Chesapeake Bay from June 1997 to May 1998 (Calvo et al. 1999).

Oyster Species	Low Salinity (<15ppt)	Medium Salinity (15-25ppt)	High Salinity (>25ppt)
Diploid Eastern Oyster	81%	100%	100%
Triploid Eastern Oyster	10%	35%	11%
Triploid Suminoe Oyster	14%	16%	16%

Figure 1.1: Eastern oyster (*Crassostrea virginica*) harvest in the Chesapeake Bay (Maryland and Virginia) from 1950 to 2000. (Data from Chesapeake Bay Office of the National Oceanic and Atmospheric Administration, http://noaa.chesapeakebay.net/).



CHAPTER TWO - A MODEL FOR ASSESSING THE LIKELIHOOD OF EXTIRPATION OF INDIVIDUAL POPULATIONS OF EASTERN OYSTERS (*CRASSOSTREA VIRGINICA*) IN CHESAPEAKE BAY

Abstract

A demographic population simulation model was developed to examine alternative fishery management strategies and their likely effects on the probability of extirpation of local eastern oyster populations in the Chesapeake Bay. Management strategies include varying the minimum shell length-at-harvest, harvest rate, and rate and frequency of stocking of oyster seed with respect to varying salinities and oyster population densities. We also examined the rate of disease-mediated mortality that can be tolerated by a viable population.

High density populations at low salinity sites remained viable under a 100% harvest rate and 76.6 minimum shell length-at-harvest due to increased fertilization efficiency, which increased reproduction. Low density populations at low salinity sites remained viable when harvest rate was set at 50% and minimum shell length-at-harvest was set at 85 mm. Neither reducing harvest rates nor raising minimum shell length-at-harvest produced a viable population at high salinity sites. The effects of disease-mediated mortality at high salinity sites were too great for these management options to decrease the probability of extirpation to zero. Supplemental stocking conducted regularly reduced extirpation probabilities to zero, and pulse stocking (every five to ten years) did as well, although reducing the extirpation probability to zero required a much larger number of oysters to be stocked. Decreasing disease-mediated mortality rates by 20% in high density populations and by 80% in low density populations reduced the

probability of extirpation to zero, suggesting the degree of genetic improvement needed to rebuild eastern oyster populations in the Chesapeake Bay.

Introduction

The eastern oyster (*Crassostrea virginica*) historically was the focus of a major, directed fishery, with harvest exceeding 142 million pounds in the 1880s (McHugh 1984). Today, however, the eastern oyster population in the Chesapeake Bay is estimated to be at only 1% of its original abundance (Newell 1985) through localized extirpations occurring throughout the Chesapeake Bay (Kennedy and Breisch 1983, Burreson 1991), which are mainly due to the effects of disease-mediated mortality and over-harvest (Gottlieb and Schweighofer 1996).

Two protozoan diseases, MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*), are the greatest causes of mortality to eastern oysters (Gosselin and Qian 1997). Several attempts have been made to decrease the prevalence and effects of Dermo and MSX in eastern oyster populations, including the use of selective breeding and interspecific hybridization (Burreson 1991, Allen et al.1993). However, the hybrids proved inviable (Allen et al. 1993), and selective breeding research has yielded mixed results, i.e., increased MSX resistance at the cost of decreased Dermo resistance (Burreson 1991). Another approach to developing a disease-free brood stock used a closed system hatchery for oyster production, although this method proved very costly (Krantz 1982).

High disease-mediated mortality also has altered harvest management strategies. When disease-mediated mortality was low, oyster seed was moved from areas of abundance to distribute the subsequent harvest over a larger geographical area (Krantz and Jordan 1996). Today, seed relocation is used to increase survival of oysters by moving seed to low salinity sites that are disease-free. Growth rate, however, is decreased in low salinity sites, thereby requiring a longer period of time before minimum shell length-at-harvest is reached. Proposed solutions to decrease the extirpation probability of local oyster populations include culture of oysters in low salinity, increasing the minimum shell length-at-harvest, and stocking oyster seed (Krantz and Jordan 1996). It is not known whether these actions would decrease the likelihood of extirpation of local oyster populations or to what degree a decrease will occur.

Management of eastern oysters can be performed at either a large scale, encompassing the entire Chesapeake Bay region, or local population scale. However, management to reduce the extirpation can be more effective at the local population level because populations differ in disease intensity and population density (Abbe 1992).

The purpose of this study was to develop a demographic population model to examine alternative management strategies and their likely effects on the likelihood of extirpation of local eastern oyster populations. Management strategies considered included varying the minimum shell length-at-harvest, harvest rate, and oyster seed stocking rate on oyster populations of different densities at different salinities. I also examined the effects of reduced disease-mediated mortality rates on maintaining a viable population. Simulation results from the model indicate management strategies that will likely decrease the probability of local extirpation while continuing some level of harvest.

Methods

Overview of Model

I developed a quantitative population model of the eastern oyster to estimate the likelihood of extirpation associated with oyster harvest under a range of environmental conditions and under a variety of management strategies. The model uses set demographic relationships and parameters (i.e. length-fecundity, oyster density-fertilization efficiency, and salinity-fecundity relationships) and user-specified variables (growth, and natural and harvest mortality rates). It includes management options for varying stocking rates, harvest rates, and minimum shell length-at-harvest. We utilized an existing eastern oyster fecundity model (Mann and Evans 1998) to estimate fecundity. Our model assumes that the oyster population is closed, i.e., that natural immigration and emigration do not occur. The model is age-structured, and uses a yearly time step. The state variable tracked through time is population size. Population growth rate is assumed to be exponential without density dependence. The final output of the model is the predicted population size of eastern oysters assuming specified demographic, environmental, and management parameters and variables. We developed the model using Visual Basic.

Modeling Approach

In each annual time step, growth occurs to the mean shell length of the age-class, then natural mortality and harvest are imposed, and then reproduction occurs for age-classes one through twelve (with age-class twelve being comprised of oysters age twelve and greater) (Figure 2.1). Because eastern oysters grow quickly in the spring and summer, the annual time step in the model starts in September after oysters have reached their average shell length for that age. Harvest mortality occurs from October to April, and natural mortality occurs at the greatest rates during the summer months. Because an annual time step is being used, the model is designed such that natural mortality and harvest are imposed simultaneously prior to the summer. Reproduction occurs during the summer months.

Model Variables, Parameters, and Equations

The initial conditions for the model are determined by the user's choice of specific values for several variables and parameters (Table 2.1, Table 2.2). Salinity is emphasized in the model because fecundity is highly dependent on salinity (Mann and Evans 1998). Biotic model parameters include mean shell length for each age-class, natural and harvest mortality for each age-class, disease prevalence, total mortality of oysters less than one year old, oyster population density, and sex ratio for each age-class (Table 2.1). Other parameter inputs are stocking rates, harvest regulations, and minimum shell length-at-harvest.

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

Mean Shell Length

I assume that the mean shell length of each age-class at the current time step does not affect the mean shell length of the age-class in the subsequent time step, because of large, highly variable annual growth rates (Calvo et al. 2001). Default shell length values were obtained from Mann et al. (1998) (Table 2.2 b ,c). However, these shell length values were obtained from oysters grown in a low salinity site, so we increased the mean shell length per age-class by 25 mm in each age class to represent faster growth rates at higher salinity sites (Table 2.2 d ,e) (Calvo et al. 2001).

Fecundity

The model simulates reproduction for fertile individuals in all mature age-classes with shell length greater then 30 mm, because the age at first reproduction for eastern oysters is at 30 mm to 47 mm in shell length (Galtsoff 1930, Gosselin and Qian 1997). Using Mann and Evans (1998), total fecundity for a population in relation to mean shell length is:

$$F_{t,i} = 39.06 * \left[0.000423 * L_{t,i}^{\ 1.17475}\right]^{2.36} * N_{t,i} \qquad (1)$$

where: $F_{t,i}$= total fecundity (number of eggs produced) at time t for age-class i having shell lengths greater than 30 mm,

$L_{t,i}$ = mean shell length (mm) at time t for age-class i having shell lengths greater than 30 mm, and

$N_{t,i}$ = population size (number of oysters) at time t for age-class i having shell lengths greater than 30 mm.

The parameter F_s represents the effect of salinity on fecundity using the mean salinity value for the area in Chesapeake Bay where a particular population of eastern oysters is located. The value of F_s ranges from zero (meaning zero fecundity) and one (meaning no effect of salinity on fecundity). For the eastern oyster, when salinity is below 8.0 ppt, F_s equals 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:

$$F_s = \frac{(S-8)}{5.5} \qquad (2)$$

where: F_s = 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, F_s is equal to one, because salinity has no effect on fecundity. When salinity is greater than 35 ppt, F_s is equal to zero (Mann and Evans, 1998).

The parameter for the effect of disease on fecundity, F_d, has a value between 1.0 (no mortality from disease) and 0.0 (all oyster spat die from disease) (Mann and Evans 1998). The user determines F_d based on the prevalence of disease in the area to be modeled. The default value for a population in low salinity (thereby experiencing low disease prevalence) was set at 0.8. The default value of F_d for a population at a high salinity site was set at 0.3 to model the significant impact of disease upon reproduction (Dittman et al. 2001). Since values for F_d have not been determined for eastern oyster population at varying salinities (Mann and Evans 1998), a sensitivity analysis on the parameter was run. The sensitivity analysis examined the effect F_d has on the probability of a local eastern oyster population becoming extirpated.

Oyster density is determined from the area over which the population occurs. Density affects gamete fertilization efficiency because more dense oyster populations (farms, reefs, etc.) have an increased fertilization rate (Mann and Evans 1998):

$$F_{ft,i} = 0.0049 * D_{t,i}^{0.72} \qquad (3)$$

where:

$$D_{t,i} = \frac{N_{t,i}}{A} \qquad (4)$$

where: $F_{ft,i}$ = fertilization efficiency at time t for age-class i having shell lengths greater than 30 mm,

$D_{t,i}$ = oyster density (oysters per square meter) at time t for age-class i having shell lengths greater than 30 mm, and

A = area (square meters).

The parameter for sex ratio, Fq_i, is the proportion of females in the population per age-class ranges from 0.0 to 1.0. Andrews (1979) reported that 90% of all eastern oysters less than 35 mm are male, and Kennedy (1983) reported that eastern oysters with shell lengths between 40 mm and 195 mm have a 0.5 sex ratio. Sex ratio values were set at 0.1 for age classes with mean shell length less than 35 mm. For age-classes with mean shell lengths greater than 40 mm, the sex ratio was set at 0.5 (i.e., equal sex ratio).

Hence, total number of offspring produced for all age-classes at each time step modified with the previous parameters (Mann and Evans 1998) is:

$$F_{total_t} = \sum \left(F_{t,i} * F_s * Fq_i * F_d * F_{ft,i} \right) \qquad (5)$$

where: F_{total_t} = modified total number of offspring produced at time t summed across all age-classes.

The number of recruits estimated by the fecundity model that survive to the next time step, thereby becoming age-class one, depends on the total number of offspring produced from 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), 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). All individuals stocked each year are age-class zero individuals. Hence, the number of individuals that will survive to enter age-class one at the next time step is:

$$N_{t,0} = \left(K_t + \left(F_{total_t} * \left(P_{met} * (1 - L_{mort})^{21} \right)\right)\right) * (1 - M_0) \qquad (6)$$

where: K_t = the number of oyster spat stocked at time t,

P_{met} = probability of successful completion of metamorphosis,

L_{mort} = daily larval mortality rate until settlement at 21 days, and

M_0 = total mortality rate for oysters less then one year old.

Mortality

The mortality parameters in the model for adult oysters are natural mortality and harvest mortality. A stochastic, age-structured natural mortality rate determines the proportion of oysters in each age-class of the population that die due to non-harvest causes each year. Stochastic values for each age-class and time step 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.

Population Size

Population size for the current year is determined from the previous year's population size minus harvest and natural mortality. Thus, for all age-classes greater than one, the next year's starting population for the next age-class is:

$$N_{t+1,i+1} = N_{t,i} * \left(1 - \left(H_{\mathrm{i}} + M_{t,i}\right)\right) \qquad (7)$$

where: H_i = harvest rate for age-class i with shell length greater than the minimum shell length-at-harvest, and

$M_{t,i}$ = natural mortality rate at time t for age-class i.

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

$$Ntotal_t = \sum N_{t,i} \qquad (8)$$

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

Model Simulations and Output

The model provides two options to the user for output. The first option shows results of one run of the simulation model. The output is a graph showing population size over a set period of time; however, because some variables are stochastic, each time the simulation model is run one time, the output will be different. Therefore, the second output option shows the distribution of outcomes resulting from running the same scenario (i.e., the same input parameter and variable values) for a set number of iterations. This output option gives the probability of population extirpation given the specified set of input conditions. Probabilities range from 0%, meaning there is a zero probability of a population becoming extirpated given a set of input conditions, to 100%, meaning that this outcome will occur every time under the given set of input conditions.

To understand the effects of key parameters, values of single parameters were manipulated while keeping all other parameters constant at default values. The parameters that were altered include harvest rate, minimum shell length-at-harvest, stocking, and natural mortality rate. Parameter alterations were examined under four different conditions: high density and low salinity (HDLS), low density and low salinity (LDLS), high density and high salinity (HDHS), and low density and high salinity (LDHS). Low salinity was set at 10 ppt and high salinity was set at 20 ppt. Low density was set at 0.66 oysters per meter square and high density was set at 214.7 oysters per meter square. These densities are representative of the highest and lowest densities from eastern oyster data collected in the James River, Virginia (Mann and Evans 1998). Each combination of parameters and variables was run for 100 years with 200 iterations.

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

Results

Effects of five major parameters on the probability of an eastern oyster population becoming locally extirpated were examined using the simulation model. These parameters were: harvest rate, minimum shell length-at-harvest, stocking, and natural mortality rate.

Harvest Rate

The impact of harvest rates on extirpation probabilities is highly dependent on the salinity of the site and density of the oyster population (Figure 2.2). In low salinity sites with high density populations, the probability of extirpation is 0% even with 100% harvest. High density populations at low salinity sites are viable because increased reproduction due to increased fertilization efficiency and reduced disease-mediated mortality allows the population to support harvest while remaining viable.

Low density populations at low salinity sites have a zero probability of extirpation until harvest rate is 0.5, after which the probability of extirpation increases as the harvest rate increases until the harvest rate reaches 1.0 at which the probability of extirpation is 62.5%. Low density populations at low salinity sites can support harvest rates less than 0.5 because when harvest rates are lower than 0.5, enough individual oysters are remaining in the water and reproducing, thereby able to maintain a viable population.

Reducing harvest rates will decrease the probability of extirpation in high salinity sites, but this action by itself will not reduce extirpation probabilities below 25% - 55%, depending on whether the population has a high or low density, respectively. For these populations, disease-mediated mortality is causing extirpation to occur in the population even in the absence of harvest mortality.

Minimum Shell Length-at-Harvest

As minimum shell length-at-harvest increases, the probability of extirpation decreases; however, the extent to which extirpation probability decreases is highly dependent on salinity and oyster population density (Figure 2.3). High density populations at low salinity sites have a zero probability of extirpation when minimum shell length-at-harvest is set at 65 mm and up. Low density populations at low salinity sites have a zero probability of extirpation when the minimum shell length-at-harvest is set at 85 mm and up because the population needs oysters in age classes with mean shell lengths from 30 mm to 85mm to stay in the water and reproduce in order to remain viable when harvest is occurring.

Increasing the minimum shell length-at-harvest reduces the probability of extirpation at high salinity sites, but is not sufficient to lower extirpation to reasonable levels. Low and high density populations at high salinity sites will have a probability of extirpation of 88% and 58.5%, respectively, when the shell length-at-harvest is 100 mm. Populations at high salinity sites have high rates of extirpation even when oysters are not being harvested until the oysters reach 100 mm because disease-mediated mortality is too severe.

Stocking

A wide range of stocking options could reduce the probability of extirpation at both low and high salinity sites. Six different stocking options were examined: a one-time stocking, stocking every year, stocking every other year, stocking every three years, stocking every five years, and stocking every ten years. When the stocking number was set at 1,000 oysters, there was zero probability of extirpation in all four conditions when stocking occurred every year, every other year, or every three years (Table 2.3). Low and high density populations at low salinity sites had a zero probability of extirpation when stocking 1,000 oysters every five years and every ten years. In order to obtain a zero probability of extirpation for high and low density populations at high salinity sites, stocking number had to be set at 2,000,000 oysters when stocking every five years and 5,000,000 oysters when stocking every ten years. One initial stocking had little apparent effect on lowering the probability of extirpation. For example, a one-time stocking of a billion oysters in a low density population at a low salinity site, resulted in a 52% probability of extirpation, whereas a population without any stocking had a 69% probability of extirpation. In low salinity sites, stocking oyster seed up to every once every ten years increases density of oyster populations, which increases the fertilization efficiency, thereby increasing reproduction and population size. Stocking oyster seed up to once every three years for oyster populations at high salinity sites acted as additional recruitment coming into the population and countered the decreased reproduction due to disease-mediated mortality.

Natural Mortality Rates

For populations of high and low densities at high salinity sites, disease was the most important factor contributing to mortality rates. In order to obtain a zero probability of extirpation, the mortality rates for a high density population needed to be reduced by 20% when the simulation model was run using all default values (Figure 2.4). For a low density population, mortality rates need to be reduced by 80% to maintain a viable population when the simulation model was run using all default values.

Sensitivity Analysis for F_d

F_d is the effect of disease on fecundity (Mann and Evans 1998). Because the exact value of F_d is unknown for different population types, a sensitivity analysis was run. Results indicated that extirpation risk is sensitive to changes of F_d from 0.1 to 1.0, except for high density populations in low salinity sites and low density populations in high salinity sites (Figure 2.5). High density populations in low salinity sites could have a zero extirpation probability when F_d was greater than 0.05. Low density populations at high salinity sites still had a 100% extirpation probability even when F_d was set at 1.0, meaning no effect of disease on fecundity.

The probability of extirpation varies with F_d in both low density populations at low salinity sites and high density populations at high salinity sites. The extirpation probability was 0.5 when F_d was set at the default value of 0.8 for a low density population at low salinity site. However, when F_d was set at 1.0, meaning no effect of disease on fecundity, the extirpation probability was reduced to 0.36. In contrast, when F_d was set at 0.1, the extirpation probability was raised to 0.87. The probability of extirpation was 0.77 when F_d was set at the default value of 0.3 for a high density population at a high salinity site. When F_d was raised to 1.0, the extirpation probability decreased to 0.17. In contrast, when F_d was reduced to 0.1, the extirpation probability increased to 100%.

Discussion

Local extirpation of eastern oyster populations caused by disease mortality and over-harvest creates both economic and ecological losses. This model examined the likely effects of various management strategies that can be used to reduce the probability of extirpation of local eastern oyster populations in the Chesapeake Bay. These management strategies included varying harvest rate, minimum shell length-at-harvest, and options for stocking. I also examined to what extent natural mortality rates need to be reduced to characterize a population that remains viable. Results indicated that changes in management strategies can have major impacts on reducing eastern oyster extirpation probabilities. However, the effects of potential changes to management strategies are highly dependent on the salinity and population density of individual populations.

Management Strategies

Changing harvest rate is one way to manage the eastern oyster population. Populations with high densities at low salinity sites can sustain a harvest of all oysters over the minimum shell length-at-harvest (76.6 mm) without risk of extirpation because disease-mediated natural mortality rates are low in low salinity areas (Burreson 1991). In contrast, populations at high salinity sites will become extirpated due to high rates of disease-mediated natural mortality independent of harvest. Low density populations in low salinity sites could have a zero probability of extirpation if the harvest rate was reduced to 0.5 and below. However, simply setting a targeted harvest rate may not be the best way to manage an oyster fishery, as it would require an annual estimation the total allowable harvest from each local population. This would be a costly process because it is very time consuming. Instead, harvest regulation could be obtained through management strategies such as setting a minimum shell length-at-harvest.

Setting a minimum shell length-at-harvest is one management option used to regulate harvest. Increasing minimum shell length-at-harvest is a management strategy that could decrease the probability of local oyster population extirpation. Krantz and Jordan (1996) suggested that reducing the minimum shell length-at-harvest would decrease recruitment. Based on our simulation results for a low density population, this appeared to hold true. However, our model indicated that high density populations at low salinity sites could sustain the impact of decreasing minimum shell length-at-harvest without greatly increasing the risk of extirpation. However, for marketing reasons, harvest of smaller oysters may not prove commercially attractive.

Stocking seed that is hatchery raised in local populations would have a large impact on decreasing the probability of extirpation. Regular stocking or large-scale pulse stocking could reduce extirpation probabilities to negligible levels. Even stocking as few as 1,000 oysters every three years reduced the probability of local extirpation to zero. However, this management strategy can prove costly. Oyster seed is relatively cheap; however, paying people to deploy the seed into oyster populations throughout the

Chesapeake Bay can be costly. For this reason, we also examined stocking every five or ten years, a less costly prospect. Under these scenarios, stocking as few as 1,000 oysters caused the populations at low salinity sites to have a zero probability of extirpation; however, for populations at higher salinity sites, stocking rate would need to increase significantly to reduce extirpation risk, significantly increasing operational cost. Although it would not be feasible to stock all oyster populations throughout the Chesapeake Bay, managers could use this model to choose populations with extirpations rates that could quickly decrease to near-zero with stocking, thereby maximizing the impact of using stocking as a management strategy.

It was apparent from these model simulations that oyster culture at lower salinity sites is more viable than culture in higher salinity sites. MSX and Dermo are intolerant of low salinity (Burreson 1991). Dermo is intolerant of salinities below 9 ppt (Mackin 1956), and needs salinities greater than 12 ppt for a full epizootic (Ragone and Burreson 1993). When salinity is less than 10 ppt for longer than two weeks, MSX disappears from oysters (Andrews 1964, Andrews 1983). Although oyster reproduction and growth rates are decreased in lower salinity areas (Krantz and Jordan 1996, Mann and Evans 1998), model results suggested that sustainable population and harvest remain possible if oyster density is very high. A high density population at low salinities was found viable because the high fertilization efficiency of a high density population compensated for the reduced fecundity at low salinities (Mann and Evans 1998).

Selective breeding for producing a disease resistant oyster have gone forward since the mid-1960s (Andrews 1965), and there has been progress towards developing disease-resistant strains. Our simulation results indicated that mortality rates need to be reduced by 20% for high density populations, and 80% for low density populations. High density population mortality rates only need to be reduced to 20% because the increased fertilization efficiency in highly dense populations (Mann and Evans 1998) overcomes the effect of increased mortality rates. Hence, reducing mortality rates by 20% and 80% for high and low density populations are the selective breeding goals for effective restoration to go forward.

Results indicated that changes in the value of F_d would affect extirpation probabilities. Although the default values for F_d are based on current literature, determining the exact value for which disease effect fecundity could improve the performance of the model. Future research should be performed to quantify the effect of disease on fecundity at different salinities throughout the Chesapeake Bay.

Modeling

Although other eastern oyster models exist, such as the time-dependent energy flow 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, Powell et al. 1996, Ford et al. 1999), we developed a new demographic model for several reasons. First, we determined that a demographic population dynamics model tracking population size over time would be the most efficient method to achieve the objective of determining population viability, a demographic process. Although the time-dependent energy flow model also tracks population size over time, all calculations are dependent on energy stocks and flow, which are translated into population size, thus making the model a bioenergetic model and not a demographic model. Second, we wanted to develop a simple model with emphasis on management strategies, so that a wide range of users could run the model and interpret the results under different management strategies.

The prevalence of disease currently is driving the decline of the eastern oyster population. Currently, there is little that can be done to directly decrease disease-mediated mortality. As a result, both population size and harvest are decreasing. This study indicates application of particular management strategies can both increase harvest and decrease the probability of local population extirpation. Management strategies including stocking and oyster culture at low salinity sites could lead to more viable populations. This model can be used as a tool to assess future management options at given areas.

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Table 2.1: Definitions of model variables and parameters.

Symbol	Parameter or Variable Definition
A	Area (square meters)
$D_{t,i}$	Oyster density (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
F_d	Effect of disease on fecundity ($0 = F_d = 1$)
$F_{ft,i}$	Fertilization efficiency at time t for age-class i ($0 = F_{ft,i} = 1$)
F_{q_i}	Effect of sex ratio on fecundity for age-class i ($0 = F_{q_i} = 1$)
F_s	Effect of salinity on fecundity ($0 = F_s = 1$)
F_{total_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
L_{mort}	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
N_{total_t}	Total population size (number of oysters) for all age-classes at time t
P_{met}	Probability of successful metamorphis
S	Salinity (ppt)
t	Time (years)

Table 2.2a: Default variable and parameter values for the model.

Variable	Default Value
A (square meters)	1000
H_i	0.8
Iterations	200
K_t	0
Minimum shell length-at-harvest (mm)*	76.6
t (years)	100

* This is the current regulation for minimum shell length-at-harvest.

Table 2.2b: Default variable and parameter values for high density (214.7 oysters per square meter) oyster populations in low salinity sites (10 ppt). The effect of disease on fecundity, F_d, is set at 0.8.

i	$N_{0,i}$	$L_{t,i}$ (mm) *	Variance of $L_{t,i}$ (mm) **	$M_{t,i}$ ***	Variance of $M_{t,i}$ **	F_{q_i} ****
1	100000	11.43	5	0.4	0.05	0.1
2	50000	31.47	10	0.4	0.05	0.1
3	30000	47.87	10	0.25	0.05	0.5
4	15000	61.12	10	0.35	0.05	0.5
5	5000	71.99	10	0.4	0.05	0.5
6	4000	80.85	10	0.4	0.05	0.5
7	3500	88.08	10	0.4	0.05	0.5
8	3000	93.97	10	0.4	0.05	0.5
9	2000	98.77	10	0.4	0.05	0.5
10	1000	102.69	10	0.4	0.05	0.5
11	800	105.88	10	0.4	0.05	0.5
12	400	108.88	10	0.4	0.05	0.5

* Mann et al. 1998
** Calvo et al. 2001
*** Burreson 1991, Calvo et al. 2001, Mann et al. 1998
****Andrew 1979, Kennedy 1982

Table 2.2c: Default variable and parameter values for low density (0.66 oysters per square meter) oyster populations in low salinity sites (10 ppt). The effect of disease on fecundity, F_d, is set at 0.8.

i	$N_{0,i}$	$L_{t,i}$ (mm) *	Variance of $L_{t,i}$ (mm) **	$M_{t,i}$ ***	Variance of $M_{t,i}$ **	F_{q_i} ****
1	100	11.43	5	0.2	0.05	0.1
2	100	31.47	10	0.2	0.05	0.1
3	100	47.87	10	0.25	0.05	0.5
4	100	61.12	10	0.25	0.05	0.5
5	75	71.99	10	0.35	0.05	0.5
6	50	80.85	10	0.35	0.05	0.5
7	45	88.08	10	0.4	0.05	0.5
8	35	93.97	10	0.4	0.05	0.5
9	25	98.77	10	0.4	0.05	0.5
10	15	102.69	10	0.4	0.05	0.5
11	10	105.88	10	0.4	0.05	0.5
12	5	108.88	10	0.4	0.05	0.5

* Mann et al. 1998
** Calvo et al. 2001
*** Burreson 1991, Calvo et al. 2001, Mann et al. 1998
****Andrew 1979, Kennedy 1982

Table 2.2d: Default variable and parameter values for high density (214.7 oysters per square meter) oyster populations in high salinity sites (20 ppt). The effect of disease on fecundity, F_d, is set at 0.3.

i	$N_{0,i}$	$L_{t,i}$ (mm) *	Variance of $L_{t,i}$ (mm) **	$M_{t,i}$ ***	Variance of $M_{t,i}$ **	F_{qi} ****
1	100000	36.43	5	0.4	0.05	0.1
2	50000	56.47	10	0.9	0.05	0.5
3	30000	71.87		0.9	0.05	0.5
4	15000	77.12	10	0.9	0.05	0.5
5	5000	86.99	10	0.9	0.05	0.5
6	4000	88.85	10	0.9	0.05	0.5
7	3500	95.08	10	0.9	0.05	0.5
8	3000	103.97	10	0.9	0.05	0.5
9	2000	108.77	10	0.9	0.05	0.5
10	1000	112.69	10	0.9	0.05	0.5
11	800	120.88	10	0.9	0.05	0.5
12	400	122.88	10	0.9	0.05	0.5

* Mann et al. 1998
** Calvo et al. 2001
*** Burreson 1991, Calvo et al. 2001, Mann et al. 1998
****Andrew 1979, Kennedy 1982

Table 2.2e: Default variable and parameter values for low density (0.66 oysters per square meter) oyster populations in high salinity sites (20 ppt). The effect of disease on fecundity, F_d, is set at 0.3.

i	$N_{0,i}$	$L_{t,i}$ (mm) *	Variance of $L_{t,i}$ (mm) **	$M_{t,i}$ ***	Variance of $M_{t,i}$ **	Fq_i ****
1	100	36.43	5	0.2	0.05	0.1
2	100	56.47	10	0.6	0.05	0.5
3	100	71.87	10	0.9	0.05	0.5
4	100	77.12	10	0.9	0.05	0.5
5	75	86.99	10	0.9	0.05	0.5
6	50	88.85	10	0.9	0.05	0.5
7	45	95.08	10	0.9	0.05	0.5
8	35	103.97	10	0.9	0.05	0.5
9	25	108.77	10	0.9	0.05	0.5
10	15	112.69	10	0.9	0.05	0.5
11	10	120.88	10	0.9	0.05	0.5
12	5	122.88	10	0.9	0.05	0.5

* Mann et al. 1998

** Calvo et al. 2001

*** Burreson 1991, Calvo et al. 2001, Mann et al. 1998

****Andrew 1979, Kennedy 1982

Table 2.3: Number of eastern oysters, *C. virginica*, stocked to obtain a zero probability of extirpation. Stocking occurred every year, every other year, every three years, every 5 years, and every 10 years. This was examined for four different population types: high density populations at low salinity sites (HDLS), low density populations at low salinity sites (LDLS), high density populations at high salinity sites (HDHS), and low density populations at high salinity sites (LDHS).

Stocking	HDLS	LDLS	HDHS	LDHS
Every Year	1000	1000	1000	1000
Every 2 Years	1000	1000	1000	1000
Every 3 Years	1000	1000	1000	1000
Every 5 Years	1000	1000	2,000,000	2,000,000
Every 10 Years	1000	1000	5,000,000	5,000,000

Figure Captions

Figure 2.1: Flow chart depicting events within the annual time step in the model for estimating likelihood of extirpation for *C. virginica* populations.

Figure 2.2: Effect of harvest rate on the probability of a *C. virginica* population becoming extirpated, keeping all other variables and parameters at default values under three different conditions: low density populations at low salinity sites (LDLS), high density populations at high salinity sites (HDHS), and low density populations at high salinity sites (LDHS).

Figure 2.3: Effect of minimum shell length-at-harvest on the probability of a *C. virginica* population becoming extirpated, keeping all other variables and parameters at default values under for different conditions: high density populations at low salinity sites (HDLS), low density populations at low salinity sites (LDLS), high density populations at high salinity sites (HDHS), and low density populations at high salinity sites (LDHS).

Figure 2.4: Effect of the percent decrease in mortality rates on the probability of a *C. virginica* population becoming extirpated, keeping all other variables and parameters at default values under two different conditions: high density populations at high salinity sites (HDHS), and low density populations at high salinity sites (LDHS).

Figure 2.5: Effect of the effect of disease on fecundity, F_d, on the probability of a *C. virginica* population becoming extirpated, keeping all other variables and parameters at default values two different conditions: low density populations at low salinity sites (LDLS), and high density populations at high salinity sites (HDHS). The default F_d value is 0.8 for low density populations at low salinity sites and is 0.3 for high density populations at high salinity sites.

Figure 2.1

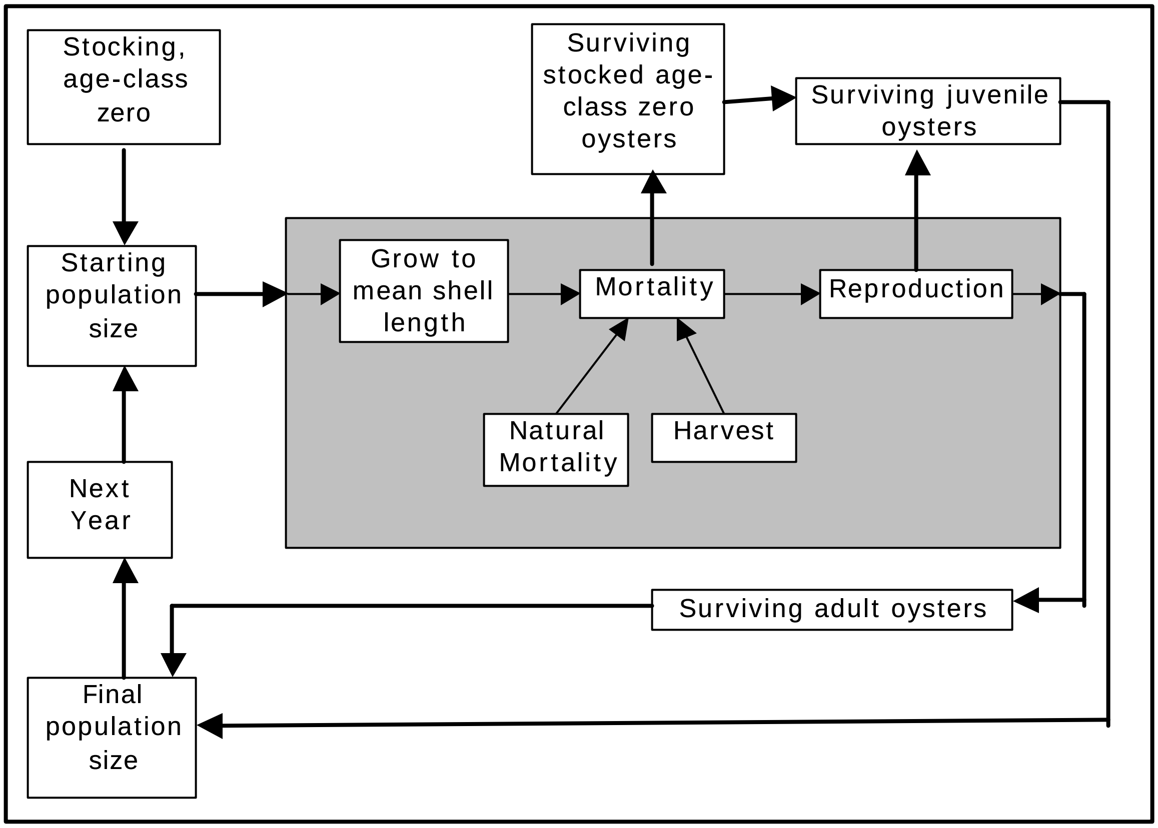

Stocking, age-class zero
Surviving stocked age-class zero oysters
Surviving juvenile oysters
Starting population size
Grow to mean shell length
Mortality
Reproduction
Natural Mortality
Harvest
Next Year
Surviving adult oysters
Final population size

Figure 2.2

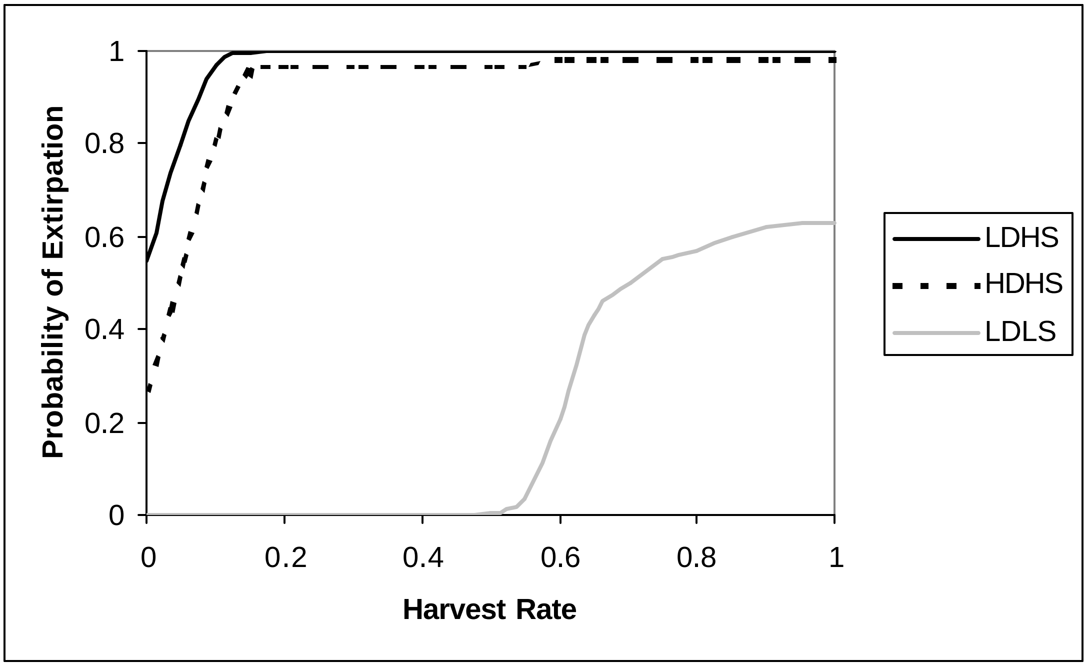

Probability of Extirpation
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
Harvest Rate
LDHS
HDHS
LDLS

Figure 2.3

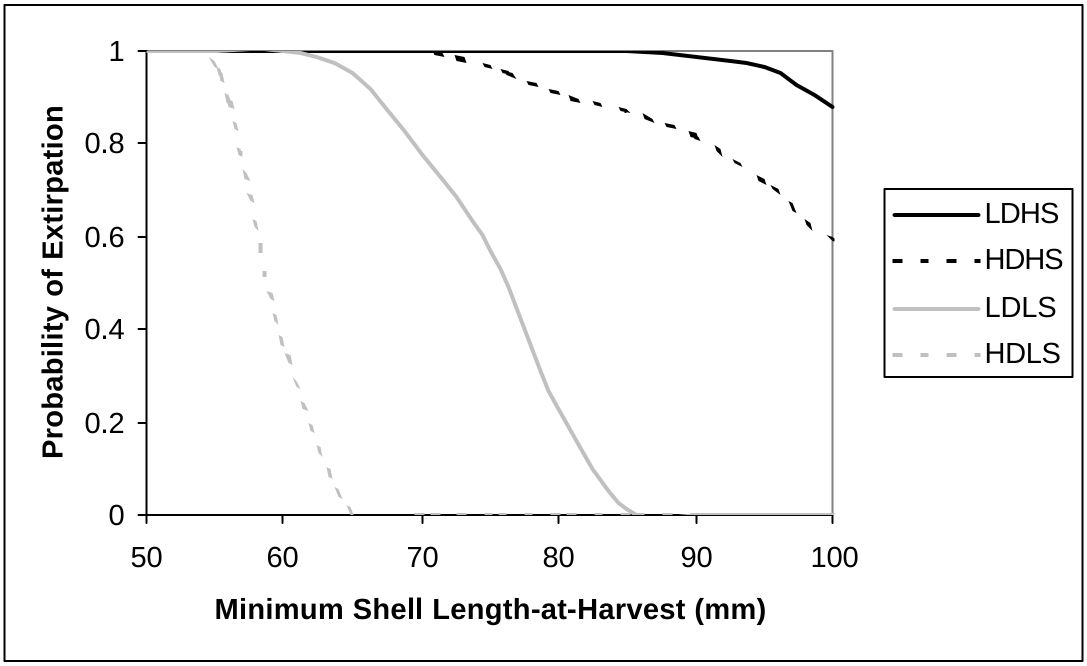

1
0.8
0.6
0.4
0.2
0
Probability of Extirpation
50
60
70
80
90
100
Minimum Shell Length-at-Harvest (mm)
LDHS
HDHS
LDLS
HDLS

Figure 2.4

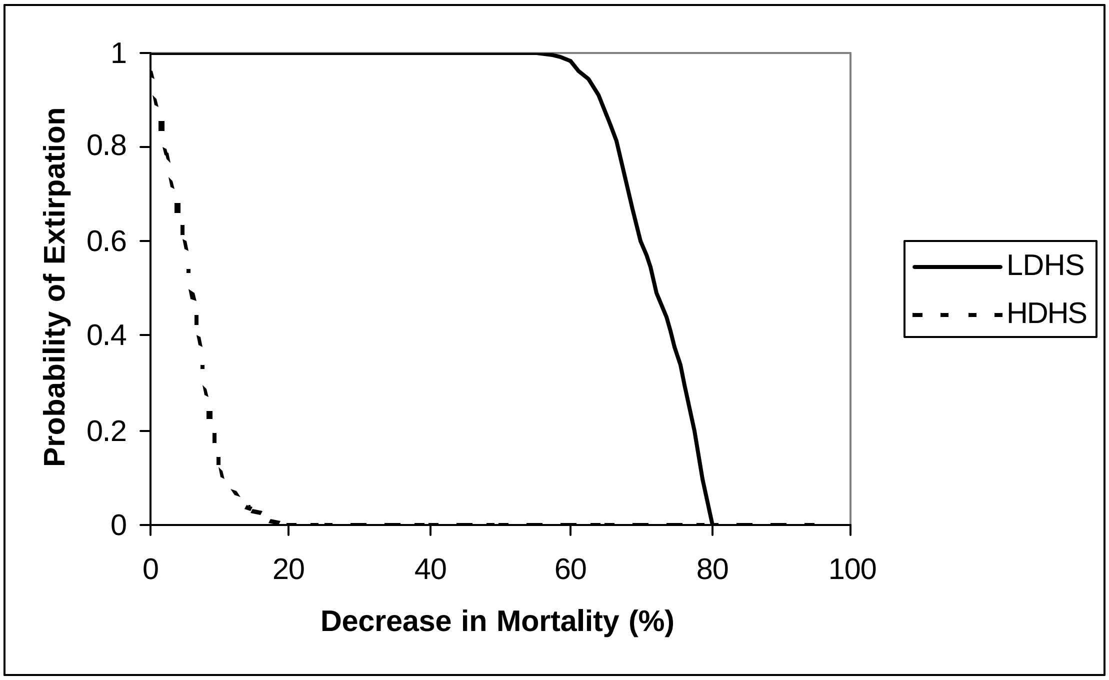
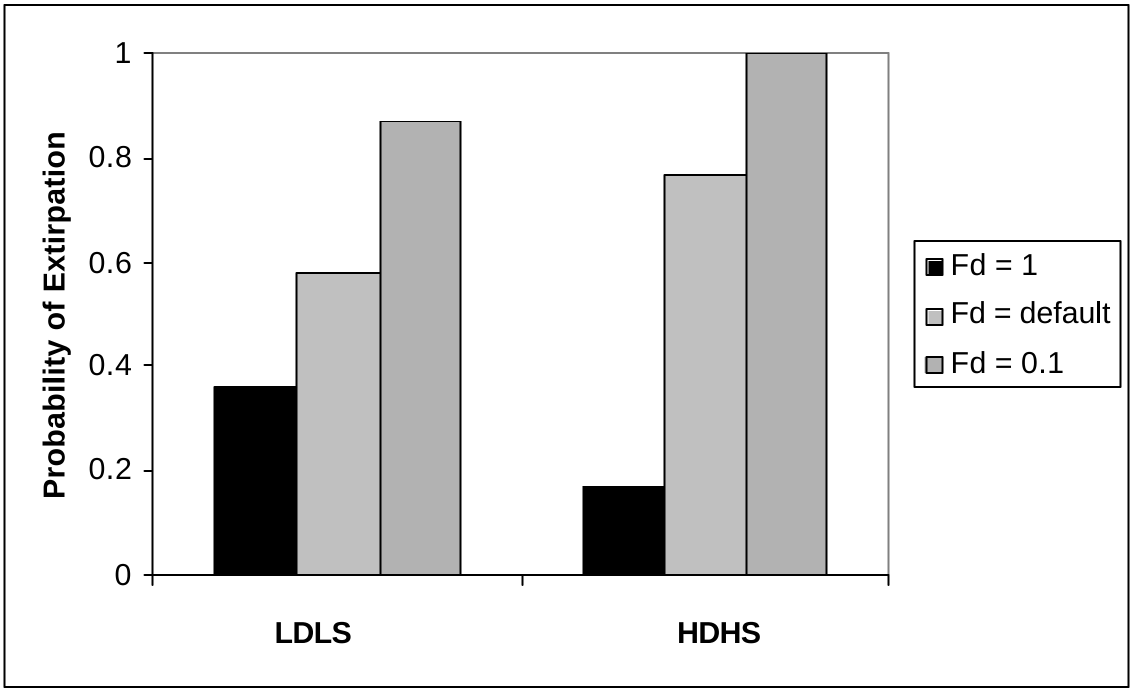

1
0.8
0.6
0.4
0.2
0
Probability of Extirpation
0
20
40
60
80
100
Decrease in Mortality (%)
LDHS
HDHS

Figure 2.5



* Default *Fd* value for LDLS is 0.8 and default *Fd* value for HDHS is 0.3.

CHAPTER THREE - A MODEL FOR ASSESSING THE LIKELIHOOD OF SELF-SUSTAINING POPULATIONS RESULTING FROM COMMERCIAL PRODUCTION OF TRIPLOID SUMINOE OYSTERS (*CRASSOSTREA ARIAKENSIS*) IN CHESAPEAKE BAY

Abstract

Culture of a non-native species, such as the Suminoe oyster (*Crassostrea ariakensis*), could supplement 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 include salinity, stocking density, reversion rate, reproductive potential, natural and harvest mortality, growth rates, and effects of various management strategies, including harvest criteria. The probability of a Suminoe oyster population becoming self-sustaining decreased 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. Based on model results, I suggest using these management strategies for decreasing 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.

Introduction

The native eastern oyster (*Crassostrea virginica*) population in Chesapeake Bay has declined due to 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 disease pressures 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 using 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, with individuals reaching 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 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 makes the use of triploids imperfect. For example, recent data showed 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 are comprised of 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. I define this hazard, “reproductively effective reversion”, as the process 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, with numerous unknown ecological consequences.

Another hazard associated with deployment of triploid Suminoe oysters is the possibility that non-triploids might be stocked inadvertently because of failure to detect them in a mixed batch of triploid and diploid individuals. While technology to produce “100%” triploids is now available, as practiced on Pacific oyster (Guo and Allen 1994b, Guo et al. 1996), the reliability of “100%” triploids in Suminoe oyster is undetermined. Diploids may enter the population from several sources, including chromosomal non-disjunction in tetraploid males producing haploid gametes, low level hermaphrodism in diploid females yielding self-fertilized embryos, and cross-contamination between diploid and triploid cultures (c.f., 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

using current technology. Should the frequency of diploids be greater than zero but less than one in a thousand, then the batch would be certified 100% triploid, posing the hazard of stocking fertile diploid oysters.

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. Hazard may be defined as an undesirable outcome resulting from an activity (Hallerman and Kapuscinski, 1995). Stocking triploid Suminoe oysters produces two hazards in this model, inadvertently stocking diploids and 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 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 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 in 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. Since 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 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.

Modeling Approach

In each annual time step for age-classes one through six (with age-class six being comprised of oysters age six and greater), growth occurs to the mean shell length of the age-class, then natural mortality and harvest are imposed, and then reproduction occurs

(Figure 3.1). Because Suminoe oysters grow quickly in autumn (Cahn 1950), the annual time step starts 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 (Table 3.1, Table 3.2). 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 3.1). Other variable inputs are stocking rates, harvest regulations, and management strategies.

Stochasticity is programmed 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, while 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, with the degree of variance 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 the subsequent time step due to 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).

Using Mann and Evans (1998), total fecundity for a diploid population in relation to mean shell length is given below:

$$F_{t,i} = 39.06 * \left[0.000423 * L_{t,i}{}^{1.17475}\right]^{2.36} * N_{t,i} \qquad (1)$$

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

$L_{t,i}$ = 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.

Equation one is used when determining the number of eggs produced by diploid oysters that survived from the previous year. Equation one must be modified to determine the number of eggs produced by triploid oysters under-going reproductively effective reversion. Diploids may enter the population through two reproduction-related processes, non-detection of diploids ($T_{t,i}$) and reproductively effective reversion ($R_{t,i}$) of triploids. First, diploid individuals may enter the population by 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 two, reproductively effective reversion is the percentage of the population that reverts from triploidy to mosaicism (i.e., containing both triploid and diploid gamete cells). We conservatively assume that reverted triploids will have full reproductive capabilities, even though this has not yet been observed (Allen, unpublished 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 for triploid oysters:

$$F_{revert_{t,i}} = 39.06 * \left[0.000423 * L_{t,i}^{\ 1.17475}\right]^{2.36} * N_{t,i} * \left(R_{t,i} + T_{t,i}\right) \qquad (2)$$

where: $F_{revert_{t,i}}$ = 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 F_s is the effect of salinity on fecundity using the mean salinity value for the area in Chesapeake Bay where a particular population of Suminoe oysters is located. The value of F_s ranges from zero (meaning zero fecundity) and one (meaning no effect of salinity on fecundity). For the eastern oyster, when salinity is below 8.0 ppt, F_s 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:

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

where: F_s = 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, F_s is equal to one denoting no effect of salinity on fecundity. When salinity is greater than 35 ppt, F_s 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), and in the absence of contrary information, these F_s values were used for Suminoe oysters.

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 suggest that the Suminoe oyster is resistant to diseases on the east coast of North America (Calvo et al. 2001); therefore, the default value of F_d 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.) have an increased fertilization rate (Mann and Evan 1998):

$$F_{f t,i} = 0.0049 * D_{t,i}^{0.72} \qquad (4)$$

where: $F_{f t,i}$ = 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 (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 (m^2). However, the density value for equation four will differ with triploid populations since 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:

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

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 equation one and two is only comprised of females. 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:

$$F_{total_t} = \sum \left(F_{revert_{t,i}} * F_s * Fq_i * F_d * F_{ft,i} \right) \qquad (6)$$

where: F_{total_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:

$$N_{t,0} = (K_t + (F_{total_t} * (P_{met} * (1 - L_{mort})^{21}))) * (1 - M_0) \qquad (7)$$

where: K_t = the number of oyster spat stocked at time t,

P_{met} = probability of successful completion of metamorphosis,

L_{mort} = 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 that die due to non-harvest causes each year. Default natural mortality rates were taken from Calvo et al. (2001) (Table 3.2b). 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:

$$N_{t+1,i+1} = N_{t,i} * \left(1 - \left(H_{\mathrm{i}} + M_{t,i}\right)\right) \qquad (8)$$

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 while allowing stochastic variables to change. This output option shows the probability of the population becoming self-sustaining given the specified set of input conditions, yielding 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 was 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 is to continue running the simulation for twenty years without stocking, reflecting a maximum longevity of 20 years for Suminoe oyster (Cahn 1950).

To understand the effects of key variables, the 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 include salinity, certainty of obtaining the desired harvest rate, minimum shell length-at-harvest, and stocking density. The second set of model runs is similar to the first, except changes were made to the values of two variables at a time while keeping all other variables 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, keeping area set at 300 m^2.

All simulation results reported below were obtained using default values for all variables (Table 3.2a, 3.2b), unless noted otherwise.

Results

Effects of four major variables on the probability of a Suminoe oyster population becoming self-sustaining were examined 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 (Figure 3.2). 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 (Figure 3.2). By harvesting the oysters sooner, there is decreased likelihood of reproductively effective reversion occurring.

Certainty in Harvest Rate

As the certainty of obtaining the desired harvest rate increased, the probability of the population becoming self-sustaining decreased (Figure 3.3). For example, if oysters were grown on the bottom, the certainty of obtaining the desired harvest rate would be lower than if cages were used. Lower certainty of harvest would increase the likelihood of reproductively effective reversion occurring 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.

I 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 (Figure 3.3). This 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 relative 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 0.82. 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 0.35.

Minimum Shell Length-at-Harvest

As the minimum shell length-at-harvest was increased, the probability of the population becoming self-sustaining increased (Figure 3.4). Increased probability of self-sustainability is because the probability of reproductively effective reversion increases the longer oysters are in the water, and the number of offspring produced by undetected diploids is 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 (Figure 3.5). Increased probability of self-sustainability is because gamete fertilization efficiency increases 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 (Figure 3.5). Absence of reproduction from undetected diploids, and the lack of reproduction in mosaic (reverted triploid) oysters until age three, 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 keeping all other variables set at the default values (Figure 3.6). 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, keeping all other variables set at the default values (Figure 3.7). Increased certainty of harvest decreased the number of oysters remaining in culture 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 and activities of the introduced species (i.e., through reproduction, competition, etc.). To a large degree, the hazards of 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 hazard 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 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 low population density of oysters stocked.

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 relationship of oyster density and fertilization efficiency are not known for Suminoe oysters, so those for eastern oysters were used. It is important to determine 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, so eastern oyster parameter values were used. For most oyster species, gametogenesis is decreased or even nonexistent at lower salinities;

however, the salinity value at which gametogenesis is decreased or absent may vary among species (Amemiya 1926, Calabrese and Davis 1970, Kennedy et al. 1996). The Suminoe oyster seems to thrive in estuarine conditions (Huang 1962, Calvo et al. 2001) and there may biological parallels to 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 (Huang 1962, Wang, personal communication), so the model may slightly underestimate fecundity 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 are comprised of both triploid gamete producing cells, unable to produce viable gametes, and also of diploid gamete producing cells, able to produce viable gametes. Continuing research with triploid Suminoe oyster should help us fill in this gap in knowledge; however, until then, we decided that the model should err on the ecologically conservative side in saying 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 detecting very low proportions of diploids could reduce risk of a triploid Suminoe oyster population becoming self-sustaining under high stocking rates. Currently, flow cytometry is used for certifying triploid batches by 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 is 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 decreasing the subsequent chance for reproduction to occur. Improved detection also could allow watermen to stock more Suminoe oysters in a smaller area.

I developed my 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, Powell et al. 1996, Ford et al. 1999) for various reasons. First, there were only two years of growth, mortality, and reversion rate data available for Suminoe oysters in the Chesapeake 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 dynamics 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 calculations are done in terms of energy, which then is converted into population size. Since 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 parameter values have yet to be determined for the Suminoe oyster.

The scope of my model could be easily expanded to investigate more detailed scenarios and outputs. Economic aspects could be modeled to examine cost and profit/loss relationships for commercial production of triploid Suminoe oyster under various assumptions. Also, 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. Additional work is needed to assess a wider range of management options and potential risks.

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Table 3.1: Definitions of model parameters and variables.

Symbol	Parameter and Variable Definition
A	Area (square meters)
C	Certainty in obtaining the desired harvest rate (0 = C = 1)
$D_{t,i}$	Oyster density (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
F_d	Effect of disease on fecundity (0 = F_d = 1)
$F_{f_{t,i}}$	Fertilization efficiency at time t for age-class i (0 = $F_{f_{t,i}}$ = 1)
F_{q_i}	Effect of sex ratio on fecundity for age-class I (0 = F_{q_i} = 1)
$F_{revert_{t,i}}$	Total fecundity (number of eggs) of reverted triploid oysters at time t for age-class i
F_s	Effect of salinity on fecundity (0 = F_s = 1)
F_{total_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
L_{mort}	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
N_{total_t}	Total population size (number of oysters) for all age-classes at time t
P_{met}	Probability of successful metamorphosis (0 = P_{met} = 1)
$R_{t,i}$	Reproductively effective reversion rate at time t for age-class i (0 = $R_{t,i}$ = 1)
$T_{t,i}$	Detection threshold at time t for age-class i (0 = $T_{t,i}$ = 1)
S	Salinity (ppt)
t	Time (years)

Table 3.2a: Default values set in the model.

Variable	Default Value
A (square meters)	220
C	0.9
Extra time-steps without stocking (years)	20
F_d	1.0
H_i	1.0
Iterations	350
K_t	10000
Minimum shell length-at-harvest (mm)	76.6
S (ppt)	15
t (years)	50

Table 3.2b: Default age-dependent variable values in the model.

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

* (Yingya et al., 1992)
** (Cahn, 1950)
*** (Calvo et al., 2001)

Figure Captions

Figure 3.1: Flow chart depicting the annual time-step in the model for estimating likelihood of establishing self-sustaining reproduction in triploid *C. ariakensis*.

Figure 3.2: Effect of salinity at deployment site on probability of a *C. ariakensis* population becoming self-sustaining, when area is set at 100 m^2, stocking size is set at 20,000 oysters, and keeping all other variables 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.

Figure 3.3: Effect of certainty in obtaining a specified harvest rate on probability of a *C. ariakensis* population becoming self-sustaining, when area is 300 m^2 and 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 3.4: Effect of minimum shell length-at-harvest (mm) on probability of a *C. ariakensis* population becoming self-sustaining, keeping all other variables at default values.

Figure 3.5: Effect of stocking density on 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 3.6: Effect of stocking density and salinity at deployment site on 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.

Figure 3.7: Effect of stocking density and certainty in obtaining the desired harvest rate on 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.

Figure 3.1

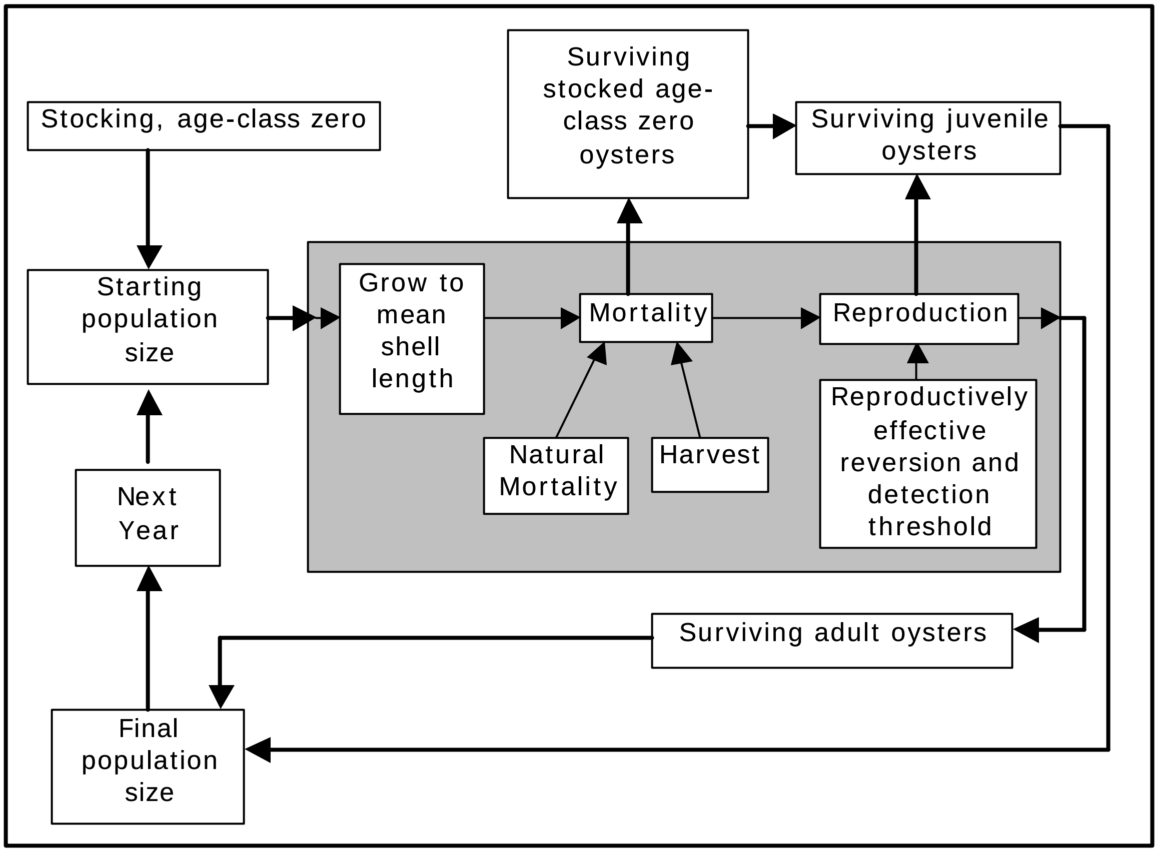

Stocking, age-class zero
Surviving stocked age-class zero oysters
Surviving juvenile oysters
Starting population size
Grow to mean shell length
Mortality
Reproduction
Natural Mortality
Harvest
Reproductively effective reversion and detection threshold
Next Year
Surviving adult oysters
Final population size

Figure 3.2

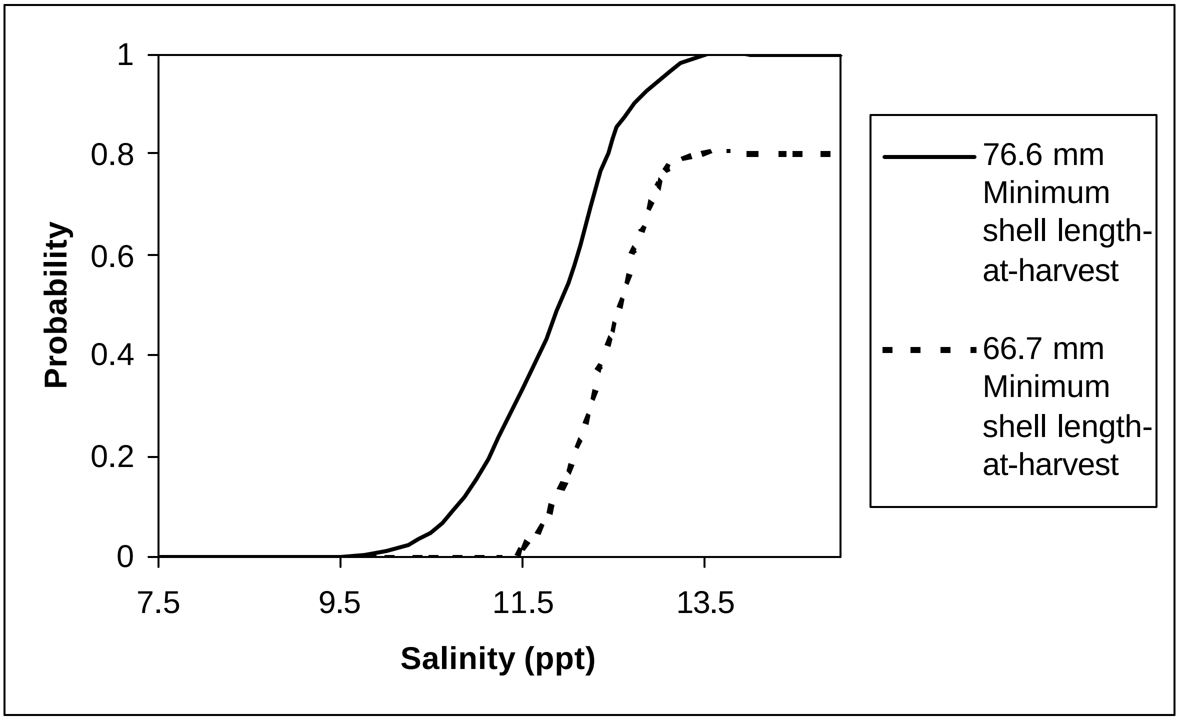

1
0.8
0.6
0.4
0.2
0
Probability
7.5
9.5
11.5
13.5
Salinity (ppt)
76.6 mm Minimum shell length-at-harvest
66.7 mm Minimum shell length-at-harvest

Figure 3.3

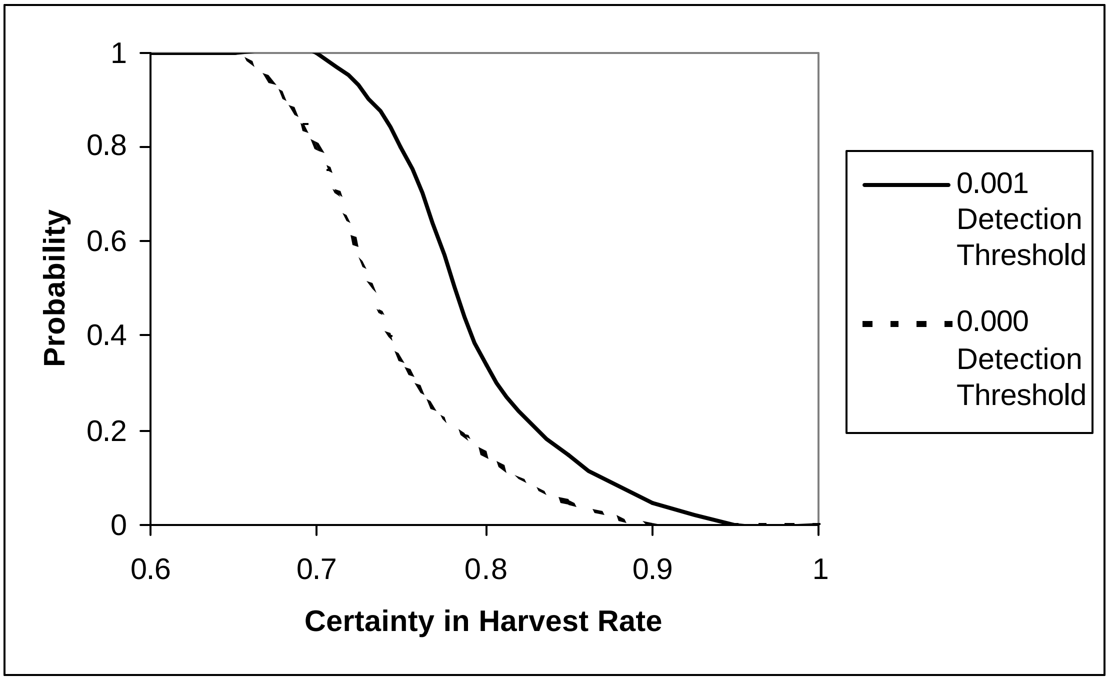
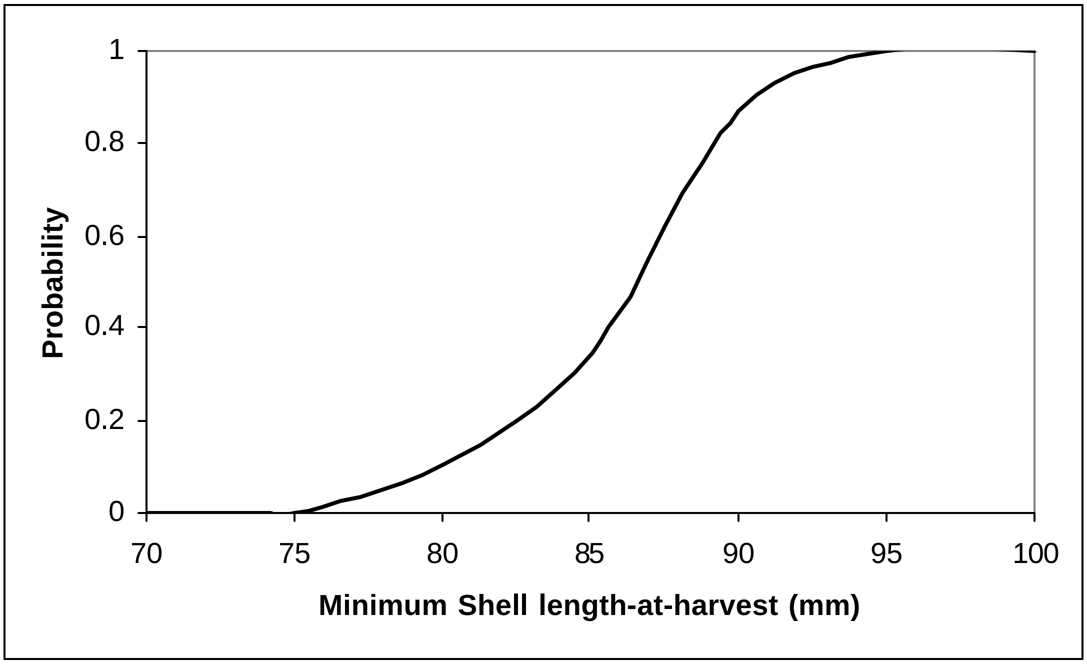

1
0.8
0.6
0.4
0.2
0
Probability
0.6
0.7
0.8
0.9
1
Certainty in Harvest Rate
0.001 Detection Threshold
0.000 Detection Threshold

Figure 3.4



1
0.8
0.6
0.4
0.2
0
Probability
70
75
80
85
90
95
100
Minimum Shell length-at-harvest (mm)

Figure 3.5

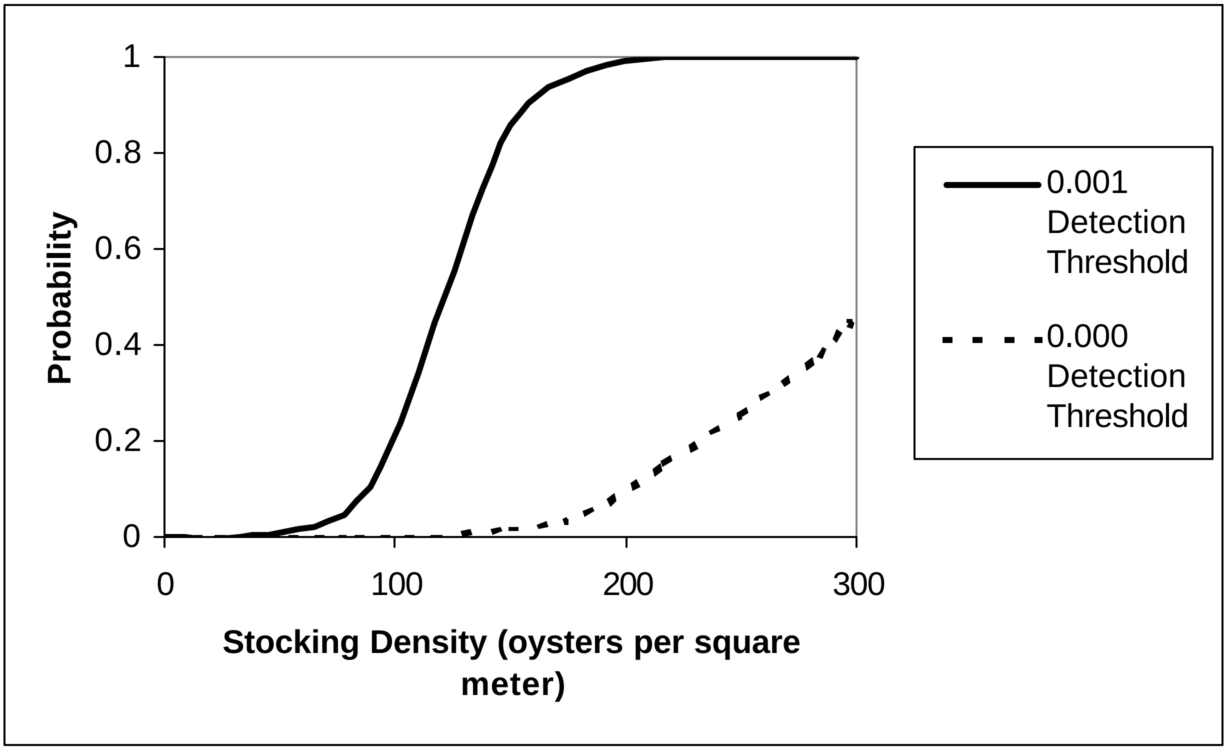

1
0.8
0.6
0.4
0.2
0
Probability
0
100
200
300
Stocking Density (oysters per square meter)
0.001 Detection Threshold
0.000 Detection Threshold

Figure 3.6

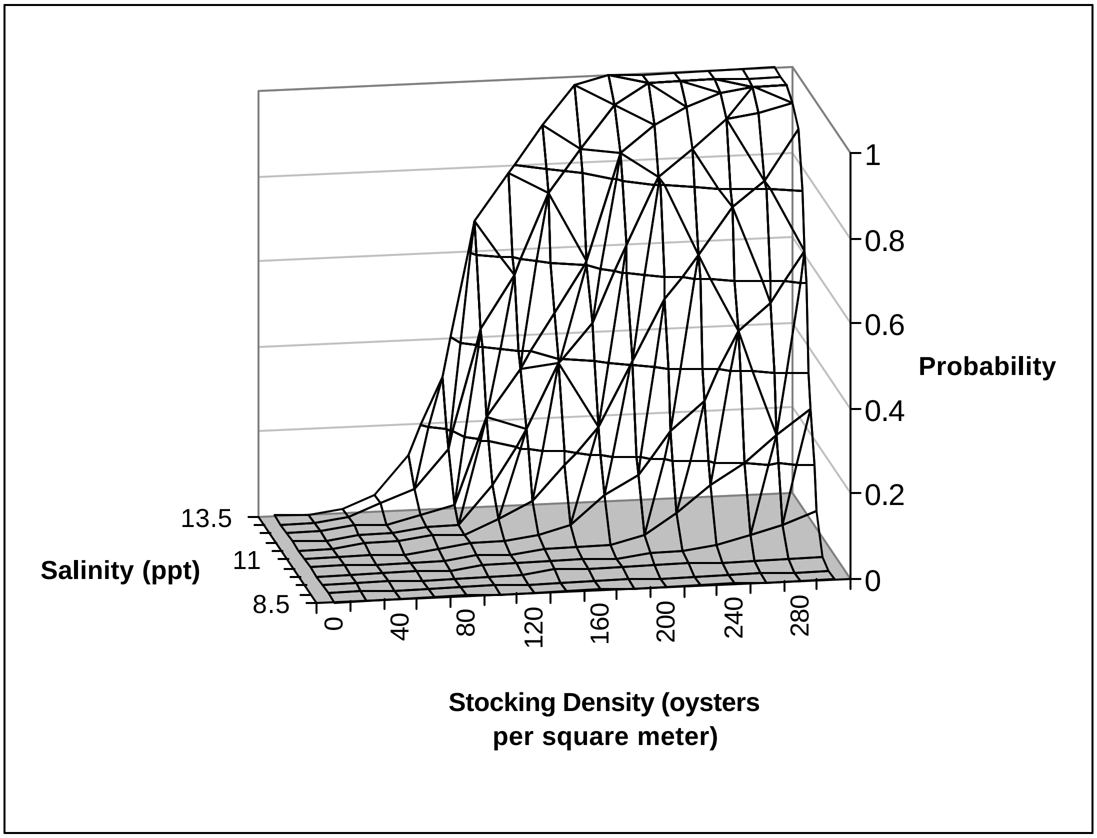
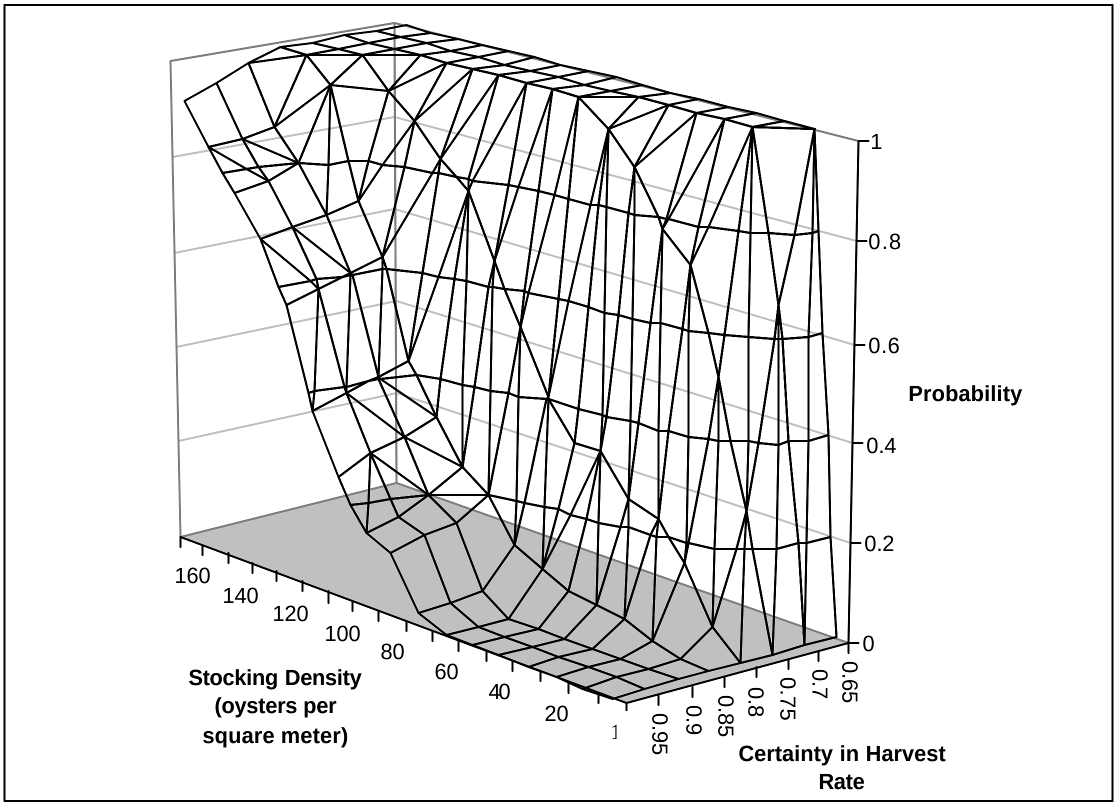

1
0.8
0.6
0.4
0.2
0
Probability
13.5
11
8.5
Salinity (ppt)
0
40
80
120
160
200
240
280
Stocking Density (oysters per square meter)

Figure 3.7


1
0.8
0.6
0.4
0.2
0
Probability
160
140
120
100
80
60
40
20
Stocking Density (oysters per square meter)
1
0.95
0.9
0.85
0.8
0.75
0.7
0.65
Certainty in Harvest Rate

CHAPTER FOUR – GENERAL DISCUSSION OF FINDINGS AND MANAGEMENT IMPLICATIONS

The eastern oyster (*Crassostrea virginica*) population in the Chesapeake Bay has declined to 1-2% of its historic abundance (Newell 1985). Due to this decline, managers are considering management strategies for stabilizing the eastern oyster population and increasing oyster harvest in the Chesapeake Bay. These management strategies include management of eastern oyster itself (i.e., harvest regulations, selective breeding, supplementation through stocking, and culture at different salinities) and supplementing the eastern oyster fishery with commercial production of a non-native oyster species, such as triploid Suminoe oysters (*Crassostrea ariakensis*).

Simulation models were developed and used to examine many of these management strategies using simulations. By using simulation models to examine population responses to management actions, managers may consider predictions regarding which management strategies would prove most efficient for increasing the eastern oyster population. Managers also may use the model to examine the population dynamics of triploid Suminoe oysters, considering the possibility of non-detection and reversion to diploidy and the effects of various management strategies (i.e., differing stocking densities, minimum shell lengths-at-harvest, harvest rates, certainty of harvest at the desired harvest rate, and culture at different salinities) on the likelihood that the non-native species would establish a self-sustaining population in the Chesapeake Bay.

Eastern Oyster Model Conclusions

Results of a series of simulations systematically varying inputs showed that disease-mediated mortality had a greater influence on eastern oyster population dynamics than harvest mortality. Hence, most harvest regulation management strategies would have little impact on decreasing the probability of localized population extirpations. Even when harvest rate was set at zero and minimum shell length-at-harvest was set at 100 mm, because of the effects of MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*), eastern oyster populations at high salinity sites still had a relatively high extirpation probability over the next 100 years. However, model results indicated that high density oyster culture in low salinity sites, along with stocking of oyster seed would stabilize the population and even begin to increase population size. Even though oysters have lower fecundity in low salinity areas (Mann and Evans 1998), high density oyster population have increased fertilization efficiency, which counters the reduced fecundity. Stocking oyster seed into low density populations at low salinity areas will increase population density so that the population will increase fertilization efficiency. This model will help managers identify which populations would most benefit from stocking acting as additional recruitment. Unless and until breeders are able to produce a sufficiently disease-resistant strain of eastern oysters suitable for stocking in high salinity areas, it seems that culture in low salinities may be the best way to maintain a viable population.

Experiments are still ongoing to develop a disease-resistant strain of eastern oysters. Thus far, some progress has been made through selective breeding (Burreson 1991). The simulation model can be used to predict the degree of improvement needed to provide biologically significant results. Results indicated that mortality rates from disease need to be reduced by 20% in high density populations and by 80% in low density populations at high salinity sites in order to maintain viable populations. Mortality only needs to be reduced by 20% in high density populations because increased fertilization efficiency at high densities and high fecundity at high salinities (Mann and Evans 1998) can counter the increased mortality from disease.

Non-Native Introductions for Commercial Production

Three stakeholder groups - watermen, scientists, and policy makers - have put great pressure on the Virginia Marine Resource Commission (VMRC) to allow research on the potential for Suminoe oyster production in the Chesapeake Bay (Hallerman et al. 2001). Industry stakeholders are urging VMRC to rapidly move forward allowing the Virginia Institute of Marine Science to provide triploid Suminoe oysters to them for commercial production. The Virginia oyster industry would like to produce 270 million triploid Suminoe oysters to send to regional markets in less than five years. Triploid Suminoe oyster production would compensate for some loss of eastern oyster harvests; however, the industry is pushing for commercial production of diploid Suminoe oysters because it is less costly, and because of hopes for a return to harvest of a self-sustaining wild oyster population (Hallerman et al. 2001).

Scientist stakeholders are more concerned with risks associated with an introduction of Suminoe oysters. While many scientists acknowledged that a complete consensus on risk may never be achieved, they agreed that a more complete understanding of the biology and ecology of the Suminoe oyster could lead to quantification of some risks (Hallerman et al. 2001). Some hazards addressed by scientists included: (1) illegal introductions of diploid Suminoe oysters, (2) a catastrophe destroying bio-confinement measures controlling spread of triploid Suminoe oysters, (3) introduction of diseases, (4) competition with the native eastern oyster, (5) Suminoe oysters converting the Chesapeake Bay to a benthic-dominated ecosystem, and (6) Suminoe oyster becoming a nuisance species, such as zebra mussel (*Dreissena polymorpha*) (Hallerman et al. 2001).

Policymaker stakeholders also are concerned with risks associated with the introduction of the Suminoe oysters; however, policy makers want the introduction of Suminoe oysters to be considered not only in terms of ecological effects, but also in terms of possible social effects. Policymakers want to achieve understanding of the basic biology of the Suminoe oyster and possible ecological consequences from the introduction examined prior to the introduction (Hallerman et al. 2001). Policymakers also want a better idea of the user conflicts that might ensue if the Suminoe oyster is introduced (e.g., effects of Suminoe oyster commercial production on blue crab and finfish fisheries, boating in the Chesapeake Bay, and effects of Suminoe oyster population accidentally becoming established on the Gulf coast) (Hallerman et al. 2001).

The controversy of whether or not to introduce Suminoe oysters for commercial production in much broader than the scope of this research. My research advances understanding of triploid Suminoe oyster population dynamics under different management strategies, and determines where more research is needed. A broader scope of research is needed to address all other concerns about Suminoe oyster introduction.

Triploid Suminoe Oyster Model Conclusions

A key hazard posed by culture of triploid Suminoe oysters is that individual oysters could revert to mosaics, successfully reproduce, and establish a self-sustaining population. Examining risk of reversion of triploid Suminoe oysters and the associated probability of a Suminoe oyster population becoming self-sustained under various management strategies using a simulation model enables managers to anticipate the population dynamics of triploid Suminoe oysters. Results from model simulations indicated the utility of adopting multiple management strategies to decrease the probability of a population becoming self-sustaining. These management strategies include: (1) growing oysters in confinements so that oysters are not accidentally left in the environment to revert to diploid, (2) practicing oyster culture in areas of low salinity to reduce fecundity of reverted triploids, (3) use of low stocking densities to decrease fertilization efficiency, and (4) adopting a small minimum shell length-at-harvest regulation so that oysters will have less time in the water, thereby decreasing the possibility of reversion. Following these management strategies, I find it possible to obtain a near-zero percent probability of a Suminoe oyster population becoming self-sustaining, thus making deployment of triploid Suminoe oysters defensible.

Because little was and is known about Suminoe oyster population dynamics, modeling allows managers to predict Suminoe oyster population dynamics without introducing the species and then examining population dynamics empirically. However, the model embodied assumptions due to the lack of biological information on Suminoe oysters, which will impact the accuracy of model predictions.

Assumptions embodied in the model suggest where scientists and managers should focus future research about the Suminoe oyster. The entire reproductive aspect of the model was approached using eastern oyster parameters because little is known about Suminoe oyster reproduction. Future Suminoe oyster research should quantify the length-fecundity relationship, salinity-fecundity relationship, oyster density–fertilization efficiency relationship, and mortality rates of larvae and spat. After experiments quantify these relationships, the model should be reparameterized, thereby increasing the performance of the model.

Another assumption in the model was that revertant triploid oysters would produce viable gametes at the same level as diploid Suminoe oysters. It is likely that fecundity would be decreased in reverted triploid oysters; although, it has not been shown. If fecundity is decreased in revertant triploids, then the model currently over-estimates fecundity, biasing the estimated probability of a Suminoe oyster population becoming self-sustaining upwards. Actual fecundity of reverted triploids should be determined so that the model may be reparameterized to include this relationship.

While future versions of the model should include additional information on Suminoe oysters, the model also could be altered to include a monthly time step, a spatial aspect, and consideration of economics of triploid Suminoe oyster production. A monthly time step may allow managers to decide whether deploying oysters at different times of the year would decrease the probability of a triploid Suminoe oyster population becoming self-sustaining. For example, if managers stocked triploid Suminoe oysters as juveniles just before spawning season and harvested oysters a year later as adults prior to the spawning season, the probability of reproduction would decrease, thus preventing the establishment of a self-sustained population. In contrast, if juvenile oysters were stocked after the spawning season and harvested as adults after the spawning season, any adult triploid oysters had that reverted could reproduce during spawning season and cause the population to become self-sustaining.

Including a spatial aspect into the model could allow managers to examine the probability of a triploid Suminoe oyster population becoming self-sustaining while considering proximity to the nearest triploid Suminoe oyster production area. If triploid Suminoe oyster production areas are proximate, this could increase fertilization efficiency of gametes, and the numbers of spat settling in nearby areas, thereby increasing the likelihood that a self-sustaining population would become established perhaps in an area far enough from production areas to escape detection.

Adding economics into the model would allow exploration of profit/loss of commercial production of triploid Suminoe oysters. Watermen will want to examine the cost included with commercial production of triploid Suminoe oysters, as well as how decreasing/increasing the level of commercial production will affect profit/loss.

Diploid Suminoe Oyster Introductions

Many enterprises are interested in commercial production of triploid Suminoe oysters, yet only want to use triploids for a short period of time. Most oyster culturists want diploid Suminoe oysters to be bottom-seeded and left to establish self-sustaining populations because it is less costly and could rebuild a more traditional oyster harvest industry. While the model in this study deals only with triploid Suminoe oysters, a similar model could be developed to examine the population dynamics of diploids, hopefully also considering ecological interactions of the Suminoe oyster and other species residing in the Chesapeake Bay.

The most important ecosystem interaction that needs to be addressed may be competition between Suminoe and eastern oysters. A small laboratory experiment of competition between Suminoe and eastern oyster spat is being performed at the Virginia Institute of Marine Science (M. Luckenbach, pers. comm.). Interspecific competition will affect survival and growth of oyster spat, which can affect population size. Information from the results of competition experiments could be used in developing a competition model for Suminoe and eastern oysters.

Although these experiments are small-scale, modeling competition will allow mangers to examine survival and growth effects on population dynamics of the two species when population sizes are larger and over a longer time frame. For example, if experiments find that juvenile Suminoe oyster survival is decreased by 20% when there is a ratio of five Suminoe oysters to 45 eastern oysters, we could include an additional variable in the model that will decrease survival of juvenile Suminoe oyster by 20% and determine if the total population size decreases significantly over the next 20 years from the additional mortality. The additional variable of juvenile mortality could be included in the eastern oyster model as well. We also could combine the Suminoe and eastern models to determine population size over time for each species simultaneously, and then determine the ratio of Suminoe to eastern oysters at each time step. After determining the ratio, we could decrease or increase juvenile survival each time step based on results found from the laboratory experiments. Including additional juvenile survival rates from competition at each time step may provide a more realist interpretation of competition affecting population size in the Chesapeake Bay.

Recommendations

The simulation model results of this study can be used to support several recommendations for oyster management in the Chesapeake Bay. I would advise oyster managers to focus efforts on eastern oyster culture in low salinity areas of the Chesapeake Bay where disease-mediated mortality is relatively low, and to stock oyster seed in these areas so that increased fertilization efficiency will counter the decreased fecundity effect of low salinity. Low salinity oysters culture and stocking will help ensure viable eastern oysters populations. Should the decision be made to introduce triploid Suminoe oysters, I would advise oyster managers to follow four management guidelines to achieve a near-zero probability of a triploid Suminoe oyster population becoming self-sustaining. The four management guidelines are growing oysters in confinements, growing oysters in low salinity areas, keeping stocking density low, and adapting small minimum shell length-at-harvest, thereby reducing the amount of time oysters are in the water.

For those managers and scientists examining the possibility of introducing diploid Suminoe oysters, I would advise them to not to do so until more is known about Suminoe oyster. Future research experiments should examine Suminoe oyster reproduction, competition between eastern and Suminoe oysters, and disease and parasite transmission. Also, future research should examine reproduction in revertant triploids, as well as continuing research on quantifying reversion rate. Continuation of experiments on growth and survival of Suminoe oysters at different salinities will provide more information on basic biology of Suminoe oysters.

Conclusion

This study was the first attempt to model the impacts of introducing a non-native triploid oyster species into the Chesapeake Bay. It also was one of the few attempts to examine localized extirpations of eastern oyster populations using a demographic approach. The model can be used to explore the effects of management strategies on oyster population size, thereby suggesting guidelines for better management of both eastern and Suminoe oysters. It has not been designed solely to study current options, but instead to assess future management options. The model is an abstraction of reality, and because of the multiple assumptions made, all results should be noted as preliminary. As with any model, this model can be updated as more information becomes available or altered to include other aspects that managers and scientists wish to explore.

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VITA

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