A Risk-Based Approach to Managing
the Intentional Introduction of Nonnative Species

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Final Report for USDA PREISM Grant #43-3AEM4-80101.

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1 This research is funded by the USDA Program for Research on the Economics of Invasive Species Management (PREISM).
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Abstract

This Report describes a risk-based approach for analyzing the potential for an intentionally introduced nonnative species to become invasive. We apply the framework to the case of introducing nonnative oysters on the US east coast. This is an urgent issue that has been a topic of heated public debate (e.g., National Research Council, 2004), and also is representative of the issues faced for the introduction of other nonnative species, including both terrestrial and aquatic introductions.

Two different institutional structures are considered. First, we consider the public management context, where a government agency makes all decisions regarding introduction and management of the introduced species, and private parties have shared access to the resource. This context is representative of management on public grazing lands or an open access fishery. Second, we consider a private management case, where a private firm makes all decisions regarding introduction and management of the introduced species, subject to a set of incentives and constraints developed by the government agency. This institutional structure is representative of introduction of a nonnative species on private property or leased submerged lands.

The public management problem is analyzed using a spatially explicit, dynamic multi-agent computer model that simulates the growth, spread and harvest of oysters over time. We find that technology-based controls in the form of introducing non-reproductive triploid oysters is an effective means of controlling the risk of invasion. In contrast, our results suggest it is much less effective to use best management practice of introducing reproductively-capable oysters in relatively isolated areas, with low connectivity to the rest of the estuary.

The private management problem is analyzed using a principal-agent model, whereby a regulating government agency acts as principal on behalf of the public, and firms proposing to introduce nonnative species act as agents. The framework determines tradeoffs between the potential social benefit of an intentional introduction versus the likelihood that the species becomes invasive and the potential harm that might result. The model is used to assess how various policy portfolios designed by the principal can provide incentives and constraints that solve problems associated with adverse selection and moral hazard on the part of agents who propose to introduce the nonnative species. Our research suggests that the private management framework may be subject to an adverse selection problem, whereby agents are more likely to participate if they are overly optimistic regarding the challenge of controlling risks of invasion.

The extant literature has found that the invasive species problem is a “weakest link” problem, whereby attempts to control invasions are only as effective as the weakest link in a chain of actions. Our results suggest that ex ante incentives to avoid invasion can result in a selection for “weak links”.

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I. Introduction

Many intentionally introduced species have become invasive, and invasive species are a rapidly growing economic and environmental problem. However, great social benefits are also provided by some nonnative species. For example, substantial benefits are associated with introduced agricultural crops, livestock species, ornamental plants and pets. Thus, wholesale prohibition on introduction of all nonnative species is not a desirable approach to controlling risks of invasive species.

Furthermore, policies based on total prohibition of nonnative species are likely to be unsuccessful, and may even increase risks of invasion. Overly conservative policies regarding intentional introductions might encourage some to illegally introduce the species, effectively circumventing measures designed to control risks of invasion.

This research develops a risk-based approach that focuses on the effectiveness of policies to control the likelihood that the species becomes invasive and the potential harm that might result. We consider a broad set of policy options, including technological controls, best management practices and incentive-based controls.

The model is applied to two fundamentally different institutional structures. First, we consider a case where a government agency makes all decisions regarding introduction and management of the introduced species, and private parties share harvest of the resource. This institutional structure is termed the public management approach, and is representative of situations where firms have shared access to the resource, such as is the case with public grazing lands or an open access fishery. Second, we consider a case where a private firm makes all decisions regarding introduction and management of the introduced species, subject to a set of incentives and constraints defined by regulations developed by the government agency. This institutional structure is termed the private management approach, and is representative of introduction of a nonnative species on private property or on leased submerged lands.

For clarity of exposition, we assume the non-native species is a commercial species that is introduced to be harvested by firms for profit. But the model also represent other introductions such as ornamental plants for landscaping, pets or etc.

The two different institutional structures require distinctly different modeling approaches. The Public Management scenario is modeled using a dynamic and spatially explicit multi-agent model that simulates the growth, spread and harvest of the introduced species over time. The Private Management scenario is modeled using a Principal-Agent model, whereby a government agency, acting on behalf of the public, is the principal, and a firm proposing to introduce a non-native species is the agent. The Principal-Agent model is used to
identify potential benefits and challenges associated with moral hazard and adverse selection.

The framework considers the control of risk through phased introduction with a set of intervention points, at which the species introduction is likely to be reversible at feasible cost, if desired. Multiple tiers of risk are considered, including (1) the likelihood that a purposefully introduced species becomes invasive, (2) risks associated with invasive “hitchhiker” species, (3) the likelihood of “rogue” introduction of species in violation of government policy and (4) financial risks associated with profitability of operations based on purposeful introduction.

As indicated above, a spatially explicit, dynamic simulation model is used to analyze the Public Management scenario. The model simulates production and investment activities for the nonnative species and interactions between species. The dynamic nature of the model is particularly important to account for phased introduction of nonnative species and potential irreversibility of the decision. The control policies are classified into three general categories: (1) input controls, such as best management practices, (2) output performance standards, like a maximum escapement rate for introduced species, and (3) incentive systems, such as property rights and liability regimes. We provide a more detailed description of the case study below.

We apply the two frameworks to the case of nonnative oysters on the US east coast, focusing on Chesapeake Bay as a case study. The case study represents an urgent issue that has been a topic of heated public debate, and has recently been the subject of study by a National Research Council committee (National Research Council, 2004).

The private management scenario is used to assess how various policy portfolios designed by the principal can provide incentives and constraints that solve problems associated with adverse selection and moral hazard on the part of agents who propose to introduce the nonnative species.

I.A. Intentional Introduction of Nonnative Species

Invasive species are a rapidly growing economic and environmental problem in the United States (e.g., USDA, 1999). The term “invasive” is applied to nonnative species that cause or are likely to cause economic losses, harm to the environment and/or adverse impacts on human health which are disproportionate to any associated social benefit (e.g., National Invasive Species Council, 2002). Invasive species can damage environmentally and/or economically important native species, adversely affect human health, cause population declines and/or species extinctions, change predator-prey dynamics, shift species niches, change habitat, reduce biodiversity and spread nonnative diseases or parasites, to which native species may have little or no resistance.

Several thousand species have been introduced in the past 200 years, and about one in seven of these introduced species have been identified as “invasive” (USDA, 1999). According to the Conservation Foundation, invasive plants currently cover 100 million acres, and are spreading at a rate of 14% per year. It has been estimated that invasive species cost the United States more than $138 billion in damages each year (Pimentel, 1999), and the problem appears to be rapidly accelerating (e.g., Perrings et al, 2002) largely due to the increasing global transportation of people and products (National Research Council, 2002). In addition, global warming has recently been
identified as a factor that facilitates non-indigenous species invasions (Stachowitz et al., 2002).

Invasive species may arrive through human or natural pathways, or a combination of the two. However, naturally occurring movement of species into the United States is relatively uncommon, and tends to occur slowly over long time periods. Rather, the majority of invasive species arrive through human activities, either intentionally or unintentionally (National Research Council, 2002). Since human actions are largely responsible for introduction, effective management requires a thorough understanding of incentives and human behavior (e.g., National Invasive Species Council, 2002).

An important pathway of introduction that must be considered by management is the “rogue” introduction of species, which might occur when individuals purposefully introduce species in violation of government policies. Rogue introductions are likely to result when agents feel that government policy is unreasonably restrictive. This pathway of introduction might reflect differing incentives that arise because some agents obtain financial benefit from introduction but pass the risk on to the larger society. Or it might reflect different expectations regarding the risks involved with the introduced species. This implies that a social decision to exclude a non-native species may be thwarted by any of a large number of agents, resulting in the so-called “weakest-link” problem (Sandler, 1997; Perrings et al, 2002).

Thus, social and economic factors are primary concerns when designing policies to control species invasions. As a consequence, control of invasive species requires an understanding of the key drivers of human behavior and carefully designed policies that account for associated incentives (National Invasive Species Council, 2001). This is particularly true for intentionally introduced species, as is the case with commercial operations or personal use (e.g., pets or houseplants), and for invasive species that are an unanticipated consequence of purposeful introductions, such as pathogens or other pests that might be harbored by purposefully introduced species. For example, potentially invasive pests like insects, pathogens, slugs, snails or weeds may be concealed within imported agricultural products, aquaculture stocks, seeds, nursery crops, flowers or timber.

There are many examples of intentional introductions that have led to problems of invasive species. Purple loosestrife (Lythrum salicaria L.) was introduced as an ornamental plant, and has subsequently invaded wetlands in nearly all contiguous US states. Loosestrife has replaced diverse native vegetation with dense monocultures, and has impacted the wildlife that depends on native wetland habitat. Mongooses were released on Caribbean Island and Hawaii in an attempt to control snakes and rats. However, snakes were only partially controlled by the mongoose, and after depleting the more easily available rats in sugar cane fields, the mongooses began to prey on native mammals and ground nesting birds. Within 20 years of its introduction into the Caribbean, the mongoose was considered the worst of all of the pests. Eucalyptus trees were planted in California and Hawaii to serve as wind breaks, but eucalyptus trees create virtual monocultures and can rapidly take over surrounding compatible areas, completely changing the ecosystem. In addition, the eucalyptus trees present extreme fire hazards. While eucalyptus trees grow rapidly, they cannot tolerate cold temperatures, and are highly susceptible to rare freezing temperatures in California. Widespread deaths of eucalyptus
trees present extreme fire hazards during dry periods.

Notwithstanding all the problems associated with invasive species, great social benefits are also provided by some nonnative species. Many nonnative species are non-invasive and support highly valued commercial activities and improve our quality of life. For example, substantial social benefits are associated with many introduced agricultural crops, livestock species, ornamental plants and household pets. Thus, it is not desirable to base invasive species control policies on a wholesale prohibition on the introduction of all nonnative species. This is recognized in extant policy guidance such as Executive Order 13112 and the associated National Invasive Species Management Plan (National Invasive Species Council, 2001), which forbid actions to introduce or enhance nonnative species unless “… the benefits of such actions clearly outweigh the potential harm caused by invasive species; and that all feasible and prudent measures to minimize risk of harm will be taken in conjunction with the actions.”

Furthermore, policies based on total prohibition of introducing nonnative species are likely to be unsuccessful in eliminating risks, and may even increase risks associated with introduced species. Overly conservative policies regarding introduction of potentially profitable commercial species might encourage some to illegally introduce the species with the intention of subsequently harvesting it. This pathway of introduction may increase risks of invasive species, since it circumvents existing measures to control spread of both the intentionally introduced species and the unintentional introduction of “hitchhiking” species that might be harbored.

II. Chesapeake Bay Oysters

Chesapeake Bay is the largest estuary in the US, and its watershed includes parts of six states: Virginia, Maryland, Delaware, West Virginia, Pennsylvania and New York (See Figure 1). Oysters were once an important species on the east coast, especially in the Chesapeake Bay region. However, the species has been subject to a dramatic decline in recent years. As shown in Figure 2, annual harvest of oysters in Chesapeake Bay were once in excess of 100 million pounds, but have dwindled to near zero in the past several years. A variety of factors have contributed to the decline, including fishing pressure and habitat degradation resulting from agricultural, industrial and residential pollution, deforestation and oyster reef destruction. However, in recent decades, the parasitic diseases MSX and Dermo have been identified as the core reasons for further decline.

MSX was first identified in the Chesapeake Bay in 1959. It is caused by the invasive protozoan parasite, *Haplosporidium nelsoni*, which was introduced to the East Coast from Asia (Burreson, Stokes and Friedman. 2000). To date, attempts to restore the oyster populations based on fisheries management efforts, use of disease-resistant strains and various oyster reef restoration programs have not been successful. The loss of the oysters has been devastating to the oyster industry and its dependent communities. Those that remain in the Chesapeake oyster-processing sector rely on oysters that are brought in from the Gulf region and other areas for their economic survival (Anderson and Whitlatch. 2004).

There is considerable controversy surrounding recent proposals to introduce the nonnative Asian oyster (*C. ariakensis*) into the east coast, in particular into the
Figure 1. Chesapeake Bay Watershed
Figure 2. Time Series of Oyster Landings in Chesapeake Bay
Chesapeake Bay region. Although the population of native oysters is currently at very low levels, there are ongoing attempts to restore native oyster populations and to develop disease resistant native strains. The introduction of nonnative oysters could be a stop-gap measure, to be used until efforts to restore native oysters prove successful. But the introduction represents a risk of undermining the recovery of native oysters or of displacing other species of shellfish. Furthermore there is a risk that the introduction of the oyster into the environment may result in the unintentional introduction of potentially invasive organisms, such as other molluscan species, worms, protozoa and seaweeds that are associated with the nonnative oysters. Of particular concern are those that may cause disease in the native oyster or other species. Indeed, it is believed that the diseases that have so devastated native oysters in the Chesapeake were introduced with nonnative oysters.

One approach that has been suggested for introduction of nonnative oysters is to release hatchery raised triploid oysters into the environment to be “grown out” on designated open-water aquaculture sites. The introduction of the hatchery farmed, triploid nonnative Suminoe oyster (*C. ariakensis*) from Asia may be a solution to this difficult problem, but it is not without risk. Triploid oysters are strains that are unable to reproduce, although there is a probability that some triploid oysters will revert to diploids (referred to as mosaics), which are capable of reproducing. Additionally, in the process of releasing triploid oysters, some number of diploids will also accidentally be introduced. Hence, introducing triploid oysters reduces the probability that the species will become invasive, but does not completely eliminate the risk.

While many questions are evident, the National Research Council, Committee on Nonnative oysters in the Chesapeake Bay concluded that there are several essential research needs which should be addressed immediately. The three identified below are the most pertinent to our proposed research: 1) Development of Standards for Regulating Nonnative Oyster Aquaculture. (National Research Council, 2004. p241) 2) Cost Minimization Model incorporating risk (National Research Council, 2004. p247) and 3) Evaluation of Alternative Institutional Structures. (National Research Council, 2004. p245).

To address these issues, we develop a simulation model to assess potential management regimes designed to mitigate the risks associated with the introduced species. The simulation model will be specific to the introduction of the farmed Suminoe oyster, *C. ariakensis*, but with appropriate data the methodology can readily be generalized to the introduction of other nonnative species within different contexts, including for terrestrial species. Indeed, controlling potential invasion by oysters has similarities with controlling invasive plants, as the adults are immobile, and transport occurs during reproduction.

There are three general scenarios considered by our model for the controlled introduction of the Suminoe oysters: seeding of hatchery-produced potentially reproductive diploid oysters on designated lease sites, seeding hatchery-produced non-reproductive triploid oysters on designated lease sites, and introduction of hatchery-produced triploid oysters in enclosed aquaculture systems. These three scenarios represent progressively reduced risk of spread of nonnative oysters at increased cost.

In addition, specific policy actions can be imposed on the introducing firms by the
government agency, which fall into three general categories: (1) input controls (2) performance standards and (3) incentive-based systems, such as property rights (Sylvia and Anderson, 2004) These categories of policies are discussed below, in sequence.

(1) Input controls

Input Controls place limits on production technologies employed by producing firms. Examples of input control are the ‘Best Available Technology’ or ‘Best Practices’. These approaches regulate such things as location, equipment design, laboratory methods, farming technology, harvest systems, etc.

Location controls limit where the non-native species can be introduced. Spread on non-natives might be reduced by allowing introductions only in areas that are not well connected to other favorable habitat. In the case of oysters, introducing non-native oysters in locations with low currents and those surrounded by poor habitat could help reduce the likelihood that nonnative oysters will spread.

Equipment design includes enclosures that facilitate harvest of a large fraction of planted oysters prior to spawning age, reducing the likelihood that nonnative oysters have an opportunity to reproduce.

Improved laboratory methods include quarantine with careful monitoring of oysters prior to planting, reducing the likelihood that planted oysters harbor unintended “hitchhiking” species, and possibly reducing the planting of reproductively capable diploids.

Similarly improved farming technologies and harvesting systems increase the fraction of planted oysters that are harvested, reducing escapement of nonnative oysters and thereby lowering the likelihood of invasion. Input controls have the advantage of being understandable and measurable, but are generally costly and inefficient to implement.

(2) Performance standards

Performance Standards are a class of management instruments that is output-based, in contrast the input-based approach above. Examples of performance standards include setting a maximum number of introduced individuals unaccounted for at harvest, or the acceptable incidence of reproductive animals detected at a given stage of production. Advantages of performance standards include the flexibility allowed for production units to select efficient input bundles. Disadvantages can include difficulties in measuring compliance with the performance standard, and potential for high costs of correction when the standard is violated.

(3) Incentive systems

This category of control involves correction discrepancies between incentives for the principal and agent, and assigning to the agent the rights and responsibilities to manage the introduction of the nonnative species. The invasive species problem is a classic example of the externality, where the economic agent that causes an invasion does not bear the full social cost. When successful, incentive systems ensure that the full social costs are recognized by the party responsible for decisions with respect to introduced species. Incentive systems include liability for damages and remedial actions associated with invasive species, providing territorial use rights, etc. Incentive-based systems are flexible and tend to promote efficiency. But careful designs for incentive schemes are important,
and strong property rights systems are often resisted in aquatic environments.

These mentioned management systems are included in the simulation model, and the portfolio of management tools will be assessed using the following criteria:

- the risk that nonnative oyster becomes invasive,
- the risk of disease-causing pathogen associated with the nonnative oyster becomes invasive,
- the social benefits associated with production of the marketed output (producer and consumer surplus).

These criteria will be used to develop outcome frontiers, which can be used by decision makers to better understand the tradeoffs faced between risk of invasions and economic values associated with the industry. Sensitivity analysis will be conducted to identify critical thresholds relevant to the successful aquaculture of hatchery-produced Suminoe oysters.

III. Public Management Scenario

This section discusses the public management scenario, where a government agency directs the introduction and management of the non-native species. We simulate the behavior of oysters using a detailed model of survival, growth, reproduction and transport of oyster populations.

III.A. Model Dynamics

Oyster Population Dynamics

The model described in this section closely follows Dew et al (2003, 2005), including all life history parameters of oysters. The model is a standard age class model, with two significant departures. First, we include detailed modeling of larval transport, which is a particularly important element of this dynamic model. Like plants, adult oysters are largely stationary, and spread of the non-native species occurs almost exclusively during reproduction. Thus, it is essential that the model focuses on transport of seed. Secondly, we examine interactions between two species of oysters, native oysters (C. virginica) and the introduced oysters (C. ariakensis). In locations where the two stocks co-exist, they compete for food and habitat. In addition, there is an important element of stock interactions at the time of reproduction, as detailed below.

Once oysters set, they are secured to hard surface (including other oysters), so that transportation of adult oysters is minimal. Rather, transport of oysters occurs almost exclusively during reproduction and the larval life stages. Various means of controlling the spread of nonnative oyster involve management actions that effectively reduce the production of gametes, such as introducing non-reproductive triploid oysters, and actions that reduce the viability of larvae, thereby reducing the production of juvenile nonnative oysters. For example, planting of non-native oysters could be restricted to isolated habitat locations, from which larvae are unlikely to spread to the larger environment. Or, since larvae are far more sensitive to salinity levels than adults, the risk of uncontrolled spread of non-native oysters could be reduced by introducing non-native oysters in locations where salinity is unfavorable for survival of larvae. Furthermore, gamete production can be controlled by harvesting a large fraction of oysters prior to their reaching reproductive age.

In order to model policies that control potential spread of nonnative oysters, we
need to carry out detailed modeling of various stages of the process from spawning through survival of young-of-the-year. For these reasons, our model focuses more extensively on modeling the details of the early life stages of oysters than is typical for bioeconomic models. Our model includes separate equations for production of gametes (sperm and eggs), fertilization into zygotes, and setting of spat on hard substrate.

At present, we utilize identical life history parameters for the two species of oysters, with the important exception of susceptibility to disease. The primary rationale for introducing C. ariakensis is its resistance to disease. Therefore, we adopt available estimates for susceptibility of the native species, C. virginica, but assume that the introduced species is not affected by disease.

First we model fecundity or the production of gametes. The number of gametes produced depends upon the number of oysters and the size of oysters, where gamete production increases at an increasing rate with size. Also, in the case of introducing non-reproductive triploid oysters, the reproductive potential is determined by the fraction of introduced oysters that revert from triploid to diploid and the fraction of diploids accidentally introduced. The equation for fecundity is:

\[
F_{tj} = 39.06 \left[0.00423L_{tj}^{1.17475}\right]^{2.36} N_{tj}(R_{tj} + T_{tj})
\]

where \(F_{tj}\) is total potential fecundity at time \(t\) for age class \(j\), \(L_{tj}\) is the length at time \(t\) for age class \(j\), \(N_{tj}\) is the number of adults at time \(t\) for age class \(j\), \(R_{tj}\) is the percentage rate of revision from triploid to diploid, and \(T_{tj}\) is the percentage of diploids accidentally released into the environment. Note that when nonnative oysters are stocked as reproductive diploids, \(R_{tj}=0\) and \(T_{tj}=1\).

Salinity is used to relate potential fecundity to actual fecundity. Although adult oysters are relatively unaffected by salinity, reproductive effects can be important. This suggests a spatially explicit policy to reduce risk of invasion by planting nonnative oysters in areas where reproduction is limited by salinity, or in areas where nonnative oysters are confined by salinity. For example, the risk of spread of the nonnative species can be controlled by limiting planting to inlets that are isolated from the rest of Chesapeake Bay by an area with salinity that is unfavorable to survival of larvae, thereby reducing the likelihood of geographic dispersal of nonnative oysters.

The fecundity adjustment factor accounting for salinity, \(F_s\), is zero for salinity less than 8 ppt, reaches a maximum at salinity of 13.5 ppt, then declines back to zero when salinity reaches 35 ppt. We specify the relationship between fecundity and salinity as a piecewise linear function of the level of salinity.

\[
F_s = \begin{cases} 
0 & \text{for } s < 8 \\
\frac{(s - 8)}{5.5} & \text{for } 8 \leq s < 13.5 \\
\frac{(35 - s)}{21.5} & \text{for } 13.5 \leq s < 35 \\
0 & \text{for } s \geq 35
\end{cases}
\]

where \(F_s\) is the salinity factor that relates potential to actual fecundity, and \(s\) is salinity measured in parts per thousand.

We introduce a disease factor to account for the effect that various diseases can have on reproductive success. The disease factor goes from 0 to 1, where zero indicates no
reproductive success, and 1 indicates no disease-related mortality. Although nonnative oysters have proven to be resistant to diseases that are prevalent on the east coast, they may be affected by other diseases. Also, the disease factor will be important when the model is used to analyze decision with within a multi-species framework, with both native and nonnative oysters.

Oysters tend to congregate in highly concentrated communities, called oyster bars. Indeed, prior to the 1800’s, oyster bars were significant hazards to shipping in Chesapeake Bay when oyster populations were at historic high levels. Oysters benefit from high concentrations in at least two ways. First, oysters require hard surface to attach to, including other oysters. Therefore, oysters provide their own habitat. Also since oysters are broadcast spawners, fertilization success increases with concentration of oysters. We specify an equation for fertilization success as:

\[ F_{ft,i} = 0.0049 * D_{t,i}^{0.72} \]

where

\[ D_{t,i} = \frac{N_{t,j} * (R_{t,j} + T_{t,j})}{A} \]

and \( F_{t,j} \) is fertilization efficiency, \( D_{t,i} \) is the density of reproductive oysters, and \( A \) is the area in square meters.

Total zygote production is the sum over all age classes of potential production, corrected for salinity (\( F_s \)), the sex ratio (\( F_d \)), the fraction not lost to disease (\( F_d \)) and the fertilization rate (\( F_{t,j} \))

\[ F_{tot,i} = \sum_j (F_{t,j} * F_s * F_{d} * F_{d} * F_{t,j}) \]

Spat are zygotes that have successfully metamorphosed, settled and attached to hard substrate. The total number of spat is sum of the number of reproduced from the population plus the number of stocked. The number of spat is determined by multiplying the number of zygotes by the probability of successful completion of metamorphosis (\( P_{met} \)), corrected for larval mortality through the time of settlement. The daily larval mortality rate is \( L_{mort} \), and it takes approximately 21 days to metamorphose. Finally, the number of one-year-old oysters is the number of spat times the total mortality rate for oysters less than one year old (\( m_0 \)). The equation relating the number of zygotes to the number of one-year-old oysters is:

\[ N_{t,1} = (K_t + F_{total,t} * P_{met} * (1 - L_{mort})^{21}) * (1 - m_0) \]

where \( N_{t,1} \) is the number of individuals at age class one at time \( t \), \( K_t \) is the number of stocked spat, \( P_{met} \) is the proportion of fertilized zygotes that successfully metamorphose, \( L_{mort} \) is the daily mortality rate for larvae, and \( m_0 \) is the mortality rate of spat prior to reaching age 1. When working in the multi-species framework, this will be extended to include a fraction of non-viable zygotes that result from hybridization between the native and nonnative species. More discussion of this issue is contained below.

Numbers of individuals at various age classes then progress through the equation:

\[ N_{t+1,j+1} = N_{t,j} * e^{-(H_i + M_{t,i})} \]

where \( H_i \) is the harvest rate for age class \( i \) and \( M_{t,i} \) is the natural mortality rate at time \( t \) for age class \( i \). Mortality rates vary by age, and also by time to account for changes in the prevalence of disease. The total number of individuals in the population is simply the sum over all age classes:
Another potentially important issue related to introduced species is the notion of a gamete sink (e.g., Meritt et al, 2005). Oysters of all species are broadcast spawners, and fertilization occurs when sperm and egg join in the environment. This raises the potentially important issue of the extent to which gametes of the two species interact. If the two species of oysters synchronize spawning, then a fraction of eggs from one species will join with a sperm from the other. This results in hybrids which in the case of oysters are not viable. This adversely affects reproduction of both species. However, the effect on the less numerous species may be far more devastating from a reproductive viewpoint.

For example, suppose that the gametes (eggs and sperm) of one species outnumber those of the other by a ratio of 3 to 1. In this case, ¼ of the gametes from the more numerous species will join with gametes from the less numerous species, and become hybrid. Since these hybrids are not viable, they die. However, ¾ of the gametes from the less numerous species will join with gametes from the more numerous species, producing hybrids which subsequently perish. This means that less numerous species in an even worse competitive position in each future generation, and their gametes will become outnumbered by an even larger ratio in the future. Hence, even in cases where the population of less numerous species is viable in the absence of the more numerous species, the potential for the gamete sink could make the species reproductively non-viable. This notion of the gamete sink is incorporated in calculating the viability of zygotes in the multi-species version of our simulation model, as discussed above.

The effect of the gamete sink could be advantageous or disadvantageous when considering potential risks of invasion by intentionally introduced species. If the gametes from the introduced species significantly outnumber those of the native species, the native species could be driven to extinction (assuming synchronized spawning), and attempts to restore the native species could be futile if a large population of reproductive nonnative species becomes established.

However, if the number of gametes from the introduced species is kept sufficiently below those of the native species, then the gamete sink effect could reduce the risk of invasion by the introduced species, and the number of gametes of the introduced species could be kept low by introducing non-reproductive triploids. Thus, even if the population of the introduced species is significantly larger than that of the native species, the number of gametes from the introduced species could be kept low by introducing non-reproductive triploids. The gamete sink effect could reduce the probability of successful reproductive by mosaics and accidentally introduced diploids.

However, it would be advised not to become too reliant upon the gamete sink notion to control the risks of invasion by the introduced oysters. If spawning is not well synchronized across the two species, then the gamete sink notion is not relevant. And even if the populations start out synchronized, one might expect selection pressures to disrupt the synchronization of spawning: oysters whose reproduction is not synchronized with the competing species might become relatively more successful, and the two populations might naturally move out of synchronization.
III.B. Spatial Distribution of Oysters

We developed a spatially explicit agent-based model that simulates the growth, transport and harvest of the native and nonnative oyster species in Chesapeake Bay. The general structure of the modeling system is presented in Figure 3. OpenMap™ (http://openmap.bbn.com/) is used to manage spatially explicit data, and passes the data onto the simulation model in array format. Simulations of the behavior of oyster populations and fishing effort are carried out within an agent-based model, which is implemented within the Recursive Porous Agent Simulation Toolkit (RePast) (http://repast.sourceforge.net/) modeling environment. Repast model results are passed back to OpenMap to create a visual representation of the dynamics of oyster population on electronic maps. The OpenMap depiction of Chesapeake Bay is presented in Figure 4. Detailed simulation results, such as the quantitative levels of oyster populations over time and space, harvest, etc. are stored for later analysis.

Each spatial grid in the simulation model is a hexagonal shape in order to assure a high degree of connectivity within the spatial model. Cell size is determined by the time step and the maximum distance that oyster larvae can be expected to travel while still surviving. For the simulations reported below, we adopt hexagonal cells that are 500m on each side.

Our simulations focused on the various tributaries in the Chesapeake Bay. Spatially explicit data (e.g., shorelines, bottom type, salinity, etc.) are managed by OpenMap, and passed in array format to the RePast simulation model. Non-spatial data, such as oyster life history parameters and economic data are imported directly into the RePast agent-based simulation model. Many of the simulation parameters can be modified using an interactive user interface, which allows easy analysis of various policy options. For example, the user can specify the size and location of the simulation area, the number, location and timing of oysters planted, the allowable catch, and time delay until the age of allowable harvest, etc.

The agent-based simulation model manages the oyster populations within each cell and the interactions among cells. The equations of the agent-based model representing oyster populations were presented in Section II.B. above. There is also an agent model representation of oyster harvesters that manages effort and catch by oyster fishermen. Currently, the oyster fishing model is particularly simple. There is a fixed allowable harvest of oysters, and harvest occurs in the cells with the highest concentrations of oysters. When a cell is targeted for harvest, the population in that cell is reduced by a fixed percentage.

Adult oysters are sedentary individuals that are physically attached to hard surfaces, including other oysters. So adult oysters do not move, but oyster larvae are transported by currents. Additionally, oyster larvae are not passive, but rather an understanding of larval behavior is necessary to best predict transport. Clearly, such an effort is beyond the scope of the present project. Rather, we use a simplified framework that we calibrate to a model funded by the Chesapeake Bay Project (North et al, 2007).

Our simplified framework models oyster transport during reproduction. Oysters produce larvae in such enormous numbers that it is essential to account for even the small fractions of larvae that is transported to other tributaries and survive. In particular, this allows larvae to colonize relatively remote and isolated habitat patches.
Figure 3. Depiction of the Modeling System Architecture.
Figure 4. OpenMap™ Depiction of Chesapeake Bay
We calibrate the larval transport for different locations within Chesapeake Bay using the detailed larval transport modeling results of the North et al (2007). North et al use a hydrodynamic model linked with behavior to simulate larval transport under weather scenarios representing water flow and winds for the years 1995-1999. They calculate a distribution on transport, and calculate mean distance traveled per year for various tributaries within the Chesapeake. The results are shown in Table 1 for Virginica and Ariakensis.

We assume that larval transport distance follows the half normal distribution, where the distribution is calibrated to the distances traveled from North et al (2007) for each tributary in the Virginia portion of the Chesapeake. All boundaries are treated as reflective, so that larvae “bounce” when meeting a boundary. Connectivity among tributaries is specified using the North et al results shown in Table 2.

We use the above methods to determine the number of larvae transported from each originating cell to each destination cell, and the survival during transport. We then simulate larvae survival from the time of arrival in the cell to the end of year 1. Survival in a particular cell is parameterized by a number of key structural variables: the cell’s environmental characteristics, such as presence of suitable habitat, salinity level and prevalence of disease. In our initial runs of the model, we limit habitat suitability to a 0/1 indicator, where there is 100% mortality of larvae that are transported to non-habitat areas, and mortality in suitable habitat is as defined in the Section II.B. for the various larval stages. More general measures of habitat quality between 0 and 1 could be used, as oyster reefs provide the most suitable habitat for oyster larvae, but rock, cobble and other hard substrate (e.g., docks or piers) also provide suitable habitat. And habitat can also be intentionally created by human actions, such as placing oyster shell on the bottom. Salinity level is also an important determinant of larval survival, and is incorporated using a piecewise linear function, as discussed above.

As discussed above, an interactive graphical user interface is used to allow changing parameter values for sensitivity analyses. With suitable modifications, the user can specify key environmental factors that are important determinants of oyster survival and transport. For example, extreme rainfall or drought events have important influences on currents and salinity, which will affect the extent to which planted oysters are transported throughout the region. Simulation results are displayed as raster images in the interface, and/or can be exported to generate shape files for user download and further analyze with GIS software.

### III.D. Policy Options and Results

We implement the simulation model discussed above. Further details of the model results are contained in Luo and Opaluch (2010). To recap, survival, growth and reproduction of oysters are modeled using the equations in Section III.B., and the spatial distribution of oysters is modeled as described in Section III.C. Catch of oysters is modeled in a very simplified manner. We assume that there is a constraint on allowable harvest of oyster, and we assume that costs are minimized by having harvest occur in the cells with the greatest concentration of oysters. We use a geospatial habitat layer, based on a 0/1 indicator of habitat and assume a constant favorable salinity level.

We consider one example policy within two of the general categories for policies. For Best Management Practices, we consider
Table 1. Larval Transport Simulations for Distance Traveled (km)

**Virginica**

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**Ariakensis**

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### Table 2. Connectivity Across Tributaries

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<th>Choptank</th>
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<th>Tangier</th>
<th>Rappahannock</th>
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<td>Virginia Mainstem</td>
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<td>Mobjck Bay</td>
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placing oysters in area of low connectivity to other areas within Chesapeake Bay. For technology based standards we consider introducing triploid non-native oysters. Triploids are not reproductively capable, but we include a probability of reproduction to account for reversion to diploid, or for human errors, whereby diploids could be mistakenly introduced. Incentive-based policies are not really appropriate within public management option, but rather are reserved for the private management scenario, discussed below.

An example run of the simulation model is presented visually in Figure 5. The blue areas in the figure represents non-habitat areas and the black areas indicate oyster habitat. Native oyster populations are indicated by green hexagonal cells, with darker green indicating higher concentrations. Non-native oysters are represented by the red cells, again with darker red indicating higher concentrations. Purple cells represent areas with both native and non-native populations. As indicated above, catch is restricted to the cells with the highest oyster densities. Catch reduces oyster densities in those cells, and changes the corresponding cell color to a lighter shade for the next time step.

This example models a case where non-native oysters are planted in the James River, which is a tributary that is relatively isolated in the “downstream” portion of Chesapeake Bay. As shown in Table 2, about 99.98% of larvae that originate in James river end up within James river. Roughly 0.02% of larve in James bay are transported to the Chesapeake mainstem, and 0.001% are transported to York river and Mobjck bay and York river. The initial simulations assume planting of reproductively capable diploid non-native oysters. The first policy considered is to employ Best Management Practices, which are assumed to be comprised of planting reproductively capable non-native oysters in relatively isolated locations within the Chesapeake watershed, combined with setting a minimum standard for oyster harvest each period in an attempt to capture as the majority of oysters before they reach reproductive age. Our simulation model finds that this approach is not sufficient to keep non-native oysters within the region they are planted, but rather non-native oysters eventually spread throughout the Chesapeake Bay.

The second policy considered is the technology based standard, where non-reproductive triploid oysters are planted within the watershed. Note that, as discussed above, although planted oysters are not reproductively capable, a fraction of oyster are reproductively capable, either because they revert to diploid status, or because due to processing errors, a limited number of diploids are mistakenly for triploids. This second policy is effective in keeping non-native oysters from spreading from the area of introduction.

IV. Private Management Scenario

Here we discuss the model of the Private Management scenario, as practiced for oyster aquaculture in Virginia. The State of Virginia leases oyster beds to private parties, who are responsible for carrying out all aquaculture operations, including planting, management and harvest. In contrast, in the public management system discussed above, the government agency carries out planting and management operations, and fishermen are licensed to harvest from publicly managed lands. An important element of our research is to do a comparative analysis
Figure 5. Illustrative Simulation Output Screenshot
of the strengths and weaknesses of these two distinct management strategies.

The Virginia system is based on a sole manager of the oyster bed who operates under constraints defined by an operating permit granted by the State government. Therefore, we use a principal-agent framework as the model for the Virginia context. The regulating government agency is viewed as the principal, acting on behalf of the public. The firm is modeled as the agent that makes planting, management and harvesting decisions subject to state regulations. The goal of the principal is to design a set of incentives and constraints that induce actions on the part of the agent that are consistent with the goals of the Principal. Two key challenges are identified in the Principal-Agent literature: moral hazard and adverse selection.

Moral hazard means that the agent has incentives that are not compatible with are goals of the principal. For example, in the insurance industry, if individuals could insure their cars for any amount of money, they would have the incentive to ensure their car for more than it is worth, then to purposefully crash their car to collect the insurance. These individuals have an incentive to act in a manner that is not consistent with the goals of the principal, which is to reduce accident rates.

Adverse selection means that undesirable agents have the incentive to participate in a contract, while desirable agents have the incentive to reject the contract. For example, suppose all insurance companies sold insurance at a low premium for young healthy people, and high premium for elderly people with poor health. Now suppose that one insurance company changed their policies so all individuals could purchase insurance at an average premium. An insurance company with such a policy would attached elderly people with poor health, but not young people in good health who could get lower rates from other companies. A company adopting such a policy would lose money since they are charging an average rate to customers who are selected to be high risk.

In the case of the Maryland system, the state has tighter controls over planting and managing oysters, but the fishery becomes, in effect, open (or limited) access. In the case of Virginia, the state sacrifices complete control over planting and management, but a single firm makes all production decisions, thus resolving the common pool problem. Furthermore, under the Virginia system, the operator can be held responsible for complying with a more complete set of regulations. For example, it is not as straightforward to set requirements for maximum escapement (or equivalently, minimum harvest) under the Maryland system, where many firms harvest form a single oyster bed.

For simplicity we assume that the regulations for controlling invasion of the nonnative species are related to escapement of adults of the introduced species. Escapement is defined as the number of adults that are not harvested prior to reaching reproductive age. Catch is the weight per individual harvested times the number harvested, and the number harvested equals the number of individuals planted minus escapement:

\[
H = \sum_{i=1}^{n} W(N(i) - E(i))
\]

where H is harvest, W is average weight of oysters, N(i) is the number planted by firm i and E(i) is escapement from firm i.

Initially we define invasion of the nonnative species as the creation of a reproductively
viable population. Since adult oysters are not mobile, invasion will not occur in the absence of reproduction. Note that this is a conservative definition of invasion, as the reproductively viable population might be confined only within the area licensed for aquaculture, while invasion implies that the population spreads around the bay in an uncontrolled fashion. However, if the population becomes reproductively viable, there is a threat of invasion, and the larger the size of the reproductively viable population, the greater the risk with all else held equal. We later confine the definition of invasion to be more restrictive, where viable adult populations are established outside the licensed area.

The probability of an invasion is a function of escapement of reproductively viable (diploid) oysters and other control actions:

\[ p(E(1),...,E(n)) = 1 - \prod_{i=1}^{n} (1 - p(E(i),A(i))) \]

where \( p(\cdot) \) is the overall probability of invasion and \( p(\cdot) \) is the probability of invasion by an individual operator, \( E(i) \) is escapement allowed by operator \( I \) and \( A(i) \) is the level of other control actions. Note that we allow for multiple invasions at different times and/or locations. Since oysters are broadcast spawners, we would expect that the probability of invasion increases at an increasing rate at low levels of escapement. We assume that the probability of invasion follows the usual logistic shape, where the probability of invasion increases at an increasing rate for small levels of escapement, and asymptotically approaches 1 for large levels of escapement.

Harvest, denoted by \( H \), is the sum of harvests over all agents, which is the weight per individual of the harvested species times the number of individuals harvested. Catch by each agent equals the total planting, \( N(i) \), minus the residual not harvested, or escapement, \( E(i) \).

The flow of social benefits of introducing the nonnative species is:

\[ B(H, I) = S(H) - C(A, H) - p(A) \cdot D(I) \]

where \( B(\cdot) \) is the net benefit of allowing introduction of the non-native species, \( H \) is harvest, \( D \) is the damage of invasion and \( C \) is the cost of operations, including control costs. Here we assume that each invasion is a discrete variable, 1 if an invasion occurs and zero otherwise, and the expected damage from invasion is the probability of invasion \( (P_{\text{inv}}) \) times the damage that results from each invasion, \( D \). Below we expand the conceptual framework to include a more detailed dynamic model of biomass of the invasive species, where invasion becomes a continuous and dynamic process.

Cost depends upon the size of the harvest, and the fraction of total planting that is harvested. For simplicity, we assume cost is a linear function of the number harvested (holding the fraction harvested fixed), where the average (=marginal) cost is a function of the fraction harvested. The cost per unit harvest cost increases at an increasing rate as the fraction harvested goes to one and escapement goes to zero. Thus,

\[ C = c(H/N,A)H = c(h,A)H \]

where \( h = H/N \) is the percentage of oysters harvested. We assume \( c_h, c_A > 0 \). The upper bound on the marginal cost is \( c(1) = c \), which may be finite or infinite. Below we assume \( c \) is finite. For example, in the case of oysters, it is possible to practice confined planting, where the oysters are contained in an enclosure. Hence, it is feasible to harvest all individuals planted, except for a low probability catastrophe (e.g., destruction from a hurricane).
The social objective is to maximize discounted expected net benefit:

\[
\max \sum_{t=1}^{T} B(H,A)(1 + r)^{-t} = \sum_{t=1}^{T} (pH - p(A)D - C(h,A)(1 + r)^{-t})
\]

The principal determines N, the size of planting by the agent and the levels of control actions, A. We assume that the principal observes invasion perfectly. More generally, the principal might observe a signal such as damages that are associated with invasion, or perhaps the principal can monitor for escapement. For example, in the case of nonnative oyster introduction, the principal may be able to monitor for larvae, or harvested oysters might be tested for reproductive diploids. If all nonnative oysters are captured prior to spawning, no larvae should be present. The larger the level of escapement, the larger the number of larvae that are likely to be found and the higher the likelihood of invasion.

As indicated above, harvest regulations will specify a maximum allowable level of escapement, and therefore a minimum level of harvest. This is in contrast to the common practice with fisheries models, where regulations target maximum allowable harvest. In the traditional fisheries model, leaving a larger population in the environment is beneficial, as it increases the reproductive potential. But in this case, having a larger reproductively capable stock in the environment has a negative social value, associated with the potential for social costs associated with invasion.

The principal can impose penalties and/or rewards when escapement varies from the target level, \( \bar{E} \), and for control actions, A. It is interesting to note that it may not as straightforward to set regulations that constrain maximum total escapement under the public management system, where many firms harvest from a single oyster bed. However, it may be possible to provide incentives for firms to increase catch beyond what might maximize profit.

IV.A. Principal Agent Model of the Private Management Scenario

As indicated above, the Private Management scenario is modeled using a Principal-Agent framework. The relationships among the key actors in this model are depicted in Figure 6. A regulating government agency acts as principal on behalf of the public, and firms proposing to introduce nonnative species act as agents.

As indicated in Figure 6, the firms introducing a nonnative species obtain inputs from the environment in order to produce consumer goods of benefit to society. The introduced species may also have positive effects on the environment. For example, oysters are filter feeders that remove suspended solids from the water column, improving water quality. However, the introduced species might also become invasive, thereby damaging the environment and reducing the flow of environmental services to consumers. Policy controls are imposed by the principal upon producing agents in order to avoid problems associated with adverse selection and moral hazard. These policy measures include technological controls, best management practices and incentive-based controls imposed on producing firms. Some examples of these policy instruments were discussed above in Section II.

As indicated in the Figure, government policy actions might also include direct interventions to protect and restore the environment, including actions that improve habitat for the native and/or nonnative...
Figure 6. Depiction of Key Relationships for Principal-Agent Model
species, monitoring actions to identify when invasions are underway and remedial actions taken to control invasion.

We assume firms apply for permits to introduce the non-native species to grow in the environment, and to harvest once the individuals reach marketable size, and the age of marketable size, \( t^M \) is assumed to occur prior to the age of sexual maturity.

Thus, within the context of non-native oysters, we start by assuming that the agency imposes regulations that allow firms to introduce reproductively viable diploid oysters, and that the potential for invasion is controlled by harvesting oysters prior to their reaching reproductive age. If all members of the introduced species are harvested, there is zero risk of invasion. However, the non-native species could become invasive if a viable population survives to maturity.

We define the notion of “reliability” to be the extent to which incentives, beliefs and behavior of the agent comply with those of the principal, and we assume that agents can be ordered in terms of reliability. This will result in a model where an important element of policy design is to encourage participation by reliable agents and discourage participation by unreliable agents.

Start by considering a three period model. In time period 1, the non-native species is introduced. In period 2, at time \( t^M \), the non-native species reached marketable size and is subject to harvest. In period 3, at time \( t^R \), the species reaches sexual maturity and reproduction occurs. The probability of invasion depends upon the number of individuals that remain in the environment in time period 3, and possibly on other factors, such as the presence of suitable habitat near the area of control of the agent.

Assume natural mortality rates of \( m_i \) in period \( i \), where mortality rate of newly planted non-natives is greater that that in future periods \( (m_0 > m_1 \geq m_2) \). Denote harvest in year \( i \) as \( h_i \). We assume that no harvest occurs in at time 1 \( (h_1 = 0) \), since the introduced species doesn’t reach marketable size until time period 2.

We define invasion as an escapement of the introduced species beyond the zone of control of the firm introducing the species. If some of the introduced species remains in the environment at the time of maturity, reproduction occurs and there is some probability that an invasion occurs. The larger the population of reproductively capable individuals, the higher the probability of invasion.

We assume that there exists a non-stochastic function, \( p(A) \), that relates actions to control invasions and other factors with the probability of invasion. We assume the function \( p(A) \) is a logistic function of the number of individuals remaining in the environment, as depicted in Figure 7. The logistic function can be shifted by environmental factors, such as salinity, distance to suitable habitat that lies outside of the zone of control of the agent etc. This function is assumed to be known by the principal, but possibly not by the agent. Rather, various agents hold different beliefs regarding the likelihood of invasion.

With multiple agents introducing the non-native species, the probability of an invasion is a function of escapement of reproductively viable (diploid) oysters.

\[
P(A_1, ..., A_n) = 1 - \prod_{i=1}^{n} (1 - p(A_i))
\]

where \( P \) is the overall probability of invasion and \( p \) is the probability of invasion by an individual operator, \( A_i \) is escapement
Figure 7. Probability of an Invasion as a Function of Cumulative Escapement.
allowed by operator $i$. Under this model, the likelihood of invasion depends upon the actions taken by all agents, and an invasion occurs even if only a single agent is unsuccessful at guarding against invasion. This is analogous to the “weakest link” notion discussed in the Section I.A. But because of the stochastic nature of the problem, even “strong links” can break with some probability, thereby causing an invasion. Invasion is avoided only when all links remain intact.

Note that this is an extreme model, where invasion full invasion occurs if invasion is not completely avoided. In fact, partial invasions might occur if, for example, the introduced species invades some locations by not others. In this context, one might also consider multiple invasions at different times and/or locations.

Reliability is modeled by the ratio of the firms’ subjective beliefs of the private cost of invasion, divided by the expected social cost held by the principal, and for purposes of this research we assume that firms expected costs are less then or equal to the “true” expected social cost. We recognize that firms’ beliefs regarding the private costs of invasion may exceed the true social costs due to legal fees, penalties, etc. But we do not consider this in the analysis below. Thus, reliability is defined as:

$$ R = \frac{E(PC)}{E(SC)} $$

where $E(PC)$ is the expected private costs associated with invasion (e.g., liability for damages) under control action $A$ and $E(SC)$ is the expected social cost. A firm is said to be reliable if their private incentives are consistent with social incentives for control actions ($R=1$). An agent is completely unreliable if they hold the belief that there is a zero expected private cost of invasion for all control actions, $A$ ($R=0$). Note that this concept is intended to represent ex ante perceptions of the agent, which drive agents’ decisions on control actions, and not on the actual ex post penalties faced by the agent.

One reason an agent may be unreliable is because they underestimate this probability of invasion. An agent may also be less than fully reliable if they believe that they may not be held liable for the full social cost of invasion. For example, a “fly-by-night” agent might attempt to flee liability. Or agents might avoid the full social costs by going bankrupt or by fighting liability in legal proceedings. Additionally, firms might avoid full social costs because existing legal institutions do not make the agents fully liable for all social costs. Firms might be liable for measureable financial losses, but not for the full suite of ecological costs, some costs might be difficult to quantify with an adequate degree of certainty, or costs might accrue only over very long time horizons, and forecasting such costs might be viewed by the courts as speculative.

Below we consider two polar scenarios for the divergence of expected private and social costs. In scenario 1, some agents underestimate the likelihood of invasion under any given set of control actions. In Scenario 2, agent hold correct beliefs, but the agent’s perceived private costs may be less than the social costs of invasion. As discussed above, this might includes examples such as when agent may not be liable for all social costs (e.g., non-monetary ecological damages).

**Case 1. Incorrect Beliefs**

In Case 1, some agents are overly optimistic about the likelihood of circumventing invasions. That is, $p^\ast(A) \in [0, p(A)]$, where $p^\ast(A)$ is the agent’s subjective belief of the likelihood of invasion under control actions.
A. For a fully “reliable” agent, \( p^a(A) = p(A) \). But in Case 1, all social costs are paid by the agent through liability (\( D=L \)). In this case, society is “made whole” for damages, since \( ex \ post \), the firm bears full social cost of invasion.

Thus, from a game theory perspective, we do not assume that agents hold equilibrium beliefs regarding the likelihood of invasion. This is a central issue in problems such as invasive species, which involve important irreversibilities. In such a one-shot game, once a belief is revealed to be incorrect, the invasion has occurred and it is too late to correct the belief. Behavior by the agent is conditioned upon \( ex \ ante \) beliefs regarding the likelihood of invasion, which may diverge from true probabilities.

An important element of policy design is to avoid adverse selection of unreliable agents. The definition of reliability presented above is a scalar measure that allows us to order agents in terms of reliability. Within the context of Case 1, we assume reliability is:

\[
R(A) = \frac{p(A)}{p^a(A)}
\]

for each value of \( A \). For simplicity of exposition, we assume that \( R(A) \) is constant for all values of \( A \).

A simplified version of this Principal-Agent model can be depicted in extensive form as in Figure 8, below. In the extensive form game, nature (player 0) first determines whether the firm is reliable or unreliable. Note that this extensive form game assumes that reliability is discrete (0/1), which we extend below so that \( R \in [0, 1] \). The firm can then choose to apply for a permit to introduce the non-native species or not apply. The principal observes whether the agent applies or does not apply, but not whether the agent is reliable. If the permit is approved, the agent selects the level of action to take to control for invasion. For simplicity of exposition, this simplified extensive form representation of the model assumes the firm can either choose to take action to control for invasion or not take action, and the probability of invasion is smaller if the firm chooses to take action. Our analysis below extends this to allow for a continuous level of control actions. If the firm chooses not to take control actions, then invasion occurs with probability \( p(0) \), \( ex \ post \) social cost of invasion is \( D \) and the firm is liable for \( L \) in social costs. If the firm takes control actions, the probability of invasion is \( p(1) \).

The goal of the principal is to design a set of regulations that induces firms to behave in the best interest of the principal. This sort of principal-agent game is solved by identifying participation constraints and incentive compatibility constraints for the agent. The incentive compatibility constraint identifies parameters for which each type of agent takes actions that are in the best interest of the principal. The participation constraint identifies parameter values under which each type of agent participates—that is, applies for a permit.

In Case 1 we assume \( L=D \) is fixed as the “true” social damages, and the principal can only determine whether to grant the permit or not. However, society is fully compensated for social damages of invasion.

We assume payoffs to the principal and agent are zero if the agent does not apply for a permit or if the permit is denied. If an agent chooses to take control actions, then the agent receives profit \( \pi - C - p(1)D \), where \( \pi \) is profit from aquiculture operations and \( C \) is the cost taking action to control for invasion. If the agent introduces the non-native species and takes action to control for invasion, then society receives some social benefit \( S \). In the case of oyster operations,
Figure 8. Extensive Form for the Principal-Agent Model of the Private Management Scenario.
this might include a cleaner bay due to filtering of water by oysters, government revenues received from aquiculture operations and possibly other social benefits from maintaining a viable shellfishing industry.

It is optimal to take action to control for invasion if:

\[ \pi - C - p(1)D > \pi - p(0)D \]

or

\[ [p(0) - p(1)]D = \Delta pD > C. \]

where \( \Delta p = p(0) - p(1) \) is the level of protection provided by actions to control invasion. From the firm’s \textit{ex ante} perspective, it is optimal to take action if:

\[ \pi - C - p^a(1)D > \pi - p^a(0)D \]

or

\[ [p^a(0) - p^a(1)]D = \Delta p^aD > C. \]

where \( \Delta p^a = p^a(0) - p^a(1) = R(p(0) - p(1)) \) and where \( R \in [0, 1] \). Thus, a firm will take action if their perceived expected liability exceeds the cost of protection actions. With a continuous distribution of reliability across firms, agents are exactly indifferent between taking action an not taking action at reliability level \( R^I \), where:

\[ R^I = \Delta p D/C \]

Firms with reliability less than \( R^I \) will not take action to control for invasion, and firms with reliability will take action if they participate.

Next we consider the Participation Constraint, which determines which agents that would choose to participate in the market. Agent with reliability greater than or equal to \( R^I \) will participate when:

\[ \pi - C - p^a(1)D > 0. \]

An agent of reliability less than \( R^I \) will participate when

\[ \pi - p^a(0)D > 0. \]

For given values of \( \pi \) and \( D \), there is some critical value of reliability, \( r \), such that:

\[ \pi - p^a D = \pi - r p(0) D = 0. \]

Firm less reliable than \( r \) will participate, while firms more reliable than \( r \) will not participate. This can be written as:

Agents participate with no action to control when reliability is less than \( r \), and do not participate when reliability is greater than \( r \). As expected damage increases, the denominator increases and \( r \) decreases. This means as activities become more hazardous, less reliable agents participate and do not take action, while more reliable agents do not participate. Thus, there is a selection bias towards less reliable agents, who underestimate the likelihood of invasion.

Assume production is profitable without actions to control invasion \( (\pi > 0) \). In this case, sufficiently “unreliable” firms will participate irrespective of social costs of invasion.

Furthermore, sufficiently unreliable firms will not take control actions, when

\[ C > R\Delta pD \]

Agents with reliability in the range:

\[ R \in [0, C/(\Delta pD)] \]

will not take control actions. Thus, if the cost of control actions is strictly positive,
then for any finite value of damages, there exists a critical level of reliability, \( \frac{C}{(\Delta pD)} \), and agents of lower reliability will not take control actions. And firms with sufficiently low reliability will choose not to take control actions no matter how high the potential social damage, so long as the cost of taking action is positive.

Taken together, these results imply that sufficiently unreliable firms are willing to participate and will not take control actions irrespective of the expected social damage. In contrast, more reliable firms will refuse to participate at sufficiently high expected social damage. Thus, the expected social damage of invasion increases, the average reliability of participating agents will decrease.

This demonstrates the potential problems of adverse selection and moral hazard. More reliable firms will choose not to participate in introductions of non-native species with higher expected social damage. And as the expected social damages associated with the introduction increases, the market will select for increasingly unreliable agents. Sufficiently unreliable firms will participate, and choose not to take control actions irrespective of the expected social damage.

The problem can also be expressed as a continuous problem, where firms can take a suite of control actions, \( A \in [0, A] \), and where the probability of invasion \( (p(A)) \) and the cost of control actions \( (C(A)) \) are both continuous functions. This continuous case is illustrated in Figures 9 and 10. Figure 9 shows that as reliability decreases from 1 to .5 to zero, the \( \text{ex ante} \) subjective optimal level of control actions decreases from \( A^*(1) \) to \( A^*(5) \) to \( A^*(0) = 0 \). The “true” expected marginal social benefit of control actions exceeds the subjective estimated marginal social benefit, so unreliable firms take too few control actions.

Figure 10 shows that as \( D \) increases, more reliable firms choose not to participate in the market, while less reliable firms continue to operate. In Figure 10, the area above the solid line represents the sets of parameters under which a reliable firm operates and takes control actions. The area above the higher dashed line is the area where firms with reliability of 0.5 would operate. Finally, completely unreliable firms (\( R=0 \)) would operate for any set of parameters in the positive quadrant, and these firms would not take control actions.

Thus, increasing damages and \( \text{ex post} \) liability drives out reliable firms in favor of unreliable firms, and unreliable firms require greater incentives to take control actions. This is a rather sobering result. When firms are liable for \( \text{ex post} \) damages and direct regulations are not imposed, only firms with lower reliability operate in the most hazardous circumstances, where potential damages are highest, while reliable firms are driven out of the market.

Note, however, in Case 1, we assume the firms pay the full social damages associated with an invasion, if one occurs. Therefore, the inefficiency associated with under providing protection actions is a private cost borne by the introducing firms. From an efficiency perspective, too many invasions occur, but the public is fully compensated for any losses. Case 2 below considers the scenario where firms are able to avoid at least some of the costs of invasion.

**Case 2. Divergence of Liability and Damage**

As indicated above, in polar Case 2, firms have the correct \( \text{ex ante} \) beliefs regarding the
Figure 9. Moral Hazard Regarding Control Actions for Partially Reliable Agents.
Figure 10. Adverse Selection for Unreliable Operators
probability of invasion, but they face incompletely liability for damages, so they do not bear the full social cost. For example, a firm might go bankrupt or might not be liable for some categories of social cost of invasion, such as ecological effects.

Thus in this case, we assume the beliefs of the agents are consistent with those of society:

\[ p^a(A) = p(A) \]

but \textit{ex post} liability is less than or equal to social damages. We model this problem using the same concept of “reliability”, but now reliability drives a wedge between liability and social damage:

\[ L = RD \]

where \( L \) is the financial liability of the agent, \( R \in [0,1] \) is the fraction of damages borne by the firm and \( D \) is the social damage. Thus, the model is virtually identical to that above, except the firm does not bear the full cost associated with invasion. The extensive form game for Case 2 is shown in Figure 11. This extensive form game is identical to that in Case 1, except social payoffs are \( S-(1-R)D \) in the event of an invasion. By construction, payoffs in Case 2 are identical to \textit{ex ante} expected payoffs in Case 1.

This extensive form game proceeds exactly like the game described in Case 1. In the extensive form game, nature (player 0) first determines whether the firm is reliable or unreliable. As noted above, in this simplified depiction of the extensive form game, reliability is discrete (0/1). However, in the analysis below, reliability is continuous, such that \( R \in [0,1] \).

Next, the player 1, the firm, chooses to apply for a permit to introduce the non-native species or not apply. The principal observes whether the agent applies or does not apply, but not the degree of reliability of the agent. If the permit is approved, the agent selects the level of action to take to control for invasion.

Since the firm only bears a fraction of the social costs of invasion, the marginal private return to investment is less than the marginal social return, and the firm under-invests in control actions. However, unlike in Case 1, society bears the full cost of invasion, and is only able to obtain liability payments for \( L = RD \leq D \), where the inequality is strict for \( R<1 \).

Thus, similar to Case 1, the firm under-invest in control actions and more invasions occur than is socially optimal. But unlike Case 1, Society bears the cost associated with error in the amount of \((1-R)D\).

Case 2 exhibits the same problems regarding adverse selection and moral hazard as shown in Case 1. Moral hazard arises because lower levels of reliability imply \textit{ex post} liability payments that are less than social damages from invasion, thereby driving a wedge between \textit{ex ante} levels of the expected private benefits social benefits of control actions. Thus, “unreliable” (\( R<1 \)) firms under-invest in control actions from a social perspective. And the lower the level of reliability, the greater the degree of under-investment relative to the social optimum.

Furthermore, the lower the level of reliability, the more profitable it appears to engage in aquaculture from an \textit{ex ante} perspective. Thus, \textit{ex post} liability selects for unreliable firms.
Figure 11. Extensive Form for the Principal-Agent Model. Case 2 of the Private Management Scenario.
V. Summary

This paper presents research on controlling risks associated with the intentional introduction of nonnative species. Introducing nonnative species embody risk of invasion, which can be ecologically and economically damaging. However, great benefits have result from introduced species, including agricultural crops, livestock, ornamental plants and pets. Hence, it is not desirable to control risks of invasive species by outright prohibition of all intentionally introduced species. Furthermore, such a policy would likely be unsuccessful, and could even increase risks due to the potential for “rogue” introduction of nonnative species, which would circumvent potential actions to control risks.

We develop a risk-based approach to model two different institutional contexts for managing the intentional introduction of nonnative species. First, we discuss a public management context, where a government agency introduces a non-native species, and makes all decisions regarding introduction and management of the non-native species. This structure is representative of managing non-native species on public grazing lands or in an open access fishery. Then we discuss a model of a private management context, where private firms introduce and manage a non-native species, subject to regulations set by a government agency. This institutional structure is representative of managing non-native species on private farmlands and ranchlands, or for managing private aquiculture operations on leased submerged lands.

Two different frameworks are used to model these two institutional structures. And we develop two separate models to account for the two major regimes of Maryland and Virginia. In Maryland, the state government takes actions with respect to planting and managing shellfish beds, and it licenses firms to harvest oysters. In contrast, management in Virginia has tended towards leasing submerged lands to private firms, who then undertake all actions with respect to planting, managing and harvesting. In the case of Maryland, the state has tighter controls over planting and managing oysters, but the fishery becomes, in effect, open (or limited) access. In the case of Virginia, the state sacrifices complete control over planting and management, but a single firm makes all decisions, and thus can be held responsible for complying with a more complete set of regulations. For example, it is not as straightforward to set requirements for maximum escapement (or equivalently, minimum harvest) under the Maryland system, where many firms harvest from a single oyster bed.

The public management structure is examined using a dynamic and spatially explicit bioeconomic model that contains a detailed simulation of various larval stages. Detailed modeling of larvae is essential for this problem, since oysters (like many plants) are largely stationary during the adult stage, and are potentially invasive during reproduction.

The detailed modeling of early life stages is essential to account for inter-specific competition in the form of gamete sinks, where hybrid zygotes made up of gametes of two species are not viable. Depending upon conditions, this could be advantageous in reducing the risk of invasion of nonnative oysters, or could be disadvantageous by adversely affecting efforts to restore native oysters.

The model compares the effectiveness of policy actions such as requiring the introduction of non-reproductive triploid oysters or introduction of nonnative species in locations that are not well connected to
other sections of the Chesapeake Bay. We find that technology based controls of introducing non-reproductive triploids to be more effective than best management practices, used alone. Of course, policy could focus on combining both approaches.

Next we examine the private management case, where private firms apply for the right to plant, manage and harvest a non-native species. We define varying degrees of reliability, where reliability is defined in terms of the consistency between firms’ subjective expected private costs of invasion and the underlying social cost of invasion. We use a Principal-Agent model to identify challenges associated with adverse selection and moral hazard.

We examine two Cases of the model. In Case 1, firms bear the full cost of liability ex post, but the firm’s ex ante expectations regarding invasion may be less than the “true” likelihood. Case 2 considers an example where the firm has correct ex ante expectation of the likelihood of invasion, but does not bear the full social cost of invasion. For example, legal liability might include some categories of social damage, but not others. Or the firm may limit liability by bankruptcy, through litigation or by fleeing legal obligations.

Case models an example where firms are overly optimistic about the likelihood of avoiding invasion, and thus hold out-of-equilibrium beliefs. But because an invasion may be one-of-a-kind event, there is no factor that enforces equilibrium beliefs. Consider an extreme example such as mutually assured destruction, where one party incorrectly believes a “first strike” will successfully eliminate the enemies ability to retaliate. If the party chooses to attack, once it learns the first strike is not successful, the world ends and there is no opportunity to adjust beliefs.

In Case 1, the firm bears the full cost of invasion, but its ex ante expected cost underestimates the “true” expected cost. Thus the firm’s ex ante expected cost of invasion is less than the true cost. This drives a wedge between private and social costs, leading to under-investment in actions to control invasion. Furthermore, the more optimistic the firm, the greater the underestimate of costs of invasion.

Similarly, in Case 2, the firms expected private cost of invasion is less than the expected social cost, so once again unreliable firms will under-invest in control actions, and will view the activity as more profitable, as compared to more reliable firms.

In both Cases, lower reliability is associated with inadequate controls for invasion. And even more problematic, ex post liability will select for unreliable firms. In other words, less reliable firms are more likely to participate and will take fewer control actions.

The key difference between our two Cases, is in Case 1 firm ultimately bear the full ex post costs of invasion. Since society is fully compensated for invasion costs, there is no incentive to reject the application for a permit to introduce the non-native species. In contrast, in Case 2, society bears the cost associated with the difference between private and social costs, so society is made better off by rejecting the application for a permit.

Thus, we find that when regulations take the form of ex post liability for damages from invasion the private management institutional structure can suffer from problems associated with adverse selection and moral hazard. Ex post liability will tend to drive out reliable agents and attract unreliable agents. Furthermore, these
problems will be most pronounced within the context of the most hazardous situation, where invasions may be irreversible and highly socially damaging. This implies that there may be a critical role for direct regulations requiring the firm to take specific actions to control the likelihood of invasion, and/or for steps taken by the government agency. For our example of introduction of non-native oysters, the government might impose technology-based standards, such as requiring introduction of non-reproductive triploid oysters, and perhaps government supervised laboratories that insure oyster stock is indeed triploid.

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Appendix A

Luo and Opaluch, “Risks of biological invasion An agent based simulation model for introducing non-native oysters in Chesapeake Bay, USA” Stochastic Environmental Research and Risk Assessment, Vol. 24
Analyze the risks of biological invasion

An agent based simulation model for introducing non-native oysters in Chesapeake Bay, USA

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Abstract Introducing non-native species can create serious environmental risks, such as changing the attributes of ecosystem, displacing the native species, clogging the natural waterways and channels. Careful examination of the possible consequences before implementation can prevent the adverse consequences of invasive species. However, policy analysis for such an action is often difficult, due to the complexity of the marine environment, and the interactions among the species therein.

This paper presents a spatial-explicit agent-based simulation model for analyzing the environmental risks of introducing non-native species, Suminoe oyster (*Crassostrea ariakensis*). It is considered to be introduced into the Chesapeake Bay, USA, where there is a native Oyster species (Eastern oyster, *Crassostrea virginica*) with declining population. The simulation result indicates that the non-native species will likely displace the native species, but this can be controlled by setting up a different harvest plan, and the location and the number of initial spat introduced.

Keywords Marine environmental risks · Biological competition · ABM simulation · Non-native species

1 Introduction

Invasive species is a rapidly growing economic and environmental problem worldwide. It has been identified as one of the leading factors causing tremendous, irreversible environmental changes at an ecosystem level (GISP 2003). Many countries have suffered from huge damage caused by invasive species. For example, in China, one-third of the endangered species problems are caused by invasion of foreign species. United States, for example, has been invaded by approximately 50,000 alien species. One study estimated that the environmental and economic cost of the invasive species amounted to $120 billion per annum (Pimentel et al. 2005). The economic damage of just one species, Pink Hibiscus Mealybug, is estimated to be $4,674 million per annum in USA (Ranjan 2006).

The term “invasive” is applied to non-native species that caused or are likely to cause economic losses, harm to the environment and/or adverse impacts on human health which are disproportionate to any associated social benefit (e.g., National Invasive Species Council 2002). Major efforts have been put in controlling invasive species from international transportation activity (Batabyal 2007; Batabyal and Nijkamp 2005). However, managing the intentional introduction of non-native species for the commercial reason is equally important in preventing the non-native species, or the “hitch hikers”, from becoming invasive in the new environment.

Despite all the risks associated with invasive species, great social benefits originate from with some non-native species. Many non-native species are non-invasive and support highly valued commercial activities and improve our quality of life. They include many introduced agricultural crops, livestock species, ornamental plants and household pets. Thus, it is not desirable to base invasive...
species control policies on a wholesale prohibition on the introduction of all non-native species. This is recognized in extant policy guidance such as Executive Order 13112 and the associated National Invasive Species Management Plan (National Invasive Species Council 2001), which forbid actions to introduce or enhance non-native species unless

‘... the benefits of such actions clearly outweigh the potential harm caused by invasive species; and that all feasible and prudent measures to minimize risk of harm will be taken in conjunction with the actions.’

Furthermore, policies based on absolute prohibition of introducing non-native species are likely to be unsuccessful in eliminating risks, and may even increase risks associated with introduced species. Overly conservative policies regarding introduction of potentially profitable commercial species might encourage some to illegally introduce the species with the intention of subsequently harvesting it. This pathway of introduction may increase risks of invasive species, since it circumvents existing measures to control spread of both the intentionally introduced species and the ‘hitchhikers’ that might be harbored.

Estimating the risks in introducing non-native species and reducing the uncertainties that the introduced species may become invasive presents a challenge due to the complex, yet most of the time unknown biological and ecological adaptation of the introduced species in the environment. It is one of the important factors in controlling the incidents of invasive species from non-intentional introduction, and the permission to intentionally introduce some non-native species into the environment, to provide satisfaction to the human being.

This paper describes a case involved in the introduction of non-native Suminoe oyster species into the Chesapeake Bay area where the oyster industry is under threat because of the declining population of the native eastern oyster. We will first briefly introduce the oyster industry in Chesapeake Bay and issues in the introduction of the Suminoe oyster. Then we will describe the simulation model, and data used in the simulation process. The simulation result will be presented at the end.

2 Background

2.1 Oyster industry in Chesapeake Bay

Chesapeake Bay is located in the middle lower part of US East Coast, across the State of Maryland and Virginia. Eastern oyster has been an important commercial industry in the Chesapeake Bay, with a harvest exceeding 142 million pounds in the 1880s. Today, the oyster population is estimated to be <1% of its original abundance due to the effects of over-fishing, channel dredging, pollutants, sediments runoff, and diseases (Gottlieb and Schweighofer 1996). However, in recent decades, the diseases MSX and Dermo have been identified as the core reasons for further decline of native oyster population. MSX, first identified in the Chesapeake Bay in 1959, is caused by the invasive protozoan parasite, *Haplosporidium nelsoni*, which was introduced to the East Coast from Asia (Burreson et al. 2000). Fisheries management efforts, use of disease-resistant strains and various oyster reef restoration programs have not been successful in restoring the oyster stock to date. The cost of restoring the native oyster population is higher than its benefit (Tarnowski 2007). The loss of the oysters has been devastating to the oyster industry and its dependent communities.

Recently, it was considered to introduce non-productive non-native Suminoe oyster into the Chesapeake Bay area, to restore the oyster industry in the region. There is considerable controversy surrounding this proposal. Although the population of native oysters is currently at very low levels, there are ongoing attempts to restore native oyster populations and to develop disease resistant native strains. The introduction of non-native oysters could be a stop-gap measure, to be used until efforts to restore native oysters prove successful. However, the introduction represents a risk of undermining the recovery of native oysters or of displacing the other species of shellfish. Furthermore, there is a risk that the introduction of the non-native oyster into the environment may result in invasive organisms, such as the other molluscan species, worms, protozoa and seaweeds that are associated with the non-native oysters. Of particular concern are those that may cause disease in the native oyster or the other species. Indeed, it is believed that the diseases that have so devastated native oysters in the Chesapeake were introduced with non-native oysters.

One approach that has been suggested for introduction of non-native oysters is to release hatchery raised triploid Suminoe oysters into the environment to be “grown out” on designated open-water aquaculture sites. The introduction of the hatchery farmed, triploid non-native Suminoe oyster from Asia may be a solution to this difficult problem, but it is not without risk. Triploid oysters are strains that are unable to reproduce, although there is a probability that some triploid oysters will revert to diploids (referred to as mosaics), which are capable of reproducing. Additionally, in the process of releasing triploid oysters, some number of diploids will also accidentally be introduced. Hence, introducing triploid oysters reduces the probability that the species will become invasive, but does not completely eliminate the risk.
2.2 Literature review

Many existing papers have studied the biological property of Suminoe oyster and how it interacts with the environment. For example, in a study for the aquaculture potential of non-reproductive Suminoe oyster in the West Coast of USA (Langdon and Robinson 1996), many life history parameters, spawning environment and period, and environmental tolerances of Suminoe oysters are discussed. Similar research includes the possibility to use triploids for oyster farming activity in France (Nell 2002), and the environmental requirements for oyster growth (Calvo et al. 2000).

Dew et al. (2003) built a simulation model for assessing the likelihood of self-sustaining populations resulting from commercial production of triploid Suminoe Oysters in Chesapeake Bay. The life-history parameters of this simulation draw heavily from a previous research by Mann and Evans (1998), which estimated the standing stock for the native eastern oyster in the James River. The variables in the simulation include salinity, stocking density, reversion rate from triploids to diploids, reproduction potential, natural and harvest mortality. The spatial interaction and the competition are not considered in the model. Similar modeling efforts using oyster population dynamics could also be found for Pacific oyster (Crassostrea gigas) in Mediterranean coastal lagoon at Thau, France (Gangnery et al. 2004), at Port Stephens, Australia (Honkoop and Bayne 2002).

A recent report on the background economic analysis for the environmental impact statement on the introduction of non-native Suminoe oyster in Chesapeake Bay (Lipton 2008) presents an extensive economic analysis for the benefits and costs with the introduction of Suminoe oyster. However, in estimating the future benefits from the introduced oyster growth, the limitation and spatial distribution of the oyster habitat on the population growth of the introduced species were not included.

Large scale simulation analysis for modeling the spatial biological interaction between species and with environment using an agent based modeling approach is not frequently seen in the literature. One of the papers addresses the ecological system problem in the Coastal lagoons ecosystem where the human being (like oyster farmer) is involved in the complex decision-making process (Pereira et al. 2004). One of the examples provided in the paper simulates the anthropogenic environmental pressure resulted from the tourism and shellfish/fish farming in Sungo Bay, People’s Republic of China. It was modeled as a 2D model including the hydrodynamic process and biochemical process in the region, based on a finite difference bathymetric staggered grid with 1120 cells and a spatial resolution of 500 m (side length of rectangular cell). This grid configuration is not optimal in modeling the homogeneous diffusion in all directions.

Our focus in this research is to simulate the spatial growth of the introduced oyster in the Chesapeake Bay. Factors considered in the model include spatial distribution of oyster habitat, competition between native and non-native species, as well as the population dynamics and life history parameters of the native and non-native oysters. This enables the analysis for possible results with different management policies, including the location and size of initial stocking, Total Allowable Catch (TAC) and initial non-harvesting period.

We use Agent Based Model (ABM) to simulate the oyster population dynamics and spatial diffusion over the oyster habitats in the Chesapeake Bay. ABM is a relatively new computational modeling paradigm, originally derived from the Computer Science and refers to the modeling of various phenomena as dynamical systems of interacting software agents. The outstanding feature of ABM is its ability to derive the intricate behavior of the whole system based on the simple, localized behavior of each individual agent. Because of this, ABM has been applied in the study of collective economic behavior (Tefsatsion 2006), biology (Politopoulos 2007), and complex social, economic, and biological system (Bobashev et al. 2007). For the same reason, we use ABM to analyze the result of spatial growth, diffusion and species competition by designing a virtual oyster population agent to manage the population dynamics and spatial diffusion of oyster, which will be explained next.

2.3 Specification of the model

This section describes the specification of the model, including the population dynamics of and the spatial movement of Oysters. The population dynamics explains the survival, growth and reproduction of oyster populations. It includes all life history parameters of oysters follows Mann and Evans (1998) and Dew et al. (2003), with two significant departures. First, we include detailed modeling of larval transport. The population dynamics specified in this section are for each specific “cell” of oyster habitat. Secondly, we examine interactions between two species of oysters, native oysters and the introduced oysters. In locations where the two stocks co-exist, they compete for food and habitat space. Also, we model stock interactions though reproduction, as discussed below.

2.4 Population dynamics of oysters

In this section, we present the detailed population model for oysters at various life stages from spawning through survival of young-of-the-year. Our model focuses more extensively on modeling the details of the early life stages of oysters than is typical for bioeconomic models, as the mobility after these stages is low.
At present, we use identical life history parameters for the two species, with the important exception of susceptibility to disease. The primary rationale for introducing *C. ariakensis* is its resistance to disease. Therefore, we adopt available estimates for susceptibility of the native species, *C. virginica*, but assume that the introduced species is not affected by disease.

### 2.4.1 Oyster fecundity with the environmental condition

The actual fecundity of Oyster is determined by the potential fecundity ($F_{tj}$), adjusted by salinity ($Fs$), fertilization success ($F_{tj,i}$), and sex ratio ($F_{qi}$). First, we model fecundity or the production of gametes. The number of gametes produced at time $t$ and age class $j$ increases with the number of adult oysters ($N_{tj}$) and the size of oysters ($L_{tj}$). For non-reproductive triploid oysters introduced, the reproductive potential is determined by the fraction of introduced oysters that revert from triploid to diploid ($R_{tj}$) and the fraction of diploids that are accidentally introduced ($T_{tj}$). The equation for fecundity is:

$$F_{tj} = 0.000423L_{tj}^{-1.17475}N_{tj}(R_{tj} + T_{tj})$$

(1)

For native oysters and non-native oysters are stocked as reproductive diploids, $R_{tj} = 0$ and $T_{tj} = 1$.

Salinity affects potential fecundity, although not affecting adult oysters. This suggests a spatially explicit policy to reduce risk of invasions by planting non-native oysters in areas where reproduction is limited by salinity, or in areas where non-native oysters are confined by salinity. For example, the risk of spread of the non-native species can be controlled by limiting planting to inlets that are isolated from the rest of Chesapeake Bay. If the salinity is unfavorable to survival of larvae, it can reduce the likelihood of geographic dispersal of non-native oysters.

The fecundity adjustment factor accounting for salinity ($S$), $Fs$, is zero for salinity <8 ppt, reaches a maximum at salinity of 13.5 ppt, then declines to zero when salinity reaches 35 ppt. We specify the relationship between fecundity and salinity as a piecewise linear function of the level of salinity.

<table>
<thead>
<tr>
<th>Salinity ($S$)</th>
<th>$S &lt; 8$</th>
<th>$8 &lt; S &lt; 13.5$</th>
<th>$13.5 &lt; S &lt; 35$</th>
<th>$S &gt; 35$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Fs$</td>
<td>0</td>
<td>$(S-8)/5.5$</td>
<td>$(35-S)/21.5$</td>
<td>0</td>
</tr>
</tbody>
</table>

We introduce a disease factor to account for the effect that various diseases can have on reproductive success. The disease factor goes from 0 to 1, where zero indicates no reproductive success, and 1 indicates no disease-related mortality. Although non-native oysters have proven to be resistant to diseases that are prevalent on the east coast, they may be affected by other diseases. Also, the disease factor will be important when the model is used to analyze the decision within a multi-species framework, with both native and non-native oysters.

Oysters tend to congregate in highly concentrated communities, called oyster bars. Indeed, oyster bars were significant hazards to shipping in Chesapeake Bay when oyster populations were at historic high levels. Oysters benefit from high concentrations in at least two ways. First, oysters require a hard surface to attach to, including other oysters, i.e., oysters provide their own habitat. Second, since oysters are broadcasting spawners, fertilization success increases with concentration of oysters. We specify an equation for fertilization success as:

$$F_{f,ti} = 0.0049D_{tj}^{0.72}$$

(2)

where $D_{tj} = \frac{N_{tj}(R_{tj}+T_{tj})}{A}$ is the density of reproductive oysters, and $A$ is the area in square meters. Total zygote production ($F_{total,t}$) is the sum over all age classes of potential production, corrected for salinity, the sex ratio ($F_{qi}$), the fraction not lost to disease ($F_{d}$) and the fertilization rate:

$$F_{total,t} = \sum_i (F_{revert,i} \times F_s \times F_{qi} \times F_d \times F_{f,ti})$$

(3)

### 2.4.2 Dynamic population of spat

Spat are zygotes that have successfully metamorphosed, settled and attached to hard substrate. The total number of zygotes is the sum of the number of reproductive diploids, and $A$ is the density of reproductive oysters. Total zygote production ($F_{total,t}$) is the sum over all age classes of potential production, corrected for salinity, the sex ratio ($F_{qi}$), the fraction not lost to disease ($F_{d}$) and the fertilization rate:

$$F_{f,ti} = 0.0049D_{tj}^{0.72}$$

(2)

where $D_{tj} = \frac{N_{tj}(R_{tj}+T_{tj})}{A}$ is the density of reproductive oysters, and $A$ is the area in square meters. Total zygote production ($F_{total,t}$) is the sum over all age classes of potential production, corrected for salinity, the sex ratio ($F_{qi}$), the fraction not lost to disease ($F_{d}$) and the fertilization rate:

$$F_{total,t} = \sum_i (F_{revert,i} \times F_s \times F_{qi} \times F_d \times F_{f,ti})$$

(3)

The equation relating the number of zygotes to the number of one-year-old oysters is:

$$N_1 = \left( F_{total}(1 - E) + \sum_{n=1}^{N} \alpha_n F_{total}^n \right) P_{meq}(1 - L_{mort})^{21}$$

(4)

where $N_1$ is the number of individuals at age class one in one cell, $F_{total}^n$ cell to this cell the total larvae from the $n$th cell, $\alpha_n$ is the percentage of the larvae from $n$th cell to this cell, $N$ is total number of cells that have larvae being transported to this cell. When working in the multi-species framework, this will be extended to include a fraction of...
non-viable zygotes that result from hybridization between the native and non-native species. More discussion of this issue is contained below.

Numbers of individuals at various age classes then progress through the equation:
\[ N_{t+1,j} = N_j(1 - M_j)(1 - H_j) \]  
where \( H_j \) is the harvest rate, and \( M_j \) is the natural mortality rate at time \( t \) for age class \( j \). Harvest also varies by time to account for changes in the different management policies over time. The total number of individuals in the population is the sum over all age classes:
\[ N_t = \sum_{j=1}^{M} N_j \]  

2.4.3 Competition of habitat space through biomass capacity

In real environment, the oyster population cannot grow over certain limit. In the simulation model, we specify the upper limit for the total weight of oyster per square meters (C). If the total weight of the oysters in one cell is larger than its capacity, the population of the oysters in all the age class will be reduced proportionally, so that the total weight will below the capacity limit.

When two species reside in the same cell, they will compete for available limited space. For example, if the total weight of native oysters in cell \( i \) at time \( t \) (\( W^n_i \)) and non-native oysters (\( W^n_i \)), \( W^n_i + W^n_i \) is larger than \( C \), then it is necessary to limit the number of oysters for each species. The upper limits for each species will be:
\[ C'^n_i = \delta \cdot C \quad \text{and} \quad C'^n_i = (1 - \delta)C \]  
where \( \delta = \frac{W^n_i}{W^n_i + W^n_i} \) is the percentage of the non-native oysters in total weight of the oyster in the cell. \( C^n_i \) and \( C'^n_i \) are the capacity limited of the non-native oysters and native oysters, respectively. Thus the species with higher growth rate will eventually dominate in the cell, if all other factors remain constant.

2.4.4 The effect of gamete sink on oyster population

Another potentially important issue associated with coexistence of two oyster species in the same area is the gamete sink (e.g., Merritt et al. 2005; Bushek et al. 2007). Oysters of all species are broadcasting spawners, and fertilization occurs when sperm and egg join in the environment. This raises the potentially important issue of the extent to which gametes of the two species interact. If the two species of oysters synchronize spawning, then a fraction of eggs from one species will join with a sperm from the other. This result in a hybrid that is not viable, which can adversely affect reproduction of both species. Therefore, whenever non-native species resides at the same cell as the native species, we compute the result of gamete sink on both species. Assume the number of gametes for native species is \( N_A \) and that for non-native \( N_B \), then \( N'_A = p_A N_A \), and \( N'_B = (1 - p_A) N_B \) are the number of gametes for native and non-native species, respectively, after the gamete sink effect. \( p_A = \frac{N_A}{N_A + N_B} \) is the ratio of the gametes of native species in the total number of gametes in this cell.

This specification shows that the effect on the less numerous species may be far more devastating from a reproductive viewpoint. For example, suppose that the gametes (eggs and sperm) of one species outnumber those of the other by a ratio of 3–1. In this case, \( \frac{1}{4} \) of the gametes from the more numerous species will join with gametes from the less numerous species, and become hybrid. Since these hybrids are not viable, they die. However, \( \frac{1}{4} \) of the gametes from the less numerous species will join with gametes from the more numerous species, producing hybrids which subsequently perish. Therefore, less numerous species is in an even worse competitive position in each future generation, and their gametes will become outnumbered by an even larger ratio in the future. Hence, even in cases where the population of less numerous species is viable in the absence of the more numerous species, the potential for the gamete sink could make the species reproductively non-viable. This notion of the gamete sink is incorporated in calculating the viability of zygotes in the multi-species version of our simulation model, as discussed above.

The effect of the gamete sink could be advantageous or disadvantageous when considering potential risks of invasions by intentionally introduced species. If the gametes from the introduced species significantly outnumber those of the native species, the native species could be driven out (assuming synchronized spawning), and attempts to restore the native species could be futile if a large population of reproductive non-native species is established. However, if the number of gametes from the introduced species is kept sufficiently below those of the native species, then the gamete sink effect could reduce the risk of invasion by the introduced species, and the number of gametes of the introduced species could be kept low by introducing non-reproductive triploids. Thus, even if the population of the introduced species is significantly larger than that of the native species, the number of gametes from the introduced species could be kept low by introducing non-reproductive triploids. The gamete sink effect could reduce the probability of successful reproduction by mosaics and accidentally introduced diploids.

However, it would be advised not to become too reliant upon the gamete sink notion to control the risks of invasion by the introduced oysters. If spawning is not well synchronized across the two species, then the gamete sink notion is not
relevant. Furthermore, even if the populations start out synchronized, one might expect evolutionary pressures to disrupt the synchronization of spawning: oysters whose reproduction is not synchronized with the competing species might become relatively more successful, and the two populations might naturally move out of synchronization.

3 Simulation the spatial movement of oysters

We developed a spatial-explicit agent-based model to simulate the growth, transport and harvest of the native and non-native oyster species in Chesapeake Bay. The agent-based framework extends Recursive Porous Agent Simulation Toolkit (RePast®), which supports general simulation activities, such as graphical user interface for starting and stopping simulation, controlling time steps, changing simulation parameters, and coordinating with basic simulation functions. Research specific simulation procedures start with the oyster model, which reads in necessary data, creates oyster habitat space, displays oyster habitat and the population agents, and records the numerical simulation results. A general structure of the simulation model is in Fig. 1.

The oyster model also creates the initial oyster population agent at the initial stocking cell for each species, and let them grow and spread in the virtual habitat space during simulation. Model results are passed back to OpenMap to create a dynamic visual representation of oyster population on electronic maps. The OpenMap depiction of simulation area in Chesapeake Bay and an illustrative view of a spatial distribution of oyster population are in Fig. 2. More detailed simulation results, such as the levels of oyster populations over time and space, harvest, etc. are stored for later analysis. Next we will explain the detail configuration of the habitat space and the simulation environment.

3.1 Spatial configuration of oyster habitats

The oyster habitats in Chesapeake Bay are scattered in different tributaries, and cover only a small part of the bay area. To enable the simulation of the spatial diffusion of oyster larva and the harvest activities for adult oysters, we divided the habitat space into many small hexagonal cells, 500 m on each side. The whole simulation area, as shown in Fig. 3, could be divided into 200 by 200 cells if all the areas were oyster habitat. This grid configuration is changeable before each simulation to fit the needs of different research purposes. In addition, we only included cells with a hard bottom type (oyster rock, shell mud, and shell sand), as oyster can only fix and grow on a hard surface.

With this arrangement of cells, each cell is identified by its coordinates $x$ and $y$, starting from the upper left corner of the simulation area (Fig. 3). This specification facilitates the conversion between coordinate system and the longitude and latitude, and calculation of the distance between any two cells. Further, it facilitates the diffusion mechanism
by simplify the algorithm in searching the neighboring cells at specific range measured by the number of rings.

Residing in each cell is one population agent that manages the population dynamics for each species in that cell. It is identified by its species name and its coordinates, has information about the life-history parameters of the species (such as age, length, growth mechanism, mortality rate, reproductive capability). In addition, it can access the environmental information such as location, bottom type, the tributary information, and whether there is another species in the same cell.

3.1.1 Spatial diffusion of oyster

Agent in one cell interacts with the other agents through spreading oyster larvae into other cells within certain range, and receiving larvae drifted from other cells. This is the main mechanism for oyster to diffuse over the bay area.

Many environmental factors participated in the movement of the oyster larvae in the water column, such as the geographical condition, hydrodynamic characteristics of the bay, tidal and water current. To simplify the simulation process, for each species (s), we used the actual observations on the transportation distance \( d^s_i \) at each tributary (i) (Table 1), and the connectivity among tributaries \( (\rho^s_{ij}) \) (Table 2) to model the zygotes movement within the same tributary (i = j), and the movements to other tributaries (i ≠ j).

To model the zygotes movements within same tributary, we first assume that the transportation distance of zygotes follows a positive portion of normal distribution. Since distances cannot be negative, using \( d^s_i \) for the mean zygotes transport distance, we can find the standard deviations \( (\sigma^s_i) \) that make the cumulative probability from origin to the mean distance \( (d^s_i) \) equal to 25%:

\[
\frac{1}{\sigma^s_i \sqrt{2\pi}} \int_0^{d^s_i} e^{-\frac{t^2}{2\sigma^s_i^2}} dt = 25\%
\]  

The standard deviations that satisfy above condition are shown in Table 1 (Std column). They are used to calculate the percentage of larvae being transported into cells at different distance. Figure 4 illustrates an example of half-normal distribution when standard deviation equal to 2. It also includes the percentage of larvae remain in the initial cell and that transported to each ring. As the cell length is 500 m, and its center is the starting point of the half-normal distribution, the first ring starts at 500 m, then each of next ring will start 1 km away from the previous one, until the cumulative probability is larger than 95%. Table 1 also includes the computed maximum distance \( (d^s_{i,max}) \). As the cell diameter is 1 km, \( d^s_{i,max} -0.5 \) is actually the number of rings for species s in tributary i. Using \( \Phi^s_{ik} \) for the cumulative probability at the kth ring, if all of the cells at that ring are oyster habitat, then the percentage of larvae \( (\lambda^s_{ik}) \) moved to any one cell at that ring is:

\[
\lambda^s_{ik} = \rho^s_{ik} \Phi^s_{ik} / 6k
\]

The diffusion to the cells not in the same tributary is simulated by randomly pick up one cell from the tributary where \( \rho^s_{ij} \neq 0 \) in Table 2, and assume all that friction of the zygotes are transported to the chosen cell. If they moved into a cell that is an oyster habitat, they can survive; otherwise, they will be parish.

In either case, the new population agent will be created if there is not a population agent in the receiving cell. Then the agent will manage the oyster population dynamics, interact with the other agents and the environment. If the oyster population in a cell becomes zero, the population agent will be removed from the system.

3.1.2 Data used in the agent-based simulation model

Data used in this simulation model includes the actual larvae movement statistics for native and non-native
species in the Chesapeake Bay (Tables 1 and 2), the GIS database for different bottom types in the Virginia part of the Chesapeake Bay (Fig. 5), and the life-history parameters and economic prices for the native and non-native species (Table 3).

Figure 5 shows that there are not so many areas in the Virginia part of the Chesapeake Bay suitable for oyster to settle down and grow. The black areas in the map are oyster rocks, shell mud and shell sand area, which are scattered in different tributaries and separated by non-habitats. The other bottom types, such as buried shell, sand, sand mud, clay, cannot be used as oyster habitat.

Owing to lack of data for non-native Suminoe oyster, we assume that non-native oyster, *C. arikansis*, has very similar life history parameters as the native one. The only

<table>
<thead>
<tr>
<th>Source</th>
<th>Destinations (V.: C. Virginica; A: C. Ariakensis)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rappahannock Planatank York (%) Virginia mainstem (%) Mobjack Bay (%) James (%)</td>
</tr>
<tr>
<td>Rappahannock</td>
<td>V 92.10  2.00  0.40  5.30  0.30</td>
</tr>
<tr>
<td></td>
<td>A 99.60  0.20  0.30</td>
</tr>
<tr>
<td>Planatank</td>
<td>V 3.40   69.40  0.50  26.30  0.40</td>
</tr>
<tr>
<td></td>
<td>A 7.70   86.50  5.70</td>
</tr>
<tr>
<td>York</td>
<td>V 93.70  0.70  5.50  0.05</td>
</tr>
<tr>
<td></td>
<td>A 97.90  0.30  1.30  0.50</td>
</tr>
<tr>
<td>Virginia mainstem</td>
<td>V 8.80   4.00  6.10  72.70  6.20  1.60</td>
</tr>
<tr>
<td></td>
<td>A 11.30  2.10  1.70  62.30  1.10  19.30</td>
</tr>
<tr>
<td>Mobjack Bay</td>
<td>V 5.90   1.80  92.30  0.03</td>
</tr>
<tr>
<td></td>
<td>A 8.80   0.60  90.60  0.01</td>
</tr>
<tr>
<td>James</td>
<td>V 0.01   0.02  0.001  0.01</td>
</tr>
<tr>
<td></td>
<td>A 98.40  0.02  0.001  100.0</td>
</tr>
</tbody>
</table>

The italic numbers are the diffusion rate in the same tributary.

**Fig. 4** Percentage of zygotes transported to different rings for standard deviation = 2

**Fig. 5** Oyster bed and other bottom types in Virginia part of the Chesapeake Bay (Dark spots in the figure (A, B) indicates oyster bed. Other bottom types are currently not suitable for oyster to grow, but possible oyster beds)
difference is their susceptibility to disease. Native species’
mortality is 80% higher than the non-native one. Besides,
due to the preference of the local people, the market price
of native oyster is higher than the non-native one. The
native oyster prices are collected *ex quay* at Chesapeake
Bay area, and non-native price are assumed to be around
40% of the native ones.

For each simulation trail, we specify initial settings for the
oyster model to build the habitat space and start the simu-
lation. They include the simulation area, grid specification
(side length of hexagon), initial stocking level and position,
biomass capacity, TAC, and certainty of catch. Certainty of
catch is the probability of harvest for legal-size oyster in a
cell. When it is less than one, this parameter actually reduces
the harvest rate for both native and non-native species. For
native species, this will increase the probability of restoring
native oysters. For non-native species, it increases the risk of
forming a self-sustaining population.

### 4 Simulation result

The benefit/cost analysis without introducing non-native
species can be inferred from the recent report by Tarnowski
(2007), which compared the cost of restoring native oysters
with its benefits. This paper focuses on the possible prob-
lems for introducing non-native species. The concern for
introducing non-native species includes whether it will
become a self-sustaining species, drive out, and replace the
native oysters in the Chesapeake Bay. The risk for it to
form a self-sustaining population depends on many factors.
Our model will analyze how it changes with the initial
stocking place and size, and the impact of the species
competition with native species. The simulation model will
provide a dynamic, visual display of the simulation result
about spatial oyster population, as illustrated in Fig. 2. Due
to data availability in the bottom types, we only simulate
the area in the Virginia part of the Chesapeake Bay.

<table>
<thead>
<tr>
<th>Table 3</th>
<th>Life-history parameters and economic price for native and non-native oysters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>0</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>0</td>
</tr>
<tr>
<td>R</td>
<td>0</td>
</tr>
<tr>
<td>T</td>
<td>0</td>
</tr>
<tr>
<td>Fq</td>
<td>0</td>
</tr>
<tr>
<td>M</td>
<td>0.98</td>
</tr>
<tr>
<td>Price ($^*_{P}$)</td>
<td></td>
</tr>
<tr>
<td>Native</td>
<td>0</td>
</tr>
<tr>
<td>Non-native</td>
<td>0</td>
</tr>
</tbody>
</table>

* US Dollar per piece. Source: Oyster landing price in Chesapeake Bay 2004

#### 4.1 Simulation scenarios

We devise several scenarios to demonstrate the simulation
results for different locations and initial quantities of the
native and non-native species, with or without harvest
activities. To show the difference with specie competition,
we will first present the result for the introduced species
only. Then we will specify the scenario for two species.
Two places considered for stocking oyster spats in the
simulation are A, in Rappahannock River, and B, in James
River, as shown in Fig. 2.

#### 4.2 Scenarios with single species

We start with the simulation with only non-native species
in the Chesapeake Bay, to show the survivability of non-
native triploids with respect to the place of stocking.

##### 4.2.1 Scenario 1: Non-native triploids at James River

In this scenario, the initial stocking population is
150 million spats at the one oyster cell in James River,
which equals to 230/m² in spat density. In the initial years,
the oyster will just stay at its original place, as spats are
fixed to the oyster bed. New larvae will only appear when
the undetected/reverted diploids become mature. These
larvae will quickly spread over the oyster habitats within
the same tributary in the first 5 years. From the 10th year, it
spreads over other tributaries. However, due to limited
density, oyster population starts to decrease at the 20th
year. At the 45th year, only the oyster bed in James River
still has some oyster left. At the year 48, all oysters dis-
appeared from Chesapeake Bay.

This scenario indicates that the risk for the introduced
species to be dominating species in the Chesapeake Bay is
low if the initial stocking site is in James River. The non-
native oyster will not be sustainable in the Chesapeake
Bay. It will disappear even without harvest activity.
4.2.2 Scenario 2: Non-native triploids in Rappahannock River

With the same amount of initial spat, the simulation result indicates that the non-native species will exist perpetually in the Chesapeake Bay, if the initial stocking place is in Rappahannock River. Because of the position of Rappahannock River, the oyster species stocked in this river can spread easily; hence have high probability to sustain.

The difference between these two scenarios can be attributed to the water current movement in the Chesapeake Bay area. In Rappahannock River, the water flow enables the spreading of the oyster larvae into other parts of the bay area. James River is at the downstream of the water flow, it larvae diffusion is not as efficient as that in Rappahannock River. The diffusion rates among the tributaries in the bay area are in Table 2.

4.2.3 Scenario 3: Non-native triploids in Rappahannock River with harvest

With the same initial spat population and the place of stocking for non-native oyster as in scenario 2, the simulation result shows that the species will not be self-sustaining if harvests are allowed after 10 years. The TAC is 20% of the oysters in the total simulation area, and the certainty of catch is 95%, as the oyster is fixed at the oyster bed. Thus 5% of the legal size oysters will be available for reproduction in each cell.

The population dynamics in the initial cell of oyster stocking are presented in Fig. 6. From the graph, we can see that the initial growth period in scenario 1 is just not long enough to sustain future growth. The difference between scenario 2 and 3 is the harvest after year 10. Comparing these two scenarios, we can conclude that it is possible to introduce a non-native species into the Bay area for economic benefits without the risk of having an invasive species.

4.3 Scenarios with competing species

With two species in the same bay area, they will interact with each other by competing for limited spaces and possible gamete behavior during the spawning time. Next several scenarios will demonstrate the simulation result under such an interaction. In both scenarios, the initial stocking number is set to 200 million spats (307/m²), to allow for this mutual impact.

4.3.1 Scenario 4: Native oyster in Rappahannock River, and non-native species in James River

Although the number of initial spat increased to 200 million, the oyster population still cannot support itself if we allow 20% TAC from the 10th year of the simulation.
Although native specie has better location, it still cannot compete with the non-native species, because its high market price, and high mortality rate. Therefore, the non-native species will begin to spread over in the Rappahannock River at 20th year, and will become dominant after that. However, as the population size is not sufficient to support reproduction, the non-native will start to diminish and disappear in the bay area.

The simulation result for the total population of native and non-native species in the whole simulation area is shown in Fig. 7. At the very beginning, the number of native oysters is larger than the non-native one, because only a very small percent of the introduced species is reproductive. However, once introduced oysters are generated from the reverted triploids, they all become reproductive, so it will have higher growth rate. It also shows that the harvest activity after the 10th year is the main factor for the diminishing of non-native oyster population. The value of the harvest could be around 75 million dollars at the peak time of the harvest.

4.3.2 Scenario 5: Native in James River and non-native in Rappahannock River

With native oyster in James River, non-native oyster will dominate the simulation area, able to sustain 20% TAC, and still exist perpetually in the bay area. Because of that, the value of the harvest could also last forever (Fig. 8). However, this scenario does not consider any possible negative impacts from the over-dominating population of non-native oyster species in the Bay area. The main concerns for the negative impact include: clogging the waterway, eradicating the native oyster species, competing with other living organisms for space and food, and changing the bio-diversity of the local environment and the biological structure of the ecosystem. These are actually the main concerns for the introduction of the non-native species.

These five scenarios demonstrate the different outcomes with different initial stocking levels at different tributaries of the bay area, with or without the interactions of the native species. For both cases (single species and two species), it reveals that non-native species will be more easily spread and fill in all the oyster beds when it is stocked in the Rappahannock River. In scenario 2, the non-native oyster will spread all over the oyster bed in the simulation area and grow to the capacity level without harvest. The risk exists for the non-native species to become invasive. As the purpose of introducing non-native species is for its economic value, scenario 3 shows that the oyster population will not last forever with harvests. This minimizes the risk for the introduced species to become invasive, and at the same time, meet the market demand for oysters. It is not an issue for the disappearing of the non-native species, as it can be re-stocked again if it is diminishing. Scenario 5 illustrates a case where the oyster population becomes perpetual even with 20% TAC, which illustrate higher catching rate or lower initial stocking level should be adopted, to minimize the risks for the introduced species to become invasive.

Scenario 4 and 5 also demonstrate the concerns on how to protect the native species that is under a threat due to both over harvest and the impact of diseases. With the introduction of non-native species with lower mortality rate, the native species is under unfavorable position in the specie competition. In both scenarios, the native species will be replaced by the non-native species. If the management decision is to protect the native species, then it is necessary to adopt a more conservative policy in introducing the non-native species.

5 Conclusion

This paper introduced the agent based simulation model for spatial population growth and species competition, and applied it to the risk analysis for the intentional introduction of the non-native oyster species into the Virginia part
of the Chesapeake Bay. It integrates the bio-economic model of Oyster population dynamics with the spatial spreading and movement of the oyster larvae over the actual distribution of the existing oyster habitats in the real environment.

Compare with Dew’s results, the simulation results from this research indicate that it should be more careful when introducing non-native triploids into the bay area. With the similar stocking density, the non-native oyster would become self-sustaining with 30 years’ stocking period in Dew’s simulation, while in our simulation only one year is necessary. This implies that the simulation without consider the distribution of the oyster bed and spatial interaction may underestimate the risks for the non-native species to become invasive, thus underestimate the risks to the Coastal marine and estuary environment.

There are a couple of limitations to this research, which may require further studies. First, the position and level of existing stock of the native oyster is not known. To enable the restoration of the native species, it is necessary to survey the existing status of the native species, and then to select a location and level of non-native species to minimize its impact on the native species. Second, the simulation model only included the Virginia part of the Chesapeake Bay, since the bottom type data are not available in upper part of the bay.

Nonetheless, this simulation model revealed one important issue regarding the policy of introducing non-native species in the marine environment. Effective measures for reducing the risks and uncertainties of introduced species could be employed, so that economic benefits could be obtained, and at the same time the local ecological environment can be preserved.

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