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Deidre F. Gilbert

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**MODELING THE ROLE OF NO-TAKE MARINE RESERVES
IN FISHERIES MANAGEMENT**

By

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A.B. Bowdoin College, 1995

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

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(in Marine Policy)

The Graduate School

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By

Deirdre F. Gilbert

Thesis Advisor: Dr. James Wilson

An Abstract of the Thesis Presented
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In recent years there has been increasing interest in the potential of no-take marine reserves to benefit fisheries management. Scientific reviews have shown that reserves often lead to substantial increases in the density, biomass, size and diversity of marine fishes inside their boundaries. However, little empirical work has been done to determine the effect of reserves on the fisheries outside their boundaries, such as potential changes in yield, size of fleet, or variability in catch.

In order to explore the interaction between the biological growth and dispersion processes of the harvested stock and the changing economic incentives of harvesters created by reserves over space and time, many researchers have turned to a modeling approach. Models are being used to construct the framework that will inform the policy decisions of how and when marine reserves are used for fisheries management. This thesis examines the information provided by these models and describes an original model developed in order to examine the effect of the management regime in place before reserve formation and outside its boundaries in a multiple species fishery.

Chapter 1 provides a review of the existing reserve models that have been developed to address questions related to the potential impacts of the creation of a marine reserve on finfish fisheries. It describes the variation in these models in terms of their construction, their biological and economic assumptions, and the specific questions they were designed to explore. It provides a summary of the conclusions that have been drawn to date with regard to the effect of reserves on modeled populations, and indicates some elements of the problem the traditional modeling approach has overlooked.

Chapter 2 describes an original multiple species bioeconomic model designed to explore the effect of reserve creation on fisheries for five species with different life history characteristics, under different biological and economic assumptions.

Chapter 3 provides information on the tests that were run to ensure that the model conformed to expectations based on basic biological and economic theory. It also presents the results generated with the model for different species under different management regimes. Unlike earlier models, we find that benefits from a reserve can accrue under optimal "sole owner" management. Our model also illustrates that the creation of a reserves will affect different species very differently, depending on parameters such as the amount of larval drift and adult spillover, as well as the management regime. Finally, it confirms results from an earlier model that reserves are likely to be useful in reducing year to year catch variability.

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Chapter 1

MODELING THE ROLE OF NO-TAKE MARINE RESERVES IN FISHERIES MANAGEMENT: A SYNTHESIS

Introduction

In recent years there has been increasing interest in the use of marine protected areas (MPAs) as a tool for improving marine conservation and resource management (see Bohnsack 1990; Rowley 1994; Allison et al 1998). The obvious impetus for the consideration of no-take MPAs (also known as marine reserves) for fisheries management is the generally poor condition of many commercial fish stocks worldwide. The latest trends show that the number of underexploited and moderately exploited fisheries resources have been declining, and the number of overexploited, depleted and recovering stocks has been increasing (Food and Agriculture Organization 2000). Particularly dramatic examples of management failures from the Northwest Atlantic include the collapse of the Canadian groundfish stocks and the depressed levels of many of the commercial species in the Gulf of Maine and on Georges Bank. As these declines in stocks have occurred despite significant and burdensome regulations placed on fishermen, the seemingly limited success of the traditional management tools suggests to many (scientists, managers, and industry members alike) that it is now necessary to consider alternative approaches.

In these early stages of developing policies regarding the use of marine reserves, a major difficulty is anticipating the effects of reserve designation. There are only a relatively small number of no-take marine reserves worldwide, estimated at less than one percent of the ocean's area. They are often small, relatively young, and generally have not been thoroughly studied. Empirical work has been complicated by difficulties in obtaining adequate controls, and in some situations, an inability to undertake long term monitoring. In some areas, the effectiveness of the reserve may have been compromised by enforcement issues. Furthermore, most empirical work has focused on the conservation benefits of reserves on habitat, and on their effects on species within the boundaries of the reserves (typically increases in average size, abundance, and/or biomass) (Roberts 1995; see Dugan & Davis 1993 and Halpern & Warner 2002 for reviews). Few studies have considered how the management rules outside the reserve might be influencing its "success", and few studies have considered the economic effect of a marine reserve on local communities (e.g. changes in the overall yield from the fishery, changes in the size of the fleet following designation). In order to explore the consequences of the interaction of both biological and economic factors, many researchers have turned to a modeling approach.

Modeling Background

Researchers develop models to assist with the understanding, and in some cases the prediction, of the patterns and dynamics of real world systems. Costanza et al (1993) characterize models as "...crude, although in many cases absolutely essential, abstract

representations of complex territory” (p. 547). Such representations are vital for the “complex territory” of the intersection of marine reserve policy and fisheries management, as relatively little guidance has thus far been provided by empirical studies incorporating both biological and economic concerns. Many questions persist regarding the potential effects of a marine reserve, both on the fishermen and the fish. The rapidly expanding reserve modeling literature attests to the current high level of interest in the insights this method of research could provide.

This chapter provides a survey of the models that have been developed to address questions related to the potential impacts of the creation of a marine reserve on a finfish fishery. It attempts to lay out the full range of variation within these models, in terms of their construction, their assumptions, and the specific questions they were designed to explore. It is intended that this analysis will provide a summary of the conclusions that have been drawn to date with regard to the effect of reserves on modeled populations, and indicate some elements the traditional modeling approach has overlooked, as well as possible directions for future research.

When evaluating the results produced by various models it is useful to keep in mind the classification scheme first suggested by Holling (1964) and later described by Costanza et al (1993). Holling’s scheme stresses the consideration of three criteria particularly useful for this discussion. They are:

Realism: “Simulating system behavior in a qualitatively realistic way”
 Precision: “Simulating behavior in a quantitatively precise way” and
 Generality: “Representing a broad range of systems’ behaviors with the same model”.

Clearly, no one model can succeed in maximizing all three of these goals.

Instead, a decision is made during model construction to place emphasis on the criteria

that will assist the modeler in achieving a prioritized objective. It is important to remember that the reserve models described here lie along a continuum from high generality conceptual models to higher precision predictive models, making direct comparisons difficult in many instances. Nevertheless, dissimilar models drawing basically similar conclusions may serve as evidence for the robustness of the particular result. Costanza et al (1993) quote Levin (1966):

“we attempt to treat the same problem with several alternative models each with different simplifications...Then, if these models, despite their different assumptions, lead to similar results we have what we call a robust theorem which is relatively free of the details of the model. Hence our truth is the intersection of independent lies.”

In addition to the differences attributable to the range of modeling goals described above, the marine reserve models differ in a number of other important respects. Both analytical and simulation models have been used to represent a variety of species, typical of fundamentally different ecosystems. These range from reef dwelling species of the Caribbean to demersal species of the Northwest Atlantic. The choice of system/species is important, since it will dictate important biological dynamics (regarding the degree of adult movement, for example). Specific model parameters, such as the intrinsic growth rate of the simulated population, will also impact the results the model produces (Sladek Nowlis & Roberts 1999).

Finally, many relationships and variables that must be defined in fisheries reserve models are not actually known with a high degree of certainty, adding another level of variability between models. True values for such parameters as natural mortality and larval survivorship are largely unknown, but must nonetheless be specified. For those relationships where there is an absence of scientific consensus, different modelers have

taken different approaches, and all reasonable constructions must be considered equally justifiable.¹ Fortunately, many parameters can be used as control variables, allowing the modeler to explore a variety of assumptions. However, for those relationships which must be specified, it is important to keep the assumptions particular to each model in mind when drawing comparisons.

Every marine reserve model must contain representations of at least two interacting sectors – the biological population subject to harvest, and the harvesters. Described below are the critical components of each of these sectors, and the range of ways modelers have found to deal with them. The critical features identified within the biological sector include 1) population structure, 2) larval dynamics and 3) adult spillover. The discussion of the economic sector focuses on 1) the methodology used to simulate fishing effort and 2) the typical time horizons of the models.

Model Construction

Biological Sector

Population Structure. The simplest way to model a harvested population is as a single, undifferentiated biomass, without regard for age/size structure. Typically, such a biomass is constrained to grow according to the logistic equation $[rN(1-N/K)]$, where r is the growth rate and N is the population size, to an arbitrarily chosen carrying capacity, K .

¹ Success of settlement/recruitment to age 1 is one such relationship, which modelers have approached in several different ways. It has been modeled as a density dependent phenomenon, either as a function of the total biomass (e.g. Sladek Nowlis & Roberts 1999, Holland & Brazee 1996) or the density of settlers (e.g. Hastings & Botsford 1999). Alternatively, some models calculate recruitment from a stock recruitment relationship, using either the Beverton-Holt or Ricker equation (e.g. Guenette & Pitcher 1999, Sumaila 1999).

This approach is favored for its analytical tractability and its logical simplicity; when the population size is far below K growth is proportional to the small population size. When the population grows larger, the rate of growth increases until the population approaches K . At this point growth slows, and at K ceases, presumably due to the presence of some limiting resource. Although it is recognized that this approach has limited empirical applicability, several researchers have determined it adequate to identify the qualitative patterns necessary for addressing operational and policy questions related to marine reserve implementation (e.g. Hannesson 1998; Lauck et al 1998; Mangel 1998; Sanchirico & Wilen 1998, 2000).

The next level of sophistication in biomass modeling incorporates a rudimentary age structure by dividing the harvested population into two age classes: eggs/larvae and adults (e.g. Hastings & Botsford 1999; Pezzey et al 2000). This distinction creates the possibility of specifying different rates of transfer between the reserve and open area for these two age classes, an important capability when exploring the long-term effects of reserve designation. Pezzey et al (2000) modify the assumption of a single undifferentiated biomass in order to allow eggs/larvae to serve as the ecological linkage between the reserve and the fishing ground. Creating a division between eggs/larvae and adults also allows the researcher to define different mortality rates for these two groups.

The last group of models utilizes a detailed age structure to characterize their species-specific populations. Most commonly this entails a specified schedule of weight-at-age and fecundity-at-age data, as well as the probabilities of having recruited to the fishery at a given age (e.g. Polacheck 1990; Guenette & Pitcher 1999; Sumaila 1998). Weight-at-age data may be calculated using the von Bertalanffy equation, or it may be

provided by measurements from actual populations. Modifications to this approach include incorporating density-dependent growth rates, where the weight of fish is determined both by its age and the population density (e.g. Holland & Brazee 1996), or categorizing the harvested population according to length, rather than age, classes (e.g. Sladek Nowlis & Roberts 1999). Length classes are used to indicate that size is likely more relevant than age in dictating fecundity and recruitment to the fishery.

Models utilizing a sophisticated age/size structure are clearly the most detailed biologically, and therefore have the capacity to address aspects of reserve theory not otherwise possible. Specifically, these models capture the capacity of a reserve to extend the age structure of populations within the reserve (in the absence of very high adult transfer rates) and can track changes in the spawning stock biomass. Since many species become exponentially more fecund with advanced age², this effect of the reserve can contribute significantly to reproductive potential of a harvested stock. If there is a relationship between increased egg production and increased recruitment, models that do not incorporate this effect may understate the value of the reserve to the fishery.

Larval Dynamics. A second important assumption of the biological sector of the model concerns the nature and extent of the movement of eggs/larvae from the reserve to the fishing grounds, and the factors influencing their subsequent settlement. A potentially very powerful way that marine reserves could contribute to stock sustainability is by exporting eggs and larvae from the reserve into the fishery (Roberts 1997; Horwood et al 1998). The difficulties inherent in tracking planktonic larvae however, have made it challenging for researchers to establish empirical estimates for larval export rates from

² A fully grown (61 cm) female Atlantic red snapper (*Lutjanus campechanus*) produces 9,300,000 eggs, 212 times the number produced by a 42 cm female, a size considered large in an unprotected fishery (Bohnsack 1990).

existing reserves (Rowley 1994). Nevertheless, it is generally believed that there is some potential for the export of larvae from reserves to augment regional fisheries.

As described above, models in which the biomass is not differentiated at least between eggs/larvae and adults are not well equipped to address the question of the contribution potentially made by larval export (e.g. Hannesson 1998; Lauck et al 1998; Mangel 1998). Even in those cases where the biomass is differentiated into age classes, not all researchers include an explicit term for larval export. Instead, these models often use a stock-recruitment relationship to generate values for recruitment in the reserve and nonreserve areas. The only biological transfer between the two areas is the subsequent movement of adults (e.g. Sumaila 1998; Guenette & Pitcher 1999).

In those models where larval export is explicit, it is typically handled in the following way: all larvae produced in both the reserve and nonreserve areas during each year are assumed to mix thoroughly and redistribute uniformly over the fishery and protected area according to their relative sizes (e.g. Holland & Brazee 1996). The factors influencing the subsequent survival of these larvae however, differ between models. In Hastings & Botsford's (1999) model, all density dependent mortality occurs at the time of settlement, and depends only on the density of settling juveniles. Sladek Nowlis & Roberts (1999) also modeled settlement as a density-dependent process, utilizing a negative exponential function to predict survivorship of new settlers in their first year. However, in their equation, the density of individuals that survivorship depends upon is the density of the entire biomass of the population, not just settling juveniles. Similarly, in Holland & Brazee (1996) survival of the larvae to recruitment at age 1 is dependent on local biomass density, including all age classes. Only recently have any modelers

considered the alternative scenario where consistent oceanographic conditions generally ensure the transport of some portion of the larvae in one direction (e.g. Tuck & Possingham 2000), although there is some evidence for the potential for such “source-sink” situations (Roberts 1998).

Adult Spillover. It is frequently hypothesized that individuals fully protected by an reserve will grow to larger sizes and higher densities than those outside the reserve. Empirical evidence suggests that this is an actual effect of no-take reserves, and that increases in density can be dramatic (Alcala 1988; Polunin & Roberts 1993; see Roberts & Polunin 1993 and Halpern & Warner 2002, for reviews). Should these individuals subsequently move across the reserve boundary (the “spill-over” effect) they would become vulnerable to the local fishery, perhaps subsidizing the loss of fishing area that occurred with the establishment of the reserve. Empirical evidence of this effect is less widely documented. The observed tendency for some fishermen to set gear close to reserve boundaries indicates that spillover can provide at least some benefit to local fishermen (Dobrynski & Nicholson 2001). In addition, there is potential for reserves to export exceptionally large fish. Merritt Island National Wildlife Refuge (MINWR), outside of Cape Canaveral, Florida, has been a no-take area since 1961. It was recently determined that higher frequencies of state and world record-sized red and black drum and spotted sea trout are caught in close proximity to MINWR than elsewhere in Florida (Roberts et al 2001).

The extent to which adult emigration from the reserve occurs will be an important factor in evaluating the effect of the reserve on the fishery. Very high transfer rates could initially help reduce the decline in catch from the fishery caused by the loss of fishing

grounds, but may ultimately also reduce the benefits of the reserve as a source of eggs and larvae. Very low transfer rates may assist in the buildup of the spawning stock biomass, but at larger reserve sizes, the increased larval production may provide only relatively little benefit to the fishery when compared to the portion of the possible harvest forfeited.

Consistent with some theories regarding the movements of coral reef fish, some models assume that following settlement, adults are sedentary within the reserve for the remainder of their lives (e.g. Sladek Nowlis & Roberts 1999; Hastings & Botsford 1999; Pezzey et al 2000). For more mobile species, other models incorporate the movement of adults and explore the effects of a range of nominal transfer rates (e.g. Sumaila 1998). Transfer rates are often further modified between simulations to reflect other conditions of the model, including reserve size (e.g. Polacheck 1990; Guenette & Pitcher 1999), and differences in density between the reserve and the fishery (e.g. Holland & Brazee 1996; Sanchirico & Wilen 1998, 2000). The modifications in relation to reserve size reflect the notion that all other things being equal, the transfer of fish out of a large reserve should be proportionally smaller than the transfer of fish out of a small reserve. This is based simply on the fact that the probability of leaving a small reserve is larger than that of leaving a large reserve. Modifications of the transfer rate based on density reflect the premise that emigration rates may be responsive to resource limitations, such that fish move away from areas of higher densities at faster rates. In these models, actual transfer rates are highest where the difference in density is large.

Economic Sector

In addition to biological processes of reproduction, growth, and dispersion, each reserve model must have a corresponding component that simulates the dynamics and impacts of the harvesting sector. Like the biological sector, these simulations may be fairly simplistic, or quite sophisticated. The construction and assumptions of the economic sector will also bear heavily on the results produced by model; the full range is therefore described below.

Fishing Pressure. The simplest approach to modeling fishing pressure is simply to designate fishing mortality as a constant percentage of the available stock. This method is used by Sladek Nowlis & Roberts (1999), who represent fishing mortality with u , equal to the proportion of fishery recruited individuals caught per year³. By varying this parameter from 0.01 to 1.00 in successive simulations, they determine the optimal size reserve for each level of mortality. Lauck et al (1998) also use u to represent the targeted harvest fraction. However, their model assumes that due to the irreducible uncertainty associated with the stock estimates, and as a result of incidental mortality, the actual harvest is uncontrollable. The actual harvest is therefore taken from a probability distribution, which has u as its mean, and which is further modified by increasing coefficients of variation.

More commonly, modelers have chosen to hold fishing effort constant for the duration of a simulation and to derive fishing mortality from the effort level (e.g. Polacheck 1990; Holland & Brazee 1996; Guenette & Pitcher 1999; Sanchirico & Wilen 2000). This method bears similarities to a fishery managed under a limited entry regime,

³ u is related to F , the more common measure of fishing mortality in the following way: $u = 1 - e^{-F}$ (Sladek Nowlis & Roberts 1999).

where the total number of harvesters allowed has been specified *a priori* and may or may not bear any relationship to the condition of the stock. Researchers compare the results of increasing amounts of effort for reserve v. non reserve regimes. In these models fishing mortality generally increases in the presence of a reserve, since effort, unable to exit the fishery, is invariably concentrated in the remaining fishing grounds. The resulting increase in fishing mortality is therefore a function of the size of the reserve, with larger reserves resulting in higher levels of fishing mortality⁴ outside their borders.

As interest in marine reserves as a fisheries management tool has increased, it has several times been suggested that models which hold either fishing mortality or fishing effort constant may not be sufficient for exploring their full implications (Hannesson 1998; Sanchirico & Wilen 1998; Sumaila 1998). Economic incentives are likely to change following the creation of reserve. If the reserve provides a benefit to the adjacent fishery there will be incentive for others to join the fishery, and effort and mortality could increase. If catches decrease in the wake of reserve creation there will be incentive for exit. In order to simulate this dynamic response, some modelers are incorporating a more robust description of the harvesting sector, mimicking in their extremes the open access nature of some fisheries, versus the ideal of optimal (rent-maximizing) management.

“Open access” refers to a management regime where no property rights exist, and entry into the fishery is not restricted. According to standard economic theory, entry into the fishery will continue until total revenues just equal total costs (including a normal profit component). If the condition of the resource declines and profits become negative, exit from the fishery will take place until profits are returned to zero. Likewise, an

⁴ Because effort is assumed to be redistributed into a smaller area, instantaneous fishing mortality is modified by the following equation: $F_{\text{fishing area}} = F \times (1-RS)$, where RS = the proportion of fishing grounds made into a reserve.

improvement in the resource and in the profits is an invitation to entry, causing a return to the zero conditions. In this way, open access inevitably results in the dissipation of potential rents generated by the fishery.⁵ In all of the models considered here, both the price of fish and the unit cost of effort used for determining profits are held constant for the duration of a simulation. This assumption is made for the sake of analytical tractability, although several researchers acknowledge the possibility that both these variables would respond to the creation of a reserve⁶. Several researchers simulated the open access situation in their models (e.g. Hannesson 1998; Sanchirico & Wilen 1998; Pezzey et al 2000), allowing the amount of effort to equilibrate in response to the condition of the stock, before and after reserve creation.

In contrast, optimal management entails the deployment of that amount of effort which will maximize rents for a given year. Because this decision must be made for the fishery as a whole, this type of management is sometimes conceptualized as operated by an idealized “sole owner” or authority, which has the knowledge and ability to limit effort according to these criteria. Hannesson (1998) uses this regime as a comparison against an open access regime, and against open access with a marine reserve. Sumaila (1998) also uses optimized (discounted) rent maximizing to characterize management in his model of the Barents Sea cod fishery. He hypothesizes that Norway and Russia, the two countries with fishing rights to the stock, will cooperate to harvest the appropriate amount of biomass in order to eliminate both biological and economic waste of the

⁵ Rents are the difference between industry revenues and industry costs over the length of the fishing season (Homans & Wilen 1997).

⁶ A reserve could have multiple and opposing effects on both price and cost. If the reserve improved the yield from the fishery, increasing supply, price could decline. However, a reserve may also ultimately change the size distribution of the catch, increasing the percentage of older, larger fish. Larger individuals may command a higher price. Costs could decrease following the creation of a reserve if fish became more abundant and easier to catch, or increase if the closed area necessitated an increase in travel time, or congestion in the open area (Sanchirico & Wilen 2000).

resource. In order to compensate for the lack of full and accurate information about the fishery due to environmental variability however, the countries enter a mutual agreement to utilize fully protected marine reserves.

Time Horizon. The majority of reserve models forecast results ranging from 28 to 60 years into the future (e.g. Holland & Brazee 1996; Lauck et al 1998; Sumaila 1998; Guenette & Pitcher 1999; Pezzey et al 2000). Sladek Nowlis & Roberts (1999) conducted the longest simulations by far, operating their model over 500 years. This length of time was considered necessary for the model to reach equilibrium, and to remove any bias created by the initial starting conditions. Knowledge of the time horizon of the model is most important in those cases where the researchers evaluate the success of the reserve based on a discounted value for the catch, rather than simply on the average size of the catch (Holland & Brazee 1996; Sumaila 1998). Using a discounted value will significantly affect the size at which, or even if, a reserve becomes beneficial. Holland & Brazee (1996) found that at a specific effort level, the optimal reserve size fell from 18% to 0% when the discount rate was raised from 0 to 20%, a value considered not unreasonable for some developing countries.

The majority of models do not explicitly discuss short-term consequences of reserve designation, i.e. the effects on fishery yield in the initial years of implementation. This is likely to be an important consideration in reality however, since the political acceptability of a reserve may in part depend on how quickly the benefits are realized. Failure to detect a benefit in a "reasonable" amount of time could cause a reserve strategy to be abandoned. Holland & Brazee's (1996) dynamic model is one of the few that provides information on the initial response of the system to reserve designation. They

calculate the minimum harvest occurring in the years immediately following reserve creation. At the optimal reserve size for moderate levels of effort (1.5 and 2 on a scale of 0.75 to 2.5), annual harvests fall by 9-13% initially. The new equilibrium harvest level is reached within 6-9 years. In those situations where a community cannot cope with the initial drop in harvests caused by the reserve, Holland & Brazee (1996) suggest the alternative approach of starting with a smaller reserve than is optimal and gradually increasing its size.

Model Results

Given the wide variety in their construction and assumptions, what can the existing models as a group tell us about the effects of marine reserves on fisheries? Many claims have been made with regard to what reserves might accomplish, but not all of these can be addressed using a modeling approach. At a minimum, most models in some way evaluate the effect of a reserve on stock size/safety, as well as the effect of the reserve on the yield from the fishery. A subset of models offer additional insights, including the effect on the discounted value of the catch, the variability of the catch, and the effect of a reserve in an uncertain environment.

Effect of Reserves on Stock Size/safety

Following the establishment of a marine reserve, the alleviation of fishing pressure will presumably allow the biomass of the fished species within the reserve to grow to a level higher than that which is likely in the absence of this protection.

Researchers consider this result to represent the *conservation* benefit of a reserve (Hannesson 1998) or the *refuge* effect (Sanchirico 2000). Regardless of its impact on the harvests from the fishery, at a minimum a reserve should present some measure of security for the stock for which the reserve is designed, and perhaps provide some degree of insurance against the potential overexploitation which could occur in the remaining open area. In fact, empirical studies have commonly found increases in the size and density of the previously harvested species within reserves (see Rowley 1994 and Halpern & Warner 2002 for reviews). It is important to note however, that there are rare instances of decreases in density of some fished species within reserves (Alcala & Russ 1990). It is likely that the creation of a reserve could initiate complex, community-level changes (Babcock et al 1999), which may be responsible for these unpredictable results. Because the existing reserve models are mainly focused on individual species and do not incorporate such ecosystem effects, all find that the standing biomass of the targeted population increased in the presence of a reserve. Increases ranged from 20-400%. The increase was greatest with larger reserves, and in instances where the adults were characterized by low to moderate transfer rates.

Polacheck (1990) adapted the Beverton-Holt (1957) yield-per-recruit (YPR) model to assess the impact of a closed area on a cohort of Atlantic cod. This model was used to compare the fraction of the cohort that survives to a given age at a constant F and at transfer rates of 0.1 and 1 in a 10% reserve regime, to identical situations in a non-reserve regime. With a reserve, at the lower transfer rate, (0.1) the probability of an individual surviving to age 10 increased by a factor of over 50. Even at the higher transfer rate (1.0) the probability of survival to age 10 increased by 1.8. The reserve was

therefore responsible for a shift in the age distribution of the local population to older individuals. This shift resulted in a substantial increase in the spawning stock biomass. The increase was especially significant in situations of lower transfer rates and higher fishing mortalities. At lower fishing mortalities the total spawning stock biomass (SSB) was already closer to the maximum possible, and therefore the contribution made by the reserve was comparatively small.

Unfortunately, Polacheck (1990) also demonstrated that the same conditions which favored a substantial increase in SSB of the targeted species often also caused a loss in yield-per-recruit to the fishery. The sole exception was the combination of large reserves (~40%) and high transfer rates (1.0) in a fishery subject to high fishing mortality. These conditions allowed a similar increase in SSB at little or no cost in YPR. Based on these results, Polacheck (1990) suggested that when fishing mortality rates are high, closed areas could be effective in increasing the spawning stock biomass with no reduction in fishing effort and under some circumstances, without loss of yield. He concluded that the primary benefit of closed areas would likely be the prevention of recruitment overfishing.

Like the Polacheck (1990) model, the Guenette & Pitcher (1999) model focuses on the effect of a marine reserve on a population of Atlantic cod. The Guenette & Pitcher (1999) model however, is a non-equilibrium dynamic pool model, which includes a stock recruitment relationship absent from Polacheck (1990). This model also demonstrates that a reserve can be instrumental in maintaining the spawning stock biomass at higher levels, especially at extreme exploitation rates. Due to the incorporation of the stock recruitment relationship, increases in the SSB in this model will have an effect on

subsequent recruitment. Guenette & Pitcher (1999) explore the results generated by both Beverton and Ricker recruitment curves and find qualitatively identical results.

As in Polacheck (1990), the spawning stock biomass in the Guenette & Pitcher (1999) model decreased as the transfer rate of adults increased. Even at the highest transfer rates however, the spawning stock biomass was maintained at levels higher than the non-reserve regime, which suggests that reserves may be useful in this regard even for highly mobile species. In addition, Guenette & Pitcher (1999) were also able to show that reserves which contained >30% of the management area significantly lowered the number of years of poor recruitment, particularly at exploitation levels greater than $F=0.3$. Of course, this result is dependent upon the appropriateness of a stock-recruitment relationship, a question for which there is currently little consensus.

Sumaila's (1998) model, based loosely on the Barents Sea cod fishery, was developed to look specifically at the benefits a protected marine reserve might provide in the face of a severe shock to the system in a rent-maximizing fishery. In this model, the shock takes the form of a severe recruitment failure for years 5-15 of a 28-year simulation. Under these circumstances the reserve yielded a clear biological benefit, since under a variety of reserve sizes (0.1-0.7) and transfer rates (0.1-0.5) stocks remained higher than under non reserve conditions. Sumaila (1998) also developed an "index of biological safety", which evaluated the average standing spawning biomass relative to the minimum safe level of spawning biomass. The larger the index, the more biologically safe the stock is expected to be. As reserve size increased from 0 to 70% of the management area, the economic rent generated from the fishery decreased 28%. At the same time, average stock size more than doubled. As expected, a larger reserve size

ensured a high biological safety index for the stock. Sumaila (1998) therefore concluded that the nature of the challenge facing fisheries managers in selecting reserve size is locating an acceptable trade-off between the current economic benefits provided by the fishery and the future biological safety of the stock.

Sanchirico & Wilen (1998) examined the potential for reserves to increase aggregate system-wide biomass, using this measure as a proxy for safety from stock collapse in an open access fishery. Interested particularly in the effect of marine reserves in systems with different biological linkages, they considered three dispersal systems. Under the closed system, there was no dispersal between the reserve and the fished area. Under a sink-source system, the biomass flow was unidirectional but strength was density-dependent. Finally, under the simple density-dependent system, biomass could flow in either direction. The closed system model produced the intuitive result that creating a reserve will always increase aggregate biomass, since the stock in the reserve will build to its carrying capacity and never become vulnerable to the fishery. In a sink-source system, under uni-directional density dependent flow, they found that closing either the sink or the source would increase aggregate biomass over the base case of an open access fishery. The same result was derived for a simple density-dependent system.

As an alternative to looking at the absolute changes in biomass, the effect of a reserve on stock safety can also be evaluated by considering the potential of the reserve to mitigate the danger of stock collapse. Pezzey et al (2000) modeled an open access fishery in which it was possible for the fishing ground stock to become momentarily extinct as a result of a sudden pulse of overfishing. However, since the reserve supplied a ready source of eggs and larvae, the stock could subsequently recover in a way that was

not possible in the absence of a reserve. Pezzey et al (2000) note this as an effect of the reserve, but do not describe how frequently this dynamic occurs. Holland & Brazee (1996) also note the ability of a reserve to provide insurance against stock collapse for fisheries under very high levels of effort. According to their analysis of a red snapper fishery, this insurance can be obtained at little cost in terms of foregone annual harvest. Specifically, a reserve covering ~30% of the fishery provided an equilibrium yield that was ~95% of MSY, at a level of effort which would have otherwise caused a stock collapse.

Effect of Reserves on the Yield from a Fishery

In the context of fisheries management, the impact of a marine reserve is measured not only by how it will affect a stock's standing biomass, but also by how it will affect the yield the fishery can sustain. Many researchers have hypothesized that under certain circumstances, marine reserves could provide a yield equivalent to that obtainable through traditional fisheries management (Hastings & Botsford 1999) or even increase the size of the sustainable harvest (Sanchirico & Wilen 1998). Models have proved useful in eliciting these circumstances, as they allow researchers to examine a wide range of both biological and economic assumptions.

There are limited empirical examples of the yield from a fishery increasing in association with the implementation of a marine reserve. The most oft-cited case is probably the indirect evidence provided by Sumilon Island in the Philippines, where in 1974 25% of the reef area surrounding the island was set aside as a no-take reserve. The reserve system broke down in 1984, and fishing resumed over the extent of the reef.

Eighteen months later both catch per unit effort and total yield from the fishery had dropped to ~50% of previous levels (Russ & Alcala 1990). Emigration of adults from the reserve to the adjacent harvest zone is suggested as the mechanism that allowed for the increased yield during the reserve years (Dugan & Davis 1993). This movement, often referred to as “adult spillover” is simulated in most reserve models through increasing transfer rates.

The earliest analyses of the effect of a reserve on yield were done with yield-per-recruit models (Beverton & Holt 1957; Polacheck 1990), and suggested that while yield-per-recruit could increase in the presence of a reserve, the increase was usually minor. The increase in yield was detected only in comparisons with non-reserve regimes experiencing very high levels of fishing mortality. The development of dynamic models, incorporating stock-recruitment relationships has modified these findings slightly. Under a wide variety of ecological and economic situations, more recent models have consistently found the critical factor in determining whether a reserve could increase the yield from the fishery was the level of fishing mortality the population was subject to prior to reserve formation, or in a non-reserve regime. Under certain circumstances, increases in yield achieved through a reserve were significant. The *size* of the yield increase depended heavily on the nature and extent of the benefits provided by the reserve, in terms of larval transport and/or adult spillover. For example, in the Guenette & Pitcher (1999) model, when the exploitation rate was held at MSY and adult transfer was 0.3, the yield was reduced 12-50% in the presence of a reserve (sized from 30%-70% of the management area). However, for exploitation rates beyond MSY, the yield without a reserve collapsed, while a reserve made possible a yield of 23% that obtainable

at MSY. At a constant exploitation rate of 0.35 (beyond MSY), increasing the transfer rate of adults from 0.1 to 0.4 increased the yield over the non-reserve situation for reserves smaller than 70%. At transfer rates higher than 0.4, yield plateaued.

Sladek Nowlis & Roberts (1999) obtained similar results using a model with the fundamentally different biological assumptions of widely dispersed larvae and sedentary adults. Using the same model to independently evaluate four different coral reef species with different intrinsic population growth potentials⁷, they determined that an increase in overall catch (compared to no reserve) would occur for every species with the use of an optimally sized reserve whenever the fisheries were exploited above the MSY level. As fishing mortalities increased, so did the size of the optimal reserve. Moderately to heavily exploited fisheries required very large reserves (>60% of the fishing area for all species except for the red hind, which required a ~45% reserve even when $\mu=1.0$) to sustain their yields. However, for the species with lower growth rates, yield was always equivalent to MSY or higher, at any exploitation rate, as long as the optimal size reserve was used. Extrapolating their results to actual Caribbean fisheries subject to very high levels of fishing mortality, their model proposed reserve sizes as large as 80% of the management area. Sladek Nowlis & Roberts (1999) concluded that although reserves provided benefits in the form of increased yield for any species that was overfished, they were particularly important for populations with low intrinsic growth rates. Such populations are at the greatest risk of overfishing, and reserves may provide an important buffer against potential collapse.

⁷ *Panulirus penicillatus* (Red Sea spiny lobster) $\lambda = 1.08$, *Balistes vetula* (queen triggerfish) $\lambda = 1.11$, *Haemulon plumieri* (white grunt) $\lambda = 1.16$ and *Epinephelus guttatus* (red hind) $\lambda = 1.31$.

In contrast to the models described above, which utilize life history data tailored to particular species, there is also a group of generic biomass models, developed to derive some basic “rules of thumb” regarding the effect of a reserve on yield. Pezzey et al (2000) used such a model to identify criteria to determine whether the creation of a reserve will result in a sustainable increase in catch in an open access fishery. They claim that knowledge of the initial stock density (prior to reserve creation) and the stock’s current proximity to the population’s carrying capacity is all that is required to anticipate reserve effects. If under open access equilibrium conditions, the fish stock is reduced to $1/2$ the density of the carrying capacity, then creation of a reserve will increase equilibrium catch. The catch maximizing proportion of the reserve approaches 50% as the initial ratio of stock to carrying capacity approaches zero. Pezzey et al (2000) took these results and applied them to actual Caribbean fisheries experiencing varying levels of fishing intensity, for which the important model parameters were known. They predicted optimal reserve sizes of 20-40% for the species examined, and increases in catch of 10-80%. Even if the increase in catch was estimated conservatively at 30%, Pezzey et al (2000) hypothesized that the use of reef fishery reserves could increase the value of the annual world catch by one billion U.S. dollars per year.

Hastings & Botsford (1999) used a generic biomass model to compare the maximum sustainable yield that could be achieved through the management of fisheries using reserves to that achieved through traditional effort controls. The traditional effort controls were simulated as either harvesting a fixed fraction or a fixed number of the population. Under the simplifying assumptions that they utilized, yields were equivalent through either of these approaches. Furthermore, the optimal fraction of coastline in

reserves (as a percentage of the entire fishing area) was always smaller than the fraction of adults that would remain unharvested under traditional management techniques.

Because they were able to demonstrate that equivalent yields are possible, Hastings & Botsford (1999) strongly urged consideration of the use of reserves in appropriate situations, since reserves could provide additional advantages, including reduced catch variability and sustainability under uncertainty that traditional effort controls may not.

Hannesson (1998) also used a general biomass model to compare the yield that could be achieved from an optimally managed (rent-maximizing) fishery, an open access fishery, and an open access fishery with a marine reserve. At a given cost level, for all reserve sizes and adult transfer rates, yield was highest under optimum management. However, at lower cost levels (which encourage higher exploitation rates under open access), catch from an open access fishery with a reserve was higher than that possible under open access conditions alone for all reserve sizes less than 95%. This result was consistent for all transfer rates greater than 0.1. The greatest yield and conservation gains over open access fishing – approaching optimal management - were achieved with reserves on the order of 70-80% of the fishing area. Despite the potential for increased yields under some circumstances, Hannesson (1998) warned that it is likely that the use of reserves would also cause the costs of fishing to increase. In addition, utilizing reserves in an open access fishery would nonetheless result in the erosion of economic rents. For this reason, in order to maximize the realized benefits, Hannesson (1998) suggested that if reserves are used, it should be in conjunction with steps to limit fishing effort and capacity.

Sanchirico & Wilen (1998) used a non-species specific bioeconomic model to explore the effect on yield of reserves employed under different ecological conditions. Their intent was to locate those circumstances where non-extractive reserves could actually increase both the aggregate biomass of the population AND the yield that is generated to the fishery. As demonstrated by earlier models, such an outcome can not be expected from any reserve policy, but will instead require special biological and economic preconditions. In contrast to the effect of a reserve on the standing biomass (described in the preceding section), the nature of the connectivity between the harvested and non harvested population proved very important in determining whether or not an increase in catch would occur. All of their analyses addressed the use of a reserve in an open access fishery.

In a closed system (where there are no ecological linkages between the reserve and the fishery), Sanchirico & Wilen (1998) determined that aggregate harvest would decrease with a reserve. In this system the reserve is providing no benefits to the fishery in the form of larval movement or adult transfer. In an open system where the nature of the connectivity is sink-source with uni-directional density dependent flow, closing the sink will decrease harvest, again because the sink is not contributing any benefits to the source. In contrast, closing the source of a sink-source system with uni-directional flow will increase the aggregate harvest if the benefit from reserve creation (the increase in dispersal of eggs/larvae or adults from the source) is larger than the loss in pre-reserve harvest. This is likely when the source patch cost/price ratios are very low, since such economic conditions would tend lead to severe depletion of the source under open access conditions. Biologically, it is more likely that the benefits from the reserve will be larger

than the cost when the dispersal of adults from the source is neither too high nor too low. Characterizing the flow as simply density-dependent rather than specifically unidirectional leads to a similar result, except that this case is somewhat complicated by the economic conditions of the open area. Increase in aggregate harvest is most likely to occur when cost/price ratios in both the open and closed areas are similar. Again, this is because this ratio will dictate the pre-reserve density each region. When the ratio is low, the prospective reserve is likely to be overfished. Therefore closing this area will not be costly in terms of the foregone harvest. In addition, it will generate a large benefit in terms of dispersal, since the density gradient between the open and closed area will be large, as the open area will have been very depleted.

In summary, following the somewhat discouraging results produced by early yield per recruit analyses, subsequent studies have located circumstances under which it is possible to meet or even substantially increase the yield obtainable from a fishery by creating an reserve. This result is seen in the full range of reserve models, from highly generalized conceptual models to models based on specific populations. The same result is also seen under a variety of biological assumptions, ranging from highly dispersed larvae and sedentary adults to local recruitment and mobile adults. Central to this result for all models is the precondition that the fishery in question has or will otherwise experience a high level of fishing mortality - certainly beyond MSY, and in some cases, high enough to have caused severe depletion. As shown by Hannesson (1998) and Sumaila (1998) the catch from optimal, rent-maximizing management in the absence of any exogenous shocks to the system, cannot be improved upon with a reserve.

Effect of Reserves on Value of Catch

As illustrated above, the effect of a reserve on the targeted fishery may be measured by the changes in the size of the catch under reserve and non-reserve regimes, at various levels of fishing mortality or fishing effort. It can also be evaluated by the changes in the value of the catch. The distinction is important because the value of the catch will depend on the discount rate employed. Small increases in yield may be nullified by large discount rates, perhaps changing the political acceptability of a reserve policy (Holland & Brazee 1996).

For those fisheries modeled as anything other than open access, it is possible to measure the value of the fishery by calculating the economic rent provided. In natural resource economics, “rents” are the benefits created by “factors of production”, and accrue to the individual who controls them. Rents are measured as the difference between what the factor is earning and what is the minimum amount its owner would accept to keep it in its current use (Thomson 1998). In an open access fishery economic rent is driven to zero, but this is not necessarily the case under other management or institutional arrangements. Sumaila (1998) simulated every combination of reserve size (0.1 to 0.6) and transfer rate (0.1 to 0.7) under a rent maximizing (sole owner) management regime, and used discounted economic rent to evaluate the economic success of the reserve. Using a discount rate of 2%, Sumaila (1998) found that for net transfer rates ranging from 0.1 to 0.3, economic rents were higher in the absence of a reserve. For high net transfer rates (0.4 to 0.6) however, the optimal reserve size jumped to 70%. According to this model, reserves are economically beneficial only at high

transfer rates and large reserve sizes. A higher discount rate would decrease the optimal size of the reserve.

As described in the section on stock size/safety, Holland & Brazee (1996) found marine reserves useful in increasing harvest biomass in heavily fished fisheries, but demonstrated that reserves by themselves will not necessarily maximize rents. Holland & Brazee (1996) calculated the present value of the harvest (PVH) of the red snapper fishery over a 60-year planning horizon using a discount rate of 5%. The MSY effort level (0.75) in the absence of a reserve provided a higher PVH than any combination of reserve size and transfer rate. However, reserves became important at very high levels of effort (2.5). At this level of effort the fishery collapsed in the absence of a reserve, while a reserve of 29% of the management area made possible a PVH 75% of that at MSY.

Holland & Brazee (1996) note that the choice of the discount rate is critical to their specific conclusions regarding the value of a reserve. Discount rate is very influential because it reflects how heavily the initial periods of the simulation are valued relative to the later periods. Since reserves almost inevitably cause an initial decrease in the harvest and benefits usually are not seen several years later, high discount rates will not favor the use of reserves. At higher discount rates the Holland & Brazee (1996) model demonstrated that both the value of the reserve would be lowered and its optimum size decreased.

Sanchirico & Wilen (2000) employed a general biomass model to simulate a fishery managed under a limited entry system, and found that for most of the range of total effort, a marine reserve would cost the industry some of the rents that could otherwise be achieved. However, at high levels of effort, as long as the reserve is not a

closed system, a reserve will increase license values, which they use as proxy for the economic status of the fishery. Again, this result is consistent with the majority of models, which find that a benefit to the industry (in both yield and value) is more likely when the fishery has been, or is vulnerable to, being severely depleted.

Effect of Reserves on Variability in Catch

Amongst the other potential benefits attributed to marine reserves, there is some speculation that reserves could serve to dampen the year-to-year variability in the size of the catch.⁸ This effect may be achieved through the capacity of the reserve to maintain higher levels of SSB (as demonstrated in the Guenette & Pitcher (1999) model), and significantly decrease the number and frequency of years of poor recruitment. Such a stabilizing effect on a fishery would be desirable to both fisheries managers and industry members, as it would increase the predictability of the fishery and improve the ability of both parties to plan for the future. Although it makes intuitive sense that a marine reserve could potentially serve as a buffer by maintaining a minimum population size, and therefore ensure more constant harvests, this effect has not yet been demonstrated empirically.

Sladek Nowlis & Roberts (1999) created a source of year-to-year variability in the catch from their modeled population by adding a stochastic component to larval survivorship. In addition, they simulated 3 levels of environmental variation in order to determine how these fluctuations might influence the benefits provided by a reserve. Catch variability, calculated as standard deviation/average annual catch, declined with increasing reserve size. This was especially the case at higher fishing mortalities for all

Sladek Nowlis & Roberts (1999) cite Bohnsack (1996) as the source of this hypothesis.

four species examined. At high fishing mortalities, the ratio of standard deviation/average annual catch was often ≥ 1 ; for some species use of a reserve size 40% of the management area reduced the ratio to < 0.2 .

The impact of a reserve on the stability of a fishery can also be illustrated by the dynamic effect of the reserve on both the density of the stock on the fishing ground (biomass) and the catch. Pezzey et al (2000) found that reserves have the potential to increase the stability of a management area, measured in terms of the speed with which the system converges on the open access equilibrium. Without a reserve neither the density on the fishing ground nor the catch ever converges at all, while with a reserve convergence always occurs. How quickly the convergence takes place depends on the size of economic adjustment parameter. Lower economic adjustment parameters prevent overshoot and allow a smoother convergence. In comparison with a non-reserve regime, a reserve tends to initially create rapid oscillations during the convergence, as a result of same level of fishing effort being suddenly confined to a much smaller fish stock. These large oscillations indicate the potential importance of redirecting some fishing effort during the creation of a reserve regime in order to ease the transition, and increase the likelihood of reserve support (Pezzey et al 2000).

Additional Benefits from Reserves

The marine environment is a very complex, highly dynamic system, both difficult and costly to study. Although scientists are often able to find *ex post facto* explanations for the patterns marine ecosystems exhibit, for all practical purposes these patterns have often defied prediction. Future stock abundance has proved particularly difficult to predict, and a relationship between spawning stock size and subsequent recruitment has yet to be convincingly demonstrated. Even more distressingly, it is not uncommon for stock collapses to occur with very little advance indication of a problem. For example, numerous studies of the Northwest Atlantic cod stocks off the east coast of Canada in the late 1980s failed to anticipate the severe depletion of these stocks, which would eventually culminate in a complete closure of the fishery in the early 1990s (Roy 1996).

The high natural variability associated with recruitment as well as the difficulties associated with maintaining current and accurate estimates of stock abundances and fishing mortalities provide a strong argument for the development of tools that would operate effectively in a environment of significant uncertainty (Lauck et al 1998). Speculation that marine reserves may be one such tool has received some preliminary confirmation through modeling efforts.

There are at least two sources of uncertainty in the marine environment, which resource managers must confront. The first is the variability in marine populations that is a result of environmental variation. The second is the uncertainty associated with managing the stock, including the accuracy of stock assessments and the ability of management measures to achieve the targeted fishing mortality. Reserve proponents

hypothesize that reserves may be invaluable tools in coping with both of these sources of uncertainty; modelers have recently assessed these claims.

Effect of Reserves in an Uncertain Environment

Environmental Uncertainty. Environmental factors can dramatically affect stock levels, but their influence may not be immediately apparent. For example, harvests from the Maine lobster fishery, which occur when the lobsters are 6-7 years old, seem to bear some relationship to water temperature at the time of larval settlement (Steneck, pers. comm). One factor contributing to the collapse of Canada's northern cod fishery may have been suboptimal environmental conditions, including unusually cold and low salinity water (Roy 1996). It is likely that there are many such factors interacting in complex ways to influence stock abundance. As a result, it seems improbable that a high degree of predictability will ever be achieved for most marine populations. It is reasonable, therefore, to seek out management tools that will be effective in the absence of complete information about the stocks. Proponents of reserves have often suggested that they would be especially useful in this capacity, and would act as a form of insurance when combined with the other tools that are traditionally used to manage fisheries (Ballantine 1995; Lauck et al 1998).

Several modelers have attempted to simulate some degree of environmental variation in their models with the goal of determining how reserves might assist in stabilizing harvests. As mentioned earlier, Sladek Nowlis & Roberts (1999) tested the effect of environmental variation by adding a stochastic component to larval survivorship and evaluating the effects of three different levels of environmental variation. Under

these circumstances reserves provided the greatest increase in catch stability when the environment was the most variable. Sumaila (1998) simulated a "shock to the system", in the form of severe recruitment failure (zero recruitment for years 5-15 inclusive of a 28 year simulation) in the fished area. As described above, this model demonstrated that in such a situation, the presence of a large reserve (40-70%) can serve to increase both the economic rent and the safety of the stock. Sensitivity analyses examining the robustness of these results under a more mild recruitment failure (zero recruitment for years 4-8 of a 28 year simulation) found the economic and biological benefits provided by a reserve reduced. Again, high adult transfer rates were crucial in ensuring an economic benefit.

Regulatory Uncertainty. The second form of uncertainty resource managers must confront is the potential for errors or biases in the data upon which management decisions are based. While the abundance of a given population may depend on any number of factors, regulations designed to manage the stock are guided largely by the estimations of only two parameters: stock biomass (or spawning stock biomass) and fishing mortality. Stock assessments will inevitably have some degree of error associated with them, and in the worse case scenario (e.g. Canadian Northern cod) a miscalculation can be catastrophic. Adding to the complexity of the problem, in the U.S. complete stock assessments for a given species are generally performed only once every three years, so data may be out of date. Accurate estimates of fishing mortality are also often difficult to obtain. Landings may not be fully reported and bycatch mortality may not be incorporated. Managers are often in a position of making decisions in the face of outdated and/or incomplete information. For these reasons, it is often difficult to

ascertain whether the management actions have been fully implemented, as well as if they are having the desired effect.

Lauck et al (1998) were particularly interested in effects of a reserve on a fishery where the target fishing mortality is difficult to achieve in practice. In their model there is a target harvest u in the open area, but it is modeled as though it were largely uncontrollable. There is a probability distribution for u with its mean fixed at the target harvest fraction. The actual harvest varies around this mean. As their criterion for successful management, Lauck et al (1998) look for circumstances where the stock remains at >60% of the carrying capacity for the length of the simulation (40 years). At a target harvest fraction of 0.5 they examined coefficients of variation ranging from 18%-61%. Results showed that at high CVs, the probability of success is <1 even if only very small areas (5%) are available for harvest. At moderate CVs (50%) the probability of success falls below 1 when the area available for harvest is greater than 30%. At a catch rate of 0.5, a reserve of 70% is necessary to ensure a 95% probability of stock protection. However, an equivalent level of protection without a reserve requires a drop in the mean catch rate to 0.1, which results in a 50% lower catch. Based on these results they conclude reserves present a viable method of protecting stocks against management uncertainty while still providing a healthy long-term catch.

Influence of Management Regime on Effectiveness of Reserves

The modeling effort directed toward understanding the potential consequences of the use of marine reserves in a fisheries management capacity has expanded rapidly over the past few years. Important strides have been made in the biological sectors of reserve

models, increasing in sophistication from early yield-per-recruit analyses to dynamic models of age structured populations. A parallel effort has taken place in the economic sector, where depictions have evolved from the straightforward equilibrium assumptions (e.g. constant fishing effort) to more realistic and responsive representations of common institutional arrangements. The fisheries economics literature has tended to focus on the two endpoints of possible institutional configurations: pure open access and optimized rent maximizing (Homans & Wilen 1997). The reserve models have adhered to this tradition, recently expanding to also include depictions of a limited entry regime (Sanchirico & Wilen 2000).

Hannesson's (1998) model illustrates the response of industry under open access management to the creation of a reserve. The improved conditions in the open area lead to the build up of excessive fishing capacity and increased fishing costs, potentially eliminating the conservation gains and certainly the economic gains generated by the reserve. Hannesson (1998) is therefore not optimistic about the use of reserves in the absence of concurrent effort controls. Pezzey et al (2000) however, follow Sanchirico & Wilen (1998) in their political economy approach to the open access fishery, valuing the sustainable increase in catch and effort that a reserve may create for its own sake, despite the continued elimination of rents. Each of these models, regardless of their concern for sustained rents, locates circumstances where the use of some size reserve will improve the yield from the fishery over that which is expected from a non reserve regime. In the Hannesson (1998) model a reserve between 70-80% of an open access area with a moderate adult transfer rate of 0.5 improves the catch ~60% and more than doubles the size of the stock. Pezzey et al (2000) find the bioeconomically optimal size reserve and

predict increases in yield in existing Caribbean fisheries assumed to be in open access equilibrium of 10-80%, using maximal reserve proportions of 20-40%.

Because Hannesson's (1998) rent-maximizing optimal management or "sole owner" regime operates in a deterministic model, a reserve would not improve yield from the fishery. Similarly, Sumaila (1998) who also modeled a rent-maximizing owner, found that in the absence of exogenous shock to the fishery, a marine reserve could not improve on the yield or the stock size. However, as described above, the Sumaila (1998) model produced a different result when a severe recruitment failure was introduced. In such a situation, a reserve of any size increased the average size of the stock, and large reserves with high adult transfer rates increased the realized economic rents. This is an important result, as it demonstrates that even the most rational management attempts can be thwarted by the environmental variability that is an ever present component of many marine ecosystems. Furthermore, reserves could provide essential insurance to safeguard rents in such circumstances.

Of course, while open access and sole owner regimes represent the virtual extremes of the fisheries management spectrum, most real world fisheries are likely to fall somewhere in between. Sanchirico & Wilen (2000) recently adapted their open access model (1998) to consider the common regulatory mechanism of limited entry. Under these regulations, legitimate participants in a fishery are identified, often through historical catch records, and the entrance of all other potential participants is slowed or prevented. Such a system creates a sort of property right, which will have value to the existing and potential participants. Some limited entry regimes allow the holders of the licenses to buy and sell them. The exact value will depend to some extent on the status of

the resource, since in equilibrium, the price of the license will equal the anticipated production rents of the fishery. Particularly strong fisheries may have extremely high license values; such high values are also thought to create an incentive for careful exploitation of the fishery, since the future price any participant will receive will depend on the probability of achieving consistently high catches.

Sanchirico & Wilen (2000) specifically model a limited entry fishery, and generate license prices, which are used as a signal for the impact of reserve implementation on fishing rents. Those circumstances where the rents increase (and therefore the license prices) are judged beneficial for the industry members, and it is suggested that finding these circumstances would be an effective method of reducing opposition to no-take reserves. They determine license prices to increase in systems where the 3 modeled metapopulations are either fully integrated or linked together in a cascade fashion and the fishery is subject to high effort levels (greater than 1.5 in the fully integrated system and greater than 1.75 in the cascade system). Notably, Sanchirico & Wilen (2000) found that closing lower productivity areas resulted in an increase of license prices over a larger range of effort levels than closing high productivity areas. Furthermore, license prices also increased over a larger range of effort levels when a higher cost area was closed.

Discussion

Although the reserve models described within this chapter are highly diverse in their approaches to both the biological and economic aspects of a harvested fishery, they

do generate consistent results indicating that there are invariably circumstances where reserves would make a valuable contribution to fisheries management efforts. Careful attention to the parameters that dictate the nature and size of this contribution should prove very instructive in these early stages of developing reserve policies.

The Evolution of Reserve Models

The evolution of reserve models has corresponded in many respects to our evolving understanding of the management problem for living marine resources. As noted by Guenette et al (1998), the earliest analyses of reserves were done with YPR models (e.g. Beverton & Holt 1957). Under limited circumstances, reserves were found to provide a marginal benefit, but it was feared that realistically, reserves would increase costs for fishermen, and require too much data to successfully implement. Traditional management tools were believed sufficient to control fishing effort, and reserves were perceived as detrimental to economic efficiency. Over the next few decades it became clear to most that traditional management tools have in fact provided inadequate protection for most fish stocks. Interest in marine reserves was renewed, and it was recognized that more sophisticated representations of the biological and harvesting sectors of models were required in order to achieve a fuller understanding of the effects of a reserve on a fishery. Today, researchers are really just beginning the process of exploring the interface between the biological growth and dispersion processes of the fishery and the changing economic incentives created by reserves over space and time. It is feared that failure to incorporate the complex reactions and interactions of both of these sectors to reserve creation would result in misinformation, contributing to policy failures.

Given the political realities of reserve designation and the much-emphasized need for industry support, it is significant that several of the more recent models are treating the question of reserve placement not only as a biological, but also as an economic problem. While ecological criteria dominate most schemes for reserve selection, it must be acknowledged that socio-economic considerations will be influential when making the ultimate decision (Roberts et al, in press). Initial work has been done to explore the relative benefits of closing high cost v. low cost areas in limited entry fisheries. The range of effort levels over which license price (a proxy for the economic effect of the reserve) increases is actually larger when high cost areas are closed (Sanchirico & Wilen 2000). A fuller understanding of such questions can be achieved through further modeling experiments, and is likely to be an important step in expediting reserve system design.

In addition to the increasing sophistication (both biological and economic) of the models, the nature of the questions being addressed with the models has also evolved. Reserves were initially promoted mainly on the strength of their ability to limit fishing mortality, and restore age structure (and therefore a higher level of reproductive capacity) to the stock. More recently, the arguments in favor of reserves have begun to swing toward their capacity to offer insurance against the inevitable and irreducible uncertainty and errors that are inherent in fisheries science and management. This uncertainty is prevalent both in estimates of stock size and fishing mortality as well as the effects of environmental variability, and can undermine the effects of even the most rational management decisions. As Sumaila (1998) demonstrated, reserves could improve the yield even under a sole owner (optimal management) regime, provided that the fishery

was subject to large environmental shocks. Simulations are increasingly beginning to address these kinds of questions, but given the pervasiveness and magnitude of the uncertainty problem, the analysis is still in its infancy.

Most approaches to reserve evaluation have relied mainly on the standard economic decision rule – “Do benefits exceed costs?” In other words, does the increase in yield and or economic rent generated by the reserve exceed that which is forfeited through the closure of fishing grounds? However, given the increasing interest in no-take reserves as a method to cope with uncertainty, that decision rule may no longer be sufficient. Instead, if reserves are considered as only one part of a bet-hedging strategy (i.e. one of a suite of management tools) it should be expected that the benefits they provide in terms of reduced risk may come at the cost of a slight decrease in the optimal yield (Lauck et al 1998). This cost need not be prohibitive, as many of the models have shown. Purely economic arguments against reserves as fisheries management tools must therefore be reconsidered. Much as in financial planning, a diversified management approach will have intrinsic value if the risk of a catastrophic loss is significantly reduced.

Model Caveats

Although models are important tools for constructing the conceptual framework that will assist with evaluating prospective reserves, there are some questions for which modeling exercises are presently not well suited. The majority of the models addressed in this review are not explicitly spatial, despite the fundamental nature of reserves as spatial management tools. This means that for the most part, there is no differentiation in

the habitat characteristics of the modeled area – there is no question of selecting the "right" location for the reserve because all of the modeling landscape is equivalent from a habitat respect. Models therefore, are not able to address such questions as the relative merits of closing spawning grounds or nursery areas as opposed to other sections of a stock's range.⁹

Along the same lines, models also do not capture the response of the benthos to the alleviation of bottom impacts. One of the reasons it is believed that reserves would be beneficial for fish stocks is that they would allow for the reestablishment of the benthic structure believed to increase survivorship of postlarval and juvenile size classes (Auster & Malatesta 1995). Empirical studies suggest improved recruit survival for some groundfish stocks following area closures on Georges Bank in 1994, perhaps through the protection of critical nursery habitats (Murawski et al 2000). At present, models do not incorporate the effects of improved habitat heterogeneity, and may therefore understate the improvement in recruitment that may occur through use of reserves. In the interest of simplicity, the biological parameters of models are often assumed to remain unchanged following the creation of a reserve. However, natural mortality and growth rates are probably not constant as simulated in most models, but may actually change following the improvements in habitat and changes in population density following reserve creation.

Similarly, a reserve is likely to necessitate a change in the economic parameters of a model. For example, costs of harvesting may increase, perhaps as a result of increased travel times to the fishing grounds or even due to increased congestion in open areas

⁹ Initial work has been done on closing "sink" v. "source" areas, but this is a separate question.

(Sanchirico & Wilen 2000). In addition, if the reserve succeeds in reestablishing stock age structure, the composition of the catch could change to include more older, larger fish, potentially commanding a higher price. Simulations exploring the impacts of changing costs and prices would be useful for future cost benefit analyses.

Finally, the process of improving reserve models would be greatly assisted by empirical research to generate a better understanding of the parameters that have already been identified as highly influential (e.g. transfer rates of adults, recruitment relationships, species interactions).

Summarized Results

This survey of reserve models illustrates that closed areas could be highly effective in rebuilding depleted populations, and reestablishing age structure, especially in cases where the transfer rate of adults from the reserve to the fishing ground is low to moderate and reserve sizes are large. In cases where fishing effort is high and stocks have been severely depleted, most models indicate that yield from the fishery could also actually increase over the non-reserve situation, either through larval drift or adult spillover. These generalized results are consistent across a range of biological and economic assumptions.

Size. How large will marine reserves need to be in order to achieve the conservation and fisheries management goals their proponents anticipate? While increases in the size and abundance of exploited species within reserves have been documented even for very small reserves (Roberts & Polunin 1994, Russ & Alcala 1996), the models indicate that more extensive protection may be needed to optimize the benefits reserves could provide.

A major focus of the modeling effort has been to clarify the effect of the size of the reserve on the size of the benefits, and how that may change with the characteristics of the species in question. The optimally sized reserve must achieve a reasonable trade off between stock protection and continued healthy yields from the fishery.

For the most part, the existing models propose much larger reserves than are currently in existence, and perhaps larger than will ever be politically feasible. Most models propose a size of at least 50% and as much as 80% of the management area in order for maximum benefits to be realized, depending on the characteristics of the species, the management regime into which the reserve is set, and the current level of effort.¹⁰ The smallest optimally sized reserve was that determined by the Holland & Brazee (1996) model, of 29% at very high effort levels. Perhaps significantly, the Holland & Brazee (1996) model was also the only one to utilize density dependent growth rates, as well as the highest discount rate. They note that simulations with density independent growth resulted in significantly larger optimal reserve sizes. Research into the appropriateness of density dependent growth is needed to clarify these results.

In some models, the nominal transfer rate is modified according to the size of the reserve (i.e. transfer rate is proportionately higher for smaller reserves, due to the increased probability of crossing reserve boundaries) (e.g. Polacheck 1990; Guenette & Pitcher 1999). The Guenette & Pitcher (1999) model nonetheless also finds the greatest increase in yield to occur at moderate to large reserve sizes (0.3 to 0.5), and that yield is basically equivalent for nominal transfer rates from 0.3 to 0.7.

¹⁰ In contrast, marine reserve advocates have generally recommended 5-20% of representative cross sections of the continental shelf by year 2020.

These indications of the benefits of large reserves is in line with the arguments made by some that in the oceans, protected areas should be the rule and fishing areas the exception (Walters 2000). The implications of this result for developing reserve policy are significant; managers are likely to find themselves in a difficult position. It will be difficult to garner support from stakeholders until the benefits from reserves are demonstrated. However, demonstrating the benefits may require a substantial initial sacrifice, for which there is likely to be little support. Furthermore, some models demonstrate a threshold effect, where the increase in economic rent induced by the reserve does not become apparent until the size of the reserve surpasses a certain level. The Sumaila (1998) model finds an increase in rent over the non-reserve scenario to occur only when adult transfer rates are high (0.4 to 0.6), but not until the reserve is at least 50% of the fishing area. If the threshold effect is not borne out in reality, Holland & Brazee (1996) suggest that in those areas where the local community is highly dependent on the fishery it may be advisable to start with reserves that are smaller than optimal. This strategy will help to avoid a severe drop in harvest; reserve size can then be increased gradually.

Timeline. It is not well known how swiftly the benefits generated by a reserve may appear. Few models have considered the initial impact on the catch caused by the creation of a reserve, instead comparing longer-term averages of with/without scenarios to evaluate their effect. Neither have they specified the likely time frame necessary to achieve the new equilibrium yield and stock sizes. One exception is the Holland & Brazee (1996) model, which calculated the minimum harvest likely to occur in the years following reserve designation, and also the time required to attain the new equilibrium

catch level. When a reserve covering 20% of the management area is imposed, annual harvests fell by 10 to 14% depending on effort levels, and reached their new equilibrium within 6 to 9 years. Pezzey et al (2000) showed that the path to the new equilibrium in an open access fishery will be affected by the rate at which the economic adjustment can occur. High adjustment rates (faster entry and exit) seem to cause substantial overshoot, causing rapid and deep oscillations in the catch level, as fishing effort is concentrated into a smaller area. This result prompted Pezzey et al (2000) to urge the inclusion of careful redirection of fishing effort in reserve plans in order to avoid this effect.

Management. It is clear from the reviewed models that the management regime in place outside the reserve is very influential in determining whether a measurable increase in yield is produced. In deterministic models an optimal management rule (maximizing sustainable rent per year) always provides a higher yield than an open access regime with a reserve of any size (e.g. Hannesson 1998; Sumaila 1998). Optimal management also maintains the stock at higher levels except for when the reserve is larger than 70-80% of the management area (Hannesson 1998; Sumaila 1998). Even optimal management however, can be frustrated by severe shocks to the system, as illustrated in Sumaila (1998). In this model, a large reserve (70% of the management area) acted to keep stock size at levels comparable to a scenario where there was no severe recruitment failure.

Although it is achievable in models, attempts to attain optimal management in reality have been considerably less successful. Most real world fisheries are more closely approximated by the models that simulate limited entry at various effort levels, or even open access conditions. In every model considered in this review, increases in yield from the fishery in question occurred with the use of a reserve whenever effort levels and

fishing mortality were high, including situations where adults did not leave the reserve.

This result suggests that reserves are potentially most useful in areas wherever effort limitation has proved technically or socially difficult (Holland & Brazee 1996).

However, although a reserve in an open access fishery may represent an improvement from a political economy perspective (i.e. an increase in sustainable amount of effort) economic rent will remain at zero. It is important to keep in mind the warnings first voiced by Hannesson (1998) that improving the condition of the resource in an open access fishery is likely to cause the buildup of even more excessive capital.

Uncertainty. Populations of many commercially harvested species are known to be highly variable. The source of the variability – human induced or environmental – is not always clear. Lauck et al (1998) asserted that “progress in fisheries management will proceed most rapidly, not from vastly increased research effort in marine biology, but from research into ways to deal with this irreducible uncertainty, or as it might be called, unknowability” (p. S74). Modeling results suggest that reserves could be effective tools for coping with management uncertainty, increasing the probability of achieving the goals of stock protection without prohibitive loss of yield (Lauck et al 1998). The alternative approach of simply lowering catch levels to the point where the same level of stock protection is achieved creates a much greater reduction in yield. Furthermore, reserves may act to stabilize catch levels, reducing year-to-year variability. As noted, some simulations showed that reserves could reduce the ratio of standard deviation/average catch from values greater than 100% down to 20% (Sladek Nowlis & Roberts 1999).

Further modeling studies are needed to better assess the capacity marine protected areas to reduce the negative effects of environmental uncertainty. The expectation is that in the presence of greater variability/stochasticity and frequent deviations from the stock recruitment curve, marine reserves may become much more important.

Future Research

It is striking that marine reserves, which are often promoted as a method to pursue an ecosystem approach to fisheries management, (EPAP 1998, NRC 1998) have mainly been evaluated using single species models, looking at the dynamics of one fishery in isolation. Conspicuously absent from the existing pool of reserve models are those which incorporate any representation of a multiple species dynamic¹¹. Clearly, different species will react differently to a release from fishing pressure; the recovery of one species could even be impeded by the recovery of another. Empirical evidence demonstrates that the abundance of some commercial species has actually decreased following the creation of a reserve (Alcala & Russ 1990).

Presumably, multiple species models have been avoided for their complicated design and the difficulties inherent in their evaluation. Nonetheless, researchers have developed models to explore other questions requiring the inclusion of multispecies fishery dynamics (Wilson et al 1991, Ruth & Lindholm 1996). Multispecies models are now needed to achieve a fuller understanding of the complexities of reserve effects. Multispecies models would help to explore how different species, with different natural

¹¹ One exception is Holland (2000), a multiple species model with regard to technical (harvesting) if not biological interactions.

history characteristics would respond to reserve creation. In addition, the inclusion of interactions between species may modify the current thinking regarding if, and under what conditions, reserves will provide increases in yield. The question of appropriate reserve size will need to be looked at in the aggregate, as well as on a single species basis.

At the same time, continuing explorations of representations of the harvesting sector that go beyond constant fishing mortality or constant fishing effort, are needed to better assess the usefulness of reserves under different management regimes. The value of reserves in coping with both management and environmental uncertainty may become more apparent in more complex modeling environments.

Chapter 2

A MULTISPECIES BIOECONOMIC MODEL OF A NO-TAKE MARINE RESERVE

Introduction

Beverton & Holt (1957) were among the first researchers to adapt a model for the purpose of exploring the effects of an area unavailable to fishing pressure (Guenette et al 1998). According to their yield-per-recruit model, the closed area would need to be large (>65% of the total fishable area) in order to generate any marked increase in yield. At low fishing mortalities ($F=0.1$) yield per recruit decreased slightly with the creation of a reserve. Despite the potential for an increase in yield under certain circumstances, most managers remained skeptical of the value of closed areas for fisheries management. At that time, traditional management tools were believed sufficient to control fishing effort, and there were concerns that arbitrarily closing areas would raise the costs of finding fish, and therefore reduce economic efficiency (Guenette et al 1998).

Over the past decades it has become clear that traditional management tools have in fact provided inadequate protection for most fish stocks (Lauck et al 1998). The modeling effort has continued and expanded as interest in marine protected areas as fisheries management tools has grown, and models have assisted greatly with the development of a theoretical framework that may provide guidance for reserve policies. A wide variety of models relying upon different assumptions have found that reserves, when properly designed, can provide benefits in the form of increased overall catches and

higher levels of safety for the stock.¹² Given the current crises in many fisheries, these preliminary results certainly warrant further investigation.

Many of the earlier modeling efforts focused almost entirely on the biological sector of the system, and dealt only superficially with the changes in the behavior of the harvesting sector that may occur following reserve designation. For example, one formulation holds fishing effort constant before and after reserve creation, i.e. the size of the fleet does not change, but effort is redistributed into a smaller area (Polacheck 1990, Guenette & Pitcher 1999). This approach fails to capture important dynamics of the interaction between the resource and the economic incentives driving the human actors. In the case of fishing effort, it is unlikely that it will remain constant before and after reserve designation, since catch, and therefore profits, will likely change for better or for worse, causing boats to either enter or exit the fishery. In recent years, researchers have increasingly called for more robust models incorporating more realistic depictions of the harvesting sector (Sumaila 1998, Sanchirico & Wilen 1998, Holland 2000). This effort is now underway, and the model described in this chapter contributes to its progress. Our model departs from those previously developed in two significant ways.

1. Our model is a multiple species model. The overwhelming majority of existing models are single species. Although our model is only one formulation of the possible dynamics of a multiple species ecosystem, it is useful to begin conceptualizing the some of the possible ramifications of reserve use in such a system. It also generates insight into how species with different life history characteristics may be affected by reserve designation. In our model, the five species fall along a continuum from long lived, low fecundity species to shorter lived, high fecundity species.
2. Our model is constructed with the specific intention of exploring the effects of at least two alternate management regimes *outside* the closed area on reserve “success” (open access v. a sole owner) under varying biological circumstances.

¹² A comprehensive review of published marine reserve models and their results is provided in Chapter 1.

Using this model it is possible to observe the interaction of the economic motivations of a fleet over space and time, in conjunction with the varied biological growth and dispersion processes of multiple species. This thus far unique combination of the biological and economic sectors is used to generate new insights into the long-term impacts of reserve use.

Model Description

The model was built using the graphical programming language STELLA 5.0 (High Performance Systems).¹³ It was developed jointly by J. A. Wilson¹⁴, D. F. Gilbert and T. R. Johnson, in order to address a variety of questions regarding the likely impacts of alternate fisheries management regimes and rules. As such, this is not a predictive model constructed to forecast specific outcomes for a particular fishery, but rather a heuristic tool that allows the researcher to explore the implications of alternate sets of assumptions. Such tools are necessary because fisheries are complex, dynamic systems, with behaviors that are heavily influenced by both biological and economic factors. Describing fisheries as complex does not mean simply that they are complicated, but that they are systems like those described by Costanza et al 1993.

“Complex systems are characterized by strong (usually nonlinear) interactions between parts, complex feedback loops that make it difficult to distinguish cause from effect, and significant time and space lags, discontinuities, thresholds, and limits. These characteristics all result in scientists’ inability to simply add up or aggregate small scale behavior to arrive at large scale results”.

¹³ Although the model was built in STELLA 5.0, it was then translated into a format to be run in Berkeley Madonna, which was significantly faster in conducting the simulations.

¹⁴ The biological sector of the model was adapted into STELLA from the FORTRAN model developed by Wilson et al (1991). The economic sector of the model is adapted from Wilson et al (1999).

For these reasons, models such as the one described below are immensely helpful as tools that assist in exploring this complexity, and its implications for various management measures.

The description of the model presented below highlights the features that are important to simulations designed to explore the potential consequences of the use of no-take marine reserves. The model is composed of a biological sector divided into two ecosystems that can be linked through larval transport and/or movement by older animals, and a harvesting sector, which simulates the economically driven behavior of industry members.

The Biological Sector

The biological sector of the model is divided into two subsystems, envisioned as two distinct yet connected, local ecosystems. Each subsystem has an identical species assemblage, consisting of five age-structured populations representing a single functional group, or trophic level. The populations are age-structured in order to allow both the weight and fecundity of an individual to increase in yearly increments, on a species-specific basis. Each subsystem also has a designated overall “carrying capacity” which specifies the upper biomass limit beyond which the system cannot grow as a consequence of energy constraints. In our baseline conditions the carrying capacity and therefore the “size” of each region are equal. However, these can be adjusted to simulate instances where one region supports a larger system biomass than the other.¹⁵

¹⁵ For example, one region can be set to a carrying capacity that is 10% of the other. We use this feature to explore the impacts of reserves of different sizes, relative to the area fished.

The two subsystems of the model can be made more or less discrete from one another, depending on the type and strength of the connections that are made. The biological flows between the two regions are separated into two types – eggs/larvae and adults. The transfer of eggs/larvae can be varied in both its strength and direction (unidirectional or bi-directional). In our initial simulations we have chosen to model the movement of eggs/larvae as a net transfer of a given percentage of the eggs produced in the reserve region to the non-reserve region. This is consistent with the ecological concept of a source-sink relationship, wherein production in the sink population is supplemented by continued immigration from the nearby source area (Pulliam 1988). An oft-cited criterion for the selection of reserves designed to generate fisheries benefits is their potential to act as a source of eggs/larvae (Ballantine 1997, Roberts 1998, Lindeman 2000, Roberts et al in press). One could imagine that the prevailing oceanographic conditions have a tendency to move the eggs in this direction. The percentage transferred can be varied anywhere from 0-100% and is the same for all species, under the assumption that they are similarly impacted by the currents.

The two subsystems of the model may also be linked through adult movement. Earlier models have taken a wide variety of approaches to modeling this movement. Most models that are based on coral reef ecosystems assume that while the eggs and larvae disperse widely, the adults are sedentary (Sladek Nowlis & Roberts 1999, Hastings and Botsford 1999, Pezzey et al 2000), consistent with some theories of coral reef population dynamics (Kramer & Chapman 1999). Another coral reef model simulated the movement of adults as a density dependent process (Holland & Brazee 1996), based on the notion that the rate of emigration will be responsive to resource limitations.

Models of groundfish populations have typically simulated the movements of adults as a random process moving in both directions (Polacheck 1990, Guenette & Pitcher 1999), or as a simple net transfer rate (Sumaila 1998). The degree of movement by adults has been identified as a key parameter by most modelers. High levels of movement will tend to reduce the ability of the reserve to increase the reproductive capacity of the stock, while too little will reduce the direct benefit of an increased harvest to the fishery, and therefore potentially reduce industry support.

We have chosen to follow Sumaila (1998) and model the movements of the adults of our five species as a net transfer from the reserve to the fished area. The transfer begins the same year that the species becomes reproductively mature, and so is different for different species. Like the transfer of eggs/larvae, the number of adults to be moved is given by specifying a percentage of each adult age class to be moved from the reserve to the fished area. The transfer of adults begins only after the reserve is created. This is intended to reflect the implicit density dependent nature of this transfer. Before the reserve is created, the two areas are fished more or less equally, and biomass is reduced to similar levels, so there is no density dependent movement. However, once the reserve is created, the size of the harvested population in the fished area relative to its carrying capacity is always less than that of the reserve, regardless of the management regime outside the reserve. Therefore, it is reasonable to assume that there may be pressure for species to move from the reserve into the fished area. The strength of that pressure is reflected in the percentage of adults that spillover. Although it is possible to make the percentage of adults transferred different for each species, or even different depending on

the age class, it makes the analysis of the results considerably more complicated. For this reason, all species “spillover” at the same rates.

The species in the model are based very loosely on the characteristics of a species assemblage present on Georges Bank, and are named for convenience: herring, cod, haddock, redfish, and a “bloom” species (such as sandlance). The species are differentiated with respect to one another on the basis of weight-at-age characteristics, fecundity-at-age, natural mortality, age of maturity, age of recruitment to the fishery, and susceptibility to density dependent constraints. Many parameters required for the model have a high degree of uncertainty associated with them. For example, the true amount of natural mortality is not well known for any of these species, but a value of 20% has traditionally been used as an estimate. The natural mortality values in our model, therefore range between 18-25%. For other parameters for which true values are similarly unknown we performed sensitivity analyses to locate the range of values which generated behavior in the population that was plausible.

Although the populations in our model are based upon members of a real world system (weight and fecundity data were used where available), they are not meant to exactly replicate them in all their characteristics. During the initial parameterization of the model we found that if the characteristics of the species were made too similar, the biomass of each species exhibited concurrent, periodic oscillations that we did not feel was a plausible dynamic. Conversely, if the species were differentiated too strongly, we often found that one species would swiftly come to dominate the system and the other species would go extinct. This too, is not consistent with our expectations for a multiple species ecosystem. Therefore, we intentionally sought to make the species sufficiently

distinct from one another in order that they would exhibit some degree of compensation, i.e. when variability in the system causes one species to decline, the biomass of other species will increase, having the effect of keeping the overall system biomass relatively constant (Laevastu & Hayes 1981, Levin 1999). This behavior is consistent with the relative dynamic stability described by Hennemuth (1979) and observed in some real world systems e.g. Georges Bank (Sissenwine 1986, Murawski & Idoine 1992, Fogarty & Murawski 1998). While individual populations may be chaotic and unpredictable, the system as a whole exhibits a greater degree of stability.

In real world ecosystems, there are hundreds of species interacting to bring about this compensation effect. Because a model of that scope was not feasible, we limited ourselves to five species and differentiated them in ways that served to qualitatively simulate this phenomenon (Figure 2.1). Consequently, species are arrayed on a continuum that ranges in its characteristics from what are traditionally considered more “r-selected” to more “k-selected” life history traits. For example, our bloom species (sandlance) is a small, fast growing, short-lived, “weedy” species that begins reproduction early, and is highly fecund. However, it is also highly susceptible to density dependent effects, such that it suffers much higher rates of mortality than other species when the total biomass of the system approaches carrying capacity. In contrast, redfish is a longer lived species that experiences lower natural mortality, begins reproduction later and is much less fecund, but is also much less vulnerable to density dependent effects.

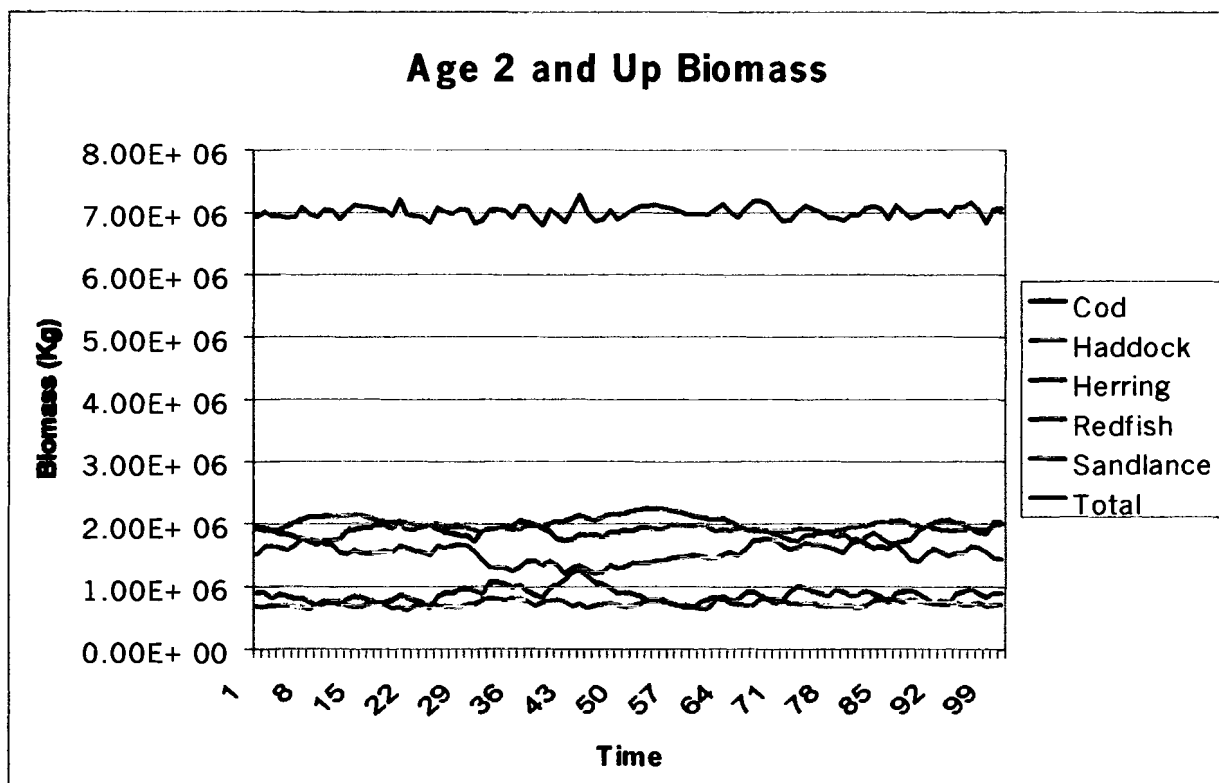


Figure 2.1: A single run showing changes in population biomass of each species (cod, haddock, herring, redfish and sandlance), as well as the overall system biomass.

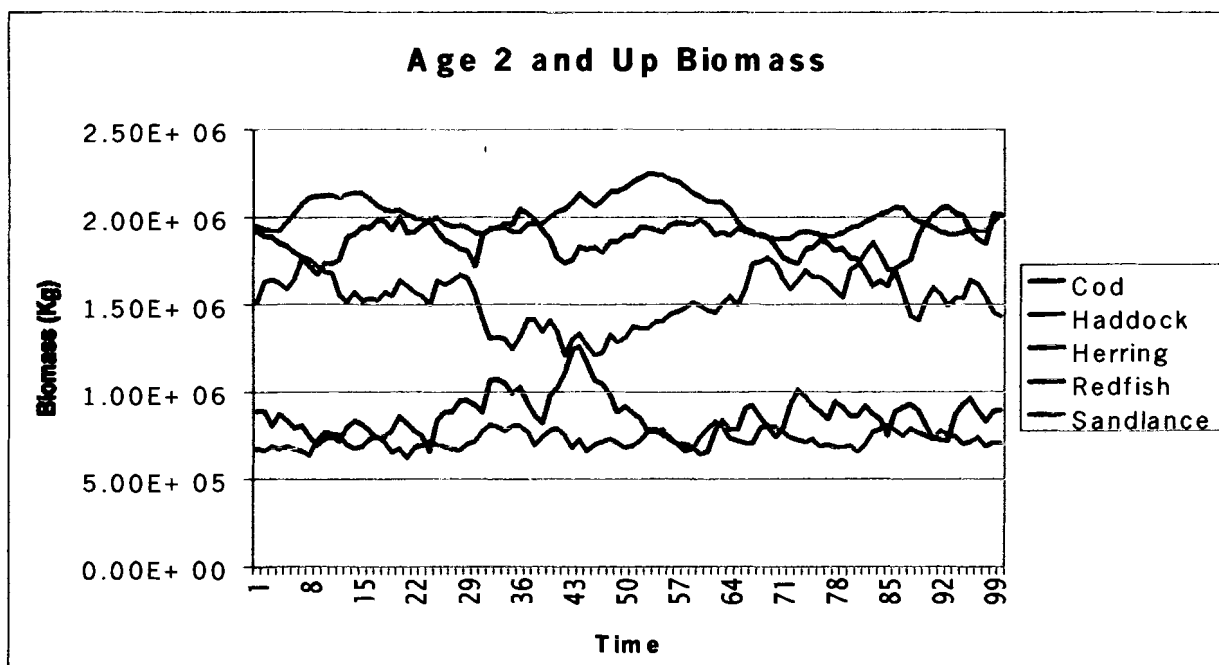


Figure 2.2: A single run showing changes in population biomass of each species (cod, haddock, herring, redfish, and sandlance).

Due to the scale, it is difficult to see in Figure 2.1 the compensation that is taking place between species which keeps the total system stable. It is more evident in Figure 2.2, which shows only the individual species. In the absence of fishing, the system is dominated by cod and redfish, the species with the lowest natural mortality and lowest susceptibility to density-dependent effects (Figure 2.2). Increases in the cod biomass are often offset by decreases in the haddock biomass, and vice versa (Figure 2.2).

In our model, compensation is brought about as a result of niche overlap through community predation¹⁶ and differences in relative fecundity that allow species to differentially take advantage of "space" in the system as it becomes available. For each species, mortality due to community predation occurs only on age 0 and age 1 fish (eggs and larvae). Community predation occurs only when the system biomass approaches the carrying capacity, and the degree of mortality is different for each species. For example, when the system carrying capacity is reached, the bloom species (sandlance) suffers higher mortality than the species that is modeled after redfish, which has a lower intrinsic rate of growth and is assumed less susceptible to density dependent effects. It is important to note that the degree of community predation that occurs on a given species in a given year does not depend on the current condition of that particular species' population, but rather on the proximity of the total system biomass to the carrying capacity. As a consequence, the year class strength of each species is highly variable and unpredictable, and it is not possible to detect a stock-recruitment relationship. The age 1 individuals that survive this mortality then suffer an additional source of mortality that is

¹⁶Community predation, as described in Sissenwine (1986), refers to the tendency of older, larger fish of all species to eat the post larval, pre recruit stages of each species. The rate at which this occurs in the model is a function of the relationship of the total system weight to the carrying capacity of the system; predation increases as the total biomass of post larval fish approaches the carrying capacity.

a randomly chosen percentage between 50-100%. This stochastic component of mortality gives the population a higher degree of variability such as might be generated by fluctuating environmental conditions.

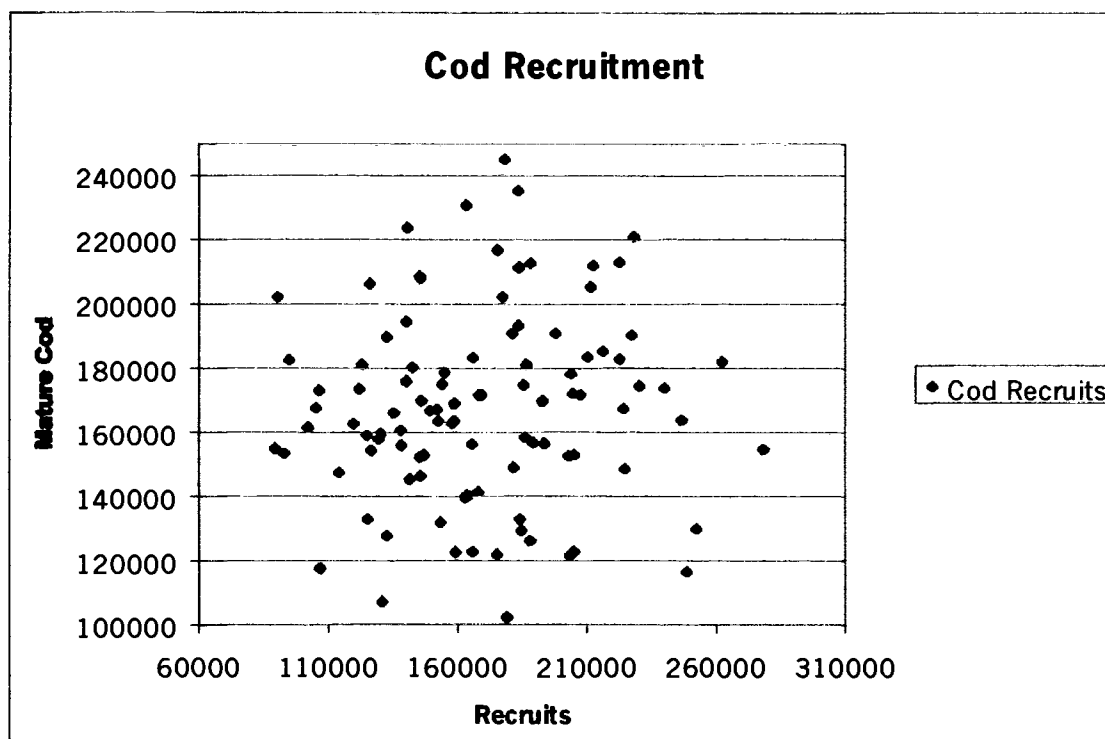


Figure 2.3: Relationship between the size of the adult population and subsequent recruitment to the fishery. No significant relationship is evident ($R^2=0.005$, $p=0.4918$).

For all age classes above age 1, mortality is imposed as a constant natural mortality rate, which differs between species (within the range of 18-25%). Fishing mortality is added at the age when the species is recruited to the fishery. Again, this occurs at different ages for different species. One of the five species (sand lance) is exempt from fishing mortality. Although sand lance comprises a relatively small portion of the biomass in an unexploited ecosystem, when fishing pressure is high on the other species, as it is under an open access regime, sand lance accounts for the majority of the

biomass. Under the baseline conditions, fishing mortality always begins the same year that the species becomes reproductively mature (starts producing eggs).

It is worth noting that if each of these populations were run in isolation from the others, they would behave in a way that is consistent with the standard single species model, i.e. logistic growth to an equilibrium population level. It is the interaction between species at the younger age classes in this model generating the variability and unpredictability within individual populations.

The Harvesting Sector

The purpose of this sector is to simulate the impacts of harvesting, given reasonable assumptions about the behavior of fishermen under two alternate management regimes. Under either regime fishermen have the opportunity to make two decisions: how many boats will be brought into or taken out of the fishery, and how these boats will be allocated amongst species and between regions. These decisions are made on the basis of the relative profitability (the value of the catch minus the costs of harvesting) of each species specific fishery or each region. For the sake of simplicity, the prices and costs are the same for each species, and both are held constant for the duration of the simulation. Holding price and cost constant regardless of the size of the harvest is consistent with many models that include an economic component (Hannesson 1998, Pezzey et al 2000). Arguably, prices in many fisheries are increasingly a function of the global market. Therefore, a decrease in abundance in one locale does not necessarily mean that prices will increase, as is suggested by the classic supply curve. Instead, the

fish may be obtained from other locations at a basically constant price. In this way, price is buffered against the variability in local supply.

Boats in the four different fisheries also have the same harvesting efficiencies. Again, for the sake of simplicity in interpreting results, efficiencies are constant across the range of biomass levels – whether the species is abundant or has been depleted. However, as a result of the changes in the relative biomass of each stock, profitability will vary, and boats are always being reallocated toward the circumstances (fisheries and/or regions) that offer higher profits.

Harvesting from the biological system takes place under two different management systems: open access or sole owner. These two rule systems represent the opposing extremes of fisheries management (Homans & Wilen 1997). Open access refers to a system in which there are no measures to limit entry. Therefore, entry continues to occur as long as average profits per harvester are positive, causing all rents to be dissipated, and often resulting in the depletion of the resource below levels which are economically optimal and perhaps biologically sustainable. In natural resource economics, “rents” are the benefits created by “factors of production”, and accrue to the individual who controls them. Rents are measured as the difference between what the factor is earning and what is the minimum amount its owner would accept to keep it in its current use (Thomson 1998). Open access completely depletes economic rent to zero. The open access result is characterized as “the tragedy of the commons”.

In contrast, a sole owner management regime is an analytical construct which assumes a single decision maker (which can be imagined as a government unit, a cooperative, or a community) managing the total number of boats and their allocation

with the goal of getting the most value from the fishery in the long term. Because the hypothetical sole owner possesses property rights over the entire fishery, they have the incentive to maximize profits, generating, rather than dissipating rents from the resource. This is generally considered optimal management, if economic criteria are considered paramount.

Operationally, under open access conditions, entry into the fishery takes place when current average profits per harvester are positive, and exit from the fishery occurs when they are negative. The extent to which this occurs is a non-linear function of profits. This rule has the effect of driving average profits to zero, and depleting the total harvestable stocks to ~30% of biomass levels in the absence of a fishery. In contrast, the sole owner manages the number of boats with the goal of maximizing profits. In this system the owner adds or subtracts boats based on recent trends in both profits and numbers of boats. For example, if both trends in profits and in the numbers of boats are positive, the sole owner will continue to add boats. If the trend in profits is negative and the trend in boats is positive, the sole owner will reverse course and begin to subtract boats from the fishery. It is necessary to use trends, rather than yearly values, because changes in profits that result from changes in the amount of effort will take a number of years to work their way through the fishery. For example, a reduction in effort may have positive consequences for subsequent recruitment, and therefore catch, but these increases will not be evident for a number of years. By using a trend we minimize the likelihood that the sole owner is reducing effort when he/she should be increasing it, or vice versa. The number of boats in the fishery is always less under sole owner

conditions, and the biomasses of the harvested species are generally maintained at significantly higher levels.

In using trends there is some danger that the sole owner will converge on a local sub-optimum rather than locate the true profit maximizing solution. In order to reduce the probability of this, the sole owner also keeps track of past circumstances that led to high profits in each fishery. Specifically, the sole owner remembers the ratio of biomass to the number of boats which existed at the time of the highest profits, and adds or subtracts boats to try to recapture those circumstances. Finally, the sole owner is also constantly comparing its profits per boat against a figure which represents what the sole owner could be making outside of fishing through alternative investments and removes boats when profits fall below that figure. Through all these calculations the sole owner is doing the best job possible of maximizing profits. However, due to the complexity of the system, the sole owner may still be stymied by biological noise and the indirect results of his/her decisions. The sole owner is therefore an extremely competent, although not perfect, manager.

In the version of the model used for this paper, harvesting rights are awarded on a single species basis. This means that while a given boat may fish in either of the two regions during the course of a year, it cannot harvest two species during the course of a single year simultaneously. The decision to allocate harvesting rights in this way was made in order to more closely approximate the current regulatory environment in New England fisheries. Historically many of Maine's fishermen harvested from a mix of species, as a function of the changes in season and changes in species relative abundance (Acheson 1988). This approach served to dampen the variability in landings that they would

otherwise experience. Over time, their ability to pursue this strategy has been largely eroded by permitting requirements, a process that fishermen describe as being confined to "little boxes". Although these rules were intended to limit the level of effort experienced by each species, they have also had the effect of severely limiting the survival strategies available to fishermen. This management trend shows evidence of continuing. Although there is currently a multispecies groundfish license that includes 13 species, species are periodically removed from this complex to be managed independently (i.e. monkfish, hake), and total allowable catch (TACs) as well as trip limits, are set on a species-by-species basis, even within the groundfish complex. Given these circumstances, we decided that a "little box" version of the model is a reasonable approximation of the current regulatory arrangements.¹⁷

Simulation Methodology

To simulate the creation of a reserve, fishing pressure on one of the biological subsystems is reduced to zero in year 200 of a 400-year run. The fishing mortality experienced in the other system depends upon the decision rule in use - open access or sole owner. The response of the sole owner is to remove 50% of its boats from the fishery when the reserve is created, since this is a logical initial reaction to losing approximately 50% of the fishable biomass. Under open access, no boats are automatically removed when the reserve is created. Instead, as profits drop below zero

¹⁷We have also developed a "big box" version of the model, in which boats may switch between species within a region, but not between regions. A comparison of the big box and little box is the focus of Teresa Johnson's thesis work. The big box model has not yet been adapted however, to address questions regarding marine reserves.

due to the overcapacity in the fleet, boats are removed in an uncoordinated way until profits are reestablished at zero.

The size of the reserve is adjusted by changing the carrying capacity of the closed subsystem relative to the fished subsystem. In one version of the model the reserve is 10% of the carrying capacity of the subsystems combined, in the other it is 50%. As explained in the description above, in addition to the size of the reserve, we can vary the amount of egg/larval transfer, the amount of adult spillover, and the management rule, and compare alternate sets of assumptions. Another key way in which the model can be varied is to change whether each species is first harvested before or after it has had an opportunity to reproduce.

In evaluating the impact of the reserve we use criteria from both the economic and biological sectors of the model. From the harvesting sector we focus on the average catch, the variability in the size of the catch from year to year, the average wealth, and the number of boats participating in the fishery, pre-reserve and post-reserve. From the biological sector we compare the species composition, the size of the total biomass, and the size of the spawning stock biomass, pre-reserve and post-reserve. In order to remove any bias created by the initial conditions of the model, and the perturbation of creating the reserve, we take our averages from years 100-199 and years 300-399. For each simulation 100 runs are performed, and the average value for each variable of interest reported. All of these indicators can be examined on an individual species basis, or in the aggregate for each subsystem.

Chapter 3

RESULTS FROM A MULTISPECIES RESERVE MODEL UNDER OPEN ACCESS AND SOLE OWNER MANAGEMENT

Introduction

The simulations conducted with the model described in Chapter 2 were designed to explore the potential benefits to fisheries management that might be derived through the use of marine reserves, as measured by changes in size of catch, variability of catch, size of fleet, economic rent, and size of spawning stock biomass. The specific intent was to examine how these potential benefits are affected by the management regime in place *outside* the closed area for different species in a multispecies fishery. Two prototypical management regimes developed in resource economics are used for the purposes of comparison: open access and a sole owner. As described in detail in Chapter 2, open access refers to a situation in which the absence of property rights over the resource leads to uncoordinated entry into the fishery, and the inevitable reduction of economic rent to zero. In contrast, in the sole owner scenario all property rights belong to a single, profit-maximizing entity. The sole owner dictates the numbers of boats allocated to each fishery and region based on its best understanding of recent trends in changes in the size of the fleet, the condition of the resource, and the profits its past actions have generated. Because the sole owner has the advantage of being able to capitalize on the benefits of its

restraint in the future, it is able to maximize profits and exploit the resource at a sustainable level.

Following a comparison between the expected yields and resource conditions for fisheries under open access and sole owner regimes, certain modifications are made to the model to explore how the basic results may change under different circumstances. These modifications reflect the different choices that might be made regarding other management rules used in concert with the management regime, the behavioral tendencies of the species in question, or the oceanographic conditions of the particular region. Management decisions include minimum size/mesh size requirements, modeled here as the age at which the species becomes available to the fishery, and the size of the reserve that is employed. The amount of adult spillover from the reserve is likely to be a function both of the natural tendencies of a given species to large-scale movements or migrations, as well as the physical placement of the reserve. Provided managers have some understanding of the extent and direction of a species movement, reserves could be placed to either facilitate or hamper the spillover of the adults. Similarly, managers may be able to capitalize on a scientific understanding of prevailing oceanographic conditions to place reserves in ways that will promote larval drift from the closed area to the fishing ground. In order to capture these effects, in addition to the management rules and reserve size, varying amounts of adult spillover and larval drift are examined.

Finally, as noted in Chapter 2, this model contains five species, which interact strongly in the early age classes. The multispecies dynamic makes this model distinct from the majority of models reported in the literature and described in Chapter 1. The species that populate the model are differentiated from one another by characteristics that

place them on a continuum with regard to their growth rates, fecundity, and susceptibility to density-dependent effects. Some species reproduce early and prolifically, but are vulnerable to density-dependent effects; others reproduce in smaller numbers later in life, but are better able to withstand pressure as the system approaches carrying capacity. When the results of a simulation are described, trends for individual species are compared and contrasted to the behavior of the system as a whole.

Consistency Tests

The characteristics of the biological and economic systems in the model were described in Chapter 2. In this chapter, we present the results of tests run to demonstrate the model's basic reliability, and to ensure that its overall behavior conformed to expectations. Specifically, we closely examine the response of each species to exploitation, and the relative impact of different management regimes on the yield generated from the individual fisheries, the wealth that is generated, the number of boats deployed, and the condition of the resource. The purpose of these exercises is to make sure the dynamic behavior of the model is consistent with normal expectations about the behavior of fish populations and harvesters.

Open Access versus a Sole Owner

It was important to ensure that the results generated under a sole owner and those generated under open access matched our intuitive and theoretical understanding of these management regimes. We compared the relevant parameters under three regimes (Table

3.1). The comparison includes the baseline sole owner, the baseline open access and a modified open access case where harvest may take place the year before reproduction begins. This latter scenario can be envisioned as a situation where the legal mesh size is smaller than biologically optimal, and for simplicity is referred to as open access, small mesh.

Under open access, entry of boats occurs until all profits are dissipated, and no wealth is accumulated. Interestingly, catch is largest under the baseline open access scenario (Table 3.1). This may be contrary to expectations, since open access implies depletion of the resource to such low levels that large catches cannot be sustained. However, the extent to which such depletion occurs is a function of the ratio of the costs of harvest to the profits of harvest, as well as additional management rules which may protect the stock. In this case, because harvest is not permitted until the age when each species begins to reproduce, the ability of the stocks to sustain consistently high catches is preserved even under open access. As expected, the number of boats deployed is much larger under open access – almost 4 times greater over all the fisheries than under a sole owner (Table 3.1). Under open access, small mesh, the overall catch is much less than the baseline open access, and less than the baseline sole owner, although the number of boats is greater than that deployed under a sole owner. In the open access, small mesh scenario, the biomass has been reduced to such a low level by high fishing mortality and low reproductive capacity, that larger catches cannot be maintained.

The biomass of age 2 and over cohorts (2+) of the harvested species is maintained at much higher levels under a sole owner than under either form of open access (Table 3.1). The biomass for the total system is nearly equivalent under sole owner or open

access because this parameter includes the biomass of sand lance. Because sand lance is not harvested, its population compensates for the depletion of the other species to whatever extent necessary to keep the system near its total carrying capacity. As fishing pressure increases, sand lance makes up a larger percentage of the total system biomass.

It is interesting to note that the relative size of the catch from each species or the fleet for each species does not stay the same for each management scenario. For example, although cod represents the largest percentage of the total catch under a sole owner and under the baseline open access, herring is the largest percentage of the catch under open access, small mesh. This implies that the different management scenarios are more than simply various levels of fishing mortality, they also affect the dynamics of the harvested species.

Stock Dynamics under Different Management Regimes

A common measurement used to gauge the health or safety of an exploited species is the size of the spawning stock biomass (SSB). It is hoped that protection of the stock can be achieved by maintaining the SSB at some level relative to that which would be expected in an unfished population. SSB is also a good metric for us to use to evaluate the impact of different management regimes on the resource.

It is clear that an open access regime results in a much larger fleet, and higher levels of fishing mortality than a sole owner regime (Table 3.1). Therefore, the depletion of the SSB is also greater under open access than it is under a sole owner, and greatest overall under open access, small mesh (Table 3.2).

Table 3.1: Average wealth, catch, fleet, and postlarval biomass for the total system and for each individual species for three different management scenarios. This average is for 100 100-year simulations.

| Management | Average | | |
|-------------------------|------------|-----------------|-----------------|
| | Sole Owner | Open Access | Open Access.SM |
| Total Wealth | 13,682,400 | NA ^a | NA ^a |
| C Wealth | 6,142,400 | NA ^a | NA ^a |
| HA Wealth | 3,625,180 | NA ^a | NA ^a |
| HE Wealth | 2,701,460 | NA ^a | NA ^a |
| R Wealth | 1,213,320 | NA ^a | NA ^a |
| Total Catch | 2,057,100 | 2,580,280 | 1,644,590 |
| C Catch | 844,616 | 955,722 | 475,397 |
| Ha Catch | 567,735 | 677,833 | 467,487 |
| He Catch | 428,976 | 770,087 | 542,792 |
| R Catch | 215,772 | 176,634 | 158,916 |
| Total Fleet | 861 | 3,194 | 1,620 |
| C Fleet | 288 | 1,188 | 450 |
| HA Fleet | 257 | 845 | 521 |
| HE Fleet | 199 | 940 | 448 |
| R Fleet | 118 | 221 | 201 |
| Total 2+ Biomass | 13,436,000 | 13,016,100 | 12,537,000 |
| C 2+ Biomass | 3,184,000 | 2,362,110 | 1,107,860 |
| HA 2+ Biomass | 2,675,790 | 1,824,630 | 934,309 |
| HE 2+ Biomass | 1,920,500 | 1,421,040 | 868,119 |
| R 2+ Biomass | 2,427,880 | 1,323,600 | 1,035,350 |
| SL 2+ Biomass | 3,227,770 | 6,084,680 | 8,591,400 |

^a Wealth is not accumulated under the open access regimes.

Table 3.2: Spawning stock biomass as a percentage of unfished spawning stock biomass for cod, haddock, herring, redfish and sandlance, and for the harvested species combined, under the three management scenarios (SO: sole owner; OA: open access; OA.SM: open access, small mesh). Sandlance spawning stock biomass increases as fishing pressure increases because it is not harvested.

| SSB | Cod | Haddock | Herring | Redfish | Sandlance | Total Harvested |
|-------|--------|---------|---------|---------|-----------|-----------------|
| SO | 61.23% | 61.53% | 89.72% | 49.81% | 214.43% | 62.72% |
| OA | 28.67% | 28.68% | 56.15% | 20.84% | 377.42% | 30.59% |
| OA.SM | 7.01% | 6.25% | 16.55% | 13.43% | 623.56% | 9.91% |

In the absence of a reserve, under a sole owner (SO), the total SSB for all harvestable species is reduced by ~37%. Under an open access system where harvest begins the same year as reproduction (OA), the total SSB is reduced by almost 70%. Finally, if fishing is allowed to begin in an open access system the year before the species become reproductive (OA.SM), the SSB is reduced by 90%. Individual species are affected to different extents, although the basic trend remains the same across management scenarios. Under a sole owner, the SSB of the redfish population is the most reduced. Redfish are the latest maturing and lowest fecundity species, and therefore very vulnerable to fishing pressure - their SSB can be quickly depleted. Conversely, herring reproduces early and is very fecund, and therefore is more resilient to fishing pressure. It is only reduced by 10% under a sole owner. Cod and haddock have very similar life history characteristics, and therefore experience very similar reductions in SSB of ~38-39%. The only species that behaves differently is sand lance. Because it is not harvested, the more other species are depleted, the more the biomass of sandlance increases. The higher the fishing pressure on the other species, the larger the SSB of sandlance.

We also examined the trend in total SSB for all harvested species over a run of 100 years, for the sole owner and open access scenarios (Figure 3.1).

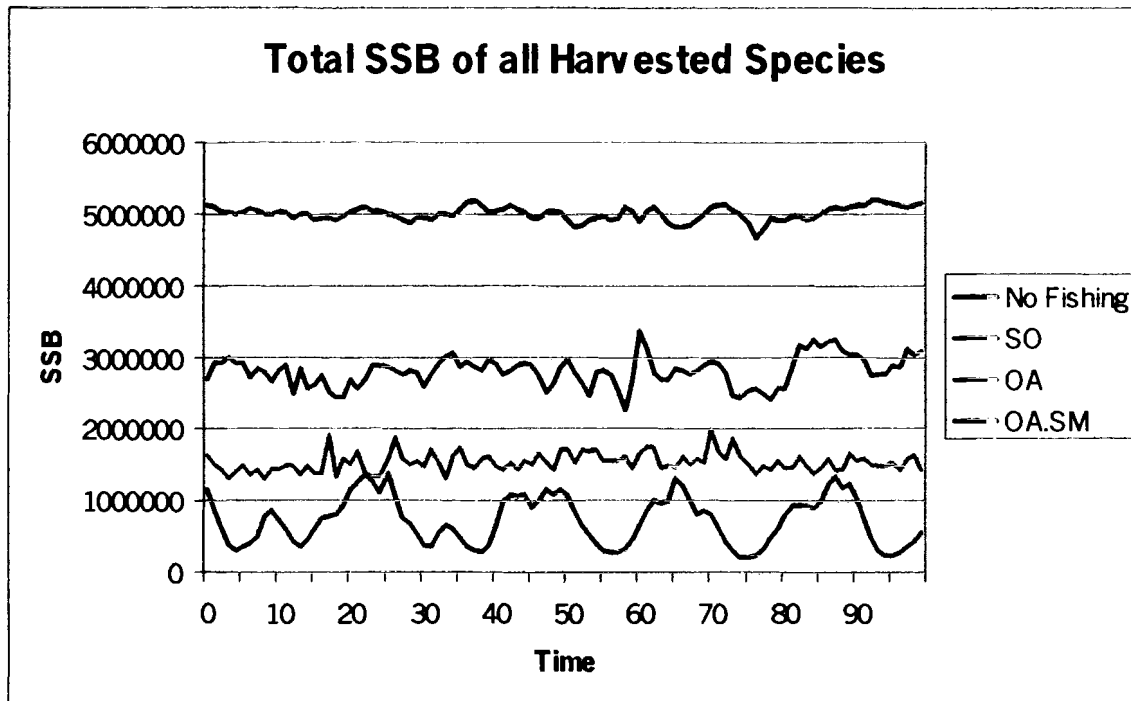


Figure 3.1: Total spawning stock biomass of all harvested species over a 100 year run, with no fishing, fishing under a sole owner (SO), fishing under open access (OA) and fishing under open access, small mesh (OA.SM).

Spawning stock biomass is least depleted under the sole owner and most depleted under an open access system where harvesting can take place before the stocks have an opportunity to reproduce (open access, small mesh). It is also evident that the variability in SSB is least when there is no fishing, and highest under open access, small mesh. This high variability is due to the dynamics that occur under open access when fishing pressure is so high. The stocks are driven to the point of near collapse, and profits become negative. Boats exit the fishery, allowing the SSB an opportunity to recover. However, as soon as profits become positive, boats flood back in, driving the SSB perilously low. This cycle is repeated over and over again, causing high variability in the

SSB for the duration of the run. In the open access, small mesh scenario, harvesting takes place before reproduction, further exacerbating this cyclic pattern. When the spawning stock biomass is driven to very low levels, its capacity for absolute growth is much smaller than with a larger biomass.

The trends observed in the levels of SSB for both individual species as well as the system as a whole under the range of management regimes examined conform to what we would expect from basic economic theory.

Response by the Fleet to the Creation of a Reserve

The baseline conditions of the model refer to simulations in which there is no connection, either by adult spillover or larval drift, between the two regions of the model. In these runs it is possible to demonstrate that the model is responding as one would expect to the closure of 50% of the area to fishing. Under sole owner, when half of the fishing grounds are closed at year 200 of the 400 year run, the sole owner automatically removes 50% of the boats. Since the sole owner has already been operating to maximize profits, this is the logical response to the contingency created by the imposition of the new reserve policy. Thereafter, using the same decisions rules as before, the model then maintains the fleet size at 50% of the pre-reserve level, providing confidence that the model adapts well to the changing conditions (Figure 3.2).

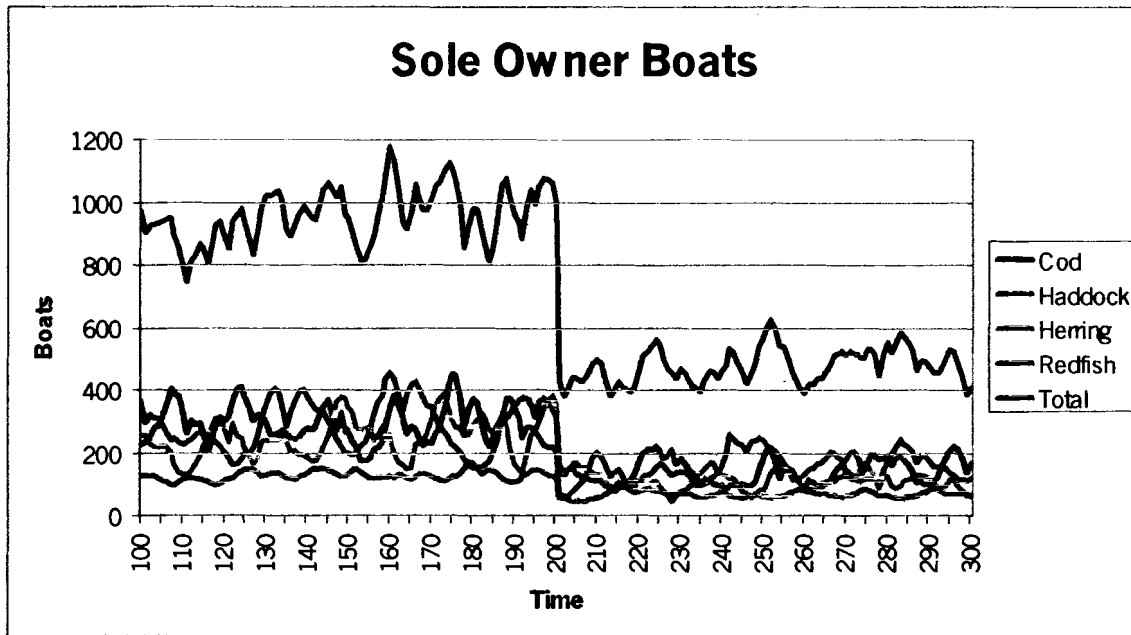


Figure 3.2: Response of the sole owner fleet to the creation of a reserve over 50% of the fishing grounds at year 200 of a 400 year simulation.

Under open access conditions, no boats are automatically removed at the time of the creation of the reserve. Instead, as profits drop below zero due to the reduction in fishable biomass, boats are removed in an uncoordinated way until profits are reestablished at zero. Providing confidence in the dynamics of the model, the post-reserve number of boats equilibrates at close to 50% of the pre-reserve levels, both on an individual species basis and for the system as a whole (Figure 3.3). Subsequent entry and exit of boats into the different fisheries in the remaining open area continues to respond to the changes in biomass of individual species. There are approximately four times as many boats deployed under open access than are considered optimal by the sole owner (Figures 3.2 & 3.3).

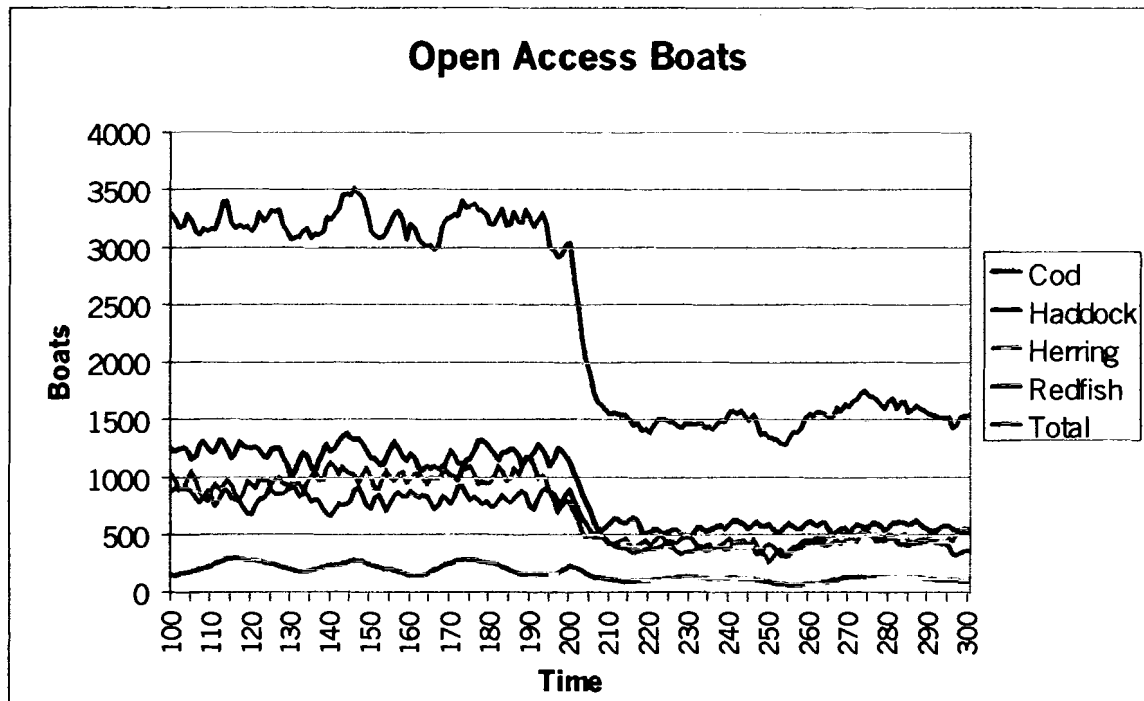


Figure 3.3: Response of the open access fleet to the creation of a reserve over 50% of the fishing grounds at year 200 of a 400 year simulation.

Response of Spawning Stock Biomass to the Creation of a Reserve

Finally, we checked the response of the populations to the creation of a reserve, with the expectation that they would rebound to higher levels following the removal of fishing pressure. All the harvested species increase following reserve creation in year 200 of the 400-year simulation (Figure 3.4). Sand lance declines sharply as the other species increase, since there is less “room” in the ecosystem for it to grow. The increase in herring following the removal of fishing pressure is the least dramatic. Herring is the most resilient to fishing pressure and its population is not significantly depleted under a sole owner (Table 3.2). Therefore, under these circumstances a reserve is of minimal benefit to the herring population.

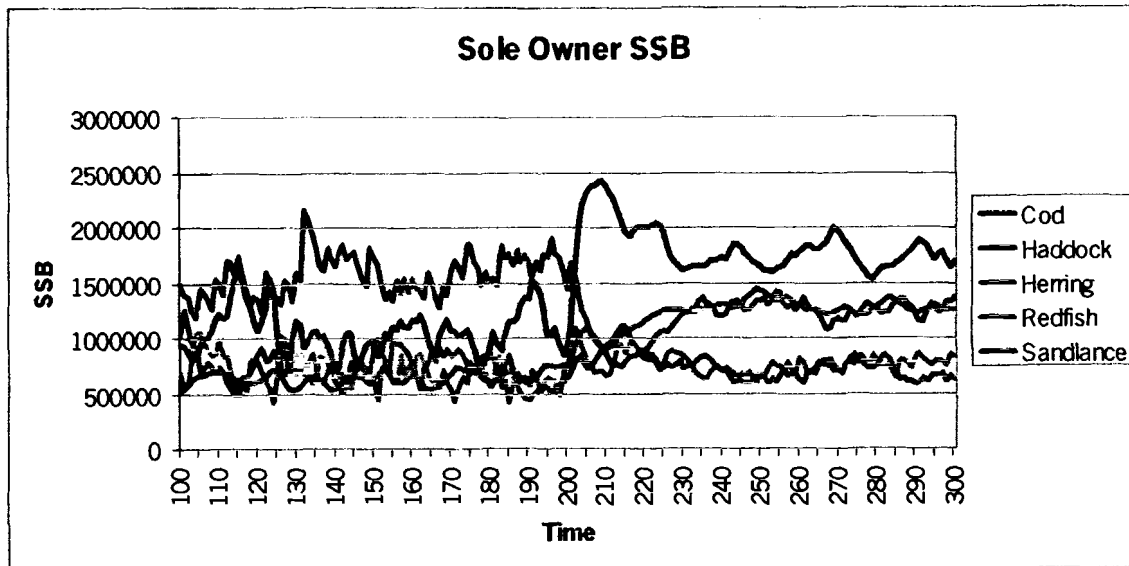


Figure 3.4: Response of the spawning stock biomass for each species harvested under a sole owner to the creation of a reserve over 50% of the fishing grounds at year 200 of a 400 year simulation

The same recovery is apparent following the creation of a reserve under open access, however the increases are more dramatic because the stocks have been further depleted by the higher level of fishing pressure (Figure 3.5).

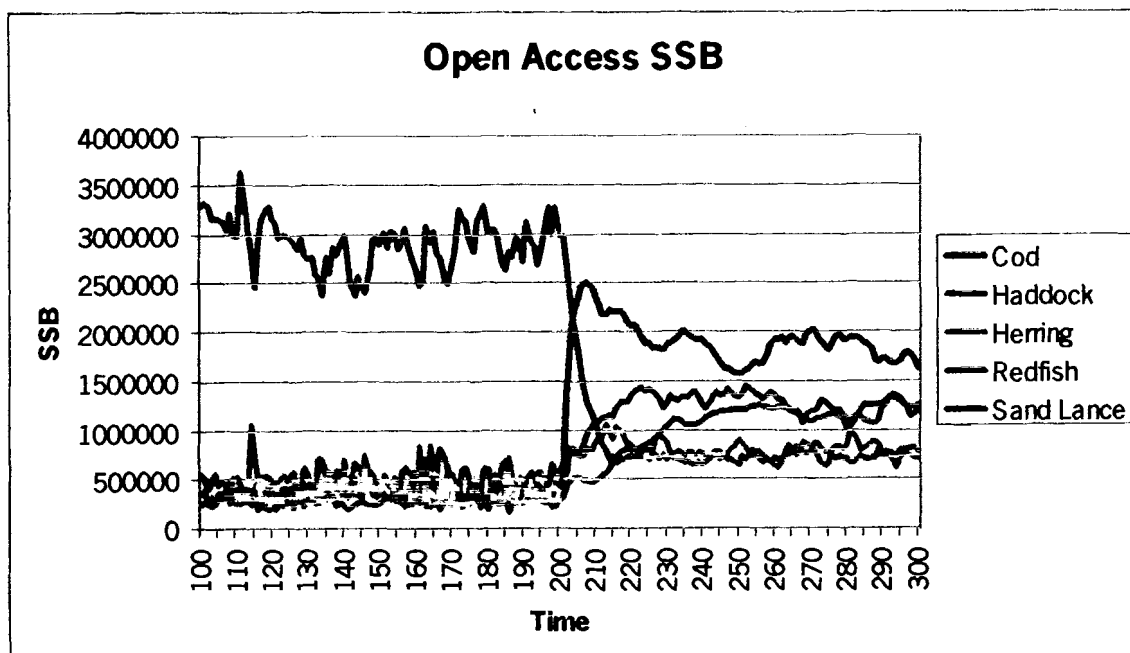


Figure 3.5: Response of the spawning stock biomass for each species harvested under open access to the creation of a reserve over 50% of the fishing grounds at year 200 of a 400 year simulation.

Simulation Methodology

As described in Chapter 1, among the arguments made in favor of the use of marine reserves is their potential to increase yield from the protected fisheries, and/or the number of boats that are able to participate in the fisheries. However, as noted by earlier researchers, the impact of the establishment of the reserve will depend upon the condition of the resource before the reserve was created, as well as the yield that the fishery had been producing in that condition (Sladek Nowlis & Roberts 1999, Pezzey et al 2000,). Both of these things will be a result of the management that is in place before and subsequently outside the boundaries of the reserve. Additionally, the characteristics of the reserve, including its size and its capacity to provide adult spillover onto the fishing grounds and larval drift outside its boundaries, will be important factors. Simulations were done comparing the results of reserve creation under the open access management rules and the sole owner. For each management regime reserves of two sizes (10% of the combined fishing ground of the two regions and 50% of the combined fishing ground) were examined, at 6 levels of adult spillover (0, 10%, 20%, 30, 40%, and 50%) and at 6 levels of larval drift (0, 10%, 20%, 30, 40%, and 50%).

Results

Sole Owner

Under a sole owner regime, the harvestable biomass is the least reduced in comparison to other management regimes (Figure 3.1). The catch from a sole owner regime is less than under the open access if rules exist prohibiting harvesting before the

age of reproduction (Table 3.1). However, by definition, greater efficiency and accumulated wealth are possible under the sole owner regime.

Sole Owner with a 50% Reserve. Because the sole owner is already employing a conservative management strategy seeking to maximize profits, creating a reserve that closes 50% of the fishery does not improve the average size of total catches, even at high levels of adult spillover or larval drift. However, yields from an individual species may increase with a 50% reserve at very high levels of adult spillover and larval drift. With a 50% reserve, the herring catch can be more than 110% of that which is achieved in the absence of a reserve, when adult spillover is 50% and larval drift is 40-50% (Figure 3.6). Herring is the only species for which an increase in catch over the pre-reserve level is seen.

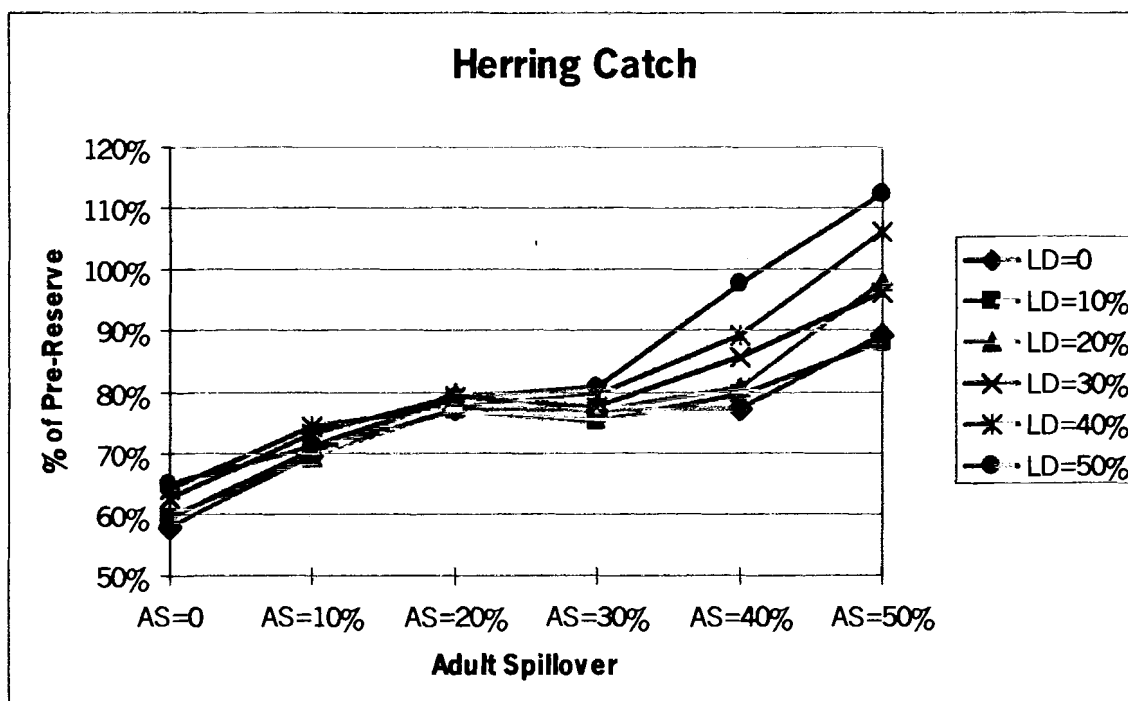


Figure 3.6: Average percentage of the pre-reserve herring catch achieved after the creation of a 50% reserve under a sole owner for levels of adult spillover 0-50% and larval drift 0-50%.

Under a sole owner, the best measurement of success of a reserve is the wealth that is generated, since that is what the sole owner is working to maximize. The total wealth approaches 85% of the pre-reserve level when adult spillover is 40% and larval drift is 50% that which is produced in the reserve (Figure 3.7). Again, the wealth generated by an individual species may be greater with a 50% reserve at high levels of adult spillover and larval drift. Herring is the only species for which this is the case (Figure 3.8).

Herring catch and wealth increases with the 50% reserve at high levels of adult spillover because of the population dynamics inside the reserve. As adult spillover increases, the reserve becomes depleted of the slower growing populations. Because herring reproduces early and is very fecund, it can quickly take advantage of the “space” in the system that is created by the spillover of other species. Beyond an adult spillover of 30%, the wealth from herring continues to increase, while cod, haddock, and redfish populations and wealth are all declining (Figure 3.9).

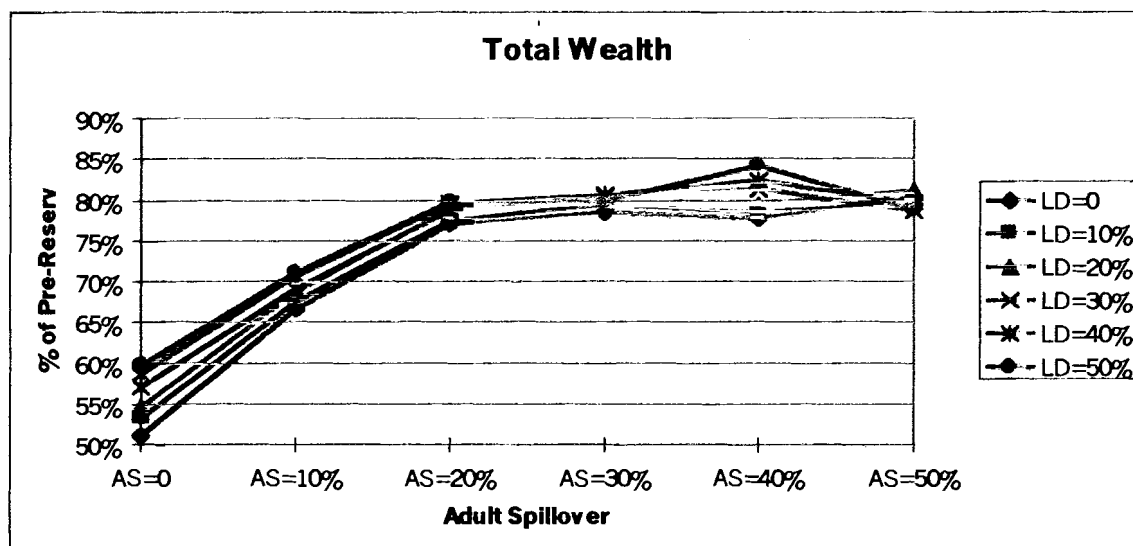


Figure 3.7: Average percentage of the pre-reserve total wealth achieved after the creation of a 50% reserve under a sole owner for levels of adult spillover 0-50% and larval drift 0-50%.

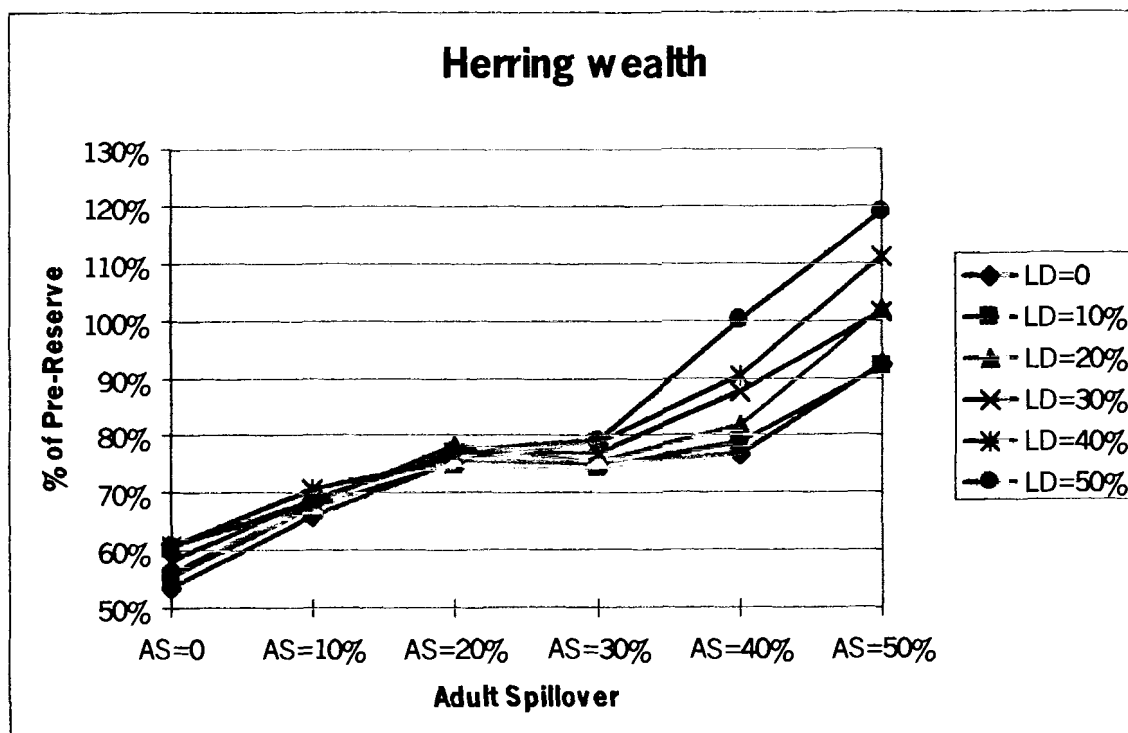


Figure 3.8: Average percentage of the pre-reserve herring wealth achieved after the creation of a 50% reserve under a sole owner for levels of adult spillover 0-50% and larval drift 0-50%.

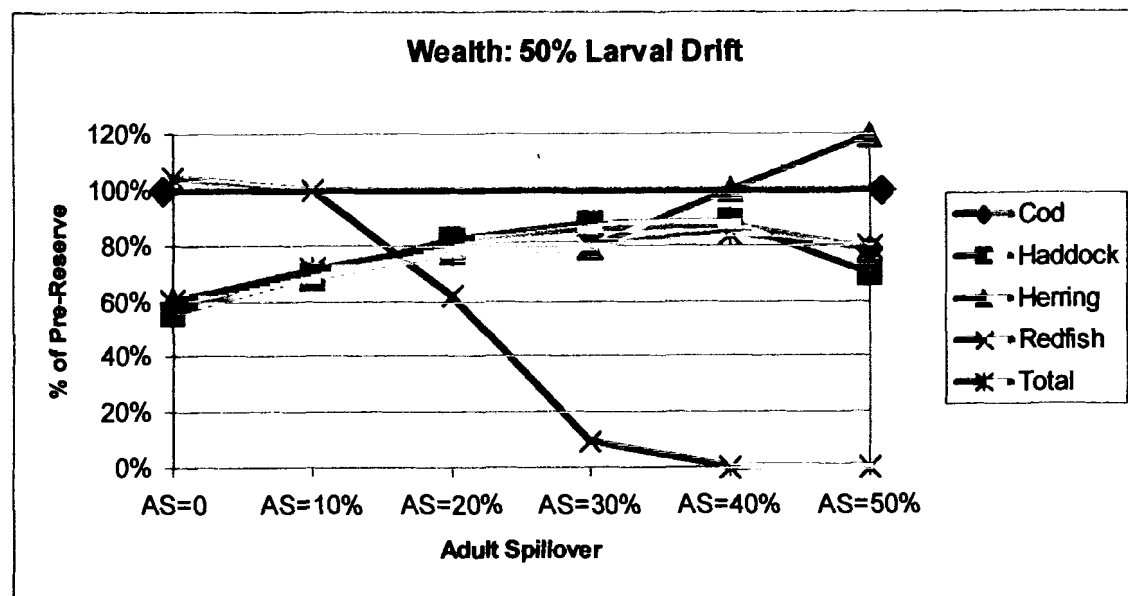


Figure 3.9: Average percentage of the pre-reserve wealth for each species achieved after the creation of a 50% reserve under a sole owner for levels of adult spillover 0-50% and larval drift = 50%.

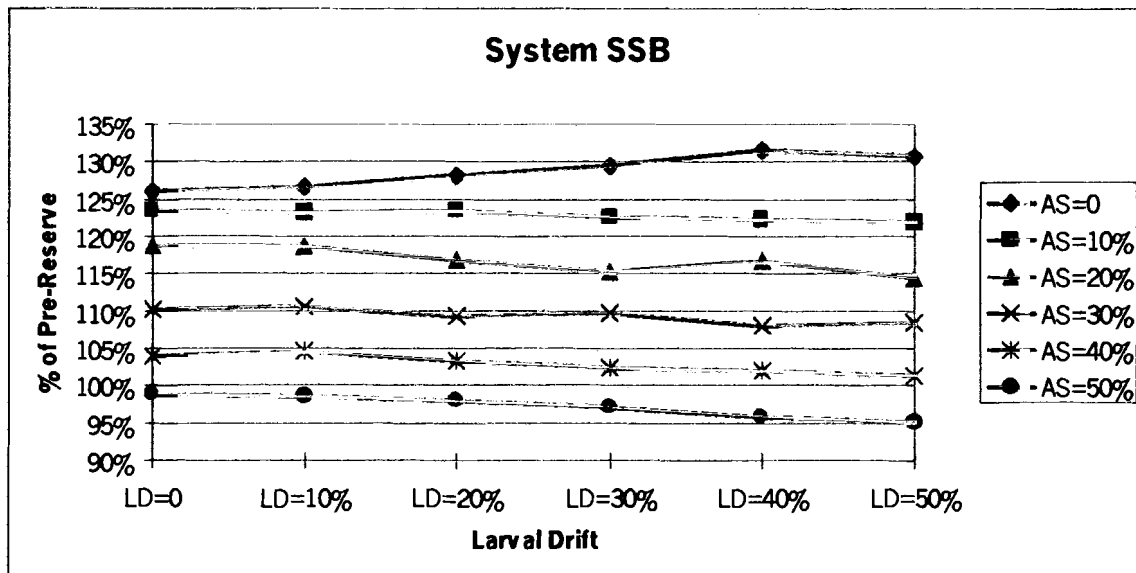


Figure 3.10: Average percentage of the pre-reserve total harvestable SSB achieved after the creation of a 50% reserve under a sole owner for levels of adult spillover 0-50% and larval drift 0-50%.

Because the sole owner does not reduce the SSB to a level that would be of concern, the insurance that is provided by the reserve in terms of increased SSB is not likely to be of interest to the sole owner. Spawning stock biomass increases the most over the pre-reserve levels when adult spillover is low (Figure 3.10). When adult spillover is as high as 50%, the total harvestable spawning stock biomass is actually less than the average that exists in the absence of a reserve (Figure 3.10). The 50% spillover out of the reserve into the open area appears to represent a greater loss to the total spawning stock biomass than is occurring under harvesting pressure. However, the trends exhibited by individual species are conflicting. At 50% adult spillover, herring achieves higher levels of spawning stock biomass with increasing larval drift, while both cod and haddock spawning stock biomass decreases with increasing larval drift (Figure 3.11).

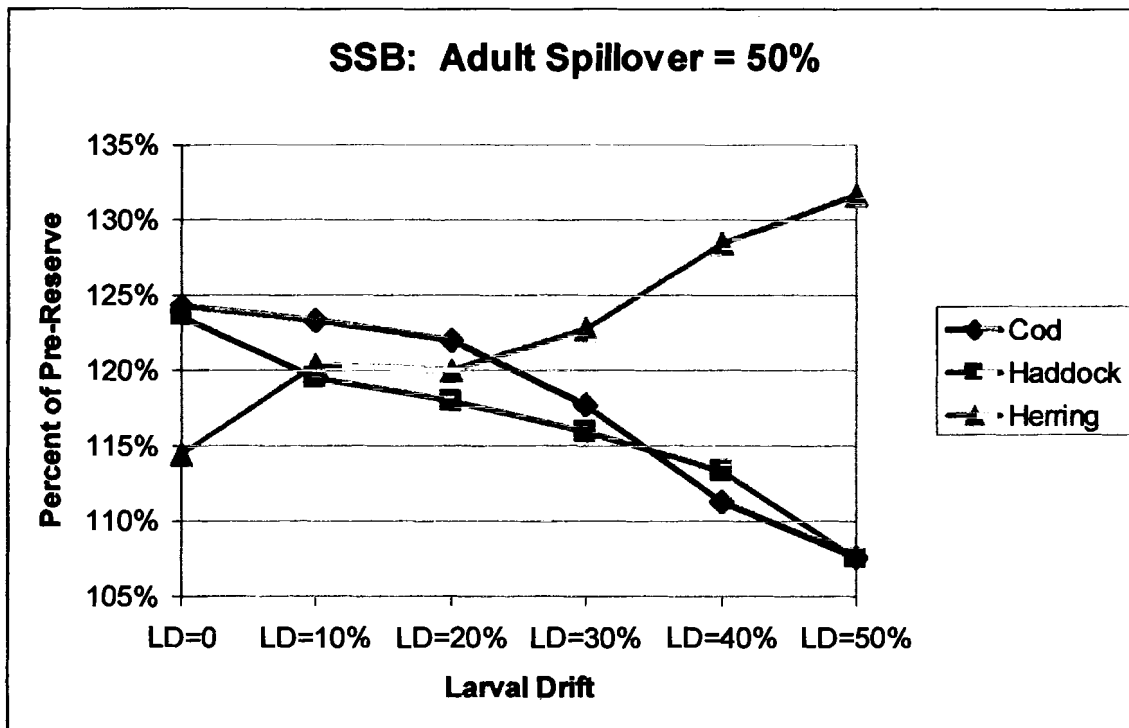


Figure 3.11: Average percentage of the pre-reserve spawning stock biomass of cod, haddock, and herring achieved after the creation of a 50% reserve under a sole owner with 50% adult spillover and larval drift of 0-50%.

Sole Owner with a 10% Reserve. Under some circumstances, a sole owner using a 10% reserve, can actually accumulate more wealth than is possible without a reserve (Figure 3.12). A high level of adult spillover (50%) is enough to ensure at least an equivalent amount of wealth as the pre-reserve situation, even with no larval drift. However, even an adult spillover of 20% is sufficient to allow wealth to exceed pre-reserve levels, if combined with a larval drift of 50% (Figure 3.12).

When adult spillover is 50% and larval drift is 50%, the average amount of total wealth is 104% of the average total wealth pre-reserve (Figure 3.12). The results for individual species can be more dramatic, as in redfish, where wealth is almost 120% of that achieved pre-reserve when there is no adult spillover, and larval drift is 40% of that present in the closed area. For every species there is some combination of adult spillover

and larval drift under which the wealth generated with a 10% reserve is equal to or greater than that which is possible without a reserve.

Although the increase is not great, this result contrasts with results of other models, which found that only when a fishery is experiencing high levels of mortality is it possible for a reserve to create an economic benefit. It is likely that the difference in these results can be attributed to using a multispecies, rather than a single species model. In this model, the sole owner is attempting to keep track of the changing abundances of four different species, and to understand the trends in those abundances as they are affected by its decisions to increase or remove effort. If this task were not difficult enough already, there are also environmental factors causing random mortality in the early age groups, and a total system constraint which is impacting each species differently. For these reasons, the sole owner does a good, but not perfect job. Closing off 50% of the fishing ground forces the sole owner to give up more catch and wealth than it gains from the reserve. However, if the sole owner closes off only 10% of the fishing ground, and the combination of adult migration and larval drift is sufficient, then a reserve can provide an important buffer in terms of a constant larval supply and adult spillover for the sole owner. Catch and wealth can achieve the same, or slightly greater levels (different for each species) relative to what is possible without a reserve, and the safety of the harvestable stock, as measured by SSB, is greater.

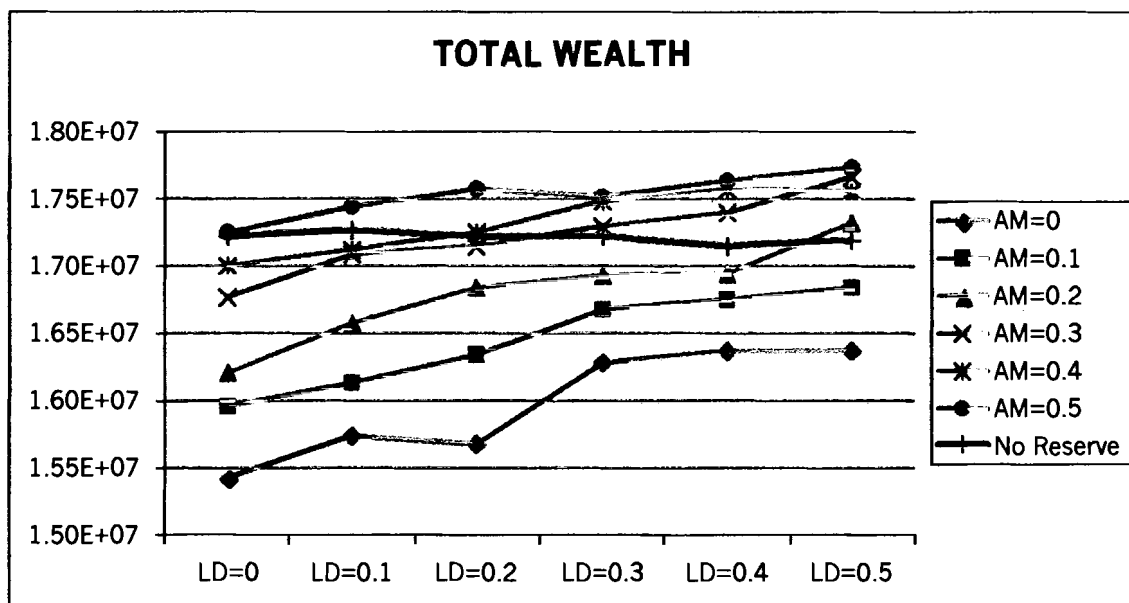


Figure 3.12: Total wealth achieved after the creation of a 10% reserve under a sole owner for levels of adult spillover 0-50% and larval drift 0-50%.

Open Access

In the baseline version of the open access model, fishing mortality is very high, and the harvestable biomass is depleted. (Table 3.2, Figure 3.1). However, remember that fishing mortality begins simultaneously with the first year of reproductive maturity. The mathematics of the model ensures at least one year of spawning before capture. The resource can therefore be fished consistently at high pressure, but maintain high productivity. In addition, the egg mortality experienced by each species each year is in part a function of that species' biomass level (the higher the species' biomass, the lower the percentage egg survival). Because the biomass has been reduced to a low level under open access, the mortality on the eggs is comparatively low. Therefore, a higher percentage of eggs survive, further ensuring the persistence of the stock.

The baseline open access model has a higher average annual catch than the baseline sole owner model¹⁸ (Table 3.1). In fact, due to the special condition of ensured reproduction, in open access, virtually the highest practical catch is achieved. In this model, the open access dynamic never drives the fishery to collapse, because as soon as profits turn negative, boats exit and the fishery has an opportunity to recover. A population base always remains to continue producing new recruitment. It is difficult for a reserve to improve on this situation, because closing any portion of the fishing ground will likely eliminate more potential catch than it will provide in benefits. Under most circumstances for the populations in this open access model, what is gained in yield through adult spillover and increased larval supply cannot compensate for the loss of fishable biomass.

Open Access with a 50% Reserve. For the baseline open access model and a reserve of 50% of the combined fishing ground, the total catch and total number of boats never reached the levels achieved before the reserve was created. With adult spillover of 30% and larval drift of 30% that created in the reserve, the total catch achieves a level of 81.8% that which is possible when the entire region is open to fishing (Figure 3.13). Similarly, the number of boats is 78.6% of the average level when there is no reserve (Figure 3.14).

Increasing adult spillover increases catch and the number of boats participating in the fishery up until an adult spillover of 30% (Figure 3.13, Figure 3.14). Higher levels of adult spillover led to a reduction in the level of catch achieved relative to pre-reserve conditions. As adult spillover increases, the size of the stock in the reserve is reduced.

¹⁸ This may seem counter intuitive, since a sole owner fleet is presumably better managed. However, the sole owner is maximizing profits, not catch. The sole owner is deploying fewer boats per unit of catch and accumulating wealth.

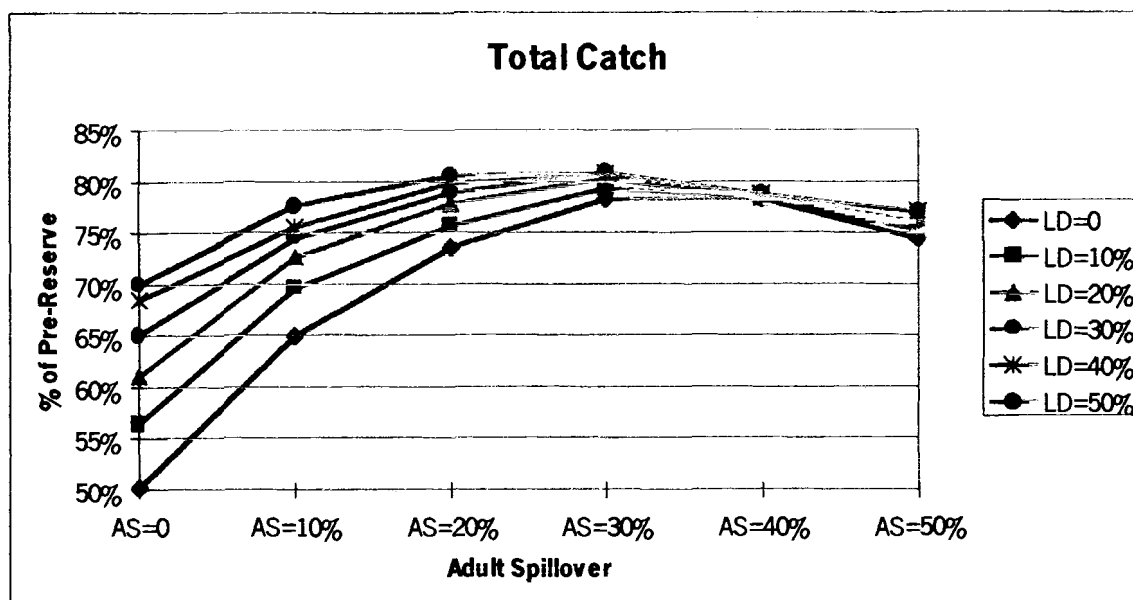


Figure 3.13: Average percentage of the pre-reserve total catch achieved after the creation of a 50% reserve under the baseline open access for levels of adult spillover 0-50% and larval drift 0-50%.

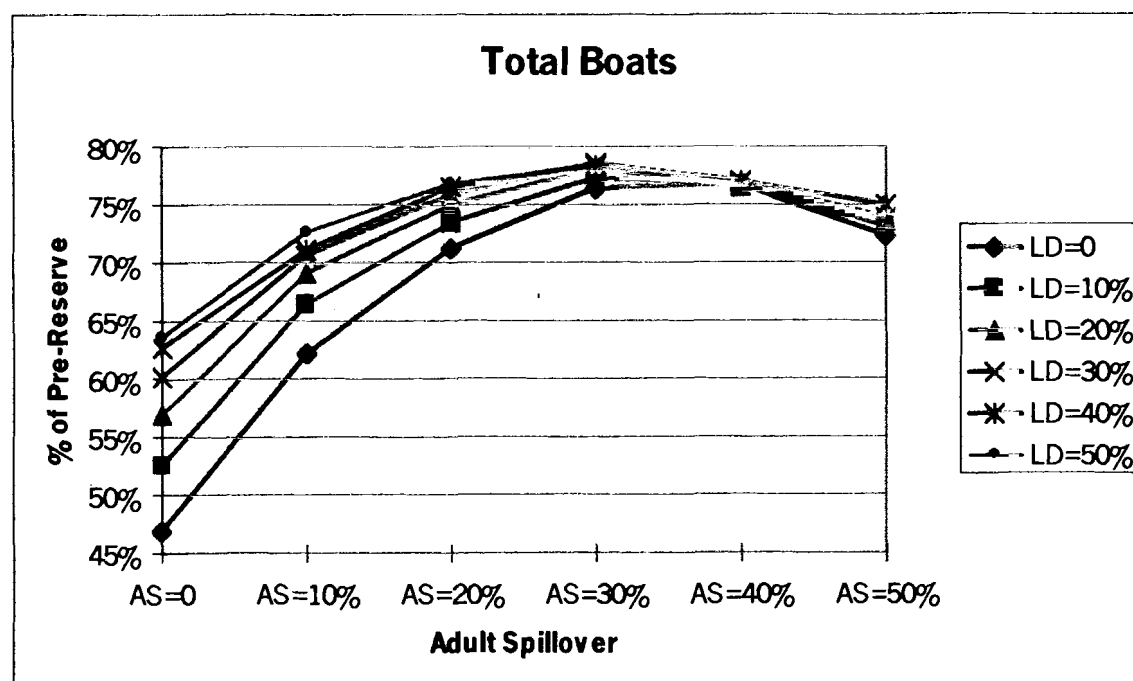


Figure 3.14: Average percentage of the pre-reserve total boats achieved after the creation of a 50% reserve under the baseline open access for levels of adult spillover 0-50% and larval drift 0-50%.

This diminishes the ability of the reserve to replenish itself, as well as to provide for subsequent spillover to the open area, both of adults and of larval drift. As a result, the amount of larval drift has a larger effect when adult spillover is at low levels. At adult spillover levels of 40%, the effect of larval drift on the size of the catch is negligible.

Another reason for the decreasing productivity of the fishery at high levels of adult spillover is the impact of the large annual influx of biomass into the open area. Such an influx will cause Region 2 (the open area) to hit its overall constraint more frequently¹⁹. Reaching or exceeding the system constraint results in higher mortality levels for the earlier age classes, and makes the open area internally less productive than it would be in the absence of this added biomass.

While the total catch from all fisheries and the total number of boats never exceeds the pre-reserve levels, due to the different life history characteristics of individual species, some do show increases above the levels achieved without a reserve. For example, as under a sole owner, at very low levels of adult spillover, redfish catch improves with a reserve. When there is no adult transfer, increasing larval drift from 0 to 50% from the reserve results in a catch that is 112% of the no reserve scenario (Figure 3.15). However, because the component of the total harvest that is redfish is less than 10% of the total catch, it does not have a noticeable impact on the overall catch. When all species have an adult transfer rate of 10%, and larval drift is 0, in the presence of a 50% reserve redfish harvests are 93% of what they are when the entire region is open to fishing. When combined with a larval drift of 20-30%, redfish catch and boats are 100% of what they were in the absence of a reserve (Figure 3.15).

¹⁹ As described in Chapter 2, the biomass of each Region is controlled by a system constraint which prevents the overall biomass from exceeding the carrying capacity of the Region.

An increasing amount of adult spillover or larval drift however, does not continue to increase the redfish harvest and fleet. Due to its low fecundity, at higher levels of adult spillover the ability of the redfish population in the reserve to sustain itself suffers greatly. The spillover is analogous to an additional source of mortality on the reserve population. Without another source to supply the reserve, the redfish population inside the reserve declines sharply. Outside the reserve, the population is vulnerable to harvesting, and is receiving little contribution from the reserve. At the highest levels of adult spillover (40-50%) the redfish catch is less than 50% of what it was before the implementation of the 50% reserve and eventually collapses (Figure 3.15).

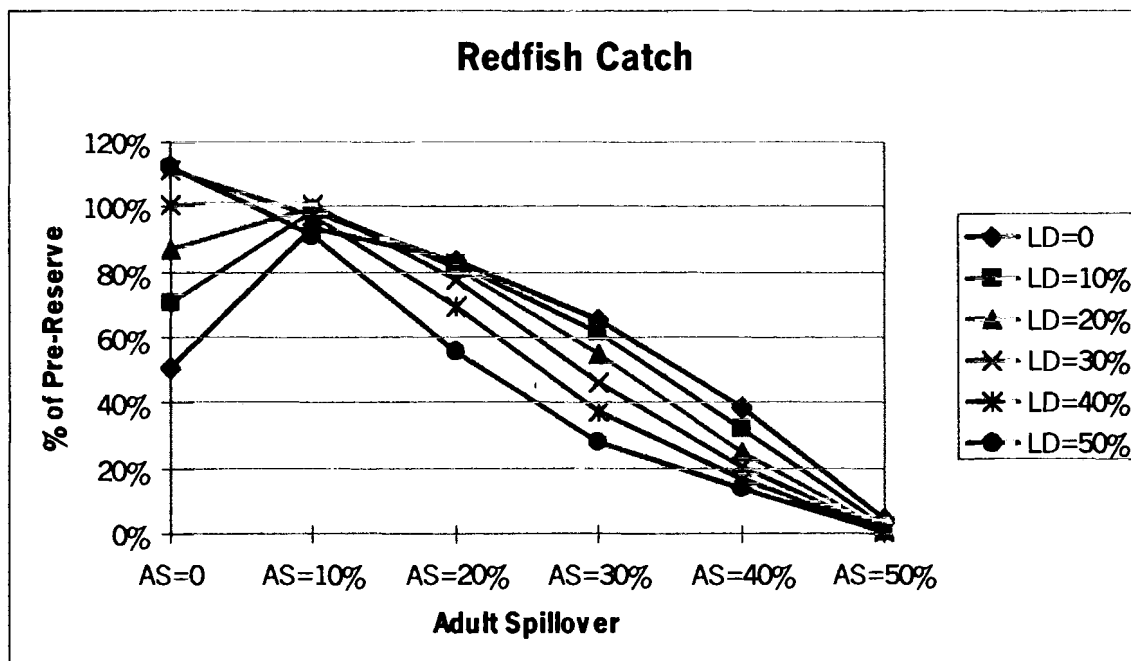


Figure 3.15: Average percentage of the pre-reserve redfish catch achieved after the creation of a 50% reserve under the baseline open access for levels of adult spillover 0-50% and larval drift 0-50%.

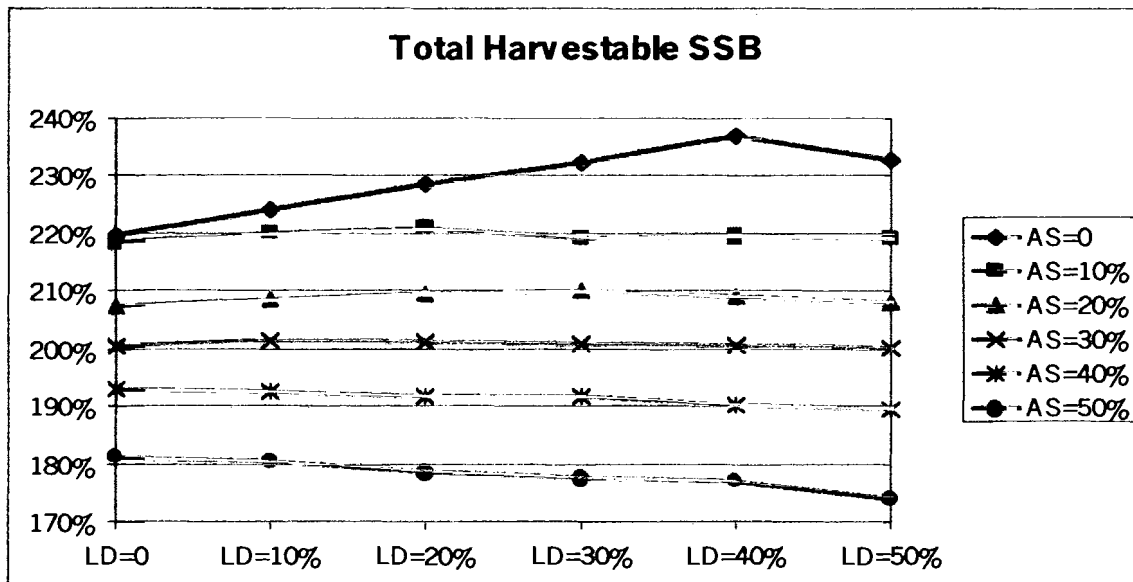


Figure 3.16: Average percentage of the pre-reserve total harvestable SSB achieved after the creation of a 50% reserve under the baseline open access for levels of adult spillover 0-50% and larval drift 0-50%.

The spawning stock biomass for all harvestable species combined across Region 1 (the reserve) and Region 2 (the open area) increases by at least 170% under every combination of adult spillover and larval drift, and by as much as 237% when adult spillover is 0 and larval drift is 40% (Figure 3.16). As expected, the size of the increase is less when adult spillover is higher. As more fish move from the reserve to the open area the capacity of the reserve to protect the spawning stock decreases. With a 50% reserve the effect of larval drift is generally small, except when adult spillover is 0.

Open Access with a 10% Reserve. For the baseline open access model with a 10% reserve, the total yield across fisheries is slightly increased (102%) under circumstances of moderate to high adult spillover (20-50%) combined with moderate to high larval drift (30-50%) (Figure 3.17).

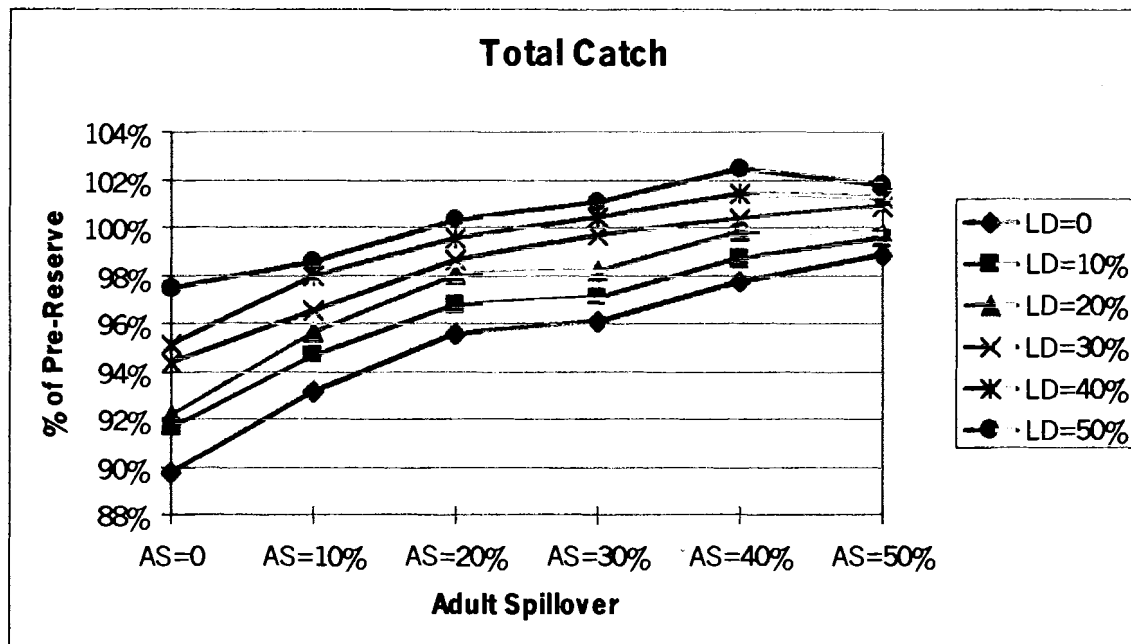


Figure 3.17: Average percentage of the pre-reserve total catch achieved after the creation of a 10% reserve under the baseline open access for levels of adult spillover 0-50% and larval drift 0-50%.

With a 10% reserve, the total catch does not begin a decline at higher levels of adult spillover, as it does when a reserve of 50% is used. Also, the contribution of larval drift to an increased catch does not decline with increasing adult spillover as it does so noticeably with a 50% reserve. The relatively improved performance of the 10% reserve is likely a result of two factors. First, the loss of fishable biomass is not so great with a 10% reserve as it is with a 50%. Therefore, the loss for which the reserve must compensate is not as great. Additionally, the open area is better able to cope with the influx of biomass from adult spillover from the smaller region. Even at the highest levels of adult spillover, the relative contribution of biomass from the reserve is very small compared to the carrying capacity of the open area. The influx does not trigger the system constraint (when the biomass reaches or exceeds the regions carrying capacity) as strongly or frequently, so it does not lower the productivity of the open area, nor will it affect egg mortality as strongly.

The results of the less drastic influx of biomass is most evident in a comparison of the redfish catch with a 10% reserve as compared with the results of a 50% reserve as adult spillover increases. The same basic pattern remains; redfish catch benefits most when adult spillover is at low levels, and larval drift is high. However, in the presence of a 50% reserve, high levels of adult spillover are enough to cause the population in the reserve to collapse, and catches to fall to near zero. Here, increasing adult spillover still causes a decline in the catch, however, it is not nearly so drastic. In fact, even at the highest level of adult spillover, the catch is only slightly less than one might expect from the closure of 10% of the fishing ground (90%) (Figure 3.18).

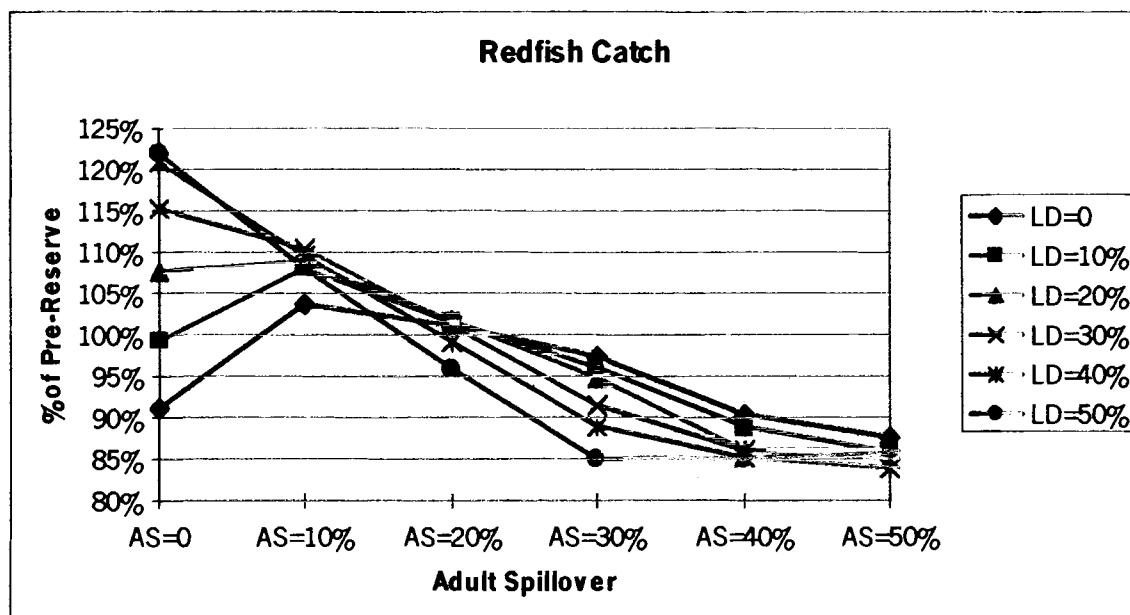


Figure 3.18: Average percentage of the pre-reserve redfish catch achieved after the creation of a 10% reserve under the baseline open access for levels of adult spillover 0-50% and larval drift 0-50%.

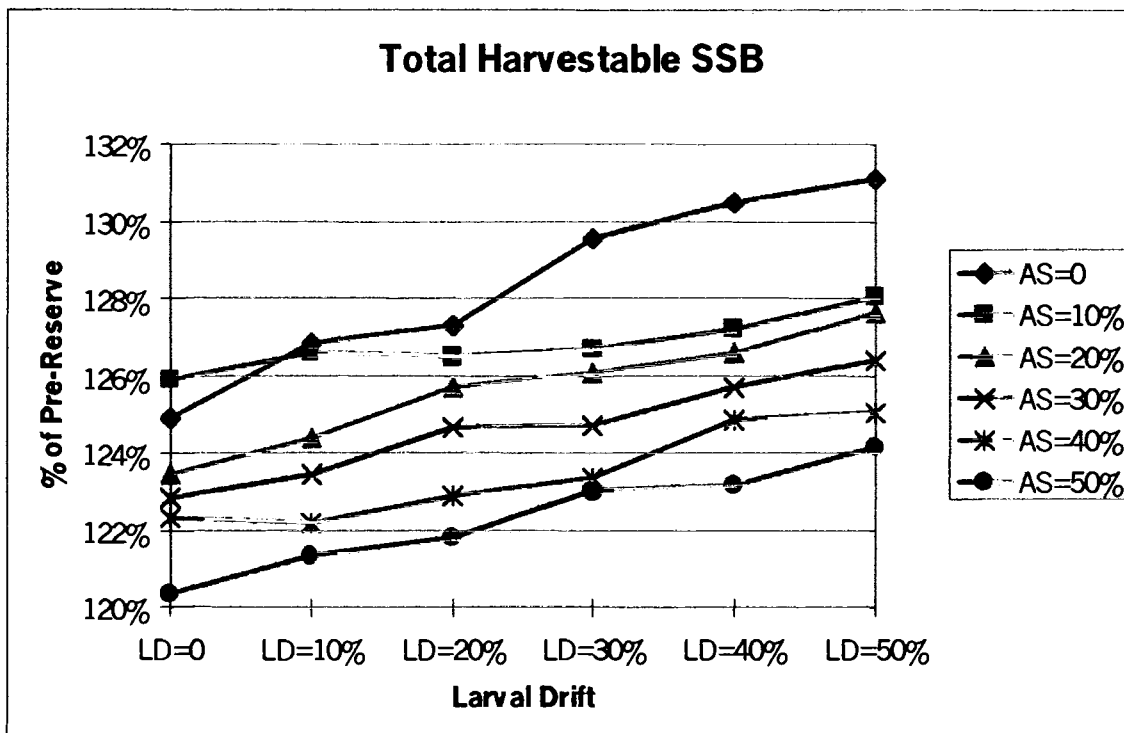


Figure 3.19: Average percentage of the pre-reserve total harvestable spawning stock biomass achieved after the creation of a 10% reserve under the baseline open access for levels of adult spillover 0-50% and larval drift 0-50%.

With a 10% reserve the increase in spawning stock biomass for all harvestable species combined is not as great as it was with a 50% reserve. The maximum increase is achieved when adult spillover is zero and larval drift is 50% (Figure 3.19). The effect of larval drift is more noticeable with a 10% reserve; the increase in spawning stock biomass increases with additional larval drift.

Open Access, Small Mesh

The second version of the open access model allows harvesting to begin the year before each species becomes reproductively mature. Such a scenario more closely approximates the reality experienced by many species, including the temperate species

complex on which this model is loosely based. This modification could be imagined as permitting a smaller mesh size than what is allowed in the baseline version of the model.

Pre-reserve, the total catch that is attainable under these circumstances is much smaller than the baseline open access model. The catch that is achieved by harvesting after the species reach reproductive maturity is 150% that realized if catch takes place before that year (Table 3.3).

Table 3.3: Average total yearly catch for three different management scenarios. This average is for 50 100-year simulations.

| Pre-Reserve | Open Access, Small mesh | Sole Owner | Open Access |
|---------------------|-------------------------|------------|-------------|
| Average Total Catch | 1,640,212 | 2,054,115 | 2,586,480 |

Open Access, Small Mesh with a 50% Reserve. At the earlier age of harvest, only at the lowest amounts of adult transfer and larval drift does the total catch fail to exceed the levels achieved before a reserve of 50% is created (Figure 3.20). For every combination where both adult spillover and larval drift are 10% or greater, the total catch with a 50% reserve increases over the pre-reserve levels.

As the amount of adult spillover increases, increasing the amount of larval drift contributes less to the increase in catch. The maximum is reached around 30%; beyond that the benefit declines. This is likely due to the depletion of the reserve by the emigrating adults, which may lower the productivity of the reserve region, both in terms of adult members of the population available to move out of the reserve in the future, and with regard to the eggs and larvae available for transport. In addition, as described earlier, when the influx of biomass becomes too large, the open area exceeds its system constraint more frequently, lowering the productivity of the open area. The initiation of the decrease takes place at different times for different species. The decline of the

increase in redfish catch begins very early, after an adult spillover of only 10% when the amount of larval drift is low. When the larval drift is higher, 30-50%, the optimal amount of adult spillover for the greatest increase in redfish catch is zero.

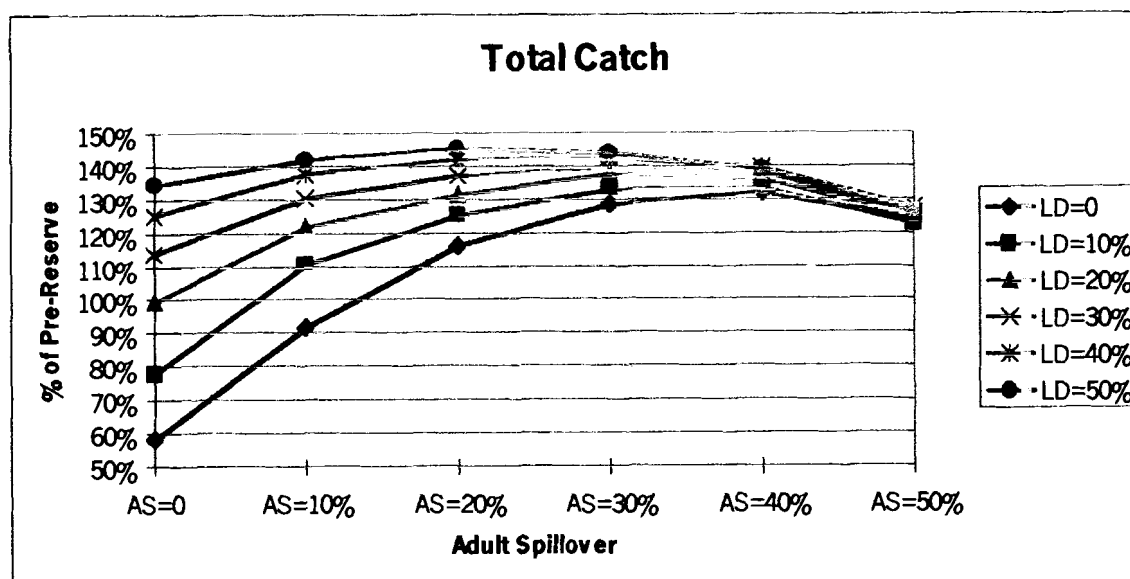


Figure 3.20: Average percentage of the pre-reserve total catch achieved after the creation of a 50% reserve under open access, small mesh for levels of adult spillover 0-50% and larval drift 0-50%.

Up to a certain level of adult migration, the trend is for increasing amounts of larval drift to lead to larger increases in the catch post-reserve. However, after a certain point (which is different for each species), as well as for the catch as a whole, increasing larval drift leads to declines in the increase of the catch. For the total catch, at the highest level of adult migration, increasing larval drift does not contribute anything to the catch. For herring, higher levels of larval drift always raises the amount of the increase in catch, for all levels of adult spillover. Both cod and haddock, in contrast, experience a decrease in catch when larval drift increases at adult spillover levels of 40% and higher and 50% and higher respectively (Figure 3.21).

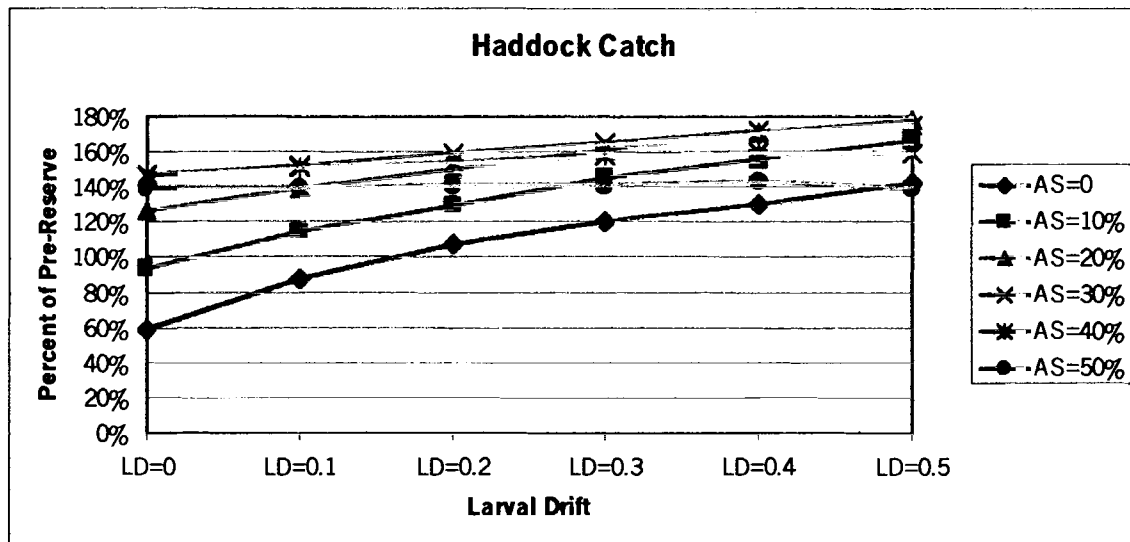


Figure 3.21: Average percentage of the pre-reserve catch for haddock after the creation of a 50% reserve under small mesh, open access for levels of adult spillover 0-50% and larval drift 0-50%.

While the total catch can increase a maximum of approximately 150% over the pre-reserve level, individual species can increase even more (Figure 3.22). For example, the cod catch is 180% of the level that is achieved in the absence of a reserve. This is the first scenario where cod has been the species that increased the most following the creation of the reserve. In contrast, when larval drift is zero and adult spillover is more than 30%, the herring catch can reach 100% of pre-reserve levels, but never gets much higher.

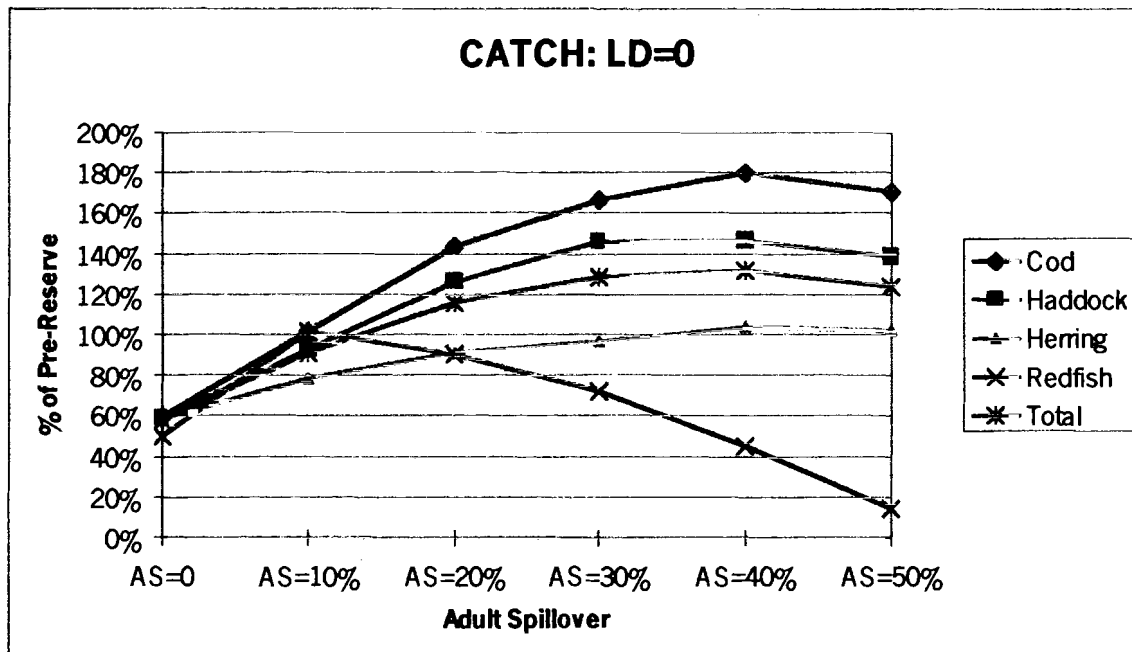


Figure 3.22: Average percentage of the pre-reserve catch for each species and for the total system achieved after the creation of a 50% reserve under small mesh, open access for levels of adult spillover 0-50% and larval drift = 0.

Open Access, Small Mesh with a 10% Reserve. Under all combinations of adult spillover and larval drift except the very lowest (AM=0-10% and LD =0-10%) the total catch under open access, small mesh with a 10% reserve always increases over the pre-reserve conditions (Figure 3.23). Although the percentage increase is generally slightly larger with a 10% reserve than with a 50%, the absolute size of the catch is less. When a 50% reserve is used the total catch begins to decline at levels of adult spillover greater than 40%; when a 10% reserve is used, catch continues to increase to an adult spillover level of 50% (Figure 3.20 & Figure 3.23).

Of all the open access scenarios with a reserve, catch is largest when capture does not occur until the species has had an opportunity to reproduce and a reserve of only 10% is used (Figure 3.23). When a reserve of 50% is used, the total catch is nearly equivalent, whether there are rules about whether harvest may occur before reproduction or not. In

this case, the reserve is providing such benefits in the form of larval drift and adult spillover, that the opportunity to reproduce in the open area becomes less critical. The smallest open access catch is achieved when capture is permitted before the age of reproduction and a reserve of only 10% is used. The smallest catch overall at lower levels of adult spillover (0-30%) is under open access, small mesh with a small (10%) reserve. Under higher levels of adult spillover the smallest total catch is under sole owner with a large (50%) reserve (Figure 3.24).

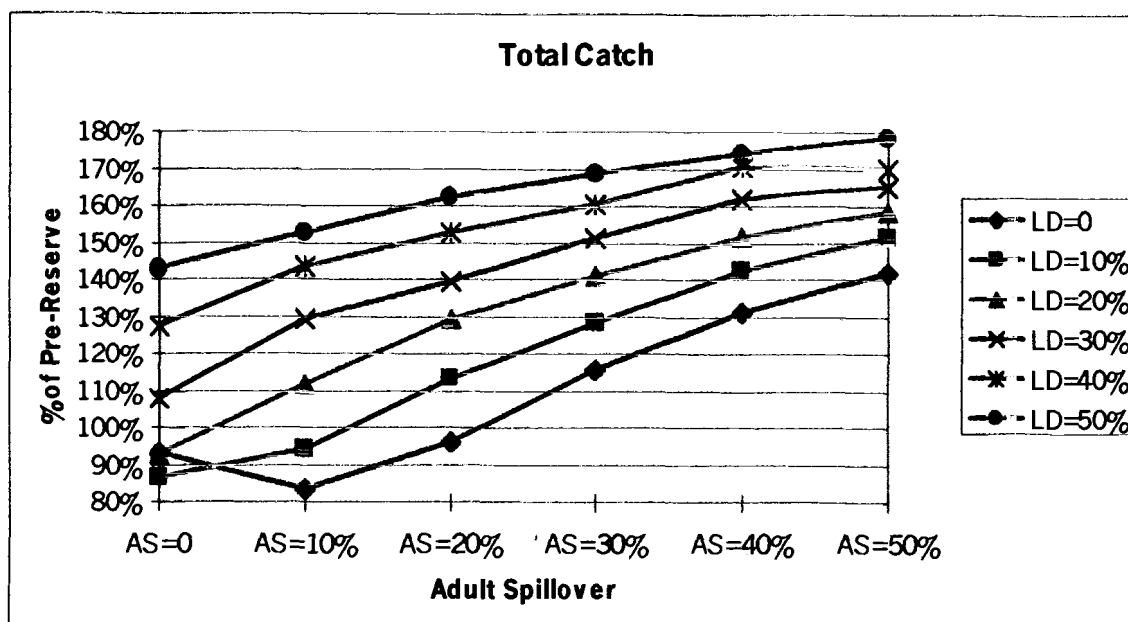


Figure 3.23: Average percentage of the pre-reserve total catch achieved after the creation of a 10% reserve under small mesh, open access for levels of adult spillover 0-50% and larval drift 0-50%.

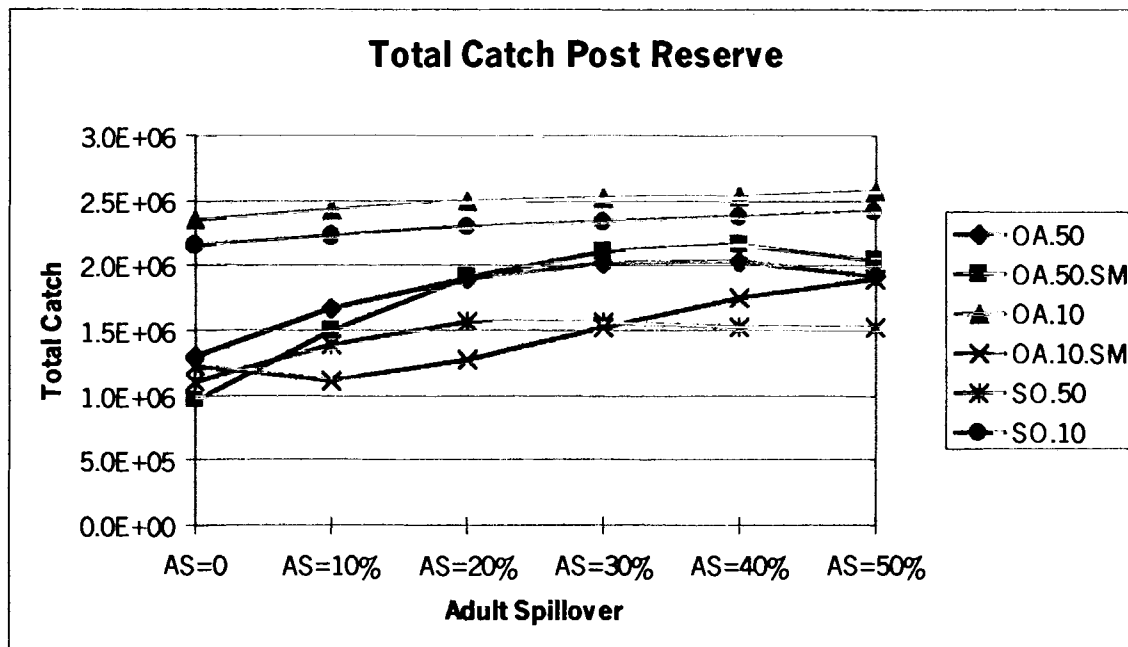


Figure 3.24: Total catch achieved after the creation of a 50% reserve under open access (OA.50); open access, small mesh (OA.50.SM); and sole owner (SO.50), for adult spillovers of 0-50%. Total catch achieved after the creation of a 10% reserve under open access (OA.10), open access, small mesh (OA.10.SM), and sole owner (SO.10) for adult spillovers of 0-50%.

Catch Variability

One hypothesized benefit of the spillover of adults and larvae from a reserve to the fishing ground is that it will not only increase catch levels, but also offer some stability to catch levels, and act as a buffer for severe recruitment failures that might result from heavy fishing pressure or poor environmental conditions (Sumaila 1998, Sladek Nowlis & Roberts 1999). We found that catches were most variable in the open access model with small mesh. An index of the variability is given by the ratio of the standard deviation to the average catch, which provides an estimate of the likelihood of fluctuations in the catch (after Sladek Nowlis & Roberts 1999).

In the open access, small mesh model, in the absence of a reserve, the catch of herring was the most variable, followed by cod, then haddock, then redfish (Figure 3.25).

The variability of the total catch from the fishery was much less than herring, cod and haddock, and very similar to redfish. This is due to the relative stability in the overall biomass, as compared to that of individual species. When the harvest from one fishery is low, it is likely that it is higher for another fishery, so the overall catch is relatively stable.

Following the creation of a 50% reserve, the variability in catch for all species except redfish is significantly lowered by high levels of larval drift (50%) (Figure 3.25). Combining 50% larval drift with a moderate amount of adult spillover (30%) brought the variability of the catches lower still. The lowest variability however, is achieved under an adult spillover of 30% alone.

When only 10% of the fishing ground is set aside as a reserve, catch variability is still lowered, but not as much as with the 50% reserve (Figure 3.26). Adult spillover levels greater than 30% do not lead to greater reductions in catch variability for the individual species or for the system as a whole. However, increasing adult spillover does increase the catch variability of redfish. As explained above, this population is reduced by increasing levels of adult spillover, and therefore changes in the size of the catch are more pronounced.

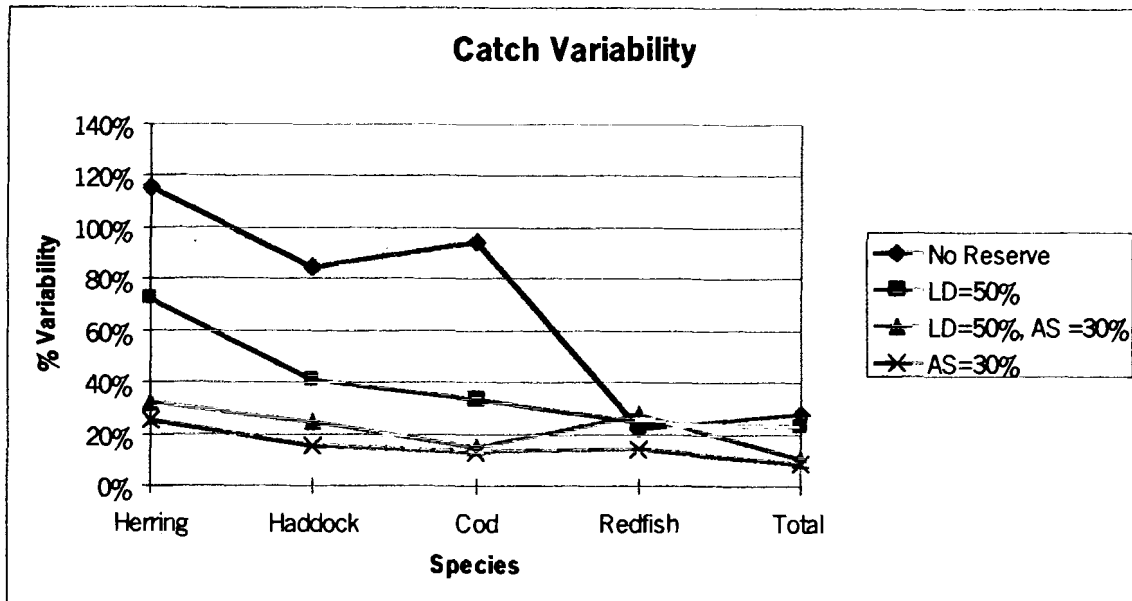


Figure 3.25: Catch variability under open access, small mesh for each species, under various combinations of larval drift and adult spillover. In the reserve scenarios the reserve is 50% of the possible fishing grounds. Catch variability is measured by the ratio of the standard deviation to the average catch, which provides an estimate of the likelihood of fluctuations in the catch.

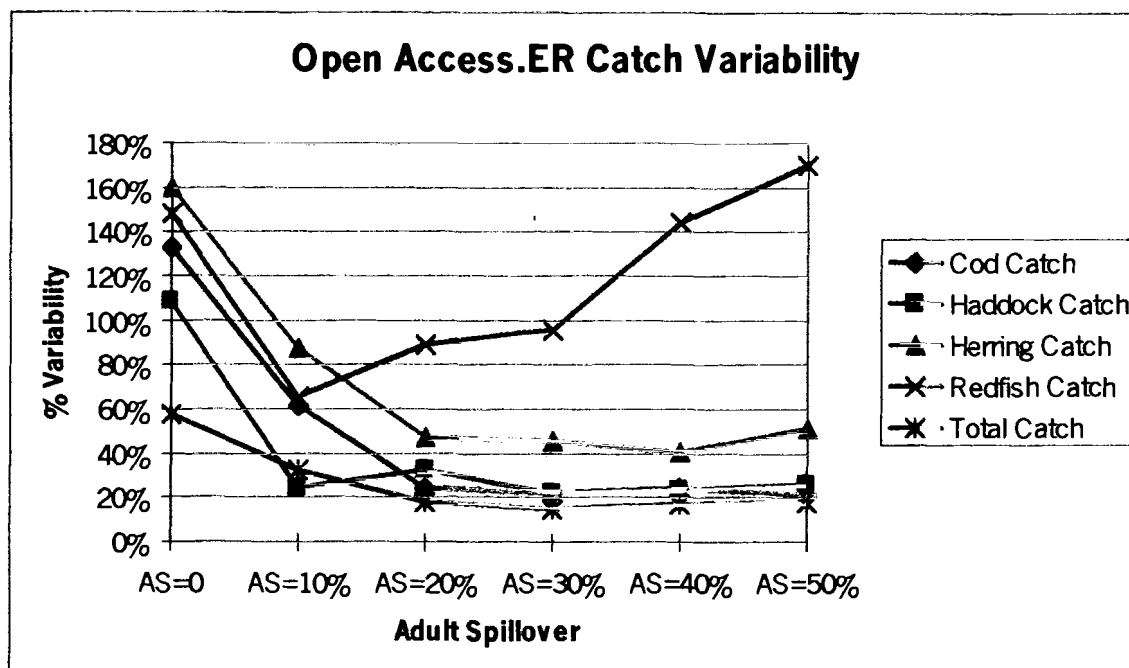


Figure 3.26: Catch variability under open access, small mesh for each species, with increasing adult spillover. The reserve is 10% of the total fishing grounds. Catch variability is measured by the ratio of the standard deviation to the average catch.

Discussion

Effect of Management Regime and Reserve Size on Total Yield Post-reserve

Earlier models have predicted that marine reserves can sometimes provide an improvement in yield to overfished fisheries, which meet certain conditions regarding the movement of adults and/or larvae. Our results support this general prediction, but with some modifications that result from the differences in our model construction. Our model is unique in its multispecies construction, and in that fishing pressure did not take the form of a constant annual fishing mortality or constant fishing effort. Instead, both under open access and a sole owner the size of the fleet, and therefore fishing pressure, responds dynamically to the changing condition of the resource. In addition, this fleet is allocating effort across two regions and amongst four harvested species with different life history traits. The multispecies nature of the model is an important factor in generating new insights into the effects of reserve use.

Unlike previous studies, we found that an increase in yield from pre-reserve conditions can occur under both open access and sole owner. Under an open access management regime where harvest cannot occur until after the first year of reproduction, a 50% reserve does not increase the total yield across species. With a 10% reserve, however, total catch is the same, or slightly more, than that achieved before the reserve. It is interesting that the smaller reserve is the one that provides an increase in yield, albeit minimal, since earlier models have indicated that the greatest benefits are achieved when the reserve is quite large, often as much as 50% or more of the total fishing ground. With effective rules ensuring at least one spawning opportunity however, the reserve here

appears to be acting less to mitigate the effects of overfishing and more to compensate for the environmental variability affecting the earlier age classes.

The effect of a reserve on yield under a sole owner is similar to that under open access with regular recruitment; a 50% reserve results in a loss of overall yield even under high levels of adult spillover and larval drift. A 10% reserve can result in slightly greater wealth (103%) at adult spillover levels of 40-50%. This is an interesting result, since the sole owner is already actively trying to maximize profits and exercising caution to prevent overfishing. Nonetheless the sole owner can benefit from a reserve because it seems to act as a buffer against mistakes the sole owner will inevitably make when trying to maximize profits in a multispecies fishery. Even with the best decision rules possible, the sole owner cannot respond perfectly in such a complex, dynamic environment. In those cases when the sole owner adds boats rather than taking them away, or transfers effort to a fishery which causes profits to decline, the reserve acts a buffer providing a steady supply of adults and larvae to maintain the fishery. Although reserves have previously been described as a buffer against biological or environmental uncertainty, this model provides further evidence that reserves can also act as buffers against management uncertainty.

Under an open access rule where harvest can occur the year before the first year of reproduction, the yield post reserve is improved by both a 50% and a 10% reserve. The absolute yield is largest with a 50% reserve, and the difference between the increase generated by the different size reserves is greatest at low to moderate amounts of adult spillover. This result is more typical of earlier studies, which found that reserves are most beneficial when the fishery has been severely depleted, and that larger reserves are

more likely to provide a larger benefit than smaller reserves. The redfish population crashes at higher levels of adult spillover, while cod and haddock yields are most increased. The herring yield increases the least as a result of the reserve, perhaps because they are already doing well due to the low biomass of other species, and their own high fecundity.

Effect of Management Regime and Reserve Size on Species Yield Post-reserve

While it is logical for the sole owner to look at the impact of a reserve on the total yield (and therefore total wealth generated), an open access fishery may be interested in the effect of the reserve on individual species as well. Under almost every combination of management regime, reserve size, and amount of adult spillover, different species will emerge with the strongest responses in terms of percentage increase of yield. This is a result of the combination of these three factors on the dynamics of the total system, in conjunction with the individual species respective life history traits.

Under all three management situations any time a 50% reserve is used and the amount of adult spillover is high, the redfish population crashes. This appears to be a result of the depletion of the reserve that occurs at high levels of adult spillover and redfish's naturally low fecundity. Out migration has the same effect as mortality on the reserve population; apparently for redfish, their mobility reaches a level where the "mortality" rate exceeds the regeneration rate. However, at low levels of adult spillover, the redfish catch can actually demonstrate the largest percentage increase in yield, such as in the baseline open access case with a 50% reserve. This is because in the absence of the density dependent effects caused by the large influx of the biomass into the open area,

the redfish population benefits significantly from larval drift the large reserve provides, which greatly supplements their own naturally low fecundity. Redfish exhibits almost an identical pattern when a 10% reserve is used with the baseline open access management.

Under the baseline open access management with higher levels of adult spillover, haddock demonstrates the largest percentage increase, followed closely by cod. Haddock also has the greatest percentage increase in yield in open access, small mesh, with a 10% reserve at high levels of adult spillover, while cod has the greatest in open access, small mesh with a 50% reserve. Finally, herring exhibits the greatest percentage increase under a sole owner with a 50% reserve. Again, the primacy of the different species under these various scenarios is a function of the changing dynamics that each combination of factors creates. Although the reason for each species increase or decline can usually be explained post hoc, it proved very difficult to predict the patterns that each species will exhibit in advance.

Effect of Adult Spillover versus Larval Drift

Other models have found that adult spillover is not a precondition of an increased catch post-reserve, but that a certain amount of larval drift may be sufficient (e.g. Sladek Nowlis & Roberts 1999). This result has important implications for the use of marine reserves in coral reef fisheries, where adults tend to have a close association with the reef (Polunin & Roberts 1996). In our model, under a sole owner or the baseline open access conditions, the increases in total yield do not occur when there is no adult spillover.

Redfish is the only species whose catch increases solely as a result of larval drift from the reserve, and that occurs under both a sole owner and open access. Under open access

with small mesh, total catch can increase in the absence of any adult spillover by as much as 140% when larval drift is 50%.

The contribution of larval drift to the increase in the catch is much more noticeable when a smaller (10%) reserve is used. With a smaller reserve, increasing larval drift provides a consistent increase in yield. With a larger (50%) reserve the increase in yield provided by larval drift declines with increasing adult spillover, and is negligible at the highest levels.

Effect of Using a Reserve or Rules that Prohibit Capture before First Reproduction

A surprising result was the apparent equivalency of absolute total yield under open access with a 50% reserve whether harvesting was permitted on the age class prior to reproduction or not (Figure 3.23). This was especially the case at levels of adult spillover 20% or higher. The large reserve appears to provide enough reproductive adults and larvae that the opportunity to reproduce in the open area becomes essentially irrelevant. Although this is not the case at lower levels of adult spillover, when adult spillover is high (50%) the yield from the open access small mesh scenario with a 10% also provides nearly the same yield as with a 50% reserve (Figure 3.23). The highest yield however, is still achieved by ensuring at least one year of spawning in combination with a 10% reserve.

Effect of Reserve Size on Spawning Stock Biomass

The creation of a reserve always increases the total SSB of the combined harvested species. In compensation for this increase, the SSB of sand lance decreases. The

percentage increase is greatest when the larger (50%) reserve is used. The percentage increase is also always greatest when adult spillover is zero, since higher levels of adult spillover expose more of the SSB to fishing pressure in the open area. Because the sole owner deploys less fishing effort in order to maximize profits, the SSB is least reduced under this management regime. Therefore, the increase in SSB from a reserve under sole owner is the smallest; on the order of 130% when a 50% reserve is used, and 115% when a 10% reserve is used. The next largest increase comes in the open access baseline case, where a 50% reserve generates an increase in SSB over the pre-reserve condition of more than 235%, and a 10% reserve generates a 130% increase. Finally, under the open access, small mesh scenario, the percentage increase in total harvestable SSB is greatest. A 50% reserve provides an increase of more than 400% for all levels of adult spillover and larval drift, and a 10% provides an increase of 225% when adult spillover is zero. The increase drops quickly to 165% however, even at a low level of adult spillover like 10%.

Ultimately, the size of the increase in SSB is meaningful only in relation to some target stock level which is expected to provide some measure of safety from collapse. Until such a level is determined for each species, it is impossible to determine what size of reserve provides a reasonable amount of protection for the SSB in exchange an acceptable reduction in the size of the catch. The model has indicated that under certain combinations of management rules and levels of larval drift and adult spillover, increases in yield are achievable, in addition to increases in SSB. These win-win (Sanchirico 1998) situations illustrate the most effective potential use of marine reserves for fisheries management.

Effect of Reserve on Catch Variability

Our model supported the Sladek Nowlis & Roberts (1999) result that catch variability decreased following reserve creation. Sladek Nowlis & Roberts (1999) found that variability decreased further with increasing reserve size. We found that the larger reserve (50%) decreased catch variability more than a smaller reserve (10%), and that beyond an adult spillover of 10%, increasing amounts of adult spillover had little effect. Although total catch variability is generally low, the reserve can have a significant effect on the variability of individual species. The variability of the herring catch drops from over 120% in the absence of a reserve to just over 20% with a 50% reserve. This range of variability is similar to what is found by Sladek Nowlis & Roberts (1999).

Conclusions

To date, there have been few empirical studies that have demonstrated an increase in fishery yield following the creation of a no-take reserve. In part, this is because the majority of the existing marine parks and reserves were not designed with thought to the ecological or economic criteria necessary for fisheries replenishment (Dugan & Davis 1993). Further, long-term experiments are necessary to demonstrate the ability of marine reserves to increase the yield from a given fishery outside the boundaries of the reserve, and these experiments may be confounded by other changes in the management regime over this time. For example, the closures on New England's Georges Bank have contributed to a reduction in fishing mortality and an increase in groundfish biomass outside the closed area (Murawski 2000), but other management measures such as trip limits and reduced days at sea have concurrently been applied. As there is currently a

great deal of interest in the ability of marine reserves to improve fisheries management, to better sustain both the fishing industry and the harvested stock, in the near-term it is likely that researchers will continue to rely on models to explore and predict reserve effects.

Obviously models are not meant to be exact replicas of the systems they are used to explore, but a pared down version of reality that contains only those elements needed to address the selected question. Almost exclusively, the models that have been used to isolate the factors controlling the size and nature of the benefit produced by using a reserve (such as harvesting pressure prior to reserve creation, reserve size, amount and nature of adult spillover, or amount and nature of larval drift) have been single species models. In general, they have confirmed the highest expectations of reserves – that under certain conditions, they are capable of providing meaningful protection to a harvested stock, while at the same time, improving the yield from the fishery. Optimal reserve size has been located for a variety of species, with different life history characteristics and different population growth rates. In reality however, many fisheries do not rely on a single harvested species, but upon a species complex, composed of species with potentially very different life histories and behaviors. Are single species models alone sufficient to answer questions about how reserves will work in a multiple species reality?

Our model allowed us to investigate the response of five different species, only one of which was not harvested, and the response of a fishing fleet operating under several different management systems, to the creation of a no-take marine reserve. When the response of the harvested biomass is looked at in the aggregate, our results were qualitatively similar to those produced by single species models under some scenarios.

However, examining the responses of individual species, showed that responses between species could differ significantly, even under the same conditions of adult spillover, larval drift and management regime. For example, there was no combination of adult spillover and larval drift where the total catch (all harvested species combined) increased following the creation of a reserve of 50% of the fishing area under a sole owner.

However, when adult spillover and larval drift were both 50%, the herring catch was 112% of what it was in the absence of a reserve. These same conditions caused the redfish catch to plummet. So even under the best possible management – in this case, a conservative sole owner - a reserve could impact species with different life history characteristics very differently. The decision by a sole owner to use a reserve or not would in part depend upon which species yield they wished to maximize.

Single species models have generally found that the likelihood that a reserve can produce a “win-win” situation, where both the population inside the reserve and the yield from the fishery, increase when the population has been overfished prior to reserve creation (e.g. Sanchirico & Wilen 1998, Pezzey et al 2000). Further, the reserve generally needs to be of considerable size, often 50% or more of the fishing ground. This size estimate was consistent across a range of disparate species that included Atlantic cod and Caribbean coral reef dwellers. Using our model however, we were able to show a small increase in the total wealth generated under the sole owner, employing a conservative harvesting strategy to maximize profits, and a reserve of only 10% of the fishing ground. When adult spillover was 30% and the larval drift was 50%, the wealth generated by haddock alone was 110% of what it was in the absence of a reserve. This result is in direct contrast to earlier sole owner models that found that the use of a reserve

would not benefit a sole owner, or at least not in absence of a catastrophic recruitment failure (Sumaila 1998). The reserve seemed to buffer against small errors made by the sole owner in their attempts to optimize harvests in four different populations, by ensuring a steady supply of larvae and adult spillover. Importantly, if a sole owner could benefit from a reserve, it is more likely that they will choose to use this form of insurance, since a sole owner has the assurance that they will benefit from the effects of their own restraint.

Single species models have also indicated that although reserves will be beneficial for any overfished population, populations with low intrinsic growth rates and high fishing mortality would benefit the most (Sladek Nowlis & Roberts 1999). This appears to be true under single species conditions, and models where there is no adult migration away from the reserve. Interestingly, the species in our model with the lowest growth rate, redfish, did provide increased yield when adult spillover was low. In fact, in an open access regime with a 10% reserve, no adult spillover, and high larval drift (50%), redfish catch is over 120% of what it was pre-reserve. However, as adult spillover increases, redfish become rapidly depleted from the reserve, and the remaining stock is unable to supply enough larvae to the open area to sustain a fishery. They also do poorly in the open area, due to the density-dependent effects that result from the high level of adult spillover. In this case, the expectations based solely on the growth rate of the species are overcome by other factors of importance in the model.

Our multiple species model also captures another potentially important aspect of inter-species interaction. The increase of biomass of any species inside a reserve may be constrained by increases in other species. An ecosystem can only support so much

biomass, and not all species can be at their maximum potential biomass at a given time. This is not to say that it is not possible that the biomass of each of the species inside the reserve will increase compared to harvested populations, but that the increase for each individual species is not likely to be as large as would be predicted if each species was considered in isolation with a single species model. Individual estimates on a species-by-species basis may create unrealistic expectations about what a reserve might actually accomplish.

It should be reiterated here that the specific results of our model, in terms of the size of the increase, or at what level of adult spillover or larval drift it occurred, is not meant to be the focus of this work. Of primary importance is the fact that such an increase is possible under certain conditions, and that these conditions will vary depending on the characteristics of the species. In addition, the patterns that are seen across species are likely robust. For example, high levels of migration out of the reserve diminish the adult population within the reserve, diminish its ability to resupply itself, and also reduce its ability to supply the open area with larvae. Therefore, for every species there is a level of adult spillover beyond which yield it gains from the reserve begins to decline. This level may be different for different species. For redfish the highest yield is achieved when there is no adult spillover, for other species the peak occurs at 30% adult spillover. Another recurrent pattern was that with larger reserves, larval drift had a bigger effect at lower levels of adult spillover. When adult spillover was high, the contribution to an increase in yield made by larval drift was negligible. Both of these patterns were robust across species.

The assumptions and omissions of any model must also always be kept in mind. Having multiple species in our model meant that we had to simplify in other ways, in order to keep the analysis tractable. Because species were differentiated from each other in a number of respects with regard to life history characteristics, we held the price that the boat received for each species constant, and the cost of harvesting each species the same. Were these prices actually significantly different from one another, the ability of a reserve to produce an increase in wealth from the fishery might depend upon whether the configuration of the reserve favored the most valuable species. We also varied the amount of adult spillover and larval drift concurrently for all species. In other words, one species did not have a greater tendency to leave the reserve than others; they left the reserve at the same rates. Different degrees of adult spillover, likely to be seen in reality, would also lead to changes in the protection and yield achieved for each species. Rates of transfer between the reserve and the areas open to fishing will be highly species dependent, and will therefore affect the potential efficacy and size requirements of refugia for a particular species (Kramer & Chapman 1999).

Our model did not capture the effects of the creation of a reserve on habitat. The main effect of the reserve in this model is to protect a portion of the population, ensure reproduction, and to provide a steady stream of larvae and spillover into the open areas. As the open access, small mesh model shows, a reserve can achieve a nearly equivalent result as waiting until after a species has had at least one opportunity to reproduce before beginning harvesting. However, it is anticipated that reserves could play an important role in allowing the recovery of three-dimensional structure that may have been reduced by the impacts of fishing gear (Auster & Malatesta 1995). Increased structure will

presumably provide better protection for postlarval and juvenile stages, and improve productivity in the reserve area. With respect to modeling, it would be possible to emulate this effect by increasing survivorship in the closed area, relative to the open area. Under those circumstances, the model that we have created might illustrate that reserves have a larger positive effect than demonstrated here.

Finally, although the model attempted to simulate realistic harvester behavior with regard to , there were no barriers to entry or exit in any of the fisheries, allowing harvesters to rapidly switch species to take advantage of spikes in their populations. In reality, fishermen often are not able to change strategies so quickly, perhaps as a result of gear restrictions or permitting requirements. In addition, harvesters often argue that while reserves might work in *theory*, they are not enforceable in practice, and therefore will not perform as claimed. Honest fishermen will sacrifice a portion of their catch so that poachers can steal the benefits, and an increase in yield for the outside fishery will never come to pass. We did not use our model to investigate “cheating” behavior, to determine how much of such violations a reserve could sustain before the benefits it provides to the outside fishery are jeopardized. If such infringement was common, it might be necessary to have larger reserves, to buffer against the losses. Further modeling work could lend some insight to this issue.

Given the large number of biological, ecological, social and economic factors that will influence the results of a reserve in the real world, it seems unlikely that scientists and managers will ever be able to predict with great accuracy the results of the creation of a reserve. Any predictions would have to take into account not only the natural history of the species involved and their behavior, but also likely changes in the behavior of the

harvesters. For accuracy, a researcher would need correct information on extent and direction of larval dispersal, natural mortality, life history, mobility and migration patterns, trophic relationships, species interactions, etc (Dugan & Davis 1993). Even in the simplified and completely controlled modeling environment it was difficult to predict the results of our simulations, and there were many surprises along the way.

Explanations for the patterns we perceived were only possible by deconstructing the model, changing variables, and running more simulations. Without these luxuries in the real world, and introducing the complexities of human behavior, it may take many years before the impact of a reserve is understood and can be fully explained. A change in the ocean currents the following year could fundamentally change the dynamics again.

What does the difficulty in our ability to forecast the results of the creation of a marine reserve with a high degree of specificity mean for fisheries management?

Interestingly, the results of single species models have rarely led to any conclusions or recommendations on how the overall management system might have to change for marine reserves to be used most effectively. Rather, they are usually considered a way to make up for failures of fisheries management. Reserves are often referred to as one more “tool” in the management “toolkit”. How this relatively new tool is combined with existing strategies will make a difference in its effectiveness.

In New England, attempts to limit fishing mortality have increasingly been pursued through restricting permitting. As harvesters are shut out of fisheries, their dependence on the ones they do maintain permits for grows. In this kind of environment, it is difficult to see how support for no-take reserves will flourish in the harvesting sector. What if the yield of the species they are licensed to harvest does not increase post-

reserve? What if, like redfish, the species they are licensed to harvest actually is suppressed as other species recover? As we have said, very few models purport to represent real world fisheries, or are meant to be predictive about the likely results of reserve creation. Given that, it is unlikely that harvesters will be willing to risk losing a small, but relatively consistent harvest against a complete unknown.

Without exception, most researchers addressing the social aspects of reserve success cite the absolute need for stakeholder “buy-in” and support (Laffoley et al 1995, Kelsey et al 1995). The use of reserves will need to be tied carefully to other management measures to ensure that the incentives for such support are there. It seems far more likely that harvesters would support the use of no-take reserves if they had some expectation that they would share in the benefits, produced by their restraint, whatever they might be. For example, if they had rights to harvest a wider variety of the commercial species, rather than a potentially permit-limited subset. When combined with a reserve, other constraints may be appropriate. Other modeling efforts (Johnson, 2001 unpublished) have suggested that when feedback to the sole owner is impaired, better decisions are made when the sole owner allocates its effort across species within a region, rather than across regions on a single species basis. This framework allows the sole owner to improve the average size of its catch, and its ability to accumulate wealth. Similarly, allowing harvesters in a multispecies fishery access to the entire complex while limiting their overall mobility, may integrate better with the use of a reserve. This would be particularly fruitful if the benefits in the outside area could be attributed to a particular reserve.

Clearly, part of the appeal of no-take marine reserves is in the contribution they could make toward the promising, but still elusive goal of ecosystem management. Modeling can help us to understand the likely impacts of reserves, isolate factors that are important, and generate non-intuitive results that will cause us to delve more deeply into understanding their application. Single species models fail to capture the complex dynamics that can result when species with different life history characteristics interact (even minimally, amongst early age classes) and how the behavior of a single species may differ from the patterns seen in the total harvestable biomass combined. The multispecies nature of our model provides some non-intuitive results that supplement the understanding of the effects of marine reserves on fisheries that is being developed through single species models. Further explorations with multiple species models are needed to determine the range of variation in results that might occur with some of the additional factors suggested above.

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