Optimal bioeconomic management of changing marine resources

by

Emily Alison Moberg

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Submitted to the MIT-WHOI Joint Program in Oceanography and Applied Ocean Science and Engineering
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Signature of author ..... Signature redacted ....
Joint Program in Biological Oceanography
Massachusetts Institute of Technology
& Woods Hole Oceanographic Institution
July 21, 2016

Certified by ... Signature redacted ....
Dr. Michael G. Neubert
Senior Scientist
Woods Hole Oceanographic Institution
Thesis Supervisor

Accepted by ... Signature redacted ....
Dr. Ann Tarrant
Chairman, Joint Committee for Biological Oceanography
Massachusetts Institute of Technology
Woods Hole Oceanographic Institution

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Abstract

Marine populations are increasingly subjected to changing conditions whether through harvest or through broad-scale habitat change. Historically, few models have accounted for such trends over time, and even fewer have been used to study how trends affect optimal harvests.

I developed and analyzed several models that explore, first, *endogenous* change caused by harvest and, second, *exogenous* change from factors (such as rising ocean temperatures) outside harvesters' control. In these models, I characterized the profit–or yield–maximizing strategy when harvesting damages habitat in a multispecies fishery, when harvest creates a selective pressure on dispersal, and when rising temperatures cause changes in vital rates. I explore this last case in both deterministic and stochastic environments, and also allow the harvester to learn about unknown parameters of the stock recruitment model while harvesting. I also develop an unambiguous definition of and describe a statistical test for a shift in a species' spatial distribution.

My results demonstrate that optimal harvesting strategies in a changing environment differ in important ways from optimal strategies in a constant environment.

Thesis Supervisor: Dr. Michael G. Neubert
Title: Senior Scientist
Woods Hole Oceanographic Institution

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Contents

Chapter 1

Introduction

A quote by Dr. Thomas Henry Huxley delivered at the Fisheries Exhibition is 1883 is often presented to illustrate the now clearly erroneous belief that the ocean's supply of fish is limitless: "...it may be affirmed with confidence that, in relation to our present mode of fishing, a number of the most important sea-fisheries, such as the cod fishery, the herring fishery, and the mackerel fishery, are inexhaustible" (Huxley, 1883). Less frequently invoked are his preceding words, noting that other fish stocks (such as salmon) might indeed be exhaustible and that human actions, such as the addition of pollutants to streams, might precipitate this exhaustion. His colleague, Mr. Charles E. Fryer, mentioned that some contemporaries blamed "overfishing" or the "burning of seaweed, building of lighthouses"... or the "wickedness of the people" for occasional fisheries fluctuations and failures (Fryer, 1883). While these words may seem comically antiquated now, they foreshadow the study and debate about how and to what extent human actions deteriorate fisheries.

In the intervening years, we have augmented the list of ways in which humans impact fish population dynamics. We now recognized that increased harvesting capacity and effort, increased human population density and its associated effluents–including the addition of heat-trapping gases such as carbon dioxide to the atmosphere–may negatively impact the health of fish stocks and their habitats. These ongoing alterations of both the oceanic environment and the removal of its inhabitants create a regime characterized by change.

Understanding how these alterations affect the interactions between exploitation and the health of marine resources is critical, as humans rely on marine resources for food and employment (Food and of the United Nations, 2012), tourism (Madin et al., 2012), and other ecosystem services (Worm et al., 2006). The repercussions of historical fisheries collapses have been long-lasting and far-reaching. For example, high unemployment, government subsidies, and low incomes among fishermen persisted long after the collapse of Newfoundland's cod fishery (Schrank, 2005). The 1970s El Niño-related fisheries declines contributed to a global drop in food production and negatively impacted the Peruvian economy (Glantz, 1979). Conflicts over fishing rights have even caused major international disputes, such as the mid-20th century Cod Wars between Iceland and the United Kingdom.

Currently, many fish stocks are declining and could provide larger, sustainable harvests (of 8 to 40% globally) if rebuilt (Costello et al., 2012); a more recent analysis suggests that the median fishery is both historically and currently being overfished and that large economic benefits could result from improved management (Costello et al., 2016). Several high profile stocks, such as the New England and Newfoundland cod stocks, have yet to recover from their collapses; recent work has further suggested that temperature induced increases in natural cod mortality might have contributed to allowing recent overfishing on the New England stock (Pershing et al., 2015). The current poor health of many fisheries, coupled with the fact that well-managed stocks may suffer if changes to the stock are not appropriately taken into account, provides strong motivation for trying to understand fishery dynamics.

Mathematical models are an important tool in building such an understanding. Fisheries models create a set of rules that describe (at a minimum) how the fish life-cycle and human harvest influence the size of the population. Environmental or demographic variability, stage structure, trophic interactions, environmental dependence, spatial structure, harvester behavior, etc. may also be added. These models may be used to determine the harvest strategies that maximize yield, profit, or conservation goals.

Many fisheries management models, however, assume a stationary environment; they assume that the underlying processes are not changing over time. There are many good reasons for the stationarity assumption including mathematical tractability and a lack of long term data to suggest trends. Our focus on stationary environments, however, leaves many unanswered questions when change is considered. The goal of this thesis is to provide theoretical models that address a few possible sources of such change in an integrated framework that includes both the fish population dynamics and the human response.

There are two ways to classify the sources of environmental change on fisheries: endogenous and exogenous. I consider endogenous change to be cases in which harvesting directly changes the environment. Exogenous change, in contrast, is caused by an agent other than the harvesters. In this thesis, I model both sources of change and organize the constituent chapters according to this classification.

I first address endogenous change. The first two chapters of the thesis focus on the feedback between harvesters' actions on either habitat suitability or on the preferential settlement of juvenile fish; these types of feedbacks–perhaps unimaginable in 1883 when the high-sea fisheries seemed limitless–have been increasingly incorporated into models in recent years. Then I address exogenous environmental change, in particular focusing on climate change. I investigate a statistical method for characterizing when a population is shifting in response to these changing conditions and then two models that characterize the optimal harvesting response to a population whose vital rates change in response to the rising temperatures.

In these next pages, I briefly describe the motivation, approach, and main results of the chapters of my thesis.

Endogenous Impacts

Harvesting fish removes biomass and acts as an additional source of mortality for fish. However, fishing activity may also damage habitat, while additional mortality to different life-stages or trophic groups may alter ecosystem structure. From a management perspective, change caused by harvesting itself is interesting because of the actions of the harvester feedback on the stock.

Habitat Damage (Chapter 2)

One clear impact of fishing–apart from the direct removal of fish–is the disturbance caused by the fishing gear itself. Understanding the impacts of fishing gear on habitat quality and on community structure has been an active area of research (e.g., Collie et al., 2000). When habitat damage is included as part of a single-species, spatial fishery model, its inclusion qualitatively changes the optimal harvesting strategy (Moeller and Neubert, 2013).

Much less, if anything, is known about how habitat damaging fishing impacts multi-species fisheries. The importance of species interactions on population dynamics has been increasingly well documented (e.g., Casini et al., 2008) and the implications of these interactions for management have also been of interest (e.g., Baskett et al., 2007; Kellner et al., 2011; Matsuda and Abrams, 2006). The analysis of optimal management of a multispecies fishery is, however, difficult due to the large number potential interactions among species that need to be accounted for (and potentially parameterized!). This difficulty is compounded by our desire to include space. To address this issue, I employ a type of model called a 'patch-occupancy' model that tracks the proportion of patches in a particular state.

Disturbance and subsequent recolonization have often been studied with patch-occupancy models (e.g., Hastings, 1980; Caswell and Cohen, 1991; Nee and May, 1992). These types of models allow the inclusion of spatial dynamics among multiple species in a relatively mathematically tractable way. I couple such a model with a simple economic harvesting model to understand how habitat damage and subsequent resettlement of the habitat influence optimal harvesting patterns, community structure, and economic productivity. I also studied the efficacy of no-take marine reserves as a management tool. I found that when ecosystems have a long recovery time, they produce lower profit and have lower optimal harvest rates. I found that while no-take marine reserves are not part of a profit maximizing harvest strategy, they incur a relatively low cost, while potentially providing a large diversity benefit.

Fisheries Induced Evolution (Chapter 3)

In addition to influencing the numbers of a fish population and potentially their habitat, fishing pressure also exerts a strong selection pressure on the fish. Evidence of so-called 'fisheries induced evolution' has been found in the life-history traits of fish (especially in age and size at maturation, e.g., Haugen and Vøllestad 2001; Grift et al. 2003; Olsen et al. 2004) and recent work suggests that accounting for this evolution changes optimal management (Eikeset et al., 2013).

Given the current interest in spatial management for fisheries, I was interested in how the evolution of dispersal would impact the optimal spatial allocation of effort. In particular, how would the evolution of a dispersal strategy that avoids harvested areas change optimal harvester response? My co-authors and I constructed a two-patch model and allowed the tendency to preferentially migrate to one patch evolve in response to fishing mortality. I found that marine reserves ceased to be part of a profit-maximizing harvest strategy, but that this strategy is unstable economically over short-time scales.

Exogenous Impacts

Exogenous impacts on fisheries are perhaps easier to identify–the introduction of pollutants or invasive species. I was interesting in investigating exogenous impacts because the lack of feedback from the harvester's actions to the source of change will likely produce different optimal management strategies. Furthermore, there are relevant exogenous stressors on fisheries–like climate change–that are currently a focus for the scientific community. I focus on climate change as the source of exogenous change.

While climate change encompasses a variety of changes, including changes in precipitation patterns and storm frequency, I consider the average increase in temperature as the motivating agent of change in this thesis. Temperature change is the hallmark of climate change and is particularly relevant for fish. Fish are generally *ectothermic*, meaning they rely on the external environment for heat, and *poikilothermic* so their internal temperature varies with their external environment. Temperature plays an important role in the metabolism and function of fish; temperature of water controls the solubility of oxygen, influences metabolic demands, and affects the ability of hemoglobin to bind oxygen (Helfman et al., 2009). Fish experiencing different temperatures may consequently have different vital rates (e.g. Munday et al., 2008; Houde, 1989; Donelson et al., 2010; Tanasichuk and Ware, 1987; Reist et al., 2006) that ultimately determine the size and growth rate of populations.

I investigate how fish stocks' responses to changing temperatures influence the optimal management of those stocks.

Detection (Chapter 4)

What gets measured gets managed. –management adage, often attributed to Peter Drucker

One common response to changing conditions is a shift in a species' geographical location to follow a suitable environment. This type of movement has been extensively studied as a 'fingerprint' of climate change impacts. There is a large body of literature reviewing range shifts (e.g., Parmesan and Yohe 2003; Root et al. 2003; Sorte et al. 2010; Madin et al. 2012) that have found evidence of poleward range shifts in many species (or shifts upwards in elevation for terrestrial species or deeper in marine environments) or phenological shifts to cooler periods in the year. However, the methodologies for testing for such shifts are not standardized. For example, some authors have focused on the mean location of individuals (e.g., Perry et al., 2005; Chen et al., 2009; Pinsky et al., 2013) while others have focused on the locations of the poleward boundary (e.g., Hickling et al., 2006; Solow et al., 2014). If distributional shifts tended to translate individuals identically, these definitions would be equivalent, but that type of shift appears to be uncommon (Hampe, 2004; Breshears et al., 2008; Sunday et al., 2012).

To address this, I describe a methodology that both defines an unambiguous distribution shift and tests for it. I borrow a concept from the economics literature–stochastic dominance–and apply it to the detection of unambiguous shifts in a species' distribution. In this chapter, I describe the concept of stochastic dominance and a test for it, and finally illustrate its usage with a fisheries example.

Changing Vital Rates (Chapter 5)

Shifts in a species' spatial distribution result from interactions between demographic rates and dispersal and may take time to manifest. Alternatively, barriers to dispersal or an organism's tracking of another component of their habitat niche may result in their experiencing different conditions. Locally, changing temperatures will impact vital rates, thus it is important to understand how to manage a stock experiencing these fluctuating vital rates. To this end, I investigate the harvest implications of a species that is experiencing changing conditions that negatively impact its vital rates. In particular, I consider a species that has a vital rate–such as mortality or fecundity–that is a function of temperature; as temperature increases, the vital rate changes. Few authors (but see e.g., Walters and Parma 1996) have investigated how optimal harvesting changes in response to changing vital rates.

I built a deterministic model to investigate how the optimal harvesting policy varies with the changing vital rate and found that even for a compensatory growth function with a monotonically decreasing vital rate, that the optimal number fish left to 'escape' in each period may not be monotonic. I show that the interplay of density dependence is critical in structuring this the shape of the optimal escapement policy.

Adaptive Management (Chapter 6)

Finally, I extend my work on the optimal management of a population with a changing vital rate to include uncertainty. Unfortunately, as Professor Huxley bemoaned in 1883, we often must regulate and manage fishing activities without perfect knowledge[1] of the dynamics of the stock. As stocks experience (warming) conditions that are increasingly outside of the historical range, it seems likely that the response of the stock to those conditions are likely to be imperfectly known.

To address this, I employ a methodology called adaptive management (Holling, 1978), which allows for the inclusion of imperfect knowledge explicitly into the optimization of the harvest. I construct several simple models that include learning about an uncertain parameter in both unchanging and changing environments to compare the optimal harvesting strategies. I highlight how adding a trend in time removes the possibility of a stationary policy over an infinite time horizon and that, for a broad class of models, the optimal escapement only depends on the initial stock size (in that period) as a constraint.

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[1] "In answer to questions relating to the habits, the food, and the mode of propagation of fishes–points, be it observed, of fundamental importance in any attempt to regulate fishing rationally–I [am] usually met with vague and often absurd guesses in the place of positive knowledge." – Professor Huxley in an address to the Fisheries Exhibition in 1883 (Huxley, 1883).

Summary

In this thesis, I explore the optimal management of stocks undergoing change with either endogenous or exogenous (to the fishery) sources of that change. Perhaps unsurprisingly, I found that including novel feedbacks and trends produce qualitatively different optimal management strategies. This suggests that the identification of the mechanisms creating change for fisheries deserve attention both empirically and from a modelling perspective.

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Chapter 2

Bioeconomics and biodiversity in harvested metacommunities: a patch-occupancy approach

2.1 Abstract

[1]We develop a coupled economic-metacommunity model to investigate the trade-off between diversity and profit for multi-species systems. The model keeps track of the presence or absence of species in habitat patches. With this approach, it becomes (relatively) simple to include more species than can typically be included in models that track species population density. We use this patch-occupancy framework to understand how profit and biodiversity are impacted by (1) community assembly, (2) pricing structures that value species equally or unequally, and (3) the implementation of marine reserves. We find that when local communities assemble slowly as a result of facilitative colonization, there are lower profits and optimal harvest rates, but the trade-off with diversity may be either large or small. The trade-off is diminished if later colonizing species are more highly valued than early colonizers. When the cost of harvesting is low, maximizing profits tends to sharply reduce

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biodiversity and maximizing diversity entails a large harvesting opportunity cost. In the models we analyze, marine reserves are never economically optimal for a profit-maximizing owner. However, management using marine reserves may provide low-cost biodiversity protection if the community is over-harvested.

Keywords: fisheries management, ecosystem-based management, marine reserves, multi-species interactions, metacommunity

2.2 Introduction

There is growing evidence that biologically diverse ecosystems provide services to society that are more valuable than the sum that would be provided by isolated individual species (Boehlert, 1996; Worm et al., 2006); that is, biodiversity has real value (Halpern et al., 2012). It follows that natural and anthropogenic threats to biodiversity, including over-harvesting and habitat destruction, have real biodiversity costs (Halpern et al., 2008). As a result, and particularly in marine systems, interest has begun to move from the management of single species or populations, and toward 'ecosystem-based management' in which the conservation of biodiversity is typically one of the explicit goals (Kellner et al., 2011).

Of course, the conservation of biodiversity will have costs. In harvested systems, maximizing biodiversity may come at the cost of reduced economic productivity or employment (Cheung and Sumaila, 2008). In order for managers and policy makers to strike a reasoned balance between economic productivity and biodiversity conservation they must be able to estimate those costs, typically with the aid of mathematical models.

Although bioeconomic modeling studies have considered the management of several interacting species (e. g., Finnoff and Tschirhart 2003; Fleming and Alexander 2003; Kellner et al. 2011), these are typically limited in the number of species that they consider. A model complex enough to capture all of the interactions both within and between its biological and economic components, for realistically large communities, is difficult to construct and often needs an prodigious amount of environmental, biological, and economic data in order to estimate its parameters (Fulton et al., 2011; Fogarty, 2014). In most cases, such data is simply not available. In addition, ecosystem-based management is "place-based" (McLeod et al., 2005; Crowder and Norse, 2008) and so requires models with a spatial component. Spatial management has become an ubiquitous part of the marine conservation toolbox (Neubert and Herrera, 2008; Botsford et al., 2009; Rassweiler et al., 2012) and, in a variety of conditions, has been shown to improve management outcomes (e. g., Thrush et al. 1998; Sanchirico and Wilen 1999; Neubert 2003; Kellner et al. 2007; Neubert and Herrera 2008; Moeller and Neubert 2013). Marine reserves—spatial management in which some areas are closed to fishing—have garnered interest as a way to potentially increase biodiversity, population sizes, resilience of communities to perturbations (including climate change), and spillover of biomass into fishable areas.

How, then, could one include multiple species in a mathematically-tractable bioeconomic framework that is complex enough to address questions of spatial management? Here we present one possibility, and demonstrate how it could be used to understand the trade-offs (or synergies) between biodiversity conservation and economic productivity. Our approach has, at its foundation, a so-called *patch-occupancy model* (e. g., Levins and Culver 1971; Hastings 1980; Caswell and Cohen 1991; Leibold et al. 2004). Such models have been used to investigate how species-specific differences in dispersal and colonization ability affect local and regional diversity patterns (Levins and Culver, 1971; Gouhier et al., 2011), as well as the role of disturbance in maintaining or eroding biodiversity (Nee and May, 1992; Prakash and de Roos, 2004).

Here we develop a patch-occupancy metacommunity framework in order to understand how profit and biodiversity are impacted by (1) the process of community assembly, (2) pricing structures that treat species harvest values either equally or unequally, and (3) the implementation of marine reserves.

In general, we are concerned with the trade-off between diversity and profit over a range of harvest rates and reserve fractions. The curves in Fig. 2-1 are intended to illustrate the different diversity and profit quantities discussed in the paper. Two quantities are useful for summarizing this trade-off: the change in diversity–the 'diversity gain'–and the change in profit–the 'foregone profit'– that accompany a change in harvest rate or reserve fraction relative to their profit maximizing levels (Fig. 2-1). These quantities are useful for compar-

Table 2.1: Definitions and concepts.

Term	Units	Definition
diversity (α)	# spp.	average number of species in a patch at equilibrium
profit (Π)	\$ per time	revenue from selling fish minus harvest costs of fish at equilibrium
profit (π)	\$ per patch per time	revenue from selling fish minus harvest costs of fish at equilibrium per patch
diversity gain	# spp.	change in diversity relative to that at profit maximizing harvest level
forgone profit	\$ per time	change in profit relative to maximum profit
open access	–	unregulated state in which profit is zero
open access diversity	# spp.	diversity at open access harvest level
profit maximizing diversity	# spp.	diversity at the profit maximizing harvest level
protected diversity	# spp.	difference between diversity at open access with and without a reserve

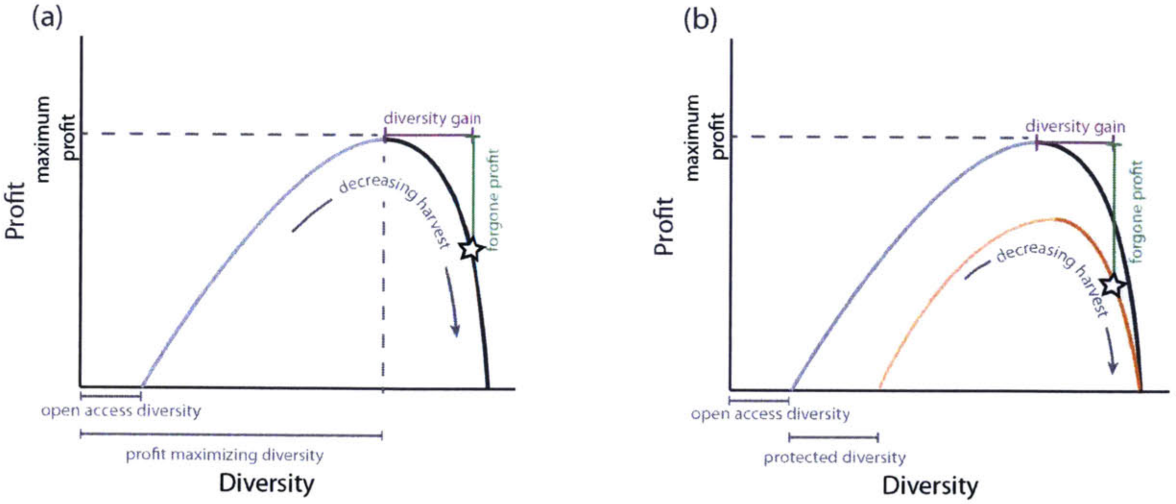

Figure 2-1: Schematic of the quantities related to profit-diversity tradeoffs with (a) effort regulation and (b) effort regulation plus marine reserves. In each panel, the grey and black curve represents the profit-diversity trade-off for a community with no marine reserve. The orange curve indicates this trade-off for a community where some habitat is protected by a marine reserve. The diversity gain (purple, horizontal bar) and forgone profit (green, vertical bar) are calculated for a particular harvest rate (star). They are measured relative to the diversity and profit at the profit maximizing harvest rate. Descriptions of 'open access diversity,' 'profit maximizing diversity,' and 'protected diversity' are in the text and Table 2.1. For each profit-diversity curve, the lighter portion of the curve indicates where profit and diversity can be simultaneously increased by harvesting less.

ing the trade-off under different management scenarios. If no reserves are implemented, the diversity gain and forgone profit result solely from a decrease in harvest rate (Fig. 2-1a). When reserves are added (as in Fig. 2-1b), the changes in diversity and profit can result from a combination of the effects of the reserve and harvest rate changes. With reserves, we also introduce the concept of 'protected diversity,' which is the increase in diversity at open access that results from implementing a reserve. The shape of these trade-off curves is determined by the biotic interactions within the community; the shape shown here was anticipated from biomass versus profit for single species models and serves as a comparison for the shape we may obtain when plotting diversity versus profit. One objective of this study is to characterise and understand how biotic interactions influence the shape of these trade-off curves. Table 2.1 details the relevant quantities that we calculate in our two illustrative models.

2.3 Patch Occupancy Framework

Patch occupancy models have several advantages over alternative approaches. First, by using spatial models, we can incorporate ecologically important processes such as dispersal and habitat disturbance. Second, because they are spatially implicit, and only consider species' presence or absence (rather than population density), patch-occupancy models tend to be more amenable to analysis than their spatially explicit counterparts. Finally, coupling the patch-occupancy model with a simple economic model enables us to optimize profit or diversity and gain insights into the trade-offs between different management objectives.

The first step in formulating a patch occupancy model is to divide a site (e. g., a bay, reef, or fishing ground) into a set of *patches.* Each of these patches is described by its *state*, as defined by the identities of the species present. Patches can change state either because they are colonized by individuals of a new species dispersing from other patches or by losing species via local extinction. The dynamics of community assembly are determined by the rules governing the colonization process—in particular how the state of a patch determines which species may invade—and the rules governing species replacement (or coexistence) after a colonization event.

In the following sections, we construct two illustrative models that capture two extreme community assembly mechanisms. In the first, *null* model, we assume that the species do not interact and may colonize any habitable patch at which they are not already present. The simplicity of this model makes it a useful baseline against which to compare more complicated and realistic processes. Such models are commonly used in community assembly studies (e.g., Weiher and Keddy 1995; Neubert et al. 2006). In the *facilitation* model we assume that species may only colonize patches already inhabited by a facilitating species. This type of obligate facilitation operates, for example, when one species provides habitat for another (e.g., anemones and clownfish (Dunn, 1981), which may be targeted for aquarium trade, or crabs in mussel beds (Silliman et al., 2011)); for other examples, see Bruno et al. (2003). In the facilitative model section below, we demonstrate the trade-offs that might be present in these communities. The facilitation model is simple and readily compared with a null model; in the discussion, we suggest possible model extensions to incorporate more complex community assembly dynamics.

In the framework we develop here, local extinction is the result of harvesting that can be regulated by a resource manager. Harvest causes extirpation of all species within a patch and renders the patch uninhabitable until the patch habitat recovers. Fishing frequently damages habitat (for example, through trawling) and has been shown to have strong effects on community composition (e. g., Thrush et al. 1998; Thrush and Dayton 2002). In addition, previous studies that have incorporated destruction of habitat have found it to be an important driver of interspecies interactions (Caswell and Cohen, 1991; Klausmeier, 2001; Prakash and de Roos, 2004) and optimal management (Moeller and Neubert, 2013). Below we present a case in which harvesting is the only source of disturbance in the community; we discuss the implications of this assumption in the discussion.

The structure of this model, the simplicity of which we exploit to facilitate analysis over these broad ranges of ecological and economic parameters and relationships, comes in the form of strong assumptions. For instance, we assume that harvesters do not know the state of any particular patch—including one that they just harvested. Harvester avoidance of recently fished areas would increase the effective fishing pressure applied to other areas. The model is also spatially implicit, which means that the survival of relict populations in space, as can occur with cellular automaton models, cannot occur. Our study of equilibrium conditions also means that the study of systems that are perturbed or far from equilibrium are not accommodated. However, as detailed below, many of these assumptions make this framework suitably tractable to be coupled with a simple economic model in order to address the role of community assembly, pricing structure, and profit-diversity trade-offs under different types of management.

2.4 Null Model

In the null model, species do not interact and are identical in colonizing ability. Species may colonize any habitable patch at which they are not already present; the rate of colonization is independent of the presence or absence of other species. Some patches are also uninhabitable until they recover.

Imagine S species which are distributed among a large set of N patches. A simple way of defining the state of a particular habitable patch is to label it with a $1 \times S$ vector, $\boldsymbol{\psi}$, composed of zeros and ones. The ith element of $\boldsymbol{\psi}$, ψ_i, is one if species i is present and zero if it is absent. An uninhabitable patch is in state ϕ. We will keep track of the number of patches in these states with the variables $X_{\boldsymbol{\psi}}$ and X_{ϕ}. In general, there will be $2^S + 1$ state variables. Table 2.2 lists the variable and parameter names for reference.

It will be notationally convenient to define Ψ as the set of all possible $\boldsymbol{\psi}$, and Ψ_i as the subset of Ψ whose members have ith element equal to one. Thus Ψ is the set of all possible habitable states and Ψ_i is the set of all states where species i is present (regardless of other inhabitants). It will also be useful to define the state where only species i is present as $\mathbf{e}_i$.

The state of an individual patch is changed when it is colonized, harvested, or recovers from harvest. Patches are harvested at rate h, causing the patch to become temporarily uninhabitable. These patches recover at rate r, becoming habitable, but empty. Thus, the number of uninhabitable patches changes at the rate

$$\frac{dX_\phi}{dt} = h \sum_{\boldsymbol{\psi} \in \Psi} X_{\boldsymbol{\psi}} - rX_\phi \tag{2.1}$$

Next, let us consider the rate of change of the number of habitable patches that are in state $\boldsymbol{\psi}$. These patches change state when they are colonized or harvested. In a given patch, colonization by species i occurs only when species i is absent; i. e., when $\psi_i = 0$. Propagules of species i are produced in state Ψ_i patches. There are $\sum_{\eta \in \Psi_i} X_\eta$ such patches. Because all species are identical in this null model, these propagules are generated at constant per-patch rates, c. Each of these propagules lands on a patch in state $\boldsymbol{\psi}$ with probability $X_{\boldsymbol{\psi}}/N$. We now sum over all species to obtain the rate of colonization of patches in state $\boldsymbol{\psi}$ as

$$\sum_{i=1}^{S} \left[(1 - \psi_i) \frac{X_{\boldsymbol{\psi}}}{N} c \sum_{\eta \in \Psi_i} X_\eta \right] \tag{2.2}$$

New state-$\boldsymbol{\psi}$ patches are created by the colonization of patches that, by the addition of a single species, become a state-$\boldsymbol{\psi}$ patch. Let us focus on one such patch that is missing species i; it is in state $\boldsymbol{\psi} - \mathbf{e}_i$. At any time, there are $c \sum_{\eta \in \Psi_i} X_\eta$ propagules of species i

Table 2.2: Null model parameters and variables.

Term	Units	Definition
Parameters		
r	time^{-1}	rate of recovery for uninhabitable patches to become habitable
c	time^{-1}	rate of propagule production from a single patch
w	$\$\text{patch}^{-1}$	cost of effort
ε	[]	efficiency of harvest
N	#	number of patches in the community
S	# spp.	number species in the community
Variables		
h	time^{-1}	rate of harvest; this renders the harvested patch uninhabitable
X_ϕ	# patches	number of uninhabitable patches
X_ψ	# patches	number of patches in state ψ
x_ϕ	[]	proportion of patches in uninhabitable state
y_i	[]	proportion of patches with species i (regardless of other inhabitants)
x_f	[]	proportion of patches in reserve, with all S species present

being produced to colonize our focal patch. Only a fraction of these propagules, $1/N$, will land on it to possibly recruit. Summing over all species that are eligible to colonize patches in state $\boldsymbol{\psi} - \mathbf{e}_i$ (those with $\psi_i = 1$) gives us the total rate of addition of new state-$\boldsymbol{\psi}$ patches:

$$\sum_{i=1}^{S} \left[\psi_i \frac{X_{\boldsymbol{\psi}-\mathbf{e}_i}}{N} c \sum_{\eta \in \Psi_i} X_\eta \right] \tag{2.3}$$

Combining the effects of harvest and colonization, we obtain

$$\frac{dX_{\mathbf{0}}}{dt} = rX_\phi - \sum_{i=1}^{S} \left[\frac{X_{\mathbf{0}}}{N} c \sum_{\eta \in \Psi_i} X_\eta \right] - hX_{\mathbf{0}} \tag{2.4}$$

and

$$\frac{dX_{\boldsymbol{\psi}}}{dt} = -\sum_{i=1}^{S} \left[(1-\psi_i) \frac{X_{\boldsymbol{\psi}}}{N} c \sum_{\eta \in \Psi_i} X_\eta \right] + \sum_{i=1}^{S} \left[\psi_i \frac{X_{\boldsymbol{\psi}-\mathbf{e}_i}}{N} c \sum_{\eta \in \Psi_i} X_\eta \right] - hX_{\boldsymbol{\psi}} \tag{2.5}$$

for $\Psi \neq 0$. By defining

$$x_\phi = X_\phi / N, \text{ and } x_{\boldsymbol{\psi}} = X_{\boldsymbol{\psi}} / N \tag{2.6}$$

(so that x_ϕ and $x_{\boldsymbol{\psi}}$ track the fraction of patches in these states) and rearranging we further simplify the null model to

$$\frac{dx_\phi}{dt} = h \sum_{\boldsymbol{\psi} \in \Psi} x_{\boldsymbol{\psi}} - rx_\phi \tag{2.7}$$

$$\frac{dx_{\mathbf{0}}}{dt} = rx_\phi - \sum_{i=1}^{S} \left[x_{\mathbf{0}} c \sum_{\eta \in \Psi_i} x_\eta \right] - hx_{\mathbf{0}} \tag{2.8}$$

$$\frac{dx_{\boldsymbol{\psi}}}{dt} = c \sum_{i=1}^{S} \sum_{\eta \in \Psi_i} x_\eta \left[\psi_i x_{\boldsymbol{\psi}-\mathbf{e}_i} - (1-\psi_i) x_{\boldsymbol{\psi}} \right] - hx_{\boldsymbol{\psi}}. \tag{2.9}$$

Eqs. 2.7–2.9 comprise the biological and harvesting component of our null model. A simple example of this model, with only two species, is illustrated in Fig. 2-2; we show the corresponding equations, for the reader's entertainment, in Appendix 2.6.

A manager of such a multispecies fishery might choose h to maximize profit. The profit depends on the cost of harvesting, the price for the harvested fish, and the intra- and in-

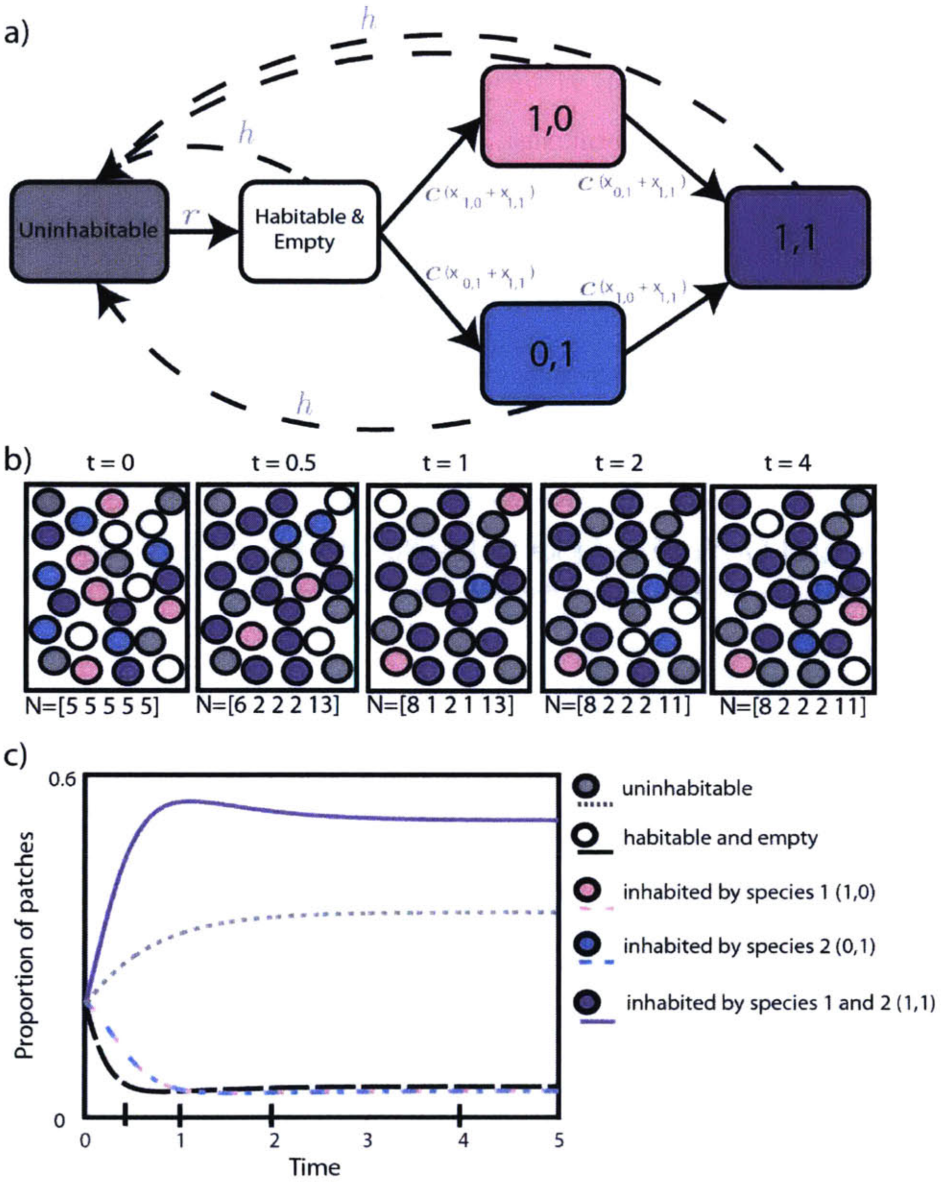

Figure 2-2: (a) Schematic of null model states (boxes), transitions (arrows; solid is colonization, dashed is harvest), and rates (arrow labels) for a community with 2 species. The model equations are described in Appendix 1. Uninhabitable patches (gray box) can recover to become habitable (white boxes) are rate r. These empty patches can then be colonized by either species 1 or 2 (pink and blue boxes) at a rate proportional to the number of patches producing propagules and the number of patches being colonized. Finally, these patches may transition to a patch with both species. All patches may become habitable but empty through harvest. (b) Schematic of how the transitions in (a) manifest for many patches. The circles, which represent patches, are colored using the same meanings as in (a). Each panel corresponds roughly to the time steps marked in (c). Note that in the last two boxes, while an equilibrium has been reached (so the number of patches in each state is the same), individual patches may change state. (c) Plot showing the simulations of the system of equations from Appendix 1 through time. While the proportion of patches started evenly distributed among states, the proportions reach equilibrium values.

terspecific interactions that determine the dynamics of the metacommunity. In the section (Null model: diversity and profit), we focus on a manager who wants to understand the potential trade-off between long-term, sustainable profit (i.e, the profit at equilibrium) and biodiversity. Before this, we explore how the equilibrium configuration of the metacommunity depends upon the control variable h, which we will take to be a constant. This allows us to formulate relatively simple static optimization problems and facilitates identification of profit-diversity trade-offs. An alternative approach, and an ambitious next step, might include the consideration of the dynamic control of harvest in time and the stability of solutions to imperfect control; the importance of such analyses in understanding fisheries collapse is illustrated for a single species by Roughgarden and Smith (1996).

2.4.1 Null Model: Equilibria

The dynamics of our null model are dominated by equilibria. While the state of any particular patch will continue to change as it is harvested, recovers, and is colonized, the proportion of patches in those states converges to a set fraction determined by the parameter values. Thus, at any time the patches are in a mosaic with some patches containing all species, some uninhabitable, et cetera. As long as all S species are initially present in the community, the fraction of patches in the uninhabitable state will converge to the equilibrium value x^*_ϕ, and the fraction of patches in the various habitable states will converge to x^*_ψ. An easy way to calculate the equilibria is to introduce the new variable $y_i = \sum_{\eta \in \Psi_i} x_\eta$ which gives the fraction of all patches that contain species i. The dynamics of y_i are given by

$$\begin{aligned} \frac{dx_\phi}{dt} &= h(1 - x_\phi) - r x_\phi, & (2.10) \\ \frac{dy_i}{dt} &= c y_i (1 - x_\phi - y_i) - h y_i, \text{ for } 1 \le i \le S. & (2.11) \end{aligned}$$

We can solve for the proportions of patches in these states at equilibrium as

$$x^*_\phi = \frac{h}{r + h} \tag{2.12}$$

and

$$y_i^* = y^* = \frac{r}{r+h} - \frac{h}{c}. \tag{2.13}$$

All S species persist as long as the harvest rate satisfies $c \geq h(r+h)/r$. At higher harvest levels, all species are extirpated and $y^* = 0$. We show that this solution is stable in Appendix 2.6.

To calculate x_{ψ}^*, we take advantage of the symmetry among species' equilibrium values and use the binomial formula. Specifically,

$$x_{\psi}^* = \left(\frac{y^*}{1-x_{\phi}^*}\right)^k \left(1 - \frac{y^*}{1-x_{\phi}^*}\right)^{(S-k)} (1 - x_{\phi}^*) \tag{2.14}$$

where k is the number of species present in state ψ (i.e., the sum of the elements of ψ). The proportion of patches with exactly i species, z_i, is

$$z_i = \frac{S!}{i!(S-i)!} \left(\frac{y^*}{1-x_{\phi}^*}\right)^i \left(1 - \frac{y^*}{1-x_{\phi}^*}\right)^{(S-i)} (1 - x_{\phi}^*). \tag{2.15}$$

At low harvest rates, most patches have all species, although there are some patches in every state (Supplemental fig. 2-3). At sufficiently high harvest levels, $c < h(r+h)/r$, all species are extirpated from the system.

2.4.2 Null Model: Diversity and Profit

We use the equilibrium values (Equations 2.14 to 2.15) to calculate diversity and profit. We focus on α diversity, or the expected number of species at a patch:

$$\alpha = \sum_i i z_i = S y^*. \tag{2.16}$$

For the null model (2.10)-(2.11), α diversity declines monotonically with harvest rate in all cases (Fig. 2-4 (a)). Higher colonization rates or recovery rates increase the diversity at a particular harvest level. When the diversity curve intersects the h-axis, all species are extirpated.

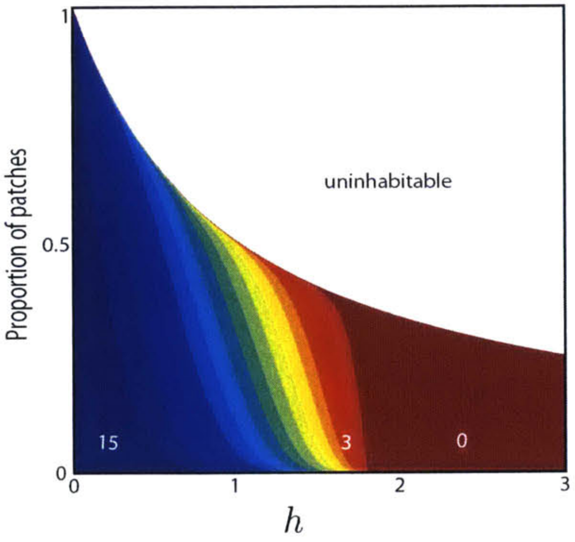

Figure 2-3: Proportion of patches with differing numbers (labelled) of coexisting species (z_i) for a fifteen-species version of the null model (equations 2.10 and 2.11). '0' includes only empty, habitable patches. $S = 15$, $c = 5$ and $r = 1$. At very low harvest levels, there are some patches in all states, just as at higher harvest levels, there are still some patches with all fifteen species.

To calculate profit, we need to specify the monetary value of the harvest from a patch in each state. Because species are identical and do not interact, each contributes the same amount of biomass and value to a patch. Without loss of generality then, we set the value of the harvest from a patch equal to the number of species that are present. Any unoccupied (or uninhabitable) patch is worth 0. We call the price of a patch with i species present, p_i; for the null model, $p_i = i$.

There is also a cost to harvest. We will assume the per patch harvest cost is w. The revenue gained from all inhabited patches, which are harvested with efficiency ε minus the effort costs is the equilibrium profit, Π:

$$\Pi = \varepsilon N h \sum_i z_i p_i - whN. \tag{2.17}$$

The per patch profit rate $\pi = \Pi/N$ gives the average profit obtained from harvest of an individual patch and is obtained by dividing equation (2.17) by N.

A manager who can regulate the harvest level is able to maximize the profit rate. Without such oversight, we will assume the system is at open-access, i.e. profits are driven to

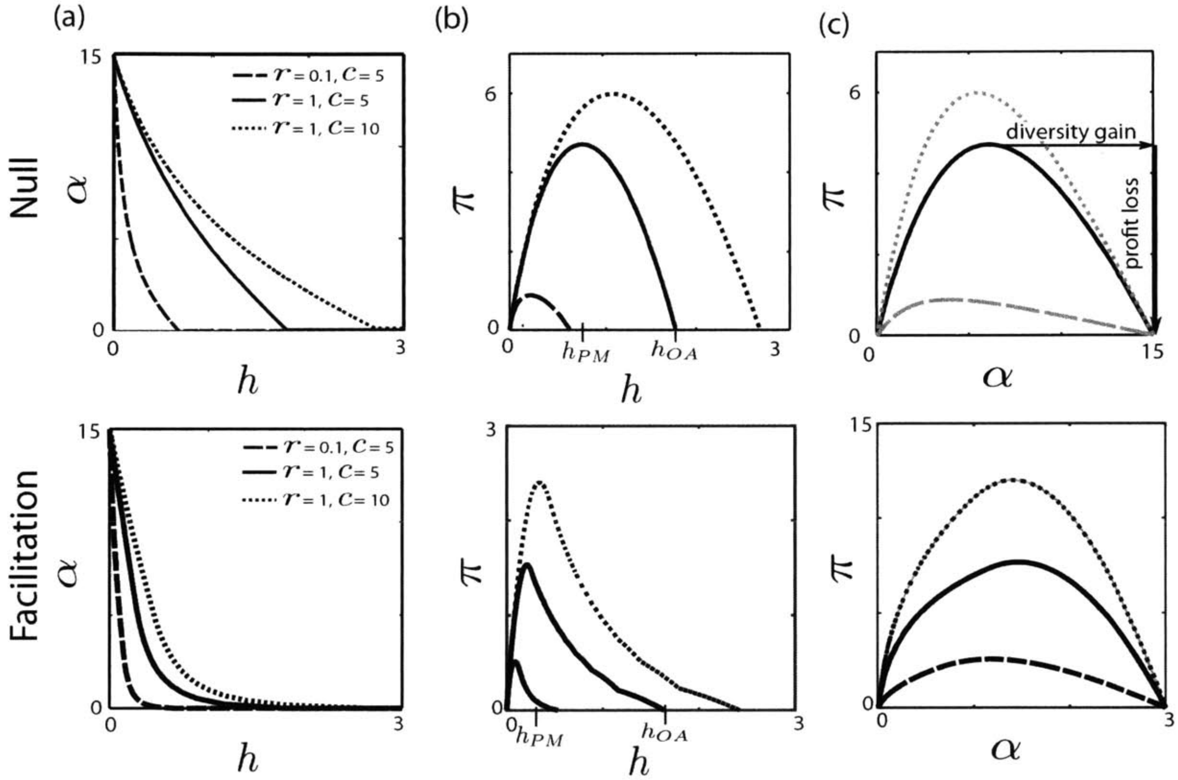

Figure 2-4: For the null model (top row; Eqns. 2.10 and 2.11) and facilitation model (bottom row; Eqs. 2.25-2.28) , α diversity (a) and profit (b) depend upon harvest rate. Together these determine the trade-off between profit and diversity and equilibrium (c). For the parameter values $r = 1$ and $c = 5$ (solid curve), the profit maximizing harvest rate is marked h_{PM} and the open access harvest rate is marked h_{OA}. The diversity gain (relative to profit maximizing harvest level) and profit loss (when diversity is maximized) are labelled in (c). For all panels, $S = 15$, $w = 0.5$, and $\varepsilon = 1$.

zero (Clark, 1973). Profit is maximized at an intermediate harvest level, h_{PM}. The open access harvest level, h_{OA}, is higher (Fig. 2-4 (b)).

We can now compare the diversity and profit at different harvest levels or among fisheries with different biological or economic parameters (Fig. 2-4 (c)). α diversity is maximized when $h = 0$, thus $\pi = 0$ as well. We focus on the maximal diversity gain (recall Fig. 2-1)– the increase in diversity from the profit maximizing harvest rate relative to the diversity at no harvest. The monetary cost of maximizing diversity is the difference in profit at h_{PM} and at the diversity maximizing level. In the null model, $h = 0$ maximizes diversity, so the 'profit loss' or cost to maximize diversity is equivalent to the maximal profit.

As can be seen in Fig. 2-5, if propagule production rates (c) are high relative to the recovery rate, both the profit lost (a) and the diversity gained (b) by maximizing diversity are more sensitive to variation in harvest costs (w) than propagule production rates. Higher propagule production rates and lower effort costs (northwest of both plots) boost the maximum profit attainable in a given community, which incentivizes a heavy harvest and thus reduces diversity.

However, the trade-off is not always large. Both low costs or high propagule production rates can make a community profitable to harvest; however, they do not impact the trade-off between diversity and profit in identical ways. For example, when propagule production rates are low, the profit loss is very low, whereas the diversity gain may still be large. When propagule production rates are low, a small increase in harvest rate increases the proportion of empty patches dramatically. As a result, even the small profit-maximizing harvest levels can cause large diversity losses. A community with low propagule production rates and high harvest costs will still face high diversity losses when harvesting occurs, but the high harvest cost reduces optimal harvest rates, so this potential diversity loss is not realized. However, it is important to note that these results are for a profit-maximizer; the costs associated with managing an open-access fishery may be very different.

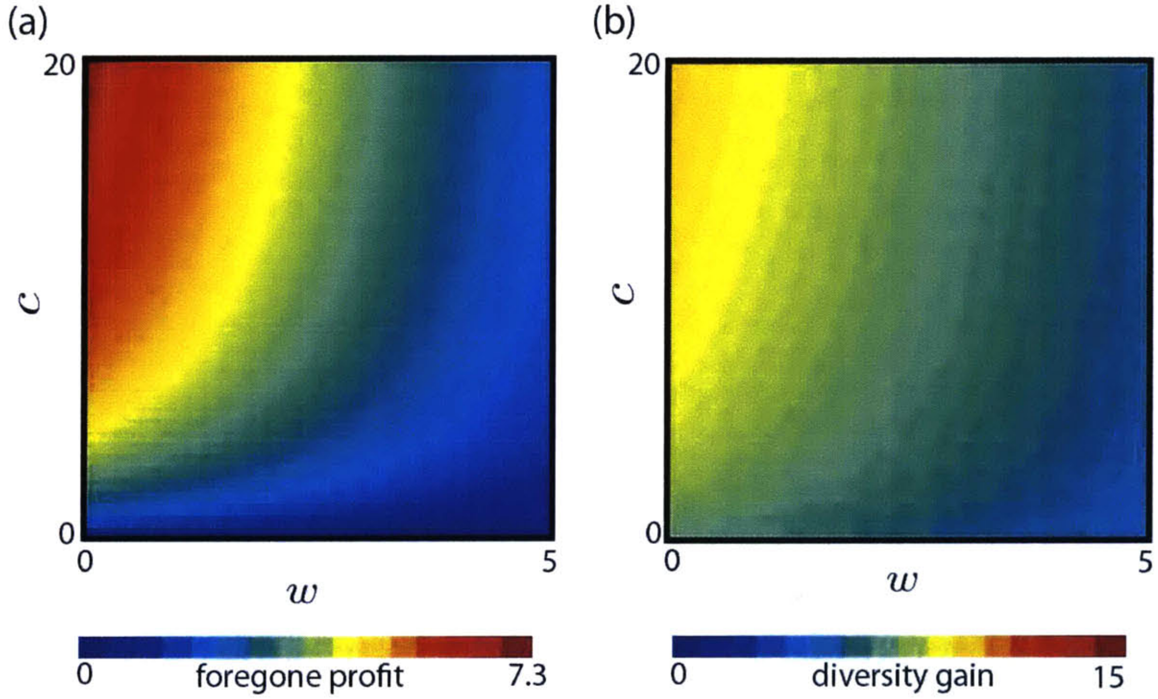

Figure 2-5: (a) Potential profit lost from harvesting at the diversity maximizing level ($h = 0$); i.e., the maximum profit. For a particular w, c combination, this is the vertical arrow shown in Figure 2-4 c. (b) Diversity gain at no harvest relative to harvesting at the profit maximizing level ($h = h_{PM}$). For a particular w, c combination, this is the horizontal arrow shown in Figure 2-4 c. For both panels, $S = 15$, $r = 1$ and $\varepsilon = 1$.

2.4.3 Null Model: Spatial Management

To investigate the cost of conserving diversity using marine reserves we modify our models to keep track of the proportion of patches that cannot be harvested. Since harvest is the only source of disturbance, we will assume that protected patches harbor all species. These reserves have the potential to provide the maximum benefit to biodiversity. Let us call the fixed fraction of patches that are set aside as protected reserves x_f. The dynamics are governed by the following systems of equations, which modify equations 2.10 and 2.11:

$$\frac{dx_\phi}{dt} = h(1 - x_\phi - x_f) - rx_\phi \tag{2.18}$$

$$\frac{dy_i}{dt} = c(y_i + x_f)(1 - x_\phi - y_i - x_f) - hy_i \tag{2.19}$$

The equilibria are then

$$x_\phi^* = \frac{h(1 - x_f)}{r + h} \tag{2.20}$$

$$y_i^* = y^* = \frac{-h + A - cx_f + \sqrt{(h - A + cx_f)^2 + 4cx_f A}}{2c} \tag{2.21}$$

where $A = c(1 - x_\phi^* - x_f)$. This is the equilibrium as long as y^* is positive (otherwise $y_i^* = 0$).

We calculate α diversity and profit, which are now

$$\alpha = S(y_i^* + x_f) \tag{2.22}$$

$$\pi = \varepsilon h \sum z_i p_i - wh \tag{2.23}$$

where z_i is modified from Eqn.(2.15) as

$$z_i = \frac{S!}{i!(S-i)!} \left(\frac{y^*}{1 - x_\phi^* - x_f} \right)^i \left(1 - \frac{y^*}{1 - x_\phi^* - x_f} \right)^{(S-i)} (1 - x_\phi^* - x_f). \tag{2.24}$$

We use these to compare the trade-off between diversity and profit (Fig. 2-6, left column).

At a particular harvest level, α diversity is always higher when reserves are present, as a set of patches with all species present is preserved. The maximum profit attainable is, however, lower if reserves are implemented (Fig. 2-6 (b)). Hart (2006) found a similar pattern in a single-species model, maximizing yield. The harvest rate that maximizes profit and the harvest rate at open access both increase. Consistent with this finding, Halpern et al. (2004) showed that concentrated effort outside reserves cannot produce comparable harvest to a community without reserves, unless there is a compensatory increase to the production rate.

In addition to increased diversity at all harvest rates, reserves provide an additional benefit: a diversity buffer. Whatever the harvest rate, diversity cannot fall below a lower limit (equal to $x_f S$). Even when the community is harvested at extreme (open access) harvest levels, some diversity is preserved. We define 'protected diversity' as the difference in diversity in the community at open-access when no reserve is present and when it is. At very high harvest rates, the diversity gain is almost entirely due to the diversity of patches in the reserve state; outside the reserves, most patches will be in uninhabitable states.

We can calculate the forgone profit necessary to achieve different combinations of the two types of diversity: protected diversity and the realized diversity gain. In Fig. 2-7 we show that the cost of adding relatively large amounts of protected diversity is consistently low (i.e., the iso-cost curves are approximately flat over large ranges of protected diversity). The white line shows the diversity at the profit maximizing harvest rate for a given amount of protected diversity. Above the white line, one can often gain protected diversity without sacrificing much profit by increasing the reserve fraction. Below the white line, for a fixed protected diversity, one can always increase the diversity gain and profit by decreasing the harvest rate. Overall, while increasing the diversity in a community (relative to the profit maximizing level) has a cost, the cost of using marine reserves to do so—which provides a degree of guaranteed diversity even if over-harvested—is relatively cheap. These patterns are consistent for other parameter values.

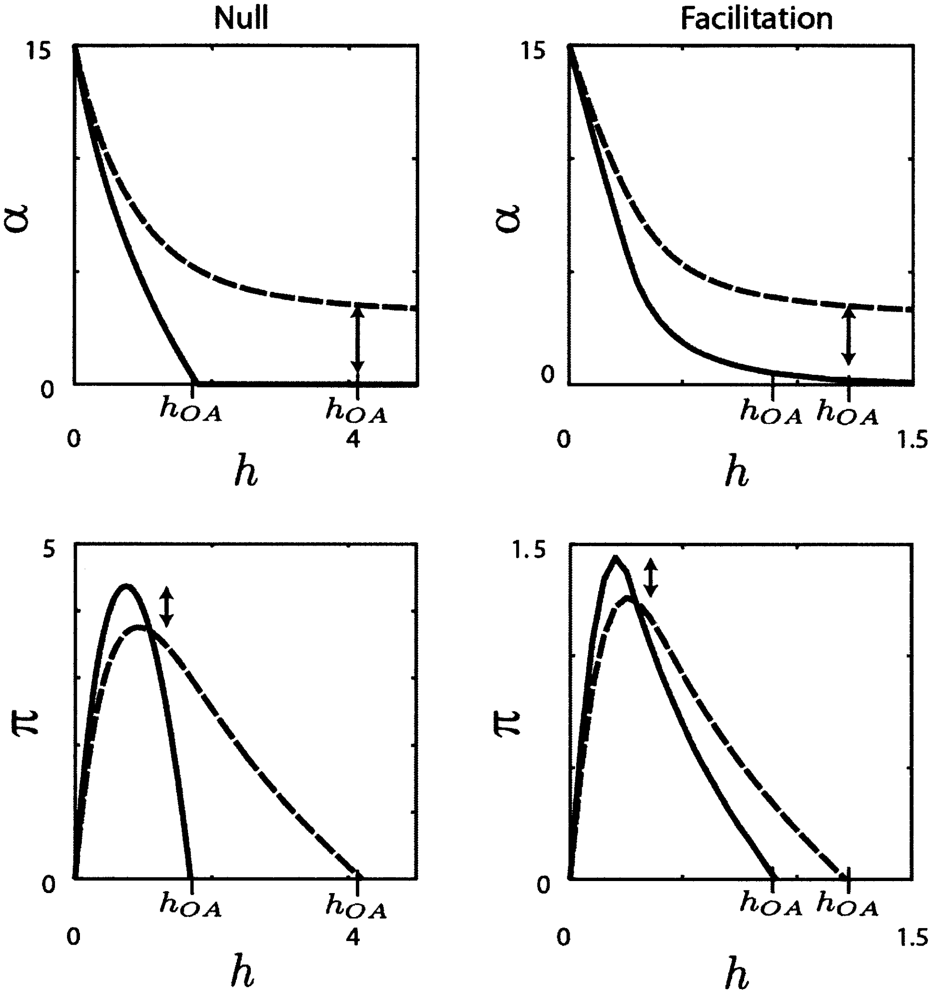

Figure 2-6: Both left panels show a fifteen-species version of the null model (Eqs. 2.18 - 2.19), while the right panels show the facilitation model (Eqs. 2.25-2.28) with parameter values $c = 5$, $r = 1$, $\varepsilon = 1$, and $w = 0.5$. The black, dashed line indicates a community with 20% in reserve and the solid line indicates a community with no reserves. (top) α diversity as a function of harvest rate. The open access harvest rates are marked. The vertical arrow shows the 'protected diversity', which is the difference between the diversity at open access with no reserves and at open access with a reserve. (bottom) Profit as a function of harvest rate. The vertical arrow shows the difference in maximal profit rate without and with a reserve.

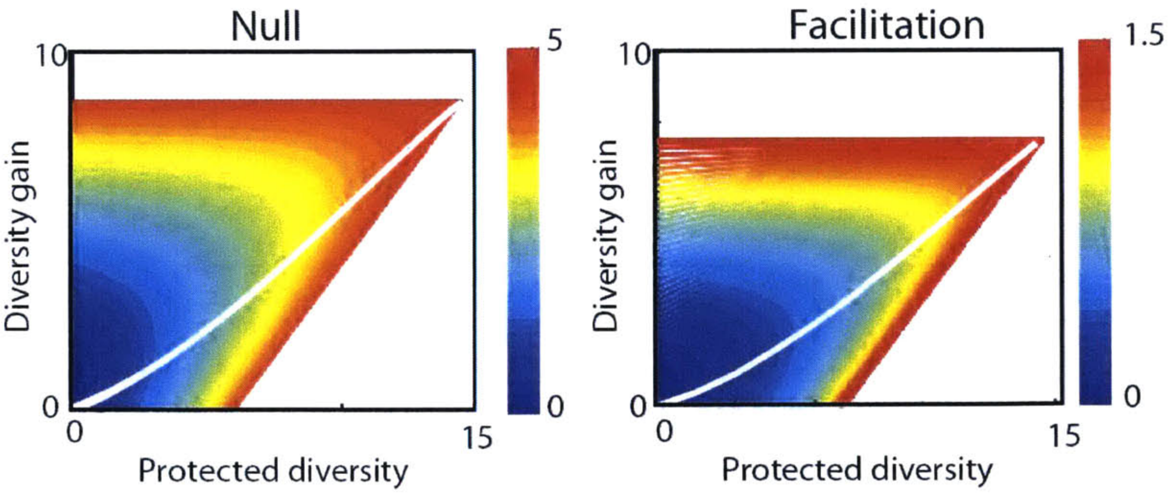

Figure 2-7: The cost, in forgone profit, necessary to achieve different levels of protected diversity and diversity gain for a fifteen-species version of the null model (Eqs. 2.18-2.19) and facilitation model (Eqs. 2.25-2.28) with parameter values $c = 5, r = 1, w = 0.5$ and $\varepsilon = 1$. Since α diversity is positive at $h = h_{PM}$, the diversity gain does not extend to $S = 15$. The white line shows the profit-maximizing diversity gain for each level of protected diversity. Points below this line are sub-optimal in both diversity and profit.

2.5 Facilitation Model

Real communities are more complicated than our null model: species interact, have different life-history traits, and are differentially valuable when harvested. In this section we present a model in which interspecies interactions are strong, as a contrast to the null model.

As in the null model, species accumulate in a patch as they colonize, but in this "facilitation" model, species colonize in sequential order, (i.e., species 2 cannot colonize unless species 1 is present, and species 3 cannot colonize without species 2, etc.). Once a species has colonized, it does not displace the previous inhabitants, so a patch with species 5 necessarily will contain species 1 through 4 as well. Uninhabitable patches, which are created by harvest, must recover from this disturbance before they can be colonized by the first species.

Because of this strong facilitative interaction, the number of states is tremendously reduced compared to the null model with the same number of species. One can now specify the state of a patch with a scalar quantity indicating the number of species in a patch. We call the proportion of patches in state i, x_i. As before, we write a system of differential

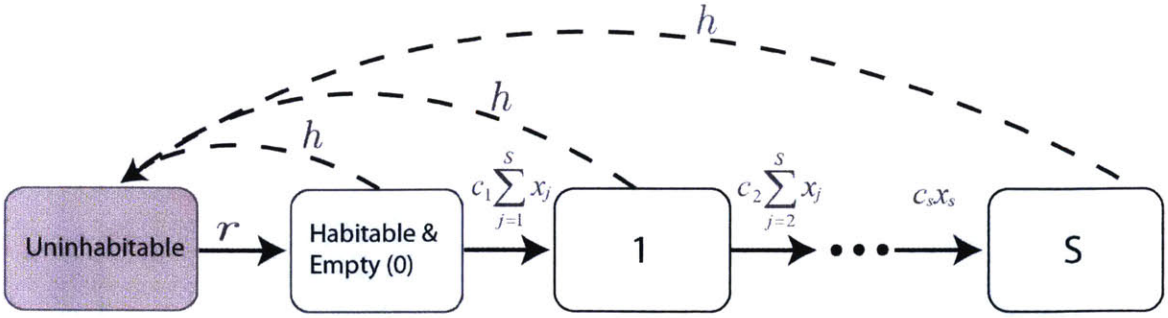

Figure 2-8: Schematic of facilitation model (Eqs. 2.25-2.28) states (boxes), transitions (arrows), and rates (arrow labels). Like in the null model, patches can transition from being uninhabitable from habitable and empty at rate r, but subsequent colonization can only be by species 1. Those patches may then be colonized by species 2, etc. at rates that are proportional to the propagule production rate c and the number of patches able to be colonized and to colonize. All patches may be harvested at rate h.

equations to track how colonization, harvest, and recovery change the proportion of patches in these states. (For parameters and variables see Table 2.3.) We again imagine N patches inhabited by S species. x_ϕ indicates the fraction of patches that are uninhabitable. These are created through harvest (at rate h) and recover at rate r:

$$\frac{dx_\phi}{dt} = h\sum_{i=0}^{n} x_i - r x_\phi. \tag{2.25}$$

Let us focus on patches in state i. The proportion of such patches changes when propagules from species i colonize state $i-1$ patches, propagules from species $i+1$ colonize state i patches, or state i patches are harvested and rendered uninhabitable. Colonization by species i occurs via propagules which are produced at a per patch rate of c_i. Combining these, we obtain (c.f. Fig. 2-8):

$$\frac{dx_0}{dt} = r x_\phi - c_1 x_0 \sum_{i=1}^{S} x_i - h x_0, \tag{2.26}$$

$$\frac{dx_i}{dt} = -c_{i+1} x_i \left(\sum_{j=i+1}^{S} x_j\right) + c_i x_{i-1}\left(\sum_{j=i}^{S} x_j\right) - h x_i, \tag{2.27}$$

$$\frac{dx_S}{dt} = c_S x_S x_{S-1} - h x_S. \tag{2.28}$$

Table 2.3: Facilitation model parameters and variables.

Term	Units	Definition
Parameters		
r	time^{-1}	rate of recovery for uninhabitable patches to become habitable
c	time^{-1}	rate of propagule production from a single patch
w	$\$\text{patch}^{-1}$	cost of effort
ε	[]	efficiency of harvest
N	#	number of patches in the community
S	# spp.	number species in the community
Variables		
hline h	time^{-1}	rate of harvest; this renders the harvested patch uninhabitable
x_ϕ	[]	proportion of patches in uninhabitable state
x_i	[]	proportion of patches with species 1 through i
x_f	[]	proportion of patches in reserve, with all S species present
ρ_j	$	the value of species j
κ	[]	constant that relates the value of patches in state $j-1$ to those in state j

2.5.1 Facilitation Model: Equilibria

As in the null model, while individual patches continue to change state, the proportions of patches in different states equilibrate. These equilibria are straightforward to calculate for arbitrary parameter values (Appendix 3). Here we focus on the case when the propagule production rate is equal among species (i.e., $c_i = c$ for all i). We illustrate this case for comparison with the null model.

For the model given by Eqns. (2.25)-(2.28), the number of species that can persist is given by

$$S^* = \min\left(S, \left\lfloor \frac{cr}{h(r+h)} \right\rfloor\right), \tag{2.29}$$

where $\lfloor \ \rfloor$ indicates the floor function.

If the harvest rate is high relative to the propagule production and recovery rates, all S species cannot co-exist in the community at equilibrium. Thus, species 1 through S^* occupy positive proportions of the habitat, while species above S^* are absent. The stable solution when $S^* > 0$ (Appendix 3) is

$$\begin{aligned} x_\phi^* &= \frac{h}{r+h}, && (2.30)\\ x_i^* &= \frac{h}{c}, \text{ for } i = 0, \ldots, S^*-1, && (2.31)\\ x_{S^*}^* &= \frac{r}{r+h} - \frac{S^*h}{c}, \text{ and} && (2.32)\\ x_j^* &= 0, \text{ for } j > S^*. && (2.33) \end{aligned}$$

The proportion of patches in the uninhabitable state is the same as in the null model. In the null model, all species are extirpated when $h(r+h)/r > c$. In contrast, in the facilitation model, species are sequentially extirpated from the community as harvest rate increases from zero, with the late colonizers being the most vulnerable to overfishing (Supplementary fig. 2-9). The earliest colonizer (species 1), which is the most resilient in the face of harvesting, is eliminated at the same harvest rate that would eliminate all species in the

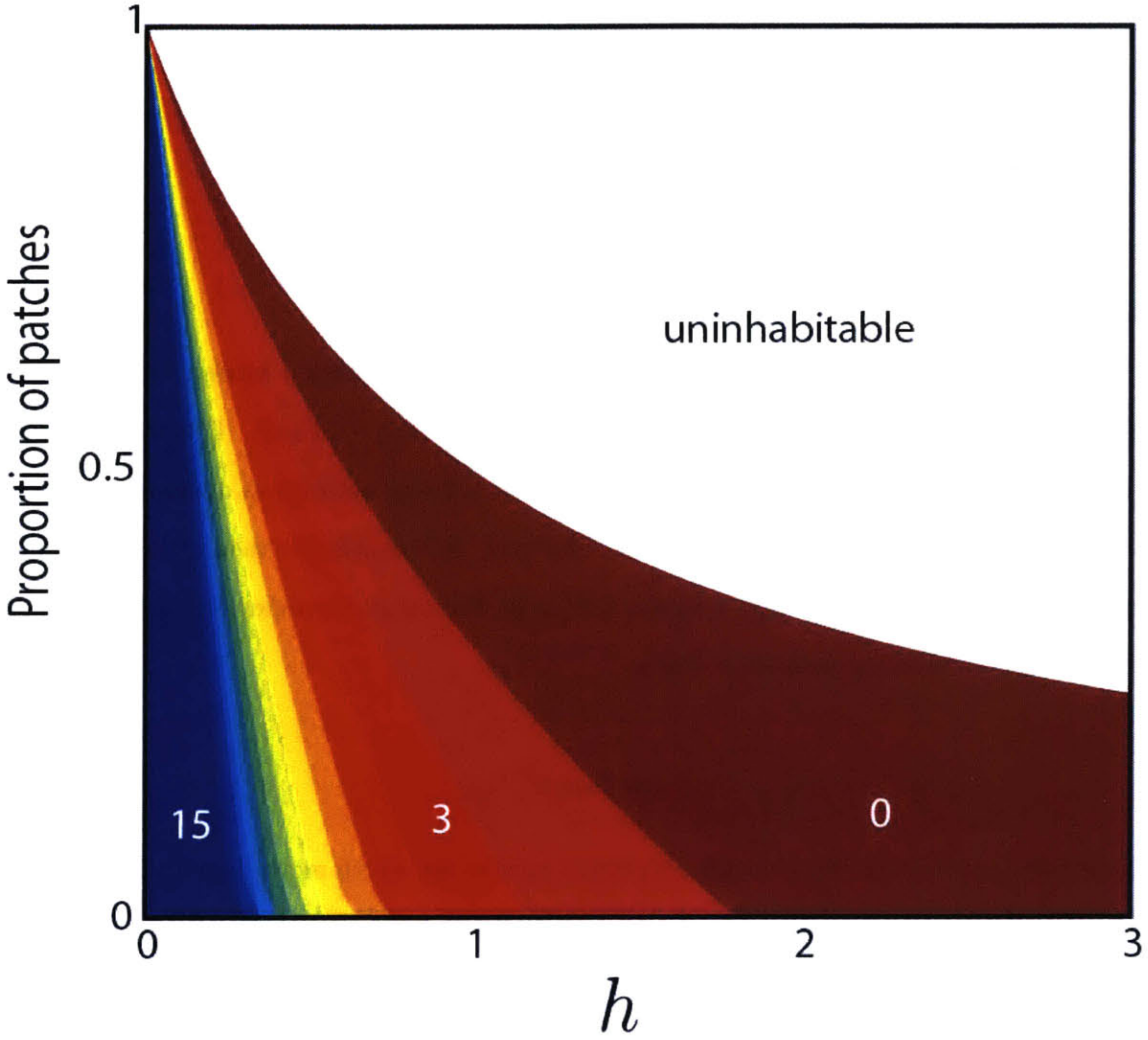

Figure 2-9: Proportion of patches with differing numbers (labelled) of coexisting species in the facilitation model (Eqs. 2.25-2.28) with parameter values $S = 15$, $c = 5$, and $r = 1$. Unlike in the null model, the number of species also uniquely identifies the patch type.

null model.

2.5.2 Facilitation Model: Diversity and Profit

Using Eqns. (2.30)-(2.33), we can calculate equilibrium diversity and profit. The expected number of species in a patch, or α diversity is

$$\alpha = \sum_{i=1}^{S} i x_i, \tag{2.34}$$

$$= \left[\frac{r}{r+h} - \frac{h(S^*+1)}{2c}\right] S^*, \tag{2.35}$$

since a patch in state i has i species present and $c_i = c$.

Diversity declines monotonically with harvest in the facilitation model, but more precipitously at low harvest levels than in the null model (Fig. 2-4 (a)). Diversity vanishes (i.e., all species are extirpated) at the same harvest rate for both types of communities.

In the facilitation model, species are not identical. It is reasonable then to allow different species to have different economic value. Let ρ_j be the value of species j. A simple model for species values is the geometric series:

$$\rho_j = \rho_1 \kappa^{j-1}. \tag{2.36}$$

If the constant κ is less than 1, early colonizing species are worth more than later colonizers; $\kappa > 1$ indicates the opposite. We use $\rho_1 = 1$ and $\kappa = 0.9, 1$, and 1.1 to explore different value relationships.

The value of a patch in state i is then

$$p_i = \sum_{j=1}^{i} \rho_j, \tag{2.37}$$

and the total harvest value is

$$\pi = h\left[\varepsilon \sum_{i=1}^{S} (x_i p_i) - w\right]. \tag{2.38}$$

As in the null model, profit is maximized at an intermediate harvest rate (Supplemental fig. 2-11). At open-access, profit is zero and the harvest rate is higher. As might be expected, profits are larger, and profit-maximizing harvest rates are smaller, if later colonizing species are more valuable relative to early colonizers (i. e., for larger κ). Profit is maximized at lower harvest rates than in the null model (compare Supplemental fig. 2-11 with Fig. 2-

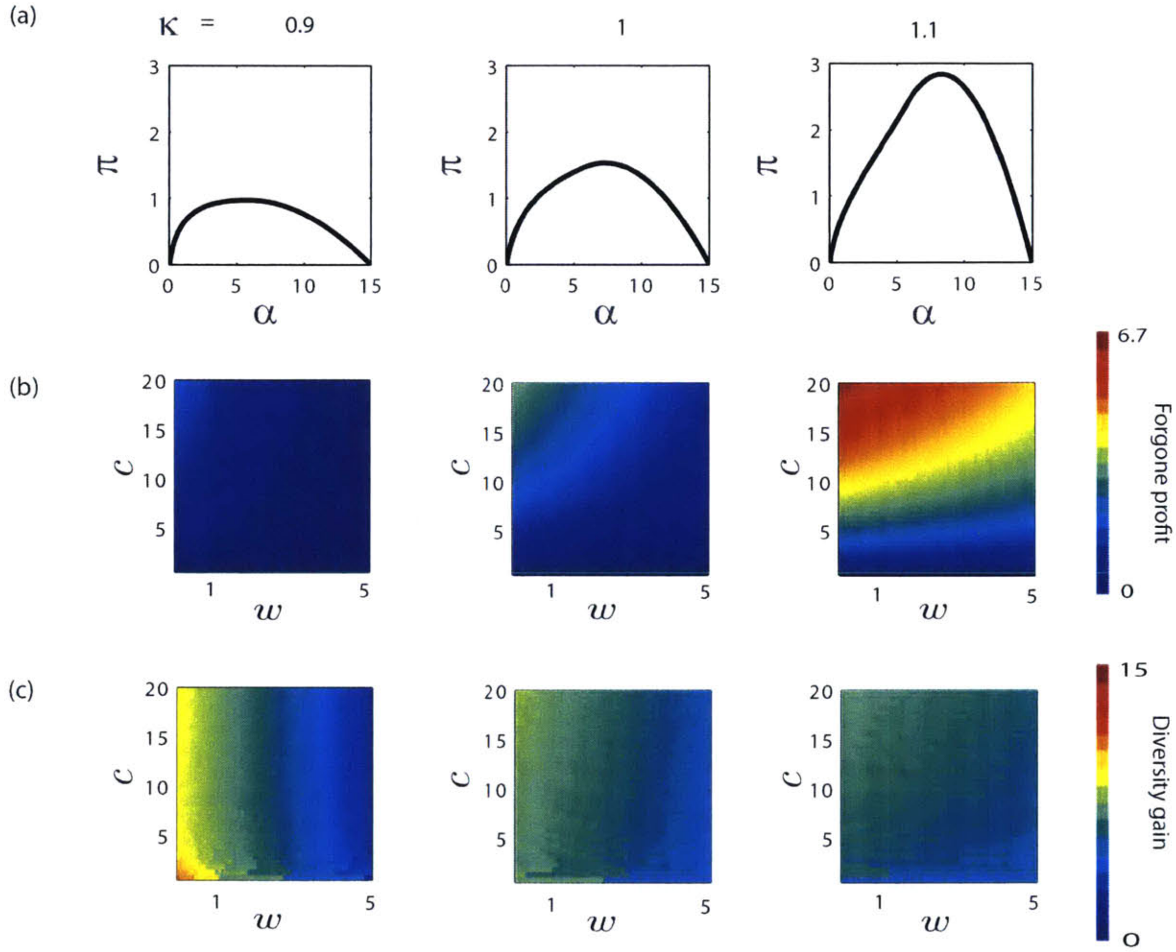

Figure 2-10: (a) α versus π for a fifteen-species version of the facilitation model (Eqs. 2.25-2.28), with $w = 0.05$, $r = 1$, $\varepsilon = 1$, and $c = 5$. Price per patch was determined by κ, as marked. (b) Potential profit lost from harvesting at the diversity maximizing level ($h = 0$). (c) The diversity gain from no harvest relative to harvesting at the profit maximizing level ($h = h_{PM}$). For all panels, $S = 15$, $r = 1$, $\rho_1 = 1$, and $\varepsilon = 1$.

4(b)). At sufficiently high harvest levels, when only early colonizing species persist, the profit is essentially independent of κ.

We can now compare the diversity and profit among fisheries with different biological or economic parameterizations (Fig. 2-10). Diversity is again maximized at $\alpha = S$ when $h = 0$ and $\pi = 0$. Fig. 2-10(b) shows the potential profit that is lost by maximizing diversity. Fig. 2-10(c) shows the diversity that is gained by not harvesting, relative to harvesting to maximize profit; this is the difference between maximum diversity, S, and the diversity at the profit maximizing-harvest level. Below, we highlight several qualitative patterns in the trade-off between diversity and profit.

First note that low harvest costs (w) and high propagule production rates (c) increase profits. In such profitable systems, the trade-off between diversity and profit is relatively large; however, as later colonizers become more valuable (higher κ), the trade-off between diversity and profit is diminished. In contrast, communities with high effort costs and low propagule production rates do not tend to have a large trade-off, as both the profit loss and diversity gain are low.

One interesting case to consider is a low κ community (first column of Fig. 2-10) with low w and low c. While the monetary loss from maximizing diversity is low, the diversity gain is still high. In this case, even though the profit maximizing harvest level is low (and thus profits are low), diversity declines even more rapidly (as the community re-builds species slowly), making the profit maximizing diversity level low. As κ increases, and the trade-off between diversity and profit decreases, this low w, low c region ceases to have such high diversity costs.

2.5.3 Facilitation Model: Spatial Management

Let x_f be the proportion of patches that are set aside in a reserve. These patches cannot be fished and we assume they are in the unharvested equilibrium state with all species present. We modify Eqns. (2.25)-(2.28) to obtain a set of $S + 2$ differential equations which describe the dynamics of a facilitation system with reserves:

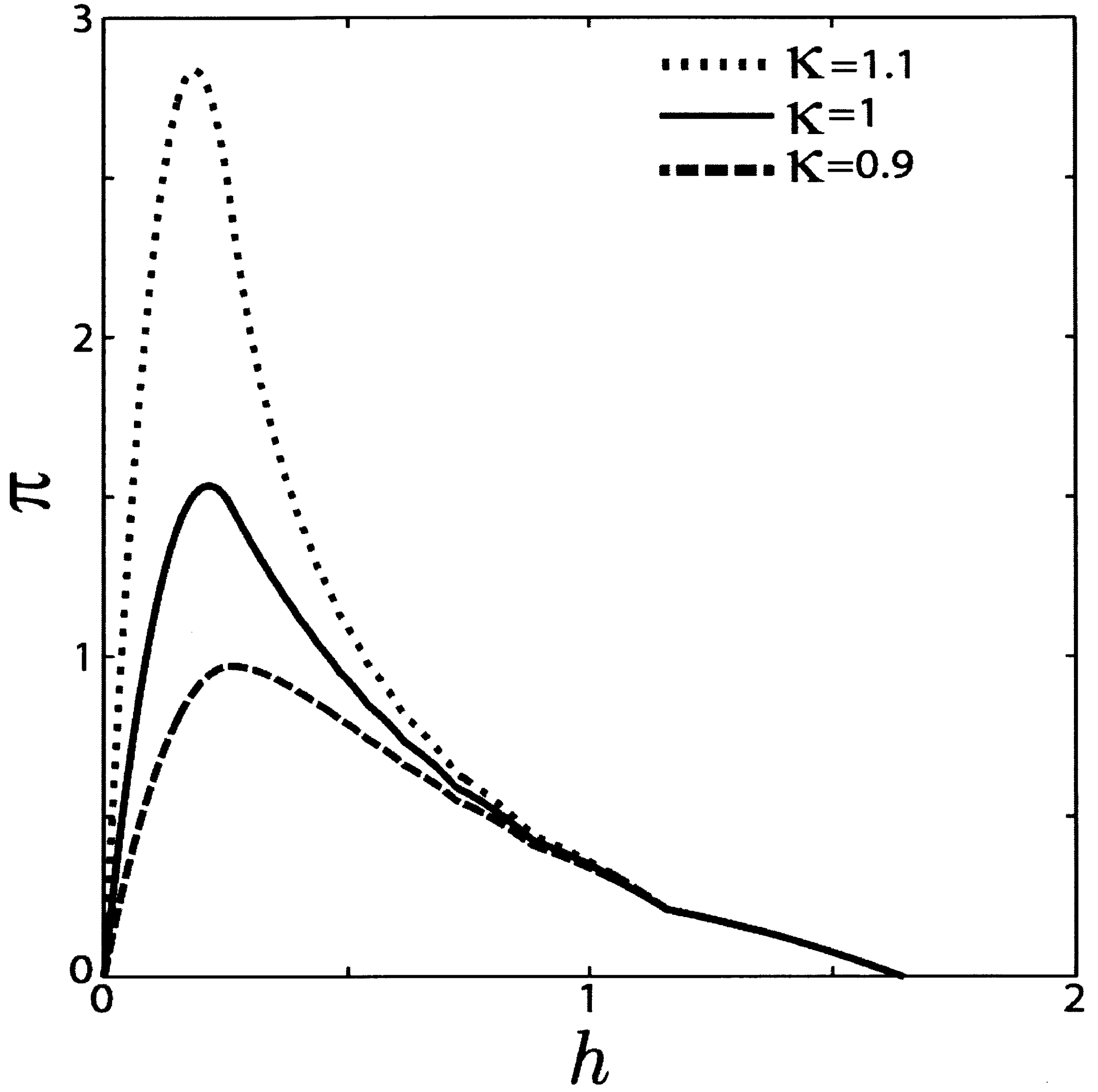

Figure 2-11: Harvest rate versus profit for the facilitation model (Eqs. 2.25-2.28) with $S = 15$, $r = 1$, $\varepsilon = 1$, $w = 0.05$, $\rho_1 = 1$, and $c = 5$. Three different pricing schemes are shown (legend). The 'kinks' in the profit curve occur when species are extirpated from the community.

$$\frac{dx_\phi}{dt} = h(1 - x_\phi - x_f) - rx_\phi, \tag{2.39}$$

$$\frac{dx_0}{dt} = rx_\phi - c_1 x_0 \sum_{j=1}^{S} x_j - hx_0, \tag{2.40}$$

$$\frac{dx_i}{dt} = -c_{i+1}x_i \left(x_f + \sum_{j=i+1}^{S} x_j \right) + c_i x_{i-1} \left(x_f + \sum_{j=i}^{S} x_j \right) - hx_i, \tag{2.41}$$

$$\frac{dx_S}{dt} = c_S(x_f + x_S)x_{S-1} - hx_S. \tag{2.42}$$

Using a modification of Eqn. (2.35) to calculate diversity:

$$\alpha = \sum_{i}^{S} ix_i + Sx_f \tag{2.43}$$

and Eqn. (2.38) along with the (numerically derived) equilibria of this system, we can calculate diversity and profit for communities with and without reserves (Fig. 2-6).

As in the null model, diversity is always higher in communities with reserves, and at high harvest levels the diversity is almost entirely within the reserves. The implementation of reserves reduces the maximum profit rate (Fig. 2-6(b)), but higher harvest levels can still be profitable. In these instances, the open-access harvest rate is larger.

We again calculate the 'protected diversity', 'forgone profit', and 'diversity gain' for all combinations of harvest rates and reserve fractions. These quantities are calculated in the same way as in the null model and are shown schematically in Fig. 2-1b. The cost in forgone profit of different levels of protected diversity and diversity gain is shown in Fig. 2-6.

Qualitatively, the trade-offs among cost and the two diversity metrics are the same as in the null model, although the maximum foregone profit and maximum diversity gains are lower in the facilitation model. For a given reserve fraction, the protected diversity is the same between the two models. The cost of adding protected diversity to a given level of diversity gain is still minimal and is generally cheaper than in the null model.

2.6 Discussion

The coupled metacommunity-economic modeling framework we have described provides a way to examine the ecological and economic factors that influence profit-diversity trade-offs. The quantities we highlighted—foregone profit, diversity gain, and protected diversity—are useful for structuring thinking about the trade-offs in a complex bioeconomic system (Fig. 2-1).

Our framework is, perhaps, best suited for identifying the types of harvested communities that are cost-effective to manage. For example, our analysis showed that in communities structured by facilitative colonization dynamics, a manager could often increase diversity without sacrificing much profit from reduced harvest, especially when propagule production rates and harvest costs are low.

An advantage of the framework is that it permits inclusion of a variety of ecological rates and types of interactions. This is important, because such variation exists in real marine systems. For example, strongly competitive systems that exhibit trophic cascades have been observed (Casini et al., 2008), while other systems show strong facilitative interactions (Silliman et al., 2011). These communities may change at vastly different rates. Recovery from harvest disturbance may take a long time—hundreds of years for deep water corals, which grow on the order of a few millimeters per year (Lartaud et al., 2012)—or a short time—for habitats which are not damaged by fishing, such as long-line fished systems or those with muddy substrates. Additionally, colonization rates can vary widely in marine metacommunities and may depend upon oceanographic features, the distribution of habitat, and species' attributes. Strategic models of the kind we developed here can accommodate this ecological variability and complement the system specific analyses that model the interactions and management of a particular community (e.g., Rassweiler et al., 2012).

In our analysis, we compared a null-community with no interactions to one with strong, facilitative colonizing interactions. The facilitative interaction results in a community that is more sensitive to harvest; it loses species sequentially as harvest rates increase. In contrast, all species persist in the null model until the harvest rate exceeds a threshold value.

Facilitative community assembly also reduces profits and profit-maximizing harvest rates. Both the magnitude and shape of the profit-diversity trade-off are changed by the type of ecological interaction (Figs. 2-5 and 2-10). Decreasing propagule production rates or colonization rates affect the diversity-profit trade-off in similar ways in both the null and facilitation models; the magnitude of the trade-off is changed, but not the shape.

The reader should not expect that the relationship between profit and diversity will always have be as simple as the curves depicted in Figs. 2-1, 2-4(c), and 2-10(a); other types of ecological interactions will produce even more interesting, complicated trade-offs. For example, in a competitive metacommunity where species displace each other at a patch (modeled by Hastings (1980)), there is non-monotonic relationship between the harvest rate and the number of species that persist. Our preliminary analysis of optimal harvest in this type of community suggests that the relationship between diversity and profit is more complex. In addition, other measures of diversity (e.g., beta-diversity or species richness) may be better suited to capturing these trade-offs.

The models we formulated can include potentially large numbers of species. The extensive literature on two species metacommunities has illustrated how important interspecies interactions are for species persistence and diversity patterns (e.g., Caswell and Cohen (1991), Nee and May (1992), Klausmeier (2001), Prakash and de Roos (2004), Gouhier et al. (2011)). When these models are extended to include marine reserves, species interactions may change the optimal reserve size and configuration (Baskett et al., 2007; Baskett, 2007). We extended these results by showing that such interactions continue to be important in much larger communities. Our results comport with those of Matsuda and Abrams (2006) who studied yield in multispecies fisheries and found, like we did, that few species are driven to extinction at yield (or in our case, profit) maximizing harvest levels. In addition, the authors found that constraining the harvest to prevent species extinction could be done without substantially reducing yield, which is analogous to our result for the cost of protected diversity.

We also investigated the cost of using marine reserves as a diversity-preserving management technique. In particular, we highlighted differences in the diversity gains achieved when the harvest rate maximizes profit or dissipates it at open access. For both the null and facilitation models, we found that that the cost of achieving some protected diversity tends to be low. At least for the theoretical communities we studied, marine reserves are an efficient way to prevent the erosion of diversity at high harvest levels.

In contrast with some previous results, we found that marine reserves are not economically optimal in this model. (I.e., reserves never increase the maximum profit attainable). Different per patch pricing methods that we examined did not reverse this result. Other, single-species models (e.g., Neubert 2003; Sanchirico et al. 2006; Neubert and Herrera 2008; White et al. 2008; Moeller and Neubert 2013) have found reserves to be economically optimal; these models incorporate spatial heterogeneity, which our models do not.

Our models also neglect natural disturbance. Thus, the inclusion of marine reserves here shows the maximum diversity benefit of reserves, as reserves have all species present. Natural disturbance primarily affects the role of marine reserves (in the non-reserve section, a disturbance rate that reduces all patches to being uninhabitable is additive with harvest and can be easily separated), as an additional $S+2$ equations to track the natural destruction and re-building of non-fished patches would be required. The magnitude of natural disturbance relative to the colonization, harvest, and recovery rates will determine whether natural disturbance is critical to the trade-offs we described here.

We assume that harvesters do not know the state of a particular patch, but rather only know the mean conditions of the entire metacommunity. They are additionally harvesting all fish present at a patch. In reality, harvesters with modern technology are increasingly able to target specific species of fish at specific locations. Allowing fishermen to target either species (species-specific harvest rates) or areas in space would dramatically increase the number of states and/or controls. This would certainly make harvesters more economically efficient and likely qualitatively change the shape of the trade-off between profit and diversity.

This framework allowed us to investigate broad scale patterns of diversity-profit trade-offs and identify regions where conservation would be cost-effective. We believe there are many interesting directions to extend this work. For example, our model is spatially implicit and does not allow us to investigate spatial patterns in connectivity (for colonization) or in harvest (such as 'fishing the line around marine reserves'). The inclusion of spatial complexity allows for spatial variation in harvest, which can result in non-intuitive configurations of harvesting effort (Wilen et al., 2002; Neubert, 2003; Kellner et al., 2007; Costello and Polasky, 2008). These analyses show that complicated patterns that are not intuitively obvious may appear when harvester behavior in space is accounted for. Spatial variation in harvest may mitigate the trade-off between harvest and biodiversity objectives.

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Appendix: Null Illustration

Fig. 2-2 is an illustration of the two-species version of the null metacommunity model. The states of this model are listed in Table 2.4. The dynamics of the state transitions are governed by

$$\frac{dx_\phi}{dt} = h\sum_i\sum_j x_{i,j} - rx_\phi \tag{2.44}$$

$$\frac{dx_{[0,0]}}{dt} = rx_\phi - c(x_{[1,0]} + x_{[1,1]})x_{[0,0]} - c(x_{[0,1]} + x_{[1,1]})x_{[0,0]} - hx_{[0,0]} \tag{2.45}$$

$$\frac{dx_{[1,0]}}{dt} = c(x_{[1,0]} + x_{[1,1]})x_{[0,0]} - c(x_{[0,1]} + x_{[1,1]})x_{[1,0]} - hx_{[1,0]} \tag{2.46}$$

$$\frac{dx_{[0,1]}}{dt} = c(x_{[0,1]} + x_{[1,1]})x_{[0,0]} - c(x_{[1,0]} + x_{[1,1]})x_{[0,1]} - hx_{[0,1]} \tag{2.47}$$

$$\frac{dx_{[1,1]}}{dt} = c(x_{[1,0]} + x_{[1,1]})x_{[0,1]} + c(x_{[0,1]} + x_{[1,1]})x_{[1,0]} - hx_{[1,1]}. \tag{2.48}$$

States	Description
ϕ	uninhabitable
$[0,0]$	habitable, empty
$[1,0]$	only species 1 present
$[0,1]$	only species 2 present
$[1,1]$	both species present

Table 2.4: Definition of states for the null model (Eqns. 2.1 and 2.2).

Appendix: Stability of the null model

The Jacobian matrix, which consists of partial derivatives of the differential equations, is:

$$J = \begin{pmatrix} -(h+r) & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ -cy_i & 0 & \cdots & c(1-x_\phi) - h - 2cy_i & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \end{pmatrix} \tag{2.49}$$

Because the determinant for this matrix is just the product of the diagonal entries, the eigenvalues of the Jacobian are described by

$$0 = (-(h+r) - \lambda)\Pi_{i=1}^{S}\left(c(1-x_{\phi}) - h - 2cy_i - \lambda\right). \tag{2.50}$$

y_is are equivalent for all i, so we can simplify to

$$0 = (-(h+r) - \lambda)\left(c(1-x_{\phi}) - h - 2cy_i - \lambda\right)^S. \tag{2.51}$$

λ thus can take two values, $-(r+h)$ or $c(1-x_{\phi}) - h - 2cy_i$. The first is always negative, since r and h are non-negative. When $y_i = 0$, $\lambda = \left(\frac{cr}{r+h} - h\right)$ is negative (and thus this solution is locally stable) whenever $c < \frac{h(r+h)}{r}$.

The other solution is $y_i = \frac{r}{r+h} - \frac{h}{c}$.

$$\lambda = c\frac{r}{r+h} - h - 2c\left(\frac{r}{r+h} - \frac{h}{c}\right). \tag{2.52}$$

Setting $\lambda < 0$, we find that this solution is stable when $c > \frac{h(r+h)}{r}$.

Appendix 3: Solutions and stability of the facilitation model

Equations 2.25 and 2.26-2.28 are set to zero to solve for the equilibria. x_{ϕ}^* is the same as in the null model and is equal to $h/(r+h)$. We then solve for the equilibrium of the next highest state, x_0^*. The roots of the quadratic are

$$x_0 = \frac{r}{r+h} \text{ and } \frac{h}{c_1}. \tag{2.53}$$

$x_0^* = h/c_1$ when $x_1 > 0$. Because when $x_0 = r/(r+h)$, $x_{\phi} + x_0 = 1$, only the second solution makes sense if there are patches in other states.

We repeat the same procedure to solve for x_1, using $x_0 = h/c_1$; the roots are

$$x_1^* = \frac{r}{r+h} - \frac{h}{c_1} \text{ and } \frac{h}{c_2}. \tag{2.54}$$

Again, the first solution corresponds to a case in which species 2 (and above) are absent. Because of this structure, we can solve for an arbitrary i.

$$
\begin{aligned}
\frac{dx_i}{dt} &= 0 = -c_{i+1}x_i \sum_{j=i+1}^{S} x_j + c_i x_{i-1} \sum_{j=1}^{S} x_j - h x_i && (2.55)\\
0 &= -c_{i+1}x_i \left(1 - x_\phi - \sum_{j=0}^{i} x_j\right) + c_i x_{i-1} \left(1 - x_\phi - \sum_{j=0}^{i-1} x_j\right) - h x_i && (2.56)\\
0 &= -c_{i+1}x_i \left[\frac{r}{r+h} - h\left(\sum_{j=1}^{S}\frac{1}{c_j}\right) - x_i\right] + c_i \frac{h}{c_i}\left[\frac{r}{r+h} - h\left(\sum_{j=1}^{S}\frac{1}{c_j}\right)\right] - h x_i
\end{aligned}
$$

x_i^* is either

$$
\begin{aligned}
x_i &= \frac{r}{r+h} - h\sum_{j=1}^{S}\frac{1}{c_j} && (2.57)\\
x_i &= \frac{h}{c_{i+1}} && (2.58)
\end{aligned}
$$

If $x_i = \frac{h}{c_i}$ pushes the sum of all uninhabitable and lower hierarchy patches higher than one, the first solution must hold. Alternatively $\frac{r}{r+h} - h\sum_{j=1}^{S}\frac{1}{c_j}$ must always be non-negative, since this expresses the proportion of patches 'left over' for state i. When $c_i = c$, this simplifies to $c \geq i\frac{h}{r}(r+h)$. The highest species number that can persist, φ is

$$\varphi = \min\left(S, \lfloor\frac{cr}{h(r+h)}\rfloor\right). \tag{2.59}$$

Thus, for that case, the total solution is expressed as

$$\mathbf{x}^* = \left[\frac{h}{r+h}, \frac{h}{c}, \frac{h}{c}, ..., \frac{r}{r+h} - \frac{\varphi h}{c}, 0, ...\right]. \tag{2.60}$$

Cases in which c_i is not the same among species follow a similar pattern.

To test local stability, we constructed the Jacobian, J, for this system:

$$\left[\begin{array}{c|c|c|c|c} -(h+c\sum_{i=1}^{S} x_i)-r & -cx_0-r & -cx_0-r & \cdots & -cx_0-r \\ \hline 0 & c\sum_{j=i}^{S} x_i & -(h+c\sum_{j=i+1}^{S} x_j)+cx_{i-1} & c(x_{i-1}-x_i) & \cdots \\ \hline \vdots & \ddots & \ddots & \ddots & \vdots \\ \hline 0 & 0 & 0 & cx_S & -h+cx_{s-1} \end{array}\right] \tag{2.61}$$

We substituted the solutions from equation 2.60 for systems with randomly generated parameter values for S, r, c over harvest rates ranging from 0 to 10. The eigenvalues, calculated with MATLAB, were always negative for these solutions, while other solutions (specifically, that for φ one species lower) were unstable.

Chapter 3

On the Bioeconomics of Marine Reserves when Dispersal Evolves

3.1 Abstract

[1]Marine reserves are an increasingly used and potentially contentious tool in fisheries management. Depending upon the way that individuals move, no-take marine reserves can be necessary for maximizing equilibrium rent in some simple mathematical models. The implementation of no-take marine reserves often generates a redistribution of fishing effort in space. This redistribution of effort, in turn, produces sharp spatial gradients in mortality rates for the targeted stock. Using a two-patch model, we show that the existence of such gradients is a sufficient condition for the evolution of an evolutionarily stable conditional dispersal strategy. Thus, the dispersal strategy of the fish depends upon the harvesting strategy of the manager and vice versa. We find that an evolutionarily stable optimal harvesting strategy (ESOHS)—one which maximizes equilibrium rent given that fish disperse in an evolutionarily stable manner—never includes a no-take marine reserve. This strategy is economically unstable in the short run because a manager can generate more rent by disregarding the possibility of dispersal evolution. Simulations of a stochastic evolutionary

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process suggest that such a short-run, myopic strategy performs poorly compared to the ESOHS over the long run, however, as it generates rent that is lower on average and higher in variability.

Keywords: *evolution of dispersal, evolutionarily stable strategy, fisheries management, marine protected areas, optimal harvesting.*

3.2 Introduction

No-take marine reserves are a type of "marine protected area" in which fishing is prohibited. Closed areas like marine reserves have been used to manage artisanal fisheries on small spatial scales for many years (Fogarty et al., 2000). The advent of geographical positioning systems (which make the possibility of enforcing closures more feasible (Pala, 2014)) combined with the decline of fish stocks, an increased demand for marine fish protein (FAO Fisheries Department, 2014), and a call for ecosystem-based management, have led not only to increased study of the efficacy of marine reserves but also to an increase in their implementation. Marine protected area coverage worldwide has increased by over 150% since 2003 (Toropova et al., 2010).

A number of studies have shown that marine reserves can contribute to the conservation of stocks and to the ecosystems that support them (e. g., Halpern and Warner, 2002; Halpern, 2003; Lester et al., 2009). Increases in individual size, biomass, population density and species diversity have been shown to increase subsequent to reserve establishment (see examples in, for example, Lester and Halpern, 2008).

The potential economic costs or benefits of reserves are less clear (Kaiser, 2005; White et al., 2008; Hart and Sissenwine, 2009; Fletcher et al., 2015, in press). Some modeling studies (e. g., Neubert, 2003; Sanchirico and Wilen, 2005; Sanchirico et al., 2006; Armstrong, 2007; Neubert and Herrera, 2008; Joshi et al., 2009; Moeller and Neubert, 2013) have shown that the establishment of marine reserves for conservation purposes does not necessarily require a reduction in economic productivity. Indeed, in some models reserves are necessary to maximize yield or sustainable rent. Others (including Polacheck, 1990; Quinn et al., 1993; Man et al., 1995; Holland and Brazee, 1996; Nowlis and Roberts, 1999; Guenette and Pitcher, 1999; Hastings and Botsford, 1999; Li, 2000; Pezzey et al., 2000; Sanchirico and Wilen, 2001; Apostolaki et al., 2002) have shown that reserves may be yield-neutral or produce minor improvements when compared with non spatial effort-control policies. In some cases, the establishment of a reserve decreases yield (Tuck and Possingham, 1994).

The optimality of reserves, then, would seem to depend both on the objective as well as the ecological and economic circumstances. One phenomena, however, emerges from all of these modeling studies, as well as from real-world observations (Fig. 3-1): the imposition of marine reserves can produce a radical redistribution of fishing effort in space. Effort is displaced from reserve areas and frequently concentrates near their borders as harvesters attempt to catch the "spillover" from the reserves. As a consequence, the establishment of marine reserves can produce sharp spatial gradients in mortality (Neubert, 2003; Kellner et al., 2007; Joshi et al., 2009; Abbott and Haynie, 2012; Moeller and Neubert, 2013).

It is easy to imagine, that as a result of these gradients, there would be strong selective pressure to evolve context-dependent dispersal (McPeek and Holt, 1992)—that is, low dispersal rates within the reserve and high dispersal rates outside—or, equivalently, the ability for dispersing individuals to detect and preferentially settle in better patches. Since the potential economic benefits of reserves rely on dispersal of individuals from reserves into fished areas, evolution of dispersal might work against the generation of sustainable rent.

In this paper we explore that possibility with the aid of a simple,"two-patch" model (Holt, 1985). We begin by briefly demonstrating that, in the absence of evolution, reserves can be economically optimal when the two patches are sufficiently different in either their biological or economic properties (Sanchirico et al., 2006). We then ask whether reserves are ever optimal (in the sense of maximizing equilibrium rent) when dispersal evolves.

Our analysis of this second problem builds on the work of Law and Grey (1989) and Grey (1993) who were perhaps the first to seriously investigate the interplay between harvest and evolution, i. e., the inclusion of evolutionary change in the constrained optimization problem of the resource manager. They developed the concept of an *evolutionarily stable optimal*

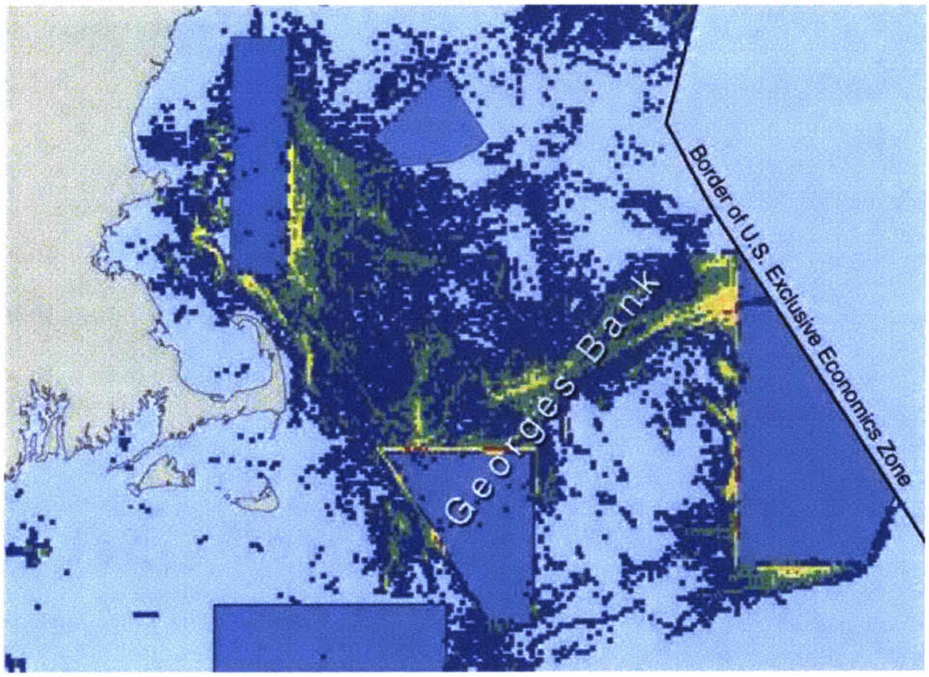

Figure 3-1: Marine reserves (blue polygons) designed to manage scallop harvest off the New England Coast. Dots indicate estimates of fishing effort in 2003, based on satellite tracking of vessels. Warmer colors (green to red) denote more intense activity. The highest intensity of fishing occurred right at MPA borders. Graphic from Fogarty and Murawski (2004).

harvest strategy (ESOHS)[2]—a harvesting strategy "which gives the greatest sustainable yield, after evolution caused by cropping has taken place." Law and Grey (1989) were particularly concerned with the problem of how age-specific harvesting selects for changes in the age at maturity, so they developed the ESOHS concept in the context of life-history theory (which generally ignores dispersal). We extend their idea here to the evolution of dispersal in a spatially managed fishery and find that evolution qualitatively changes the nature of the optimal distribution of fishing effort.

3.3 Model

The model we use is similar to those of Clark (1990, pg. 337) and Sanchirico et al. (2006), both of which derive from the classic model of Gordon (1954). The model describes the dynamics of a stock distributed across two spatial locations, or "patches," connected by dispersal. Each patch is characterized by an intrinsic rate of growth r_i and a carrying capacity k_i. Individuals leave a patch at a constant per capita rate m and enter a common pool of dispersers. From this pool a fraction ε (instantaneously) choose to settle into patch 1; the remaining fraction, $1 - \varepsilon$, settle in patch 2. In this sense, ε can be thought of as a disperser's preference for patch 1. Patches are harvested at nonnegative patch-dependent effort rates E_i. If the population size of the stock in patch i is x_i, this fishing effort generates yield at the rate $q_i E_i x_i$. The proportionality constants q_i are called the "catchability coefficients."

Under this model, the dynamics of the stock in the two patches are given by the ordinary differential equations

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) - m(1-\varepsilon)x_1 + m\varepsilon x_2 - q_1 E_1 x_1, \tag{3.1}$$

$$\frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{k_2}\right) + m(1-\varepsilon)x_1 - m\varepsilon x_2 - q_2 E_2 x_2. \tag{3.2}$$

If the price of fish is p, and the cost per unit of effort in patch i is c_i, then the rent

---

[2] We prefer the pronunciation *ess-oh-ess* for this acronym.

generated by harvesting is

$$\pi[E_1, E_2; \varepsilon] = \sum_{i=1}^{2} (pq_i x_i - c_i)\, E_i. \tag{3.3}$$

At first, we concern ourselves with the case in which a manager is able to control the levels of effort in each of the patches (for example by limiting the number of boat-days available for fishing or by taxing effort) and does so with the objective of maximizing the rent, π, at equilibrium.

It is a simple matter to numerically calculate the equilibrium stock sizes from equations (3.1) and (3.2) for any combination of E_1 and E_2. These can be substituted into formula (3.3) to determine the equilibrium rent. We call the effort levels that maximize the equilibrium rent E_i^*, the corresponding stock sizes x_i^*, and the maximum equilibrium rent π^*.

The optimal solution in patch i will fall into one of three categories depending upon the signs of E_i^* and the marginal rent in patch i, $pq_i x_i^* - c_i$. If

1. $E_i^* > 0$, we say the patch is *fished*; if
2. $E_i^* = 0$ and $pq_i x_i^* - c_i \leq 0$, we say the patch is *unfished*; and if
3. $E_i^* = 0$ and $pq_i x_i^* - c_i > 0$, we say the patch is in *reserve.*

We distinguish between unfished and reserve patches because the latter would require enforcement by the regulator—an individual harvester would have incentive to fish in that patch, but doing so would reduce the total rent at equilibrium. In unfished patches the marginal rent is negative, and rational harvesters (which we assume) avoid it of their own accord.

The optimal equilibrium effort levels in each patch are determined by the model parameters (Fig. 3-2). When the patches are economically and ecologically identical, and dispersers settle indifferently (i. e., $\varepsilon = 0.5$), the optimal strategy is to ensure that both patches are harvested at the same rate (or not fished at all if $pq_i k_i - c_i \leq 0$). Asymmetric settlement, or differences in intrinsic growth rates, carrying capacities, or harvest costs can

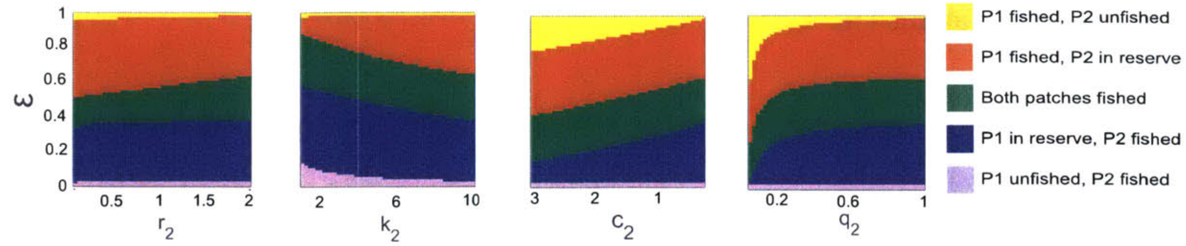

Figure 3-2: Optimal fishing effort, in the absence of evolution, in each patch as patch 2 quality varies. Patch 2 is the 'poorer' patch in every case, with variations in patch 2 parameters noted on the abscissae. All other parameters are equal between patches, with $k_i = 10, r_i = 2, q_i = 1, c_i = 0.25, m = 4, p = 1$. Note that the axis for c_2 is flipped, because patch 2 becomes 'better' (less costly to fish) as c_2 decreases.

result in the optimal closing of one patch (blue and red regions of Fig. 3-2). For the rest of the paper, we will explore cases in which patch 1 is in one way (and only one way) better (for the harvesters) than patch 2; that is, all of the inequalities

$$r_1 \geq r_2, \quad k_1 \geq k_2, \quad c_1 \leq c_2, \quad q_1 \geq q_2, \tag{3.4}$$

are satisfied and only one is satisfied as a strict inequality. This is the case for all of the parameter combinations encompassed by Fig. 3-2 and subsequent figures.

3.4 Evolution of dispersal and the ESS

In general, the optimal harvesting effort, and thus the per capita mortality rate, in each patch will differ. The dispersal strategy may evolve in response to this mortality gradient. Evolution, in turn, affects optimal fishing strategies, including the optimality of reserves, through changes in dispersal. Here, we consider the evolution of ε, the proportion of dispersers that settle into patch 1. We derive the evolutionarily stable strategy (ESS), $\hat{\varepsilon}$, the dispersal phenotype against which no alternative phenotype can increase under selection. In this section, we find an expression for $\hat{\varepsilon}$ and show that it is a "weak form ESS." This ESS is also convergence-stable, making it an evolutionary attractor to which the population will converge in the long run.

3.4.1 Calculating the ESS

To determine $\hat{\varepsilon}$, we begin by considering a population composed of a single "resident" phenotype with dispersal preference ε. The equilibrium stock sizes, $\bar{x}_1$ and $\bar{x}_2$, satisfy

$$\left[r_1\left(1-\frac{\bar{x}_1}{k_1}\right)-q_1E_1\right]\bar{x}_1-m(1-\varepsilon)\bar{x}_1+m\varepsilon\bar{x}_2=0, \tag{3.5}$$

$$\left[r_2\left(1-\frac{\bar{x}_2}{k_2}\right)-q_2E_2\right]\bar{x}_2+m(1-\varepsilon)\bar{x}_1-m\varepsilon\bar{x}_2=0. \tag{3.6}$$

We will find it useful to define α_i as the per capita growth rate, including fishing mortality, in patch i if it were isolated (i. e., if $m=0$). That is,

$$\alpha_i=\left[r_i\left(1-\frac{\bar{x}_i}{k_i}\right)-q_iE_i\right]. \tag{3.7}$$

α_i can be thought of as the fitness of an individual in patch i at equilibrium.

The phenotype that characterizes the resident population evolves through invasions (and sequential replacement) by rare mutants—alternative phenotypes that appear at low frequencies. Mutants are identical to residents, save for their dispersal preference, which we will denote as ε'. A mutant's fate depends on its *invasion fitness*—its initial growth rate in the resident population. When it first appears, the mutant is rare, and its effect on the resident's population dynamics is negligible (Metz, 2008). Thus if x_1' and x_2' are the mutant populations in the two patches, their dynamics are initially given by the linear system

$$\frac{d}{dt}\begin{pmatrix} x_1' \\ x_2' \end{pmatrix}=\mathbf{A}'\begin{pmatrix} x_1' \\ x_2' \end{pmatrix} \tag{3.8}$$

where

$$\mathbf{A}'=\begin{pmatrix} \alpha_1-m(1-\varepsilon') & m\varepsilon' \\ m(1-\varepsilon') & \alpha_2-m\varepsilon' \end{pmatrix}. \tag{3.9}$$

The invasion fitness is then given by the dominant eigenvalue of $\mathbf{A}'$ (which is always real):

$$\lambda'=\frac{1}{2}\left(\alpha_1+\alpha_2-m+\sqrt{(\alpha_1-\alpha_2)^2+2(\alpha_1-\alpha_2)(2\varepsilon'-1)m+m^2}\right). \tag{3.10}$$

Note that the invasion fitness is a function of both the mutant phenotype and the resident phenotype (because the α's depend upon the equilibrium population sizes of the resident, which, in turn depend on ε).

If the invasion fitness (3.10) is positive, the mutant can replace the resident, inducing evolutionary change; if negative, the mutant will be extirpated. An ESS, $\hat{\varepsilon}$, is a resident phenotype that cannot be replaced by any ε', making it resistant to further evolution (Geritz et al., 1998). A condition that must be satisfied by any ESS is that the selection gradient $d\lambda'/d\varepsilon'$ vanishes when $\varepsilon' = \varepsilon = \hat{\varepsilon}$. Differentiating the invasion fitness (3.10) with respect to ε' and evaluating at $\varepsilon' = \varepsilon = \hat{\varepsilon}$ gives

$$\left.\frac{\partial \lambda'}{\partial \varepsilon'}\right|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} = \frac{(\alpha_1 - \alpha_2)m}{\sqrt{(\alpha_1 - \alpha_2)^2 + 2(\alpha_1 - \alpha_2)(2\hat{\varepsilon} - 1) + m^2}} = 0. \tag{3.11}$$

Since we have assumed that m is positive, a vanishing selection gradient (3.11) implies that $\alpha_1 = \alpha_2$; but, adding (3.5) and (3.6) we find that

$$\alpha_1 \bar{x}_1 + \alpha_2 \bar{x}_2 = \alpha_1(\bar{x}_1 + \bar{x}_2) = 0. \tag{3.12}$$

Thus, when the resident population sizes are positive, $\alpha_1 = \alpha_2 = 0$. That is, when the patch preference is at its ESS value, $\hat{\varepsilon}$, the per capita growth rates in the two patches (including fishing mortality) are identical and zero.

By setting $\alpha_1 = \alpha_2 = 0$ in equilibrium equations (3.5) and (3.6), we see that the only potential ESS is

$$\hat{\varepsilon} = \frac{\hat{x}_1}{\hat{x}_1 + \hat{x}_2}, \tag{3.13}$$

where

$$\hat{x}_i = k_i \left(1 - \frac{q_i E_i}{r_i}\right) \tag{3.14}$$

are the corresponding population sizes.

Substituting the condition $\alpha_1 = \alpha_2 = 0$ into (3.10), we see that the invasion fitness of any mutant is 0 whenever the resident phenotype is given by (3.13). Because the invasion fitness is never positive, no mutant phenotype can increase under selection, confirming that

(3.13) is a local ESS. Because the invasion fitness is always 0, however, every mutant will have the same fitness as the resident, making (3.13) a 'weak form ESS' (*sensu* Uyenoyama and Bengtsson, 1982).

3.4.2 Convergence stability of the ESS

As we show next, the evolutionarily stable dispersal strategy (3.13) is also convergence stable—an evolutionary attractor to which a monomorphic population will converge through small, successive mutations (Geritz et al., 1998). We thus expect the settlement preference to evolve to, and remain at, $\hat{\varepsilon}$.

We demonstrate the convergence stability of $\hat{\varepsilon}$ using the second derivatives of the invasion fitness (3.10). Convergence stability requires that

$$\left(\frac{\partial^2 \lambda'}{\partial \varepsilon \, \partial \varepsilon'} + \frac{\partial^2 \lambda'}{\partial \varepsilon'^2} \right) \bigg|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} < 0. \tag{3.15}$$

That is, the sum of these second derivatives, taken with respect to the resident and mutant phenotypes, must be negative at the ESS $\hat{\varepsilon}$ (Eshel, 1983; Geritz et al., 1998).

Because α_1 and α_2 do not depend on the mutant strategy ε', it follows that $\partial^2\lambda'/\partial\varepsilon'^2 = 0$ when $\alpha_1 = \alpha_2$. Thus, (3.13) will be a convergence-stable ESS if $\partial^2\lambda'/\partial\varepsilon\,\partial\varepsilon' < 0$ at $\varepsilon' = \varepsilon = \hat{\varepsilon}$.

To calculate $\partial^2\lambda'/\partial\varepsilon\partial\varepsilon'$, first differentiate the invasion fitness (3.10) with respect to ε':

$$\frac{\partial \lambda'}{\partial \varepsilon'} = \frac{(\alpha_1 - \alpha_2)m}{\sqrt{(\alpha_1 - \alpha_2)^2 + 2(\alpha_1 - \alpha_2)(2\varepsilon' - 1)m + m^2}}. \tag{3.16}$$

Next, recall that α_1 and α_2 depend on the resident trait ε, and rewrite the equilibrium conditions (3.5) and (3.6) as

$$\alpha_1 = m \left[1 - \frac{\varepsilon(\bar{x}_1 + \bar{x}_2)}{\bar{x}_1} \right], \tag{3.17}$$

$$\alpha_2 = m \left[\varepsilon - \frac{(1-\varepsilon)\bar{x}_1}{\bar{x}_2} \right]. \tag{3.18}$$

Note that the equilibrium stock sizes $\bar{x}_1$ and $\bar{x}_2$ are both functions of ε.

We can substitute (3.17) and (3.18) into (3.16), and then differentiate with respect to ε to obtain $\partial^2\lambda'/\partial\varepsilon\partial\varepsilon'$. After evaluating the resulting expression at $\varepsilon' = \varepsilon = \hat{\varepsilon}$, as given by (3.13), we find that

$$\left.\frac{\partial^2\lambda'}{\partial\varepsilon\,\partial\varepsilon'}\right|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} = \frac{m}{\hat{x}_1\hat{x}_2}\left[\hat{x}_2\frac{d\bar{x}_1}{d\varepsilon} - \hat{x}_1\frac{d\bar{x}_2}{d\varepsilon} - (\hat{x}_1+\hat{x}_2)^2\right]. \tag{3.19}$$

The derivatives $d\bar{x}_1/d\varepsilon$ and $d\bar{x}_2/d\varepsilon$ can be found by differentiating the equilibrium equations (3.5) and (3.6) with respect to ε. When evaluated at $\varepsilon' = \varepsilon = \hat{\varepsilon}$ and $\bar{x}_i = \hat{x}_i$, as given by (3.14), these derivatives are

$$\left.\frac{d\bar{x}_1}{d\varepsilon}\right|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} = \frac{mk_1r_2\hat{x}_2(\hat{x}_1+\hat{x}_2)^2}{mk_2r_1\hat{x}_1^2 + r_2\hat{x}_2\left[mk_1\hat{x}_2 + r_1\hat{x}_1(\hat{x}_1+\hat{x}_2)\right]}, \tag{3.20}$$

$$\left.\frac{d\bar{x}_2}{d\varepsilon}\right|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} = -\frac{mk_2r_1\hat{x}_1(\hat{x}_1+\hat{x}_2)^2}{mk_2r_1\hat{x}_1^2 + r_2\hat{x}_2\left[mk_1\hat{x}_2 + r_1\hat{x}_1(\hat{x}_1+\hat{x}_2)\right]}. \tag{3.21}$$

After substituting (3.20) and (3.21) into (3.19), we find that

$$\left.\frac{\partial^2\lambda'}{\partial\varepsilon\,\partial\varepsilon'}\right|_{\varepsilon'=\varepsilon=\hat{\varepsilon}} = -\frac{m}{\hat{x}_1\hat{x}_2}\left(\frac{r_1r_2\hat{x}_1\hat{x}_2(\hat{x}_1+\hat{x}_2)^3}{mk_2r_1\hat{x}_1^2 + r_2\hat{x}_2\left[mk_1\hat{x}_2 + r_1\hat{x}_1(\hat{x}_1+\hat{x}_2)\right]}\right) < 0. \tag{3.22}$$

It follows that inequality (3.15) is satisfied and the ESS settlement preference (3.13) is a convergence-stable strategy.

3.5 The ESOHS and effects of evolution on optimal management

In general, the rent that is generated in each patch depends upon the fishing effort in both patches. This is not the case when the patch preference ε is at its ESS value $\hat{\varepsilon}$, which becomes clear upon substituting the equilibrium stock sizes (3.14) into the rent (3.3):

$$\pi[E_1, E_2; \hat{\varepsilon}] = \hat{\pi} = \sum_{i=1}^{2}\left(pq_ik_i\left(1 - \frac{q_iE_i}{r_i}\right) - c_i\right)E_i. \tag{3.23}$$

This means that when we maximize rent over E_1 and E_2, we are maximizing the rent in the patches independently of each other. Thus, a reserve cannot be part of an ESOHS; a patch should never be closed unless it is unprofitable to harvest (i. e., falls in the 'unfished' category). Specifically, the ESOHS is

$$\hat{E}_i^* = \begin{cases} \frac{r_i(pq_ik_i - c_i)}{2pq_i^2k_i} & \text{if} \quad pq_ik_i - c_i > 0, \\ 0 & \text{otherwise.} \end{cases} \tag{3.24}$$

The resulting stock sizes in each patch at the ESOHS are

$$\hat{x}_i^* = \begin{cases} \frac{1}{2}\left(k_i + \frac{c_i}{pq_i}\right) & \text{if} \quad pq_ik_i - c_i > 0, \\ k_i & \text{otherwise.} \end{cases} \tag{3.25}$$

The evolutionarily stable settlement preference at optimal harvest, $\hat{\varepsilon}^*$, can be calculated using (3.13) with stock sizes $\hat{x}_i = \hat{x}_i^*$.

Spatial heterogeneity in biological or economic parameters is reflected in the ESOHS (Fig. 3-3). When the patches differ in their biological parameters (r or k), the ESOHS effort level in the worse patch is smaller than it would be if the patches were identical and the parameter values were equal to their values in the good patch (Fig. 3-3, first two columns). If the only difference between the patches is due to a difference in intrinsic growth rate (i. e., if $r_2 < r_1$), the ESOHS settlement preference, $\hat{\varepsilon}^*$, remains $1/2$, and the stock sizes are equal to one half of the (identical) carrying capacity in each patch. In contrast, when the carrying capacities of the two patches differ (i. e., $k_2 < k_1$), $\hat{\varepsilon} > 1/2$, and settlement in patch 1 is more frequent than settlement in patch 2. In combination with the lower carrying capacity, this dispersal asymmetry results in a smaller equilibrium stock size in patch 2. When the patches differ in one of their economic parameters (either c or q; Fig. 3-3, last two columns), $\hat{\varepsilon}^* < 1/2$; that is, settlement is more frequent in the economically poorer patch. If the patches only differ in the cost of fishing (i. e., $c_2 > c_1$), then the ESOHS effort in the more expensive patch, as expected, is lower than in the less expensive patch. Combined with the settlement asymmetry, this results in a larger standing stock in the poorer patch. Similarly, there is a larger standing stock in patch 2 when fish are harder to catch there

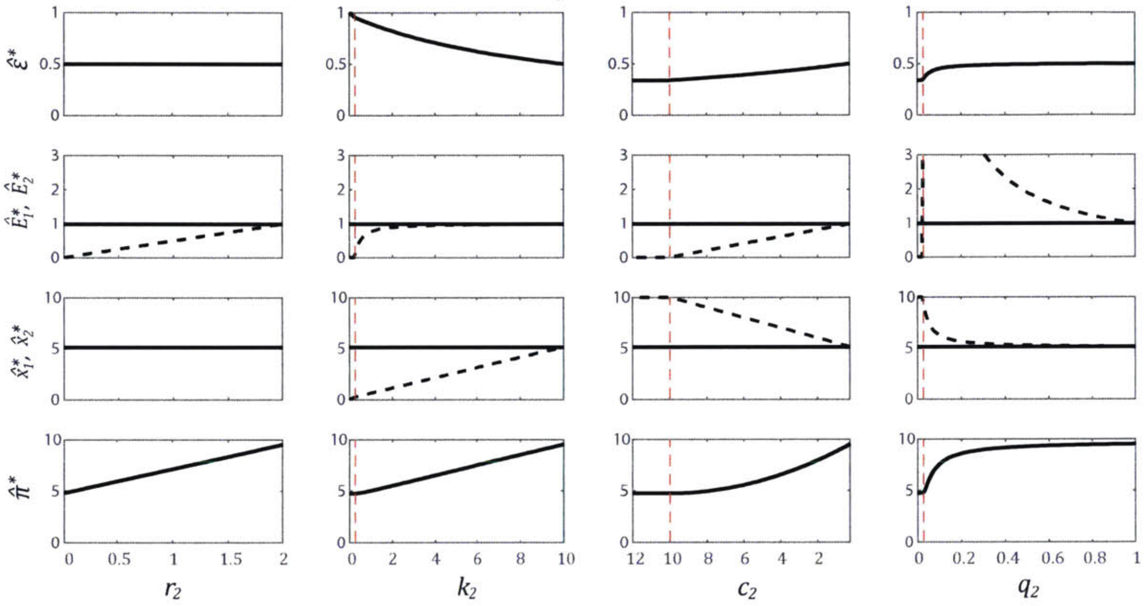

Figure 3-3: ESOHS settlement preference ($\hat{\varepsilon}^*$), fishing efforts ($\hat{E}_i^*$), stock sizes ($\hat{x}_i^*$) and sustainable rent ($\hat{\pi}^*$). Parameters not plotted are the same as in Fig. 3-2. In the middle two rows, the solid curves indicate effort or stock size in patch 1; the dashed curves depict the same quantities in patch 2. Note that the abscissa is reversed when it denotes the value of c_2. This makes those figures consistent with the rest in that patch 2 becomes either biologically or economically "worse" as one moves from right to left along the abscissa. Patch 2 is unfished for parameter values to the left of the vertical, red, dashed line in each plot.

(i. e., $q_2 < q_1$). In contrast with differences in cost, however, the ESOHS effort level in the patch with lower catchability ($\hat{E}_2^*$) is higher than it is in the patch where fish are easier to catch (at least until fish become so difficult to catch that it is no longer worth harvesting in patch 2 at all).

3.5.1 Management with reserves

Marine reserves may be part of an economically optimal, equilibrium management strategy when dispersal does not evolve; however, as (3.24) shows, this is not the case when dispersal does evolve. While marine reserves are not part of the ESOHS, they may be desirable for other purposes. It is therefore interesting to know how the establishment of a reserve would impact profits. The impact of a reserve is contingent upon whether the organisms evolve in response to differences in growth or mortality conditions.

We placed either patch 1 or patch 2 in reserve and calculated the unconstrained rent-maximizing level of effort in the other patch. We also calculated the effort level when the resulting settlement preference was constrained to be evolutionarily stable. We found that using reserves when the settlement preference ε evolves can produce dramatically lower profits (Fig. 3-4). When a patch is placed in reserve, ε evolves to increase the tendency of fish to disperse to that patch (i.e., when patch 1 is in reserve, ε increases relative to its value when both efforts are optimized to the ESS settlement preference). At least for the parameter values we studied, ε varies most with variation in k_2 and varies least with r_2 (Fig. 3-4, top row).

3.5.2 Is the ESOHS economically stable?

The ESOHS represents the best equilibrium harvesting strategy under the constraint that the strategy will not produce further evolutionary change. At the ESOHS no mutant phenotypes can invade and displace the resident phenotype. We have assumed that those mutants are rare, so that there will generally be a long time between mutation events. In between such events, however, the ESOHS is suboptimal. More rent could be extracted from the resource if the manager were to set the effort levels at their *unconstrained* levels

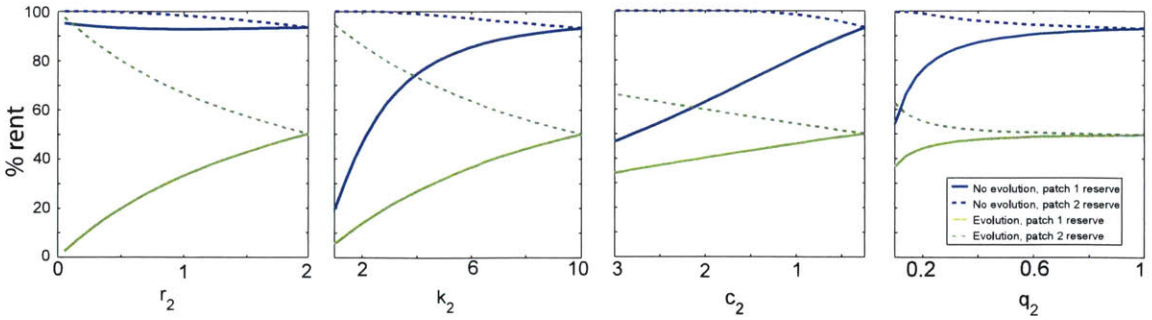

Figure 3-4: Percent of equilibrium rent lost, relative to an optimally managed system with no evolution (in blue) or with evolution (in green). Either patch 1 is in reserve (solid line) or patch 2 is in reserve (dashed line), and effort in the other patch is managed so as to maximize equilibrium rent. Note that when there is no evolution, closing patch 2 may be part of the optimal management strategy (when the dashed blue line is at 100%). Parameters are the same as in Fig. 3-2.

(i. e., $\pi[\hat{E}_1^*, \hat{E}_2^*; \hat{\varepsilon}^*] \leq \pi[E_1^*, E_2^*; \hat{\varepsilon}^*]$), and the manager will be sorely tempted to do so. As a result, we should not expect the ESOHS to be economically stable.

As a consequence of fishing at (short-term) optimal levels, rather than according to the ESOHS, the resident phenotype would no longer be an ESS and would be vulnerable to an invasion by a more fit mutant. Of course the manager could simply change his or her harvesting strategy to optimize the rent given this new phenotype. Because of the way it disperses, the potential profitability of a new phenotype would likely be different than that of the resident. Imagine that this iterative process—harvesting at rent-maximizing rates, invasion of a new phenotype, adjustment of the harvesting rates, etc.—continued for a long time. At some times the instantaneous rent would be larger than that that could be generated by the ESOHS; in some instances, it would be less.

We simulated this "reactionary" policy by introducing a mutant phenotype according to a Poisson process with rate constant μ. We drew the mutant phenotype ε' from a normal distribution with mean equal to the resident phenotype ε, and standard deviation σ, truncated so that $0 < \varepsilon' < 1$. Whenever a mutant appeared, we computed the invasion fitness (3.10). If the invasion fitness was positive, we replaced the resident by the mutant phenotype and calculated a new harvesting policy that would maximize equilibrium rent for the new phenotype. (In doing so, we implicitly assume that invasion implies displacement. For sufficiently small mutations, Geritz et al. (2002) have proved that this substitution does occur.)

We show a single realization of such a reactionary harvesting policy in Fig. 3-5. When the mutant invades, the efforts in each patch, the population levels, and the profits also fluctuate. In the case illustrated, ε tends to be less than the ESOHS ε value, while the effort and population levels tend to be higher than the ESOHS level in patch 1 (blue lines) and lower in patch 2 (orange lines). The rent derived from the reactionary policy tends to be less than the ESOHS rent for this realization. We simulated this stochastic process for a variety of parameter values to assess the average performance of a reactionary versus ESOHS harvesting policy; we found that the rent generated by the ESOHS always exceeded the average rent generated by reactionary harvesting (Fig. 3-6, top row). It appears that, on average, harvesting at rates that maximize short-term profits selects for new phenotypes that are inimical to expected long-term sustainable rent. In addition to boosting average rent, using the ESOHS has the additional advantage of reducing (to zero) the variability in profits that would accompany reactionary harvesting (Fig. 3-6, bottom row). Our simulations suggest that the more different the two patches are, the lower and the more variable are the reactionary rents.

3.6 Discussion

In a simple two-patch model, we have shown that almost every optimal harvesting strategy is unstable in the face of dispersal evolution. The exception is a unique evolutionarily stable optimal harvesting strategy, or ESOHS, where dispersal, as described by the settlement preference, is a convergence-stable, weak-form ESS. The ESOHS, however, is potentially economically unstable: in the short term, a manager could always generate more rent using a different distribution of effort (sometimes using a reserve), at least until a new phenotype invades. A manager who employs a myopic, reactionary strategy of constantly maximizing equilibrium rent, assuming that the current phenotype will not change, suffers reduced average rent, and higher variation in rent, over long timescales. In the real world, there would be economic and social benefits of a consistent harvest strategy, compared to one that changed unpredictably in response to evolutionary changes.

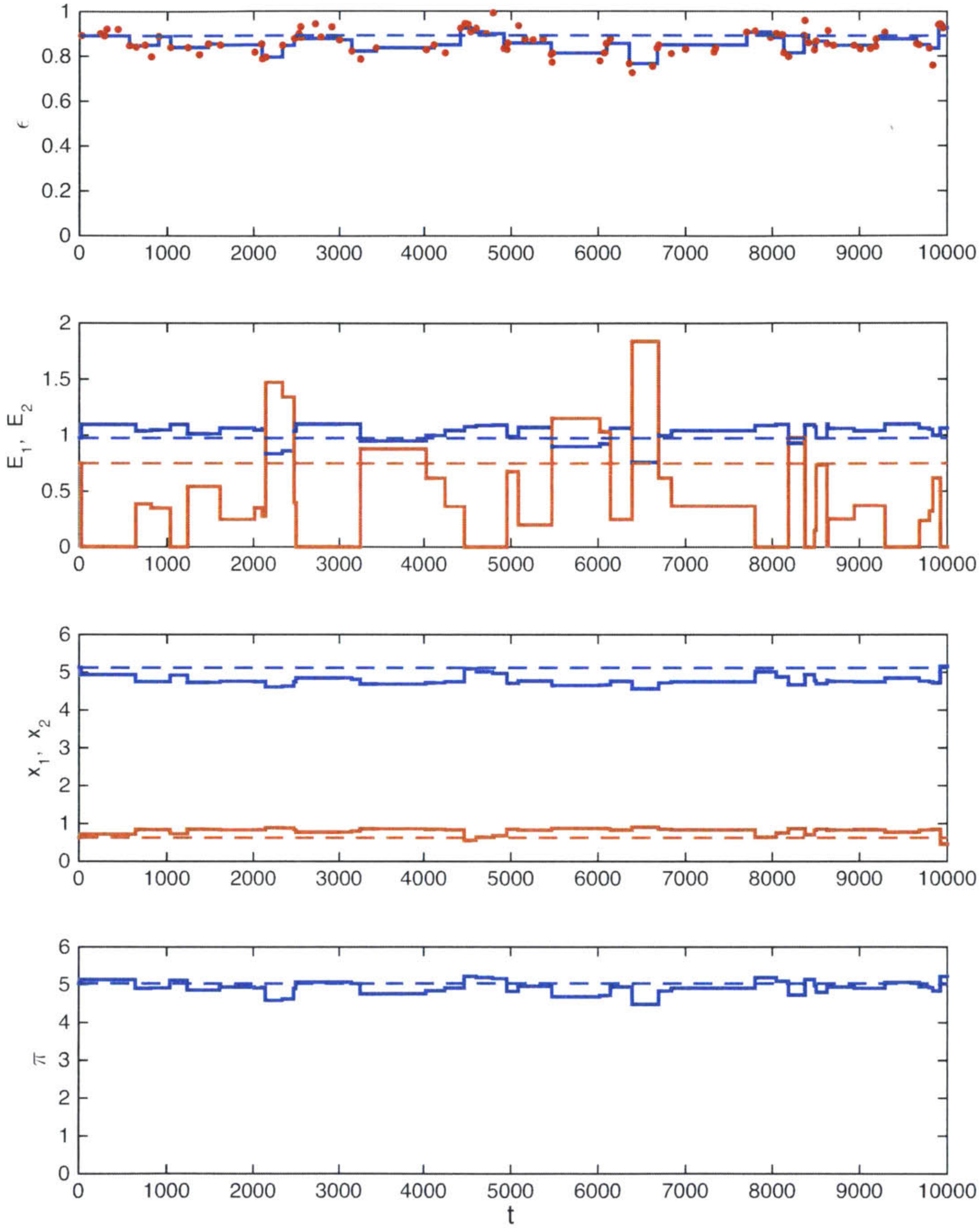

Figure 3-5: ESOHS harvesting (dotted lines) versus "reactionary" harvesting (solid lines) in which the manager sets effort so as to maximize rent at the current settlement preference (ε) without regard to evolutionary stability. Effort and stock size in patch 1 are shown in blue; in patch 2, orange. Mutants (red dots) appear according to a Poisson process with rate $\mu = 0.01$. Each mutant phenotype ε' is drawn from a normal distribution with mean given by the resident phenotype ε, and standard deviation $\sigma = 0.05$, truncated so that $0 < \varepsilon' < 1$. Parameters are the same as in Fig. 3-2, except $k_2 = 1$.

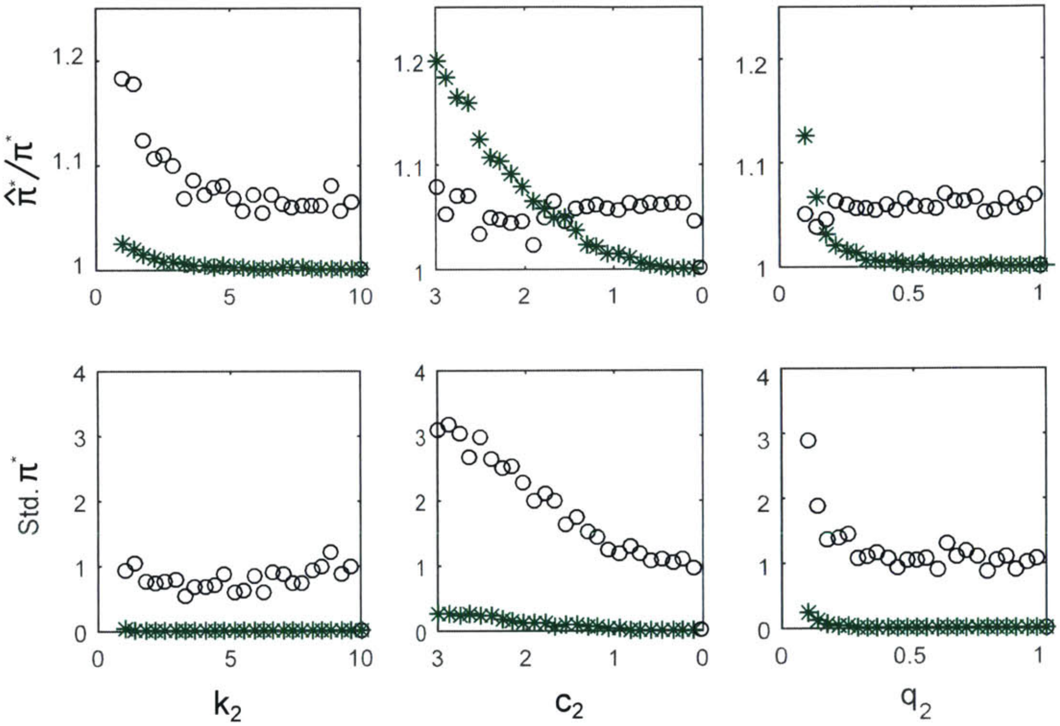

Figure 3-6: Ratio of average rent (top row) and standard deviation in rent (bottom row) of the ESOHS strategy ($\hat{\pi}^*$) compared to "reactionary" harvesting (π^*) in which the manager sets effort so as to maximize rent at the current settlement preference (ε) without regard to evolutionary stability (cf. Fig. 3-5). As in earlier figures, all parameters are equal between patches, except that which is noted on the abscissa. Mutants appear according to a Poisson process at the rate $\mu = 0.01$; their phenotype is drawn from a normal distribution with mean given by the resident phenotype, and standard deviation $\sigma = 0.05$ (green stars) or $\sigma = 0.5$ (black circles), truncated so that $0 < \varepsilon' < 1$. Averages were calculated over the time interval [0, 100,000].

Marine reserves do not play a role in the ESOHS for the two-patch model. This is because evolution of dispersal acts to equalize fitness between the two patches and push population densities to levels that result in no net movement between them. Without this net movement of individuals, or "spillover," from the reserve patch into the fished patch, reserves only reduce economic benefits. The equilibration of fitness across habitats is the sine qua non of the so-called *ideal free distribution* (Fretwell and Lucas, 1969). Based on our results with the two-patch model, we conjecture that, more generally, marine reserves will never be economically optimal when the dispersal behavior of individuals leads to the ideal free distribution of the population. The evolution of dispersal, however, does not inevitably lead to the ideal free distribution. In particular, the ideal free distribution does not emerge as the result of an evolutionary stable dispersal strategy when the environment has a source-sink structure and is characterized by temporal variability in fitness (Holt and Barfield, 2001; Schreiber, 2012). Describing the ESOHS in such circumstances, if one exists, would be challenging.

Our results, when combined with the results from Baskett et al. (2007), who found that increased fragmentation of a reserve network tended to reduce dispersal distance (i. e., increase local retention), suggests that evolution of dispersal may be an important consideration for spatially managed fisheries. However, our understanding of the likely effects of dispersal evolution on optimal management is still nascent. For example, dispersal may encompass a host of traits, including larval duration, the proportion of offspring which disperse or migrate (à la Baskett et al., 2007; Dunlop et al., 2009), or adaptive movements of mature individuals (à la Abrams et al., 2012). How reserves impact population sizes and selection pressures will depend on the particular dispersal trait.

Of course, settlement preference is not the only life history trait that may evolve in response to harvesting (Borisov, 1978; Jørgensen et al., 2007; Allendorf et al., 2008; Heino and Dieckmann, 2009). Most other studies have focused on size-selective harvest, evolution of age or size at maturity (Kuparinen and Merilä, 2007) and the consequences (both negative and positive) that such fisheries induced evolution can have on sustainable yield or rent(Law and Grey, 1989; Heino, 1998; Law, 2000; Ratner and Lande, 2001; Eikeset et al., 2013).

Intriguingly, it has been suggested that marine reserves might ameliorate the consequences of fisheries induced evolution of such traits (Baskett et al., 2005; Miethe et al., 2010). The ramifications of marine reserves in real evolving systems are likely to be complicated by the simultaneous evolution of multiple traits which may have countervailing effects.

While our study suggests that evolution of dispersal may reduce the efficacy of reserves as a rent-maximizing strategy, our analysis focused on equilibrium management on very long timescales. As Sanchirico et al. (2006) highlighted, solving for the optimal harvest trajectory between two patches through time is much more difficult; different results regarding marine reserve optimality may emerge in this case.

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Chapter 4

Testing for an Unambiguous Shift in a Species Distribution

4.1 Abstract

Climate change is expected to lead to a shift in the distributions of many species. Although there is considerable interest in detecting such shifts in recent historical data, existing methods can be sensitive to changes that do not constitute an unambiguous shift. Here, we propose stochastic dominance as an unambiguous way to characterize such a shift and describe a test for it. We describe a test for stochastic dominance using a one-sided Kolmogorov-Smirnov test statistic. We first conduct a simulation study to assess the validity and power of the test. We then illustrate the test on locational data for Atlantic cod. The described test reliably rejects dominance when appropriate, especially at larger sample sizes ($\geq$500). Our illustration shows one case in which the null hypothesis is rejected and another in which it is not. Stochastic dominance has yet to be applied in ecology, although it has the potential to allow better comparison and comprehensive understanding of species distributional changes. This unambiguous definition of a distributional shift may be a useful tool in ecology.

4.2 Introduction

One of the clearest predicted impacts of climate change is a shift in the distributions of plant and animal species (e.g., higher in elevation or in the direction of their local temperature gradient) (IPCC, 2007). Such shifts can have both ecological and economic consequences (Sumaila et al., 2011; Pinsky and Fogarty, 2012) and numerous methods have been proposed for detecting them in recent historical data. In broad terms, these methods involve focusing on some property of a species distribution - such as the mean latitude / location of individuals (e.g., Perry et al., 2005; Chen et al., 2009; Pinsky et al., 2013) or the location of the poleward boundary (e.g., Hickling et al., 2006; Solow et al., 2014) - and determining whether the observed locations of individuals in two periods are consistent with a shift in this property. These methods implicitly define a distributional shift in different ways and can give contradictory results. However, these disparate properties of the distribution-and the implicit definition of a shift that accompanies them-are likely to differ; distributional shifts that translate population density uniformly in a single direction appear to be exception rather than the norm (e.g., Hampe and Petit, 2005; Breshears et al., 2008; Sunday et al., 2012); see also Fig. 4-1 for examples of distributional changes, many of which may produce contradictory results depending on what character the shift is defined for. An unambiguous definition of a shift across an entire distribution fills a necessary gap in our study of the impact of environmental change on species (Tingley and Beissinger, 2009). The definition we propose characterizes the difference between two spatial distributions at every point in space, capturing information about the changes in central tendency and in the 'tails' of the distribution. This strict, unambiguous definition of a shift thus allows comparison among data-sets in which shifts occur in different ways.

Here, we propose as a novel definition of an unambiguous poleward distributional shift based on the notion of stochastic dominance. Stochastic dominance is commonly used in economics to compare income distributions or returns on uncertain investments (Davidson, 2008). However, it appears not to have been used in ecology. We go on to describe a test for stochastic dominance and apply it to some survey data for Atlantic cod (*Gadus morhua*) in the northwest Atlantic. It is important to emphasize that we are not simply proposing

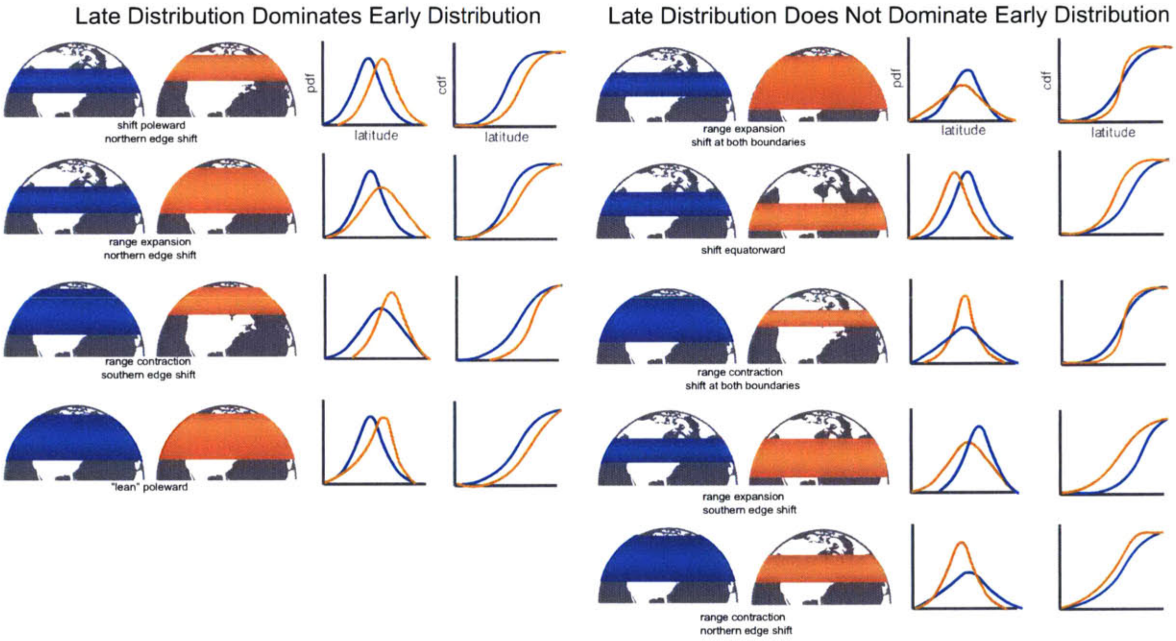


Figure 4-1: Schematics of common types of distributional changes between an early (blue) and later (orange) time period, along with their descriptions and probability density functions. The left column shows later distributions which dominate the earlier distribution.

a new test for a poleward shift, but a new and unambiguous definition of a poleward shift. Existing tests are based on definitions that are not unambiguous. For example, the mean location and the range boundaries may shift in opposite directions. Because the underlying definitions do not comport with each other, the test we propose is not comparable to earlier tests and we make no such comparison here.

4.3 Method

4.3.1 Definition

Suppose that in the first time period n_1 individuals are observed at coordinates $(x_{1j}, y_{1j}), j = 1, 2, \ldots, n_1$. These locations are assumed to arise from a 2-dimensional Poisson process with rate function $\lambda(x, y)$. It is a general result that, conditional on n_1, these locations represent a random sample from a bivariate distribution with probability density function (pdf) $f_1(x, y)$ that is proportional to $\lambda(x, y)$. It follows that, conditional on n_1, the latitudes y_{1j} of these locations represent a random sample from the corresponding marginal distribution with pdf $f_1(y) = \int f_z(x, y)dx$ and cumulative distribution function (cdf) $F_1(y)$. Similarly, the latitudes y_{2j}, $j = 1, 2, \ldots, n_2$ of n_2 individuals observed in a later period represent a random sample from a distribution with cdf $F_2(y)$. For concreteness, we focus on a Northern Hemisphere species so that y increases toward the pole. However, stochastic dominance can be defined along other one-dimensional axes, such as elevation or in the direction of a pertinent climate velocity (*sensu* Pinsky et al. (2013)).

Our interest centers on whether the latitudes in the later period lie poleward of the latitudes in the earlier period. This can be formalized through the notion of (first order) stochastic dominance. By definition, a random variable Y_1 with cdf F_1 is dominated by another random variable Y_2 with cdf F_2 if $F_1(y) \geq F_2(y)$ for all y with the inequality strict for at least one value of y. Importantly, if Y_1 is dominated by Y_2 then it is possible to transform F_1 into F_2 solely by shifting probability mass to the right. It is in this sense that stochastic dominance constitutes an unambiguous shift to higher values.

In the situation considered here, Y_1 represents the location of an individual in an earlier period and Y_2 the location of an individual in a later period. The stochastic dominance of Y_1 by Y_2 means that the density of individuals has shifted only in the poleward direction with no local shifts toward the equator. For this to be true, the mean of Y_2 is larger than that of Y_1. Figure 4-1 shows a number of common types of distributional changes and identifies those that constitute an unambiguous shift according to this definition. Note that some of these examples may conflict with the mean or boundary shifts; in particular, for a 'lean' polewards (*sensu* Breshears et al. (2008)), neither range margin moves, or for a range expansion or contraction, the mean and one may shift northward, while the other boundary shifts southward.

4.3.2 Statistical Test

We turn now to the general problem of testing stochastic dominance based on samples from two distributions. It is fair to say that the literature in this area is unsettled. Briefly, one body of work in this area focuses on testing the null hypothesis that two (or more) random variables have the same distribution against the alternative of stochastic dominance (e.g., El Barmi and Mukerjee, 2005). This formulation is not useful here because such a test is sensitive to alternatives other than dominance (e.g., a bi-directional range expansion). A number of tests have been proposed of the null hypothesis that one random variable dominates another against the alternative hypothesis of the reverse (e.g., Linton et al., 2010). Again, this formulation is inadequate here; it rules out the plausible possibility that neither random variable dominates the other. Most common are tests of the null hypothesis that one random variable dominates another against the alternative that it does not (e.g., McFadden, 1989; Schmid and M., 1996; Barrett and Donald, 2003; Ledwina and Wylupek, 2011). Finally, Davidson and Duclos (2013) described a test of the more natural null hypothesis of non-dominance against the alternative hypothesis of dominance but only over a restricted range of values of the random variables. While this proposal deserves further study, we will follow the bulk of the literature here and test the null hypothesis $H_0 : F_1(y) \geq F_2(y)$ for all y against the alternative hypothesis $H_1 : F_1(y) < F_2(y)$ for at least one y.

Let

$$\hat{F}_1(y) = \frac{1}{n_1}\sum_{j=1}^{n_1} I(y_{1j} \leq y) \tag{4.1}$$

be the empirical distribution function of the observed latitudes in the earlier period where we define the indicator function $I(y_{1j} \leq y) = 1$ and 0 otherwise. Similarly, let $\hat{F}_2(y)$ be the empirical distribution function of the observed latitudes in the second period. A natural statistic for testing H_0 against H_1 is the one-sided Kolmogorov-Smirnov statistic:

$$T = \max_y \left(\hat{F}_2(y) - \hat{F}_1(y)\right) \tag{4.2}$$

with H_0 being rejected for large values of T.

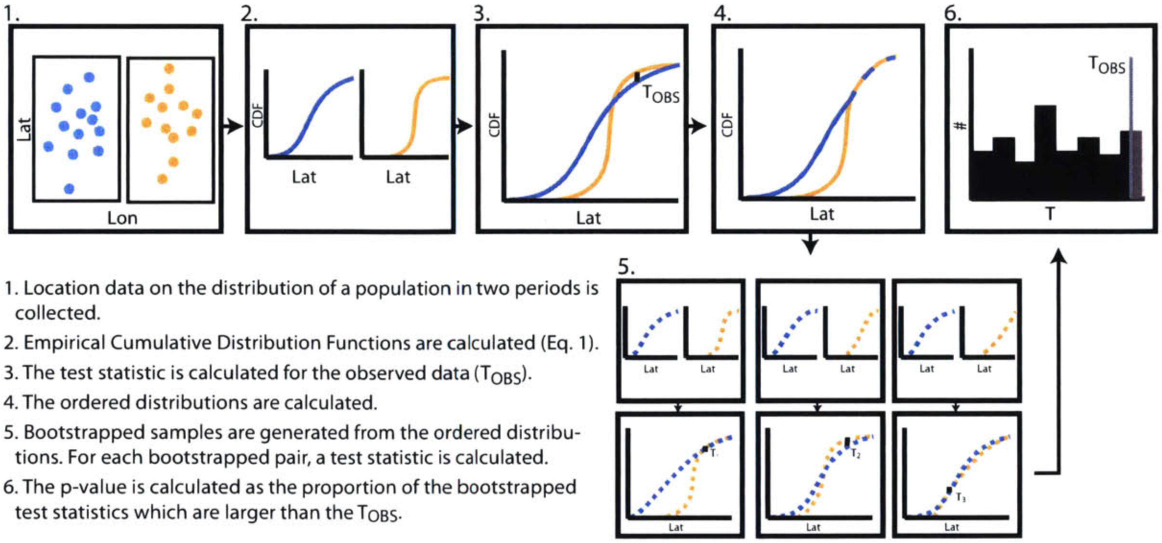
The significance level of T can be assessed through the following bootstrap procedure (Fig. 4-2). Let $\tilde{F}_1$ and $\tilde{F}_2$ be the maximum likelihood estimates of F_1 and F_2 under the restriction that $F_1(y) \leq F_2(y)$ for all y. These are given by

$$\begin{aligned}
\tilde{F}_1(y) &= \hat{F}_1(y), \tilde{F}_2(y) = \hat{F}_2(y) \text{ if } \hat{F}_1(y) \geq \hat{F}_2(y) && (4.3)\\
\tilde{F}_1(y) &= \tilde{F}_2(y) = \frac{n_1}{n_1+n_2}\hat{F}_1(y) + \frac{n_2}{n_1+n_2}\hat{F}_2(y) \text{ otherwise} && (4.4)
\end{aligned}$$

(El Barmi and Mukerjee, 2005). Simulate multinomial samples of sizes n_1 and n_2 from $\tilde{F}_1$ and $\tilde{F}_2$, respectively, and form the corresponding value T^* of T. Repeat the procedure a large number of times. As the test is one-sided, in sampling under H_0, the distribution of T^* will have a point mass at 0. For this reason, we use the so-called mid-p method (Berry, 1995) specifically, H_0 is rejected at significance level α if the proportion values of T^* that exceed the observed value of T plus one-half the proportion values of T^* that are equal to the observed value of T is less than α. In the next section, we present simulation results showing that this test works well.

4.4 Simulation Results

We conducted a simulation study aimed at assessing the performance of the test described in the previous section. All calculations were carried out using MATLAB (Mathworks,



1. Location data on the distribution of a population in two periods is collected.
2. Empirical Cumulative Distribution Functions are calculated (Eq. 1).
3. The test statistic is calculated for the observed data (T_{OBS}).
4. The ordered distributions are calculated.
5. Bootstrapped samples are generated from the ordered distributions. For each bootstrapped pair, a test statistic is calculated.
6. The p-value is calculated as the proportion of the bootstrapped test statistics which are larger than the T_{OBS}.

Figure 4-2: Schematic of the test for stochastic dominance described in the text. The blue color indicates the early distribution, while the orange indicates the later distribution, as in other figures. Note that a p-value which is less than the nominal significance level means we reject the null hypothesis that the late distribution dominates the early.

R2015a). The study proceeded in the following way. For selected values of n_1 and n_2, sample locations were simulated from selected distributions F_1 and F_2, chosen as realistic representations of species distributions. The test was applied (with 200 bootstrap samples) to each such pair of samples at nominal significance level 0.05. The procedure was repeated 500 times and the rate at which H_0 was rejected was recorded. As noted above, because they are based on potentially conflicting definitions of a range shift, we do not present results for other tests.

The first part of the simulation study was aimed at assessing the agreement between the nominal and achieved significance levels of the test. In testing a composite null hypothesis like H_0, the significance level is defined as the maximum rate at which the null hypothesis is rejected when it is, in fact, true. This maximum rate occurs when $F_1 = F_2$. As reported in Table 4.1, the estimated rate at which H_0 is rejected when $F_1 = F_2$ is in all cases close to 0.05. We conclude that the test is valid.

The second part of the simulation study was aimed at assessing the power of the test. In this case, sample locations were simulated from distributions satisfying $F_1(y) < F_2(y)$ for at least one value of y. The results are summarized in Table 4.2. In overall terms, the

Early Dist.	**Late Dist.**	**Rej. Rate ($n_1 = 250$, $n_2 = 500$)**	**Rej. Rate ($n_1 = n_2 = 500$)**	**Rej. Rate ($n_1 = 500$, $n_2 = 250$)**
N(0,1)	N(0,1)	0.064	0.066	0.048
B(2,2)	B(2,2)	0.058	0.040	0.046
U(0,1)	U(0,1)	0.054	0.048	0.062

Table 4.1: Results of simulated data drawn from equal distributions. The first and second columns show the distributions from which the simulated data were drawn (N indicates a normal distribution, B is a beta distribution, and U is a uniform distribution; the numbers in parentheses give the parameter values for the distributions). The grey columns show the rejection rate at the 5% significance level for different sample sizes (as marked).

test has good power provided n_1 and n_2 are not too small. Simulations across a range of samples sizes indicate that the power is largely controlled by the size of the smaller sample.

4.5 Illustration

In this section, we illustrate the described test through an application to trawl survey data for the commercially important Atlantic cod (*Gadus morhua*) in the US northwest Atlantic. Cod are associated with cool bottom waters, and temperature appears to impact their condition, spawning, growth rates as juveniles and adults, and egg incubation (Drinkwater, 2005). Temperature may also indirectly influence cod through their food, the composition and abundance of which has been changing (Friedland et al., 2013). The expected response of different cod stocks to increasing temperatures is different; some are expected to increase in size, while others are expected to decrease or have no change (Drinkwater, 2005). Analysis of the cod survey data in this region show that the catch rate decreases with increasing bottom temperatures, in addition to an overall decline in abundance with time (Fogarty et al., 2008).

Annual surveys for cod (and other groundfish) have been conducted by Northeast Fisheries Science Center (NEFSC) in this region since 1968. Briefly, NEFSC conducts trawls in a stratified random sampling design in this region twice a year. This stratified design takes into account hydrological and geographic features relevant for marine species. At each sampling location, the abundance and biomass per species is reported. Here, we use

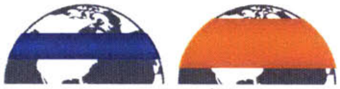
	Early Dist.	**Late Dist.**	**Rej. Rate** ($n_1 = 250$, $n_2 = 500$)	**Rej. Rate** ($n_1 = n_2 = 500$)	**Rej. Rate** ($n_1 = 500$, $n_2 = 250$)
 range expansion shift at both boundaries	U(0,1)	U(-0.125,1.125)	0.948	1	0.908
	N(0,1)	N(0.1,1.7)	0.982	0.994	0.968
	N(0,1)	N(0,1.5)	0.926	0.984	0.892
 shift equatorward	N(0,1)	N(-.1,1)	0.272	0.392	0.294
	N(0,1)	N(-.2,1)	0.718	0.872	0.768
 range contraction shift at both boundaries	U(0,1)	U(0.125,0.875)	0.99	1	1
	N(0,1)	N(0.1,0.5)	0.996	1	0.998
	N(0,1)	N(0,0.5)	1	1	1
 range expansion trailing edge shift	U(0,1)	U(-0.25,1)	1	1	1
	B(1,2)	B(3,1), -0.5 shift	0.946	0.994	0.844
 range contraction leading edge shift	U(0,1)	U(0,0.75)	1	1	1
	G(2,2)	G(9,0.5)	0.85	0.982	0.886

Table 4.2: Results of simulated data drawn from distributions in which the later distribution does not dominate the earlier distribution, i.e., for which the null hypothesis is false. The first column shows the qualitative description of the type of shift which has occurred. The second and third columns show the distributions from which the simulated data were drawn (letter indications of distribution types are as in Table 1). The grey columns show the rejection rate at the 5% significance level for different sample sizes (as marked).

the total number of Atlantic cod at each location as our data. Details on the collection methodology and sampling design are provided in Grosslein (1969). The data are available at `http://www.nefsc.noaa.gov/epd/ocean/MainPage/ioos.html`. Cod in this region are considered to belong to two stocks, a Georges Bank stock in the south and a Gulf of Maine stock in the north; these stocks are defined geographically (Mayo et al., 2009).

In this application, we tested the null hypotheses that latitude over the period 1968-1975 was dominated by latitude over the period 2005-2011 for the George's Bank stock and that the latitude over the period 2005-2011 was dominated by latitude over the period 1968-1975 for the Gulf of Maine stock. The latter case may reflect that Gulf of Maine currents often travel southward (Ruoying et al., 2005). Sample sizes for George's Bank cod were $n_1 = 4203$, $n_2 = 6528$ and $n_1 = 6084$, $n_2 = 2841$ for the Gulf of Maine. The empirical cdfs of the latitudes for each stock are shown in Figure 4-3, along with a map of cod abundance. The p-value for the George's Bank stock based on 1000 bootstrap samples was less than 0.001, so the null hypothesis can be rejected at the 0.05 significance level, indicating that an unambiguous northward shift did not occur between the two periods; the mean may have shifted, but the population did not shift only northwards. In contrast, the p-value for the Gulf of Maine stock was 0.50, indicating an unambiguous southward shift between the two periods.

4.6 Discussion

The purpose of this paper has been to propose an unambiguous definition of a directional shift in a species distribution based on stochastic dominance and to describe and illustrate a test of such a shift. While existing methods can provide useful information, they can also give contradictory results. For example, Nye et al. (2009) identified significant southward shifts in the mean and northern boundary of the distribution of Gulf of Maine cod but a significant northward shift in the southern boundary. The possibility of this kind of contradiction has been recognized in the literature, leading to ad hoc approaches involving multiple criteria. The test described here assumes that the observed locations follow a Poisson process. Note that this assumption, which appears to be implicit in other methods,

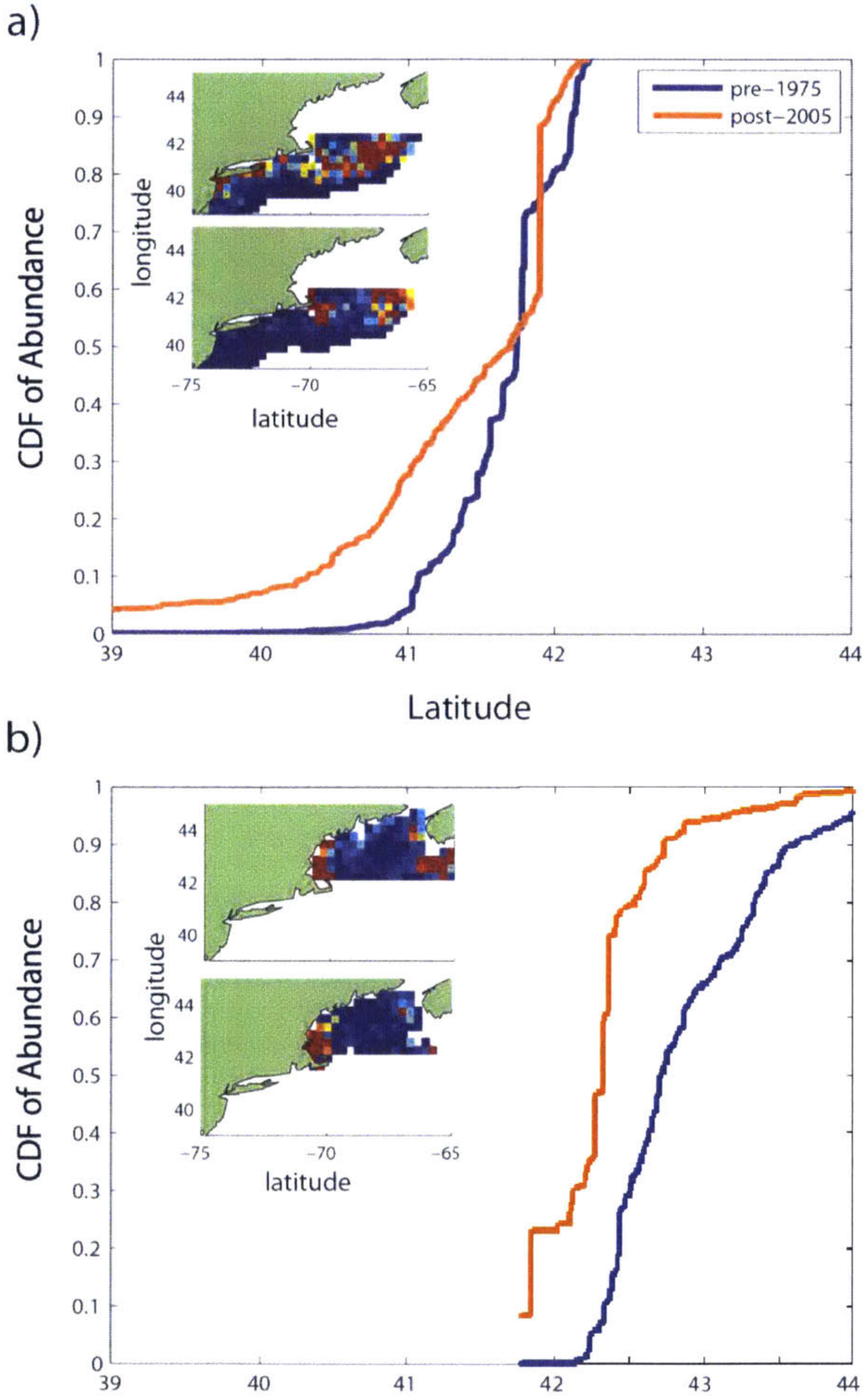


Figure 4-3: Latitudinal distribution of cod abundance in survey trawls 1968-1975 (blue) and 2005-2011 (orange). (a) Distribution of the Georges Bank stock. (b) Distribution of the Gulf of Maine stock. Insets show the spatial distribution of the observations; navy blue shows locations which were sampled but contained no cod, while the dark magenta shows locations with more than 50 cod. For the insets (not for data analysis), observations were binned in 0.3 lat. and lon. squares.

applies to the locations of individuals that are sighted and not necessarily to the locations of all individuals. Even if the latter are not Poisson, under some conditions on the observation process, the former will tend to be (e.g., Westcott, 1976). In addition, it is assumed that the spatial sampling of individuals is unbiased. This would not be the case, for example, if the allocation of spatial sampling effort changes over time. In addition, this methodology tests for stochastic dominance along a specified axis. Here, this axis was chosen because of the presumed influence of climatic change acting along that axis. However, it is important to distinguish that other factors in this case, spatially heterogeneous harvesting of the cod, changes in depth, or movements in space for non-temperature related reasons may influence the spatial distribution. Thus, the signal of distributional change may be eroded or enhanced by other factors. Finally, as noted, in keeping with the bulk of the literature, the test proposed here takes stochastic dominance "rather than non-dominance" as the null hypothesis. Although there are good technical reasons for this, it is somewhat unnatural. We are currently exploring the approach of Davidson and Duclos (2013) as an alternative. Extending this test to more than two periods may be an attractive area of future investigation.

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Chapter 5

Optimal Harvest in a Deteriorating Environment

Abstract

[1]Deteriorating environmental conditions (e.g., due to climate change) negatively impact the vital rates of marine fish, with implications for fisheries management. While the rent-maximizing harvesting strategy in a constant environment has been well characterized, optimal management under changing conditions is less understood. We develop a bioeconomic model for a fishery with compensatory growth and decreasing marginal harvest cost in a deteriorating environment. With it we show that (1) optimal escapement is largely independent of the stock size; (2) the stock is 'fished down' to a rent-dissipating level at a characteristic time after which fishing ceases; and (3) non-monotonic escapement policies are often optimal. Using the Beverton-Holt stock-recruitment model with Schaeffer harvest costs, we show that non-monotonic escapement can be optimal when fecundity decreases in time. Analysis of a simpler piecewise-linear model shows that non-monotonicity generally arises from an interaction between the deteriorating vital rate and density-dependent mechanisms of population regulation.

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Keywords

optimal harvest; fisheries; climate change; habitat; dynamic programming

5.1 Introduction

Recent human impacts on Earth's biota are dramatic and unprecedented (Ceballos et al., 2015). These impacts can take many forms, ranging from habitat degradation to climate change. Some populations are able to adapt to local impacts by moving to more favorable locations (Parmesan and Yohe, 2003). Other populations, however, cannot track their habitat niche (or all parts of it), and, as a result, experience changing environmental conditions that may alter their vital rates. These vital rates ultimately determine the growth rate and size of the population. This paper concerns the optimal management of a population subject to a systematically deteriorating environment.

Fish are particularly vulnerable to temperature changes. They are generally *poikilothermic*–their internal temperature depends on the external temperature–and temperature strongly impacts their metabolism and health. Studies have found temperature effects on, for example, individual growth (Munday et al., 2008) and developmental (Houde, 1989) rates, breeding probability and spermatogenesis (Donelson et al., 2010), and fecundity (Tanasichuk and Ware, 1987). Temperature may also influence food availability, exposure to toxins, predation, disease, and foraging behaviour (Reist et al., 2006). The response to temperature trends may be heterogenous across species (see, for example Persson, 1986).

While the scientific literature examining the many ways that species may be impacted by changing conditions is growing, little research examines how continuing environmental change affects management. Recently, the importance of these interactions was highlighted for the western North Atlantic cod stock. Pershing et al. (2015) determined that this stock has been overharvested, in part due to improper accounting for temperature driven declines in recruitment and increases in mortality.

In this paper, we focus on the coupled biological-economic system of a harvested population in a deteriorating environment. While managers of wild populations may have many (potentially conflicting) goals—including employment, conservation, and rent—we focus on rent maximization here as it is easily quantifiable and is likely important. It is also necessary for estimating the costs of alternative management policies.

There is a well developed theoretical literature on the optimal exploitation of stocks in unchanging environments (see, e.g., Reed, 1979; Moussalli and Hilborn, 1985; Costello et al., 2001; Clark, 2010). A classic result is that constant escapement strategies, in which a fixed number of fish are left unharvested each time period, are optimal for a wide range of growth and cost functions in temporally constant (or stationary, stochastic) environments (Reed, 1979). Mathematical models suggest that the optimal harvest strategy in changing conditions may be qualitatively different. For example, Walters and Parma (1996) found that when fish mortality rates increase, the best constant exploitation-rate strategy (in which a fixed *proportion* of the population is harvested each time period) dramatically outperforms the best constant escapement policy for maximizing yield. Polasky et al. (2011) characterized environmental change as an exogenous probability of a regime shift, and suggested the optimal policy may be unaffected by the potential regime shift. We extend these analyses by focusing more generally on how the properties of deterministically deteriorating vital rates can qualitatively alter optimal harvest strategies. We then demonstrate these effects with examples of climate-change impacted fisheries.

A priori, we might expect that as conditions deteriorate, optimal escapement ought to decrease because unharvested individuals will be less productive, eroding their in situ value. Indeed, for a forecast of poor conditions in a stationary stochastic environment, the optimal escapement is reduced for just this reason (Costello et al., 2001). Carson et al. (2009) arrive at a similar conclusion for populations subject to cyclical population dynamics. However, this logic oversimplifies the potential for a complex interplay between changing vital rates and density dependence. We show that, for some vital rates, deteriorating conditions can actually first necessitate a temporary increase in escapement followed by decreasing escapement after conditions deteriorate sufficiently.

5.2 Optimal Harvest in a Constant Environment

We first consider a population in an unchanging environment managed by a single harvester. We define x_t as the population size at time t; the function $f(x_t)$ projects the population to the next time period.

In each period, the harvester knows the size of the population as well as the population projection function f and its parameters and can make a harvesting decision based on this information (closed-loop decision making, *sensu* Bertsekas (2000)). By setting the harvest size, h_t, the harvester controls both the population size and her revenue stream. The fish that are left behind after harvest $(x_t - h_t)$ are able to reproduce and grow, so that the population grows (or shrinks) according to:

$$x_{t+1} = f(x_t - h_t). \tag{5.1}$$

It will be mathematically convenient to track the escapement, $y_t = x_t - h_t$, rather than h_t.

Assume the harvester's goal is to maximize the present value of the stream of discounted rent resulting from her choice of escapement over a period from $t = 0$ to T. This rent results from the revenue gained by selling the harvest at price p, per unit biomass, minus harvest costs. The harvester is price-taker, so p is not influenced by the harvester's actions. Harvest costs are incurred when effort is exerted for harvest. We assume that the cost of a given harvest is a function of the population size, with higher marginal costs, $c(x)$, associated with smaller populations, (i.e., $c'(x) < 0$). Thus, the cost of harvesting a stock from size x down to size y is $\int_y^x c(s)ds$. The rent attained in a period is then discounted by factor δ $(0 \leq \delta \leq 1)$, which relates the value of money in earlier and later periods. The present value of the total rent is

$$\Pi(y_0, y_1, ..., y_T) = \sum_{t=0}^{T} \left[p\,(x_t - y_t) - \int_{y_t}^{x_t} c(s)\,ds \right] \delta^t. \tag{5.2}$$

The manager's problem is to choose the escapement sequence, y_t, with $0 \leq y_t \leq x_t$, so as to maximize Π given the population projection function (5.1) and a given initial stock size x_0. We will denote this optimal escapement policy by $\{\tilde{y}_t\}$.

It will be useful to define y_∞ as the escapement at which marginal revenue equals marginal cost; i.e., y_∞ satisfies

$$p = c(y_\infty). \tag{5.3}$$

Harvesting below y_∞ incurs higher costs than revenue, making it economically unattractive, even in the short-run. Since $c(x)$ is a strictly decreasing function, there is at most one positive value of y_∞. If $p > c(0)$ then y_∞ is zero.

Following Reed (1979) and Costello et al. (2001), we will use dynamic programming to maximize Π. Those authors found it useful (as will we) to introduce the immediate harvest value, $Q(x_t)$:

$$Q(x_t) \equiv p(x_t - y_\infty) - \int_{y_\infty}^{x_t} c(s)ds. \tag{5.4}$$

$Q(x_t)$ is the maximum one-period profit at time t given the stock size x_t. With $Q(x_t)$ in hand, we can break the problem of maximizing $\Pi(y_t)$ into subproblems consisting of two pieces. The first piece is the value of the harvest in time t, which, conveniently is $Q(x_t) - Q(y_t)$. The second piece is the value of the remaining future harvests, given that these harvests are optimal from time $t+1$ to the end of the time horizon given x_{t+1}. Let us define this second piece as $V(x_{t+1})$. Putting these two pieces together we have

$$\begin{aligned} V(x_t) &= \max_{0 \le y_t \le x_t} \Big[Q(x_t) - Q(y_t) + \delta V(x_{t+1})\Big] && (5.5) \\ &= Q(x_t) + \max_{0 \le y_t \le x_t} \Big[- Q(y_t) + \delta V(f(y_t))\Big]. && (5.6) \end{aligned}$$

To find the optimal escapement policy $\tilde{y_t}$, we first find $\tilde{y_T}$ by maximizing $Q(x_T) - Q(y_T)$. Typically, $\tilde{y_T} = y_\infty$. We then use the recursion (5.6) to calculate the optimal escapements, $\tilde{y}_{T-1}, \tilde{y}_{T-2}, \dots, \tilde{y}_0$.

Reed (1979) showed that if $f(x)$ is a differentiable, strictly concave, and non-decreasing function (i.e., $f'(x) \geq 0$ and $f''(x) < 0$ for all $x \geq 0$), and $c(x)$ is non-increasing, then a

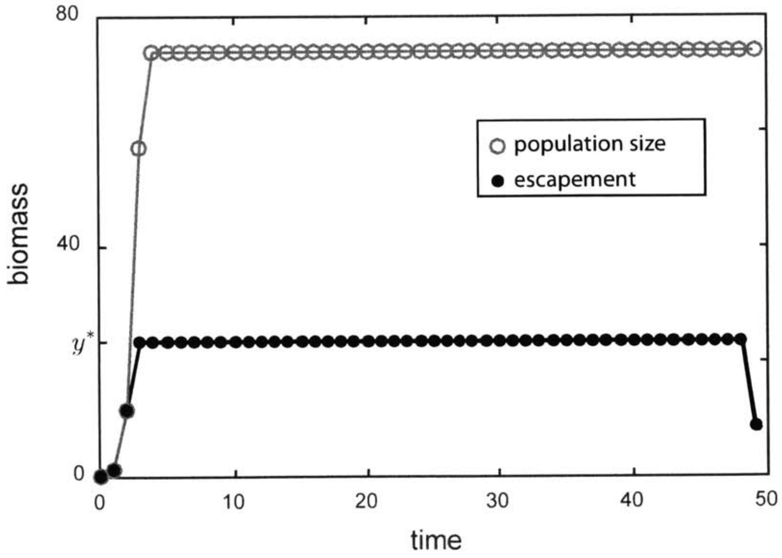

Figure 5-1: Schematic of the typical 'constant escapement policy' for an unchanging environment. In this example, initially no harvest occurs to allow the population to build. In the last period, the population is harvested down to y_∞. In intervening periods, the population and escapement are constant.

'constant escapement policy' is optimal (Figure 5-1);

$$\tilde{y}_t = \begin{cases} y^*, & \text{if } x_t \geq y^*, \\ x_t, & \text{if } x_t < y^*, \end{cases} \tag{5.7}$$

where y^* is a time-invariant optimal escapement level that we call the 'interior solution.' We impose these same conditions on $f(x)$, along with the slightly more restrictive condition that $c(x)$ be strictly decreasing.

5.3 Optimal Harvest in a Deteriorating Environment

Now we prescribe that one of the vital rates of this population changes in time; in general, let this changing parameter be θ_t. To explicitly recognize this change, we now write the population projection function as

$$x_{t+1} = f(y_t, \theta_t). \tag{5.8}$$

Noting that θ_t has no effect on the function $Q(\cdot)$, we can rewrite the value function $V(x_t)$ (5.6) as

$$V(x_t, \theta_t) = Q(x_t) + \max_{0 \leq y_t \leq x_t} \Big\{ - Q(y_t) + \delta V[f(y_t, \theta_t), \theta_{t+1}] \Big\}. \tag{5.9}$$

We say conditions are deteriorating for all $y > 0$ if $f(y, \theta_t) \geq f(y, \theta_{t+1})$, with strict inequality for at least one t. That is, the population projection function does not yield more fish for the same escapement in period $t+1$ than it would in period t. Deteriorating environments can produce an increase in θ (e.g., if θ is a mortality rate) or a decrease in θ (e.g., if θ is fecundity). Thus, $\partial f(y, \theta)/\partial \theta$ may be either positive or negative.

5.3.1 Interior Solution

To find $V(x_t, \theta_t)$ we must find the escapement $\tilde{y}_t$ that maximizes the term in braces in equation (5.9). We seek $\tilde{y}_t$ by setting the derivative of the maximand with respect to y_t equal to 0:

$$0 = \left[-\frac{dQ(y_t)}{dy_t} + \delta \frac{dV(f(y_t, \theta_t), \theta_{t+1})}{dy_t} \right] \Bigg|_{y_t = y_t^*}. \tag{5.10}$$

We define y_t^* as the escapement that satisfies equation (5.10); it is analogous to y^* in equation (5.7), excepting that we do not expect it to be constant over time.

Equation (5.10) can be interpreted as stating that at the escapement level y_t^*, the marginal loss from leaving an additional unit of escapement is balanced by the marginal gain of leaving that individual unharvested and harvesting it or its progeny later. If y_t^* satisfies $y_\infty < y_t^* < x_t$, we call it feasible.

From equation (5.9), observe that the derivative of $V(x_t, \theta_t)$ with respect to x_t is equivalent to the derivative of $Q(x_t)$. Using this fact and upon applying the chain rule, the first-order condition for an interior optimum (5.10) becomes

$$0 = \left[-\frac{dQ(y_t)}{dy_t} + \delta \frac{dQ(u)}{du} \Bigg|_{u = f(y_t, \theta_t)} \frac{\partial f(y_t, \theta_t)}{\partial y_t} \right] \Bigg|_{y_t = y_t^*}. \tag{5.11}$$

Note that y_t^* does not depend on the stock in period t (or any other period). This observation leads directly to our first result:

Proposition 1 *For a population growing according to equation (5.8) (with* $\partial f(x,\theta)/\partial x \geq 0$ *and* $\partial^2 f(x,\theta)/\partial x^2 < 0$ *for all* $x \geq 0$*) and marginal harvesting cost* $c(x)$ *decreasing in* x*, the interior solution escapement,* y_t^**, does not depend on the stock size at the beginning of the period or on vital rates (*θ*) in other periods.*

Thus, for a stock subject to a changing vital rate (non-constant population projection function), there exists a feedback control law that is pseudo-independent of the stocks, analogous to the 'constant escapement policy' in Reed (1979):

$$\tilde{y}_t = \begin{cases} y_t^*, & \text{if } x_t \geq y_t^*, \\ x_t, & \text{if } x_t < y_t^*, \end{cases} \tag{5.12}$$

while $y_t^* > y_\infty$ (see section 5.3.2). Thus, if the stock is initially small (for example, due to overfishing), $\tilde{y}_t < y_t^*$ (no harvest) while the stock recovers.

Following Costello et al. (2001), we establish a condition under which y_t^* is a unique maximum. Equation (5.11) can be rewritten as

$$\frac{1}{\delta} = \frac{dQ(f(y_t,\theta_t))}{df(y_t,\theta_t)} \left[\frac{dQ(y_t)}{dy_t}\right]^{-1} \frac{df(y_t,\theta_t)}{dy_t}. \tag{5.13}$$

Call the right-hand side of equation (5.13) $\Phi(y_t,\theta_t)$. When Φ is non-negative and $d\Phi/dy_t$ is negative (for $y_t > y_\infty$)[2], $\Phi = 1/\delta$ for at most one value of y_t, at y_t^*. The negativity condition on $d\Phi/dy_t$ is equivalent to the second-order condition, guaranteeing y_t^* is a maximum.

Note that in each period t, the interior solution y_t^* is equal to the constant optimal escapement in an unchanging environment with parameter $\theta = \theta_t$.

In some cases, the interior solution will be blocked by the constraint $\tilde{y}_t \leq x_t$. If $y_t^* > x_t$, the optimal escapement $\tilde{y}_t$ is x_t (no harvest). This allows the stock to recover and approach the interior solution for harvest at a later time. If the interior solution y_t^* falls below y_∞, the harvester makes her final harvest, leaving the escapement $\tilde{y}_t = y_\infty$, and exits the fishery.

---

[2] At y_∞, the second-order condition is undefined, but the limit from from positive direction is arbitrarily negative

The time at which this last harvest occurs we call $\hat{t}$.

5.3.2 Exiting the Fishery

Unlike a harvester in a constant environment, a rent maximizing fisherman in a deteriorating environment may choose to exit the fishery prior to the time horizon, T, if conditions have declined sufficiently. This early exit time, $\hat{t}$, is independent of the specified time horizon T.

Proposition 2 *If there exists a time $\hat{t} < T$ such that $f(y_\infty, \theta_t) \leq y_\infty$ for all $t \geq \hat{t}$, then at $t = \hat{t}$ the optimal escapement $\tilde{y}_{\hat{t}}$ is y_∞, and $\tilde{y}_t = x_t$ (no harvest) thereafter.*

When $t > \hat{t}$, the interior solution y_t^* is no longer optimal, because $y_t^* < y_\infty$. To see this, let us calculate the conditions for which $y_\infty = y_t^*$. From equations (5.3) and (5.4), $\frac{dQ(u)}{du}|_{u=y_\infty} = 0$, so it follows that equation (5.13) (which defines y_t^*) holds only if $\frac{dQ(f(u,\theta_{crit}))}{df(u,\theta_{crit})}|_{u=y_\infty} = 0$. This θ_{crit} is, by definition, the value of the vital rate at which the escapement y_∞ yields y_∞ fish in the next period; i.e., $f(y_\infty, \theta_{crit}) = y_\infty$. Once θ_{crit} is passed, $y_t^* < y_\infty$; future stock sizes will be below y_∞ and no fishing will occur.

To develop an intuition as to why this occurs, it is helpful to consider this same process in a different way. Let us define $\hat{y}_t$ as an escapement such that $\hat{y}_t = f(\hat{y}_t, \theta_t)$. $\hat{y}_t$ is interesting first because y_t^* must be less than $\hat{y}_t$. In order that the first-order condition (5.13) is satisfied, at $\hat{y}_t$, both derivatives the $dQ(y_t)/dy_t$ and $dQ(f(y_t))/d(f(y_t))$ have the same value, while the derivative of f at that point must be less than 1. Recall that δ is also less than 1. At $y > \hat{y}$, $f(y)$ will be smaller and thus the derivative of Q with respect to $f(y, \theta_t)$ will be smaller than that with respect to y alone; equation (5.13) cannot be satisfied above $\hat{y}_t$. $\hat{y}_t$ is also non-increasing in time. Because $f(y, \theta_t) \leq f(y, \theta_{t+1})$, if, at time t, $\hat{y}_t$ fish yields a recruitment of $\hat{y}_t$ in the next period, leaving $\hat{y}_t$ will yield fewer than $\hat{y}_t$ fish; thus, $\hat{y}_{t+1}$ must be smaller. This also implies that once the harvester fishes down to y_∞ at $\hat{t}$, the future stocks sizes will be less than or equal to y_∞.

Note that if $f(y_\infty, \theta) > y_\infty$ for all t, the harvester will fish down to y_∞ only the end of the time horizon, T.

5.3.3 Qualitative Behavior of Optimal Escapement Policy

In most cases, the basic structure of the optimal harvest has three parts: an approach to the 'interior solution', a series of periods during which the interior solution is optimal, after which harvest ceases. This is similar to the optimal escapement policy in a non-deteriorating environment, except that the interior solution changes in time and the fish-down time may come prior to T. In this section, we focus on the qualitative behavior of the interior solution, y_t^*, as it depends on θ_t, and in particular on $dy_t^*/d\theta_t$.

Since y_t^* is a function of θ_t, we use implicit differentiation of equation (5.13) to calculate $dy_t^*/d\theta_t$. If we define F as

$$F(\theta_t, y_t) = \left[-\frac{dQ(y_t)}{dy_t} + \delta \frac{dQ(u)}{du}\bigg|_{u=f(y_t,\theta_t)} \frac{\partial f(y_t,\theta_t)}{\partial y_t} \right], \tag{5.14}$$

then equation (5.13), which implicitly defines y_t^*, is $F(\theta_t, y_t^*) = 0$.

It follows that

$$\begin{aligned} \frac{dF(\theta_t, y_t^*(\theta_t))}{d\theta_t} &= 0 && (5.15)\\ \frac{\partial F}{\partial \theta_t} + \frac{\partial F}{\partial y_t^*}\frac{dy_t^*}{d\theta_t} &= 0 && (5.16)\\ \frac{dy_t^*}{d\theta_t} &= \frac{-\partial F/\partial\theta_t}{\partial F/\partial y_t^*}. && (5.17) \end{aligned}$$

Because y_t^* is a maximum, the second-order condition $\partial F/\partial y_t^* < 0$ holds. Thus the sign of $dy_t^*/d\theta_t$ is the sign of $\partial F/\partial\theta_t$. In turn,

$$\begin{aligned} \frac{\partial F}{\partial \theta_t} = \quad & \delta \left[\frac{\partial^2 f(y_t^*,\theta_t)}{\partial\theta_t \partial y_t^*} [p - c(f(y_t^*,\theta_t))] \right. \\ & \left. - \frac{\partial f(y_t^*,\theta_t)}{\partial y_t^*} \frac{\partial c(f(c_t^*,\theta_t))}{\partial f(y_t^*,\theta_t)} \frac{\partial f(y_t^*,\theta_t)}{\partial \theta_t} \right]. \end{aligned} \tag{5.18}$$

Most of the terms in equation (5.18) do not change sign as θ_t changes. Following from our assumptions about the cost and population projection functions we have: (i)

$[p - c(f(y_t^*, \theta_t))]$ is positive when $y_t^* > y_\infty$, so it will be positive for all interior maxima; (ii) $\frac{\partial f(y_t^*, \theta_t)}{\partial y_t^*}$ is positive; (iii) $\frac{\partial c(f(y_t^*, \theta_t))}{\partial f(y_t^*, \theta_t)}$ is negative; (iv) $\frac{\partial f(y_t^*, \theta_t)}{\partial \theta_t}$ has a fixed sign by our definition of deteriorating conditions. The sign of $\frac{\partial f(y_t^*, \theta_t)}{\partial \theta_t}$ may be negative or positive depending on how θ_t appears in the population projection function, but it does not change.

The term $\frac{\partial^2 f(y_t^*, \theta_t)}{\partial \theta_t \partial y_t^*}$, however, may change sign as time progresses and the vital rate θ_t changes. This raises the possibility that $dy_t^*/d\theta_t$ may change sign as well, i.e., optimal escapement may *not* be monotonic even if θ_t changes monotonically. This is the basis of our third proposition:

Proposition 3 *For a fishery governed by a relatively simple compensatory population projection function* $(f'(x) > 0, f''(x) < 0)$ *and marginal cost function* $(c'(x) < 0)$*, the resulting optimal escapement policy defined by the 'interior solution' may be non-monotonic in the monotonically varying vital rate,* θ_t.

The non-monotonic optimal escapement policy appears to be the result of the countervaling effects of biological parameters that delay the onset of density dependent mortality and those that hasten it; the former tends to increase optimal escapement levels while the latter tends to decrease it. For some parameters (e.g., per capita fecundity) the behavior shifts depending on the value of the parameter (see Section 5.5).

The existence of both monotonic and non-monotonic optimal escapement policies is shown by example. In the next section, we develop a Beverton-Holt model, and allow one of two vital rates to vary–density dependent morality or per capita fecundity. The former (examined in section 5.4.1) produces a strictly decreasing y_t^* trajectory while the latter (section 5.4.2) produces non-monotonic optimal escapements.

5.4 Example: Beverton-Holt Stock Recruitment Model

A simple characterization of stock dynamics that accounts for both density-independent and density-dependent mortality is the Beverton-Holt stock recruitment model (Beverton and Holt, 1957; Clark, 2010). Let x_{t+1} be the individuals that escaped harvest in period t and survived until the next period plus their progeny which also survived (Figure 5-2).

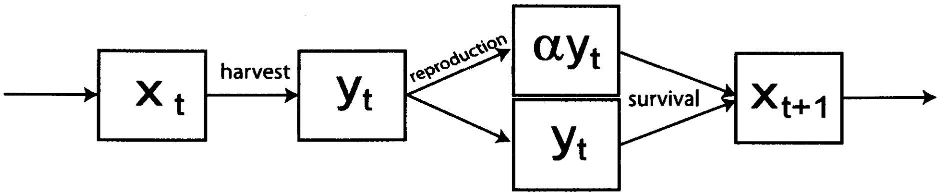

Figure 5-2: Schematic of the life-cycle of the iteroparous fish population. The initial x_t fish are harvested down to y_t, the escapement. The escaped fish then reproduce at a per capita rate α, to produce αy_t new fish. The fish that survive (governed by $f(y_t, \theta)$) are described by x_{t+1}; in this case, both the newly hatched and adult fish survive into the next period.

If each adult produces α offspring, there are αy_t initial juveniles at time t. If those juveniles experience density-independent mortality at rate μ_1 and density-dependent mortality at rate $\mu_2 \alpha y_t$, the proportion to survive to $t+1$ is

$$\frac{\mu_1 e^{-\mu_1}}{\mu_1 + \mu_2 \alpha y_t (1 - e^{-\mu_1})}. \tag{5.19}$$

During the period between t and $t+1$, the mortality rates and fecundity are constant; changes to these vital rates occurs between discrete periods and the value at t governs until $t+1$.

The adults survive with probability σ. Thus, the number of fish in the next period is

$$x_{t+1} = f(y_t) = \sigma y_t + \frac{\mu_1 e^{-\mu_1} \alpha y_t}{\mu_1 + \mu_2 (1 - e^{-\mu_1}) \alpha y_t}. \tag{5.20}$$

We may investigate a semelparous species by setting $\sigma = 0$.

Now, we analyze two examples where vital rates are functions of time, reflecting deteriorating conditions. First, we imagine the density-dependent mortality rate μ_2 increases in time ($\mu_{2,t} = \mu_{2,0} + \beta t$). Second, we let the fecundity α decrease in time ($\alpha_t = \max\{\alpha_0 - \beta t, 0\}$). These two cases produce qualitatively distinct patterns of optimal escapement.

5.4.1 Increasing density-dependent mortality rate (μ_2)

First, we allow the density-dependent mortality rate, μ_2, to increase with time. Figure 5-3 shows an example when the cost function is $c(x) = c_0/x$. The rapid decline in escapement initially, followed by a long tail approaching y_∞ is typical for increasing μ_2.

In fact it can be shown that $dy_t^*/d\mu_{2,t}$ is always negative. Recall that it is the sign of $\partial F/\partial\theta_t$ (equation (5.18)) in the numerator that determines the sign of the optimal escapement. There are two components of equation (5.18) that have signs dependent on the population projection function. The value of these terms is

$$\frac{\partial^2 f}{\partial\mu_{2,t}\partial y_t^*} = \frac{-2\mu_1^2\alpha^2 y_t^* e^{-\mu_1}(1-e^{-\mu_1})}{[\mu_1+\mu_{2,t}(1-e^{-\mu_1})\alpha y_t^*]^3}, \tag{5.21}$$

and

$$\frac{\partial f}{\partial\mu_2} = \frac{-\mu_1\alpha^2 y_t^{*2} e^{-\mu_1}(1-e^{-\mu_1})}{[\mu_1+\mu_2(1-e^{-\mu_1})\alpha y_t^*]^2}. \tag{5.22}$$

The derivatives (5.21) and (5.22) are always negative, so $dy^*/d\mu_{2,t}$ is also always negative. As mortality increases, the optimal escapement always decreases, in agreement with our initial intuition.

5.4.2 Decreasing fecundity (α)

In contrast, if α varies in time, we find that the optimal escapement policy may not be monotonic. In particular $\frac{\partial^2 f}{\partial\alpha_t\partial y_t^*}$ may change sign as α_t changes and may then also change the sign of $dy_t^*/d\alpha_t$.

As fecundity decreases, the optimal escapement often changes from increasing to decreasing (Fig. 5-4).

The reason for this non-monotonic behavior is more apparent in a simpler model, developed in the next section.

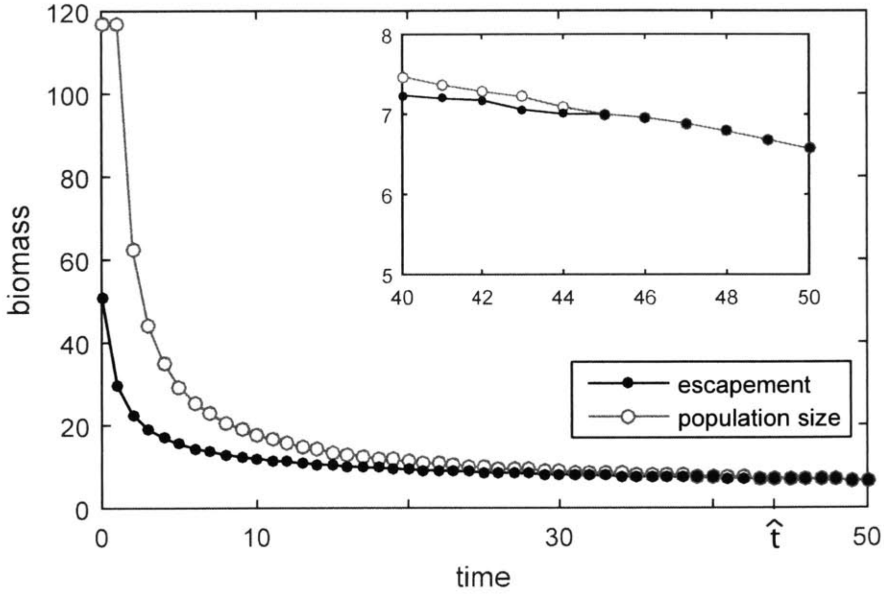

Figure 5-3: Optimal escapement for a population in which μ_2 increases at rate β. The stock is fished down to y_∞ at $\hat{t} = 45$, although harvest is very small for a while prior (see inset). $\alpha = 10$, $\sigma = 0.7$, $\beta = 0.01$, $c_0 = 7$, $p = 1$, $\delta = 0.95$, $\mu_1 = 0.05$, $\mu_2,_0 = 0.01$.

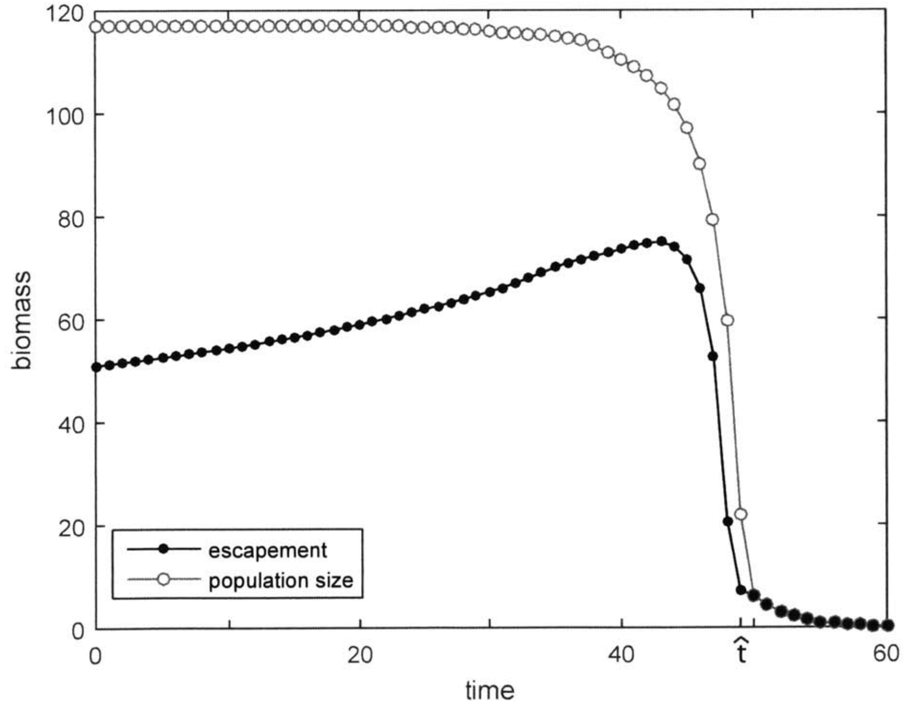

Figure 5-4: Optimal escapement for a population in which α changes over time at rate β. Initial population size is the resulting population size for an optimal escapement corresponding with the initial conditions. The population is fished down to y_∞ at $\hat{t} = 49$. $\alpha_0 = 10$, $\sigma = 0.7$, $\beta = 0.2$, $c_0 = 7$, $p = 1$, $\delta = 0.95$, $\mu_1 = 0.05$, $\mu_2 = 0.01$.

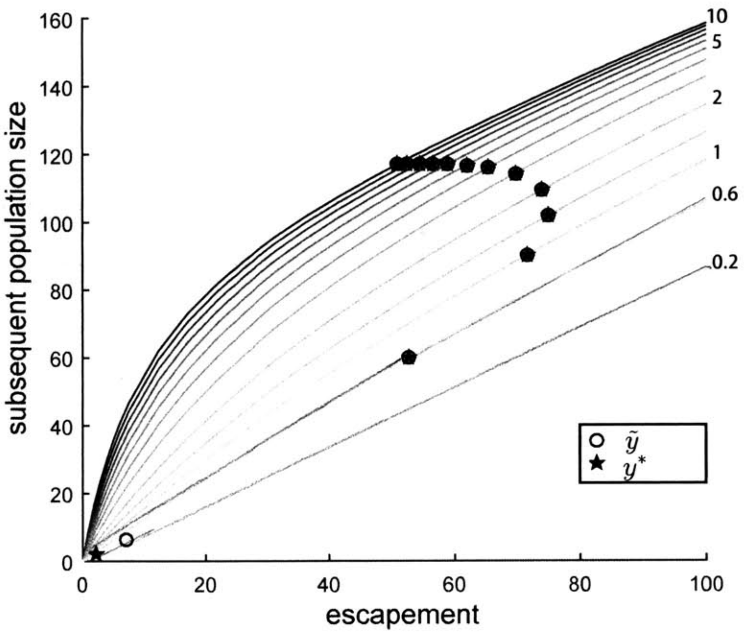

Figure 5-5: Schematic of how a Beverton-Holt model's recruitment (y-axis) varies with escapement (x-axis) over a decreasing fecundity (shaded lines) for the same parameters as Fig. 5-4. Selected α values are labeled on the right margin. The stars show optimal, interior solution. Circles show the optimal $\tilde{y}_t$ policy; once the interior solution is below the stock size, no harvest occurs.

5.5 Yield Maximizing Harvest

To develop our intuition, we constructed a model that is simpler than (5.2) and (5.20) in two ways. First, we set $c(x) = 0$ for all x and $p = 1$, reducing the objective (5.2) to the maximization of discounted yield

$$\Pi(y_0, y_1, \ldots, y_T) = \sum_0^T (x_t - y_t)\delta^t. \tag{5.23}$$

Second, we replace the nonlinear recruitment function (5.20) with the piecewise linear function:

$$x_{t+1} = \begin{cases} a y_t & \text{if } y_t \leq \eta \\ k & \text{if } y_t > \eta; \end{cases} \tag{5.24}$$

where $\eta = k/a$ is the escapement at which the two pieces intersect (Fig. 5-6a). The population grows at rate a when the population is small; for stock sizes larger than η, strong density dependence caps the population at the size k. We can imagine that either the carrying capacity k or the low-density growth rate a decreases in time as the environment deteriorates (Fig. 5-6b,c).

Recall that in an environment in which a vital rate θ_t is changing in time, the optimal escapement in period t is the same as the optimal (constant) escapement in an unchanging environment in which $\theta = \theta_t$ for all t. For the constant environment model (5.24), the optimal escapement is η:

$$\tilde{y} = \begin{cases} \eta & \text{if } x_t \geq \eta \\ x_t & \text{otherwise,} \end{cases} \tag{5.25}$$

as long as $\delta a > 1$. Thus η is our interior solution, y^*, towards which we build the stock if $x_0 < \eta$ or reduce the stock via harvesting, if $x_0 \geq \eta$. To see why, first note that it is not optimal to allow an escapement larger than η because a smaller harvest does not increase subsequent recruitment. We can also show that η is preferable to a smaller escapement, provided $\delta a > 1$.

Harvesting for T periods to η (starting with a stock size, larger than η) yields

$$\Pi(\eta, \eta, \ldots, \eta) = (x_0 - \eta) + \left(\frac{\delta - \delta^T}{1 - \delta}\right)(a\eta - \eta). \tag{5.26}$$

Similarly, the yield obtained from harvesting to a smaller escapement, ζ, is

$$\Pi(\zeta, \zeta, \ldots, \zeta) = (x_0 - \zeta) + \left(\frac{\delta - \delta^T}{1 - \delta}\right)(a\zeta - \zeta). \tag{5.27}$$

The difference between these two constant escapement policies is

$$(\eta - \zeta)\left[(a - 1)\left(\frac{\delta - \delta^T}{1 - \delta}\right) - 1\right]. \tag{5.28}$$

By construction, $\eta - \zeta$ is positive, so the relationship between a and δ determines whether, overall, harvesting the entire expression is positive ($\tilde{y} = \eta$) or negative ($\tilde{y} = 0$). As T goes to infinity, we find that $a\delta > 1$ for η to be the optimal escapement. If there is no discounting ($\delta = 1$), the stock must be self-sustaining ($a > 1$) for the constant escapement policy to outpeform removing all fish in the first period. If we are discounting, this growth rate must be slightly higher to incentivize sustained harvest.

Now let us imagine that the vital rate of the population changes between periods. In each period, we choose the optimal escapement as if it were a constant environment.

First let us consider a case in which the maximum population size, or carrying capacity k, for the stock decreases (Fig. 5-6b). This manifests as a decreasing η; saturation of the population occurs at smaller escapement levels. Thus, we have the behavior we initially expected–decreasing optimal escapement as conditions decline, until eventually we harvest all the remaining fish.

Now consider a case in which a–the initial rate of growth–declines. This merely slows the approach the the ultimate population size; the onset of that saturation now occurs at larger escapement levels. The intersect point, η, increases as a decreases, implying a larger optimal escapement each period. Eventually, we expect $a\delta$ to decline below 1, at which point it is optimal to harvest all the fish to maximize yield.

These two cases show how processes that induce saturation of the population at lower or higher escapement levels tends to decrease or increase the optimal escapement respectively. Parameter changes in more complicated biological models (e.g., Beverton-Holt) tend to change the shape of the entire recruitment curve (Fig. 5-5), making the overall behavior a mixture of the two processes in this simpler model. For some parameter values (e.g., high per capita fecundity in (5.20)), the population projection function changes more similarly to a decrease in initial growth rate, while at others (e.g., low fecundity) it behaves more similarly to a decreasing carrying capacity. Ultimately, it is this property that determines how the optimal escapement changes and allows a non-monotonic optimal escapement.

5.6 Discussion

Numerous studies have documented the ways that climate change may impact the physiology, development, or behavior of individuals and how these impacts determine vital rates (Wood and McDonald, 1997). Nevertheless, few analyses (e.g. Walters and Parma, 1996) focus on the implications of changing vital rates for fishery policy design. In the face of

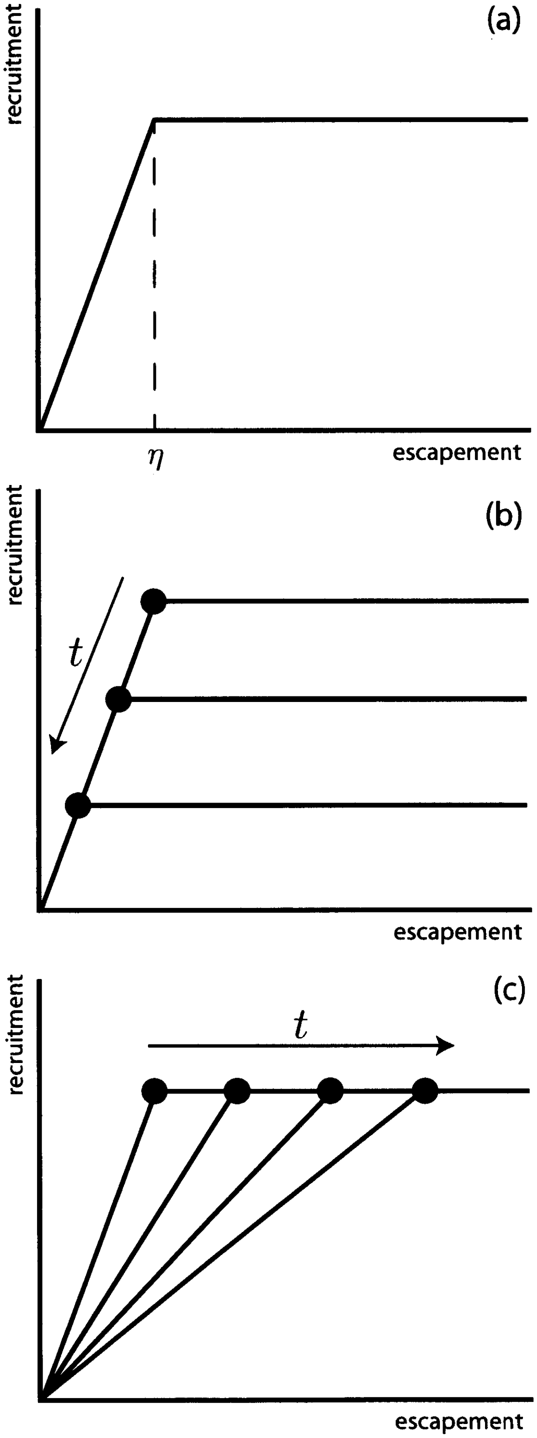

Figure 5-6: (a) Simple recruitment function with linear growth at low density (escapement less than η) and saturated growth at high densities (escapement larger than η). (b) Recruitment curves, when the size of the saturating population decreases. (c) Recruitment curves, when the slope of the initial growth is lowered.

deteriorating environmental conditions, a naive strategy might be to decrease escapement over time. We find that such a strategy may not be optimal. In particular, we find that decreasing fecundity may mitigate the impacts of density dependence and, as a result, temporarily increase the optimal escapement. This result holds even for simple models with compensatory stock-recruitment and monotonic harvest cost functions. We suggest that more attention should be paid to the consequences of dynamic vital rates in optimal management.

We analyzed deterministic models. Fish populations, in contrast, frequently suffer the slings and arrows of stochastic environmental variability. A preliminary investigation suggests that environmental stochasticity does not change our results qualitatively. In numerical simulations, we applied a multiplicative, uniform shock to the stock-recruitment function, $f(x, \theta)$, at each time step[3] and calculated the escapement policy that maximizes the expected rent using stochastic dynamic programming (Appendix 1). These simulations suggest that the the interior solutions are quantitatively similar to their deterministic counterparts.[4]

We also investigated the impact of simultaneous variation in two or more vital rates, a likely outcome for populations experiencing changing conditions. We found that monotonic or non-monotonic optimal escapement may result, although we have not found non-monotonic escapement to result from changing two variables that would only produce monotonic escapements in isolation.

Another ecological complication that our analysis ignores is the possibility of overcompensation (negative population growth at high population densities) which is a common phenomenon (Abrams, 2009; Schroder et al., 2014). An analysis similar to section 5.3.3 with the Ricker model (Ricker, 1954), $f(y_t) = y_t e^{r(1-y_t/k)}$, showed that non-monotonic optimal escapement can be optimal; we confirmed this result numerically.

We also investigated the importance of our assumption that the harvester is a price-taker (i.e., that p is not influenced by the harvester's actions). We calculated optimal

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[3] The uniform shock had mean 1, lower bound $1 - w$ and upper bound $1 + w$ for $0 < w < 1$.

[4] For a given realization, the main difference is that if the population is stochastically driven below the interior solution, it is allowed to rebuild, and if, after $\hat{t}$ the population grows larger than y_∞ for a period, it is fished down to y_∞ in that period.

escapements numerically with a price that depends on the size of harvest (isoelastic demand: $p_t = a(x_t - y_t)^b$). The optimal policies produced are no longer of the 'constant escapement' type with a threshold escapement level (i.e., target escapement varies with all stock sizes). Trajectories through time may be non-monotonic as a vital rate declines.

The optimal exploitation of a continually degrading renewable resource is an interesting hybrid between a renewable resource problem (in stationary conditions, e.g., Reed (1979)) and an exhaustible resource problem. It resembles the 'cake-eating' problem (e.g., Gale (1967)), in which a finite resource (the cake) has a fixed-lifespan (because it spoils) and discounted future utility; the optimizer's choice is how much to consume in each period. The optimal eating strategy is to eat slightly less cake each period, until the entire cake is consumed. Our problem differs in that the total amount of the resource to be consumed depends on the manager's actions, since escapement determines recruitment in the next period.

Finally, it has not escaped our attention that our analyses are applicable both to other taxa and to forms of environmental degradation other than increasing temperature. Commercially exploited species besides fish (e.g., game birds, Bethke and Nudds (2007)) have been impacted by climate change or environmental degradation. In addition, these types of analysis are equally applicable to increasingly favorable conditions, which may be encountered by species invading a newly suitable habitat.

5.7 Appendix: Stochastic Case

Let us consider the case in which the population is influenced also by environmental perturbations, or shocks. These shocks, z_t, at time t alter how the population projects to the next time period. The random variable z has expectation 1, and has finite support ($\underline{z} \leq z \leq \bar{z}$ such that $\underline{z} \geq 0$ and $f(x, \underline{z}) > 0$ for $x > 0$ (i.e., the shocks will not drive the population to extinction). We will now denote the population projection function as $f(y_t, \theta_t, z_t)$:

$$x_{t+1} = f(y_t, \theta_t, z_t). \tag{5.29}$$

For this example, we used the following function, modified from (5.20):

$$x_{t+1} = \left(\sigma y_t + \frac{\mu_1 e^{-\mu_1} \alpha y_t}{\mu_1 + \mu_2 (1 - e^{-\mu_1}) \alpha y_t} \right) z_t. \tag{5.30}$$

Instead of maximizing rent, we maximize the expectation:

$$V(x_t, \theta_t, z_t) = \max_{0 \le y_t \le x_t} \left[Q(x_t) - Q(y_t) + \delta E_t V(f(y_t, \theta_t, z_t), \theta_{t+1}, z_{t+1}) \right] \tag{5.31}$$

where the expectation is taken over z.

To investigate the influence of these shocks on the model, we specified z as a uniform distribution with lower bound $1 - w$ and upper bound $1 + w$, for $0 < w < 1$. We calculated optimal policies numerically, using 50 time steps and 113 stock sizes, which were more closely spaced near y_∞; we interpolated the value function using spline-interpolation between these stock sizes. Using the optimal policies calculated, we then simulated the policy forward in time, with the stock experiencing a shock in each period. Figure 5-7 shows an example of such a realization. The optimal policy is very similar to that in the deterministic case for the same biological and economic parameters.

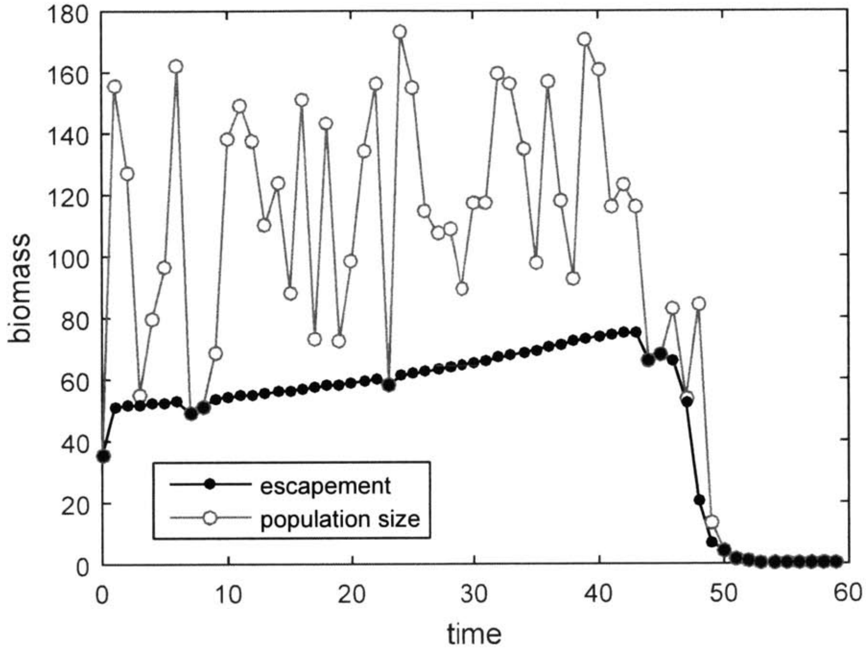

Figure 5-7: A single realization of an optimal escapement policy with stochasticity ($w = 0.6$); compare with Fig. 5-4. Parameter values are the same as in that figure.

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Chapter 6

Adaptive managment in stationary and changing environments

6.1 Introduction

The study of changing conditions—in particular, of the changing climate—on ecological processes has underscored how much about ecological systems we have yet to learn. In fact, uncertainty is such a ubiquitous feature that we often discuss the different types we may encounter: environmental uncertainty (e.g., from weather), state uncertainty (i.e., from imperfect measurements of the system), or structural and parameter uncertainty (i.e., wherein the correct model or parameter values are unknown). The last two types, structural and parameter uncertainty, are 'reducible' in that we are able to learn about them over time. Weather, in contrast, which may still exert a stochastic forcing even if we perfectly know its properties).

Climate change provides an additional source of this uncertainty; as Conroy et al. (2011) note, "the challenge posed by climate change is that predictions based on historical observations and experiences may no longer be appropriate." Managed ecological systems, like fisheries, are potentially entering previously unobserved regimes. Such changes may have profound implications for the management of such systems. For example, choosing a harvest level without knowing the dependence of vital rates on temperature has been implicated as a reason for overfishing (e.g. Pershing et al., 2015). However, the management of natural resources does not stop while we reduce our uncertainty (e.g., via the collection of additional observations or the execution of focused experiments). How then, can we achieve management objectives (such as maximizing yields over time) given imperfect information? Adaptive management (Holling, 1978)—that is, management in which learning is explicitly incorporated—is an attractive option.

The basic idea of adaptive management is that management actions are treated as data collection opportunities, or even as experiments. The processes of managing and studying a resource occur in tandem and mutually support each other. Lancia et al. (1996) note that "in adaptive resource management, learning is not simply a byproduct, but is formally acknowledged as an integral objective of the management process." Adaptive management has been investigated for its utility in fisheries (Walters and Hilborn, 1976), threatened species management (Chades et al., 2012), and the control of invasive species (Haight and Polasky, 2010; Regan et al., 2011), among others. There are many approaches to adaptive management, ranging from a periodic model update from routinely collected data (e.g. Varley and Boyce, 2006; Hobbs et al., 2015), to experimentation on small portions of a larger management area.

I focus on the simple case of managing a single stock of fish, one management action (escapement), and uncertainty about the dynamics of the system. I then model both the stock and our knowledge about the system to choose the optimal series of actions to meet various objectives (e.g., maximization of rent). In this chapter, let x_t denote the size of the stock at time t. The stock at time $t+1$, x_{t+1}, will depend on the escapement (the fish left after harvest that reproduce and survive); a stock-recruitment function f projects this escapement, y_t to the next period; $x_{t+1} = f(y_t, \theta)$. θ denotes a parameter of interest, in particular, one about which we hope to learn.

Core to adaptive management is the *belief state*, which quantifies our confidence that a particular model or parameter value is correct (Figure 6-1). The belief state is typically a probability distribution over a set of beliefs. For example, if we were unsure if a population had a high or low carrying capacity, we might assign a probability ρ that the carrying

Figure 6-1: *'Why, sometimes I've believed as many as six impossible things before breakfast.'* – the Queen in Carroll (1871), who likely would be comfortable with the concept of belief states. The image is a plate from the 1871 edition of that book, illustrated by John Tenniel.

capacity is high and probability $(1 - \rho)$ that it is low; the belief state would be ρ. If instead, we were unsure of the population growth rate, we might assign equal probability to all potential values within a reasonable range–say a uniform distribution across λ_{small} to λ_{large}. We would then treat this belief state as a part of the model in the same way we would treat a state like the size of the population.

Now, in addition to modeling population or harvesting dynamics, we can also model how the belief state changes over time. To do this, we need a mathematical construct that will allow us to update the belief state as new observations are collected. One straightforward way to do this, that I will employ throughout this chapter, is through Bayesian updating. If $\mathscr{I}(\theta)$ is the belief state for some parameter value θ and we observe a stock size x, we can update the the belief state to $\mathscr{I}^+$ using Bayes' rule:

$$\mathscr{I}^+(\theta) = \frac{Pr(x|\theta)\mathscr{I}(\theta)}{Pr(x)}. \tag{6.1}$$

If the probability of x is low for a given value of θ, say $\hat{\theta}$, we may reduce our belief that $\hat{\theta}$ is correct (i.e., $\mathscr{I}^+(\hat{\theta}) < \mathscr{I}(\hat{\theta})$). On the other hand, as we accumulate data points that are in agreement with a different value, we may increase our belief that that value is correct.

With a way to update belief states in hand, we can incorporate the belief state into our management framework. Let us consider a (closed-loop, *sensu* Bertsekas (2000)) system in which at each period we use the belief state and information about the current state of the stock to make a decision for that period. The next period, we again observe the system and may update our belief state. Our goal is to characterize the optimal policy, or rule dictating what escapement to choose if we encounter a specific state in any given period, given our management objective.

We typically update the belief state in one of two ways: passively or actively. While passive adaptive management is easier to implement numerically, active adaptive management is more intuitive. Under active adaptive management, we forecast the impact of a management action on both the dynamics of the ecological system (e.g., the population size) and the belief state. We can imagine considering an action, such as harvesting intensely, that would allow us to learn more about the population dynamics at low density, thereby changing our belief state. The resulting improvement in the accuracy of our belief state may then allow us to make better decisions in the future. This feedback between the action and the belief state is what makes a policy 'active'. However, we can also imagine a case in which we do not model the feedback of our action on the belief state; we make our decision, ignoring the possibility that modulating our actions could produce learning benefits, but then update our belief state after our decision and its outcome have been observed. This may seem to be a subtle difference, but the computational differences between these types of policies can be marked!

In adaptive management, learning for learning's sake is typically not the objective, but rather is ancillary to achieving our primary objective, whether that be a large yield through harvest or a large population size to be conserved (Walters, 2002). In this chapter, I will focus on yield or profit maximization from a harvested species. While there are many other potential objectives, this formulation has a long history (e.g., Clark, 2010; Reed, 1979; Costello et al., 2001) with which to compare and build our intuition.

I start by describing the general properties of adaptive management solutions in a stationary environment and develop a few tractable examples to build our intuition about how these systems are optimally managed. They also serve as a comparison with the later models, in which we introduce a trend in the growth-recruitment function.

I find that the differences between adaptive and non-learning policies may be particularly dramatic when vital rates change in time, as the choice of the correct parameter value determines when the stock should be depleted; depleting the stock too early can cause severe population and yield losses.

6.2 Stationary Case

6.2.1 Model

Let us consider a population that is of size x_t at time t. A harvester fishes this population down to the escapement y_t. This escaped population then changes as result of reproduction and possibly survival according to the stock recruitment function $f(y_t)$. Population change may have a stochastic component; at time t, an independent and identically distributed random shock, Z_t, modulates the population size.[1] Let θ be a parameter of the stock recruitment function. The growth process is thus

$$X_{t+1} = f(y_t, Z_t, \theta) \tag{6.2}$$

and a particular realization of that process is

$$x_{t+1} = f(y_t, z_t, \theta). \tag{6.3}$$

The management of such a stock has been extensively studied in the theoretical fisheries literature. Reed (1979) studied the problem of maximizing the net present value of the rent generated by the harvest of a fish stock governed by a stock recruitment function $X_{t+1} = f(y_t, \theta)Z_t$ over an infinite time horizon. He showed that when the growth of the population is compensatory (that is, $\partial f/\partial y > 0$ and $\partial^2 f/\partial y^2 < 0$) and the marginal cost of harvest is a non-increasing function of stock size, then the optimal harvest rule is a 'constant escapement' policy,[2]. Other authors (e.g., Costello et al., 2001) have extended this result to more general functional forms, including when the shock does not multiply f. I too will

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[1] Throughout this chapter we will use capital letters to denote random variables and a lowercase letters to denote realizations of those random variables

[2] In Chapter 5 I further describe a constant escapement policy. As a reminder, a constant escapement policy is a type of threshold policy or bang-bang rule. When the stock size at a time t is larger than some time-invariant optimal escapement level, that escapement is optimal; if the stock size is lower than that threshold, no harvest occurs until the stock rebuilds.

focus on the maximization of the present value of a stock governed by a compensatory stock recruitment function and non-increasing marginal harvest costs. Reed, however, assumed that all parameters were perfectly known. I seek to describe some general properties of optimal escapement policies when there is also uncertainty regarding a parameter that we hope to learn about.

Let us assume the parameter θ is imperfectly known. We model our uncertainty in θ at time t by treating it as a random variable Θ_t and describing our belief that $\hat{\theta}$ is the true value, θ, as $\mathscr{I}_t(\hat{\theta}) = \Pr(\Theta_t = \hat{\theta})$. We update this belief state as we accumulate observations of the system. In particular, for each perfectly known escapement y_t and resulting perfectly observed population size x_{t+1} we learn about this unknown parameter. I define the information state's update as

$$\mathscr{I}_{t+1} = g(\mathscr{I}_t, y_t, x_{t+1}). \tag{6.4}$$

We will use Bayes' rule (equation 6.1) to update $\mathscr{I}_t$. Note that we do not observe the value of z_t; we only know the distribution of Z_t. We therefore may not be able to tell if a particular x_{t+1} is the result of a large shock or an extreme value of Θ_t.

Our goal is to maximize the expected stream of discounted rents over a fixed time horizon ending at T or over an infinite time-horizon by choosing a sequence of escapements y_t. We take the expectation of both the shock and our belief state. The objective is thus

$$\Pi(y_t, x_0, \mathscr{I}_0) = \sum_{t=0}^{T} \left(\underset{Z_t,\Theta_t}{E} \left[p(X_t - y_t) - \int_{y_t}^{X_t} c(s)ds \right] \right) \delta^t \tag{6.5}$$

where p is the price per unit harvest, $c(x)$ is the marginal cost of harvesting a stock of size of size x, and δ is the discount factor.

Infinite Time Horizon

First, let us explore the properties of the optimal management policy over an infinite time horizon. In this case, I will assume that we have a discount factor $\delta < 1$. In addition, I will restrict the shocks, Z_t, to have finite support. Because the shocks are multiplicative, I specify that their expectations are unity.

In this case, a 'stationary' policy is optimal; that is, in each period, the stock size and the belief state determine the optimal escapement rule, but this *rule* does not vary over time. This result follows from the basic theory of dynamic programming on infinite time horizons ([e.g., Bertsekas, 2000). Because there is a finite profit (or yield)[3] per time period and the discount factor is less than 1, a stationary policy is optimal .

Finite Time Horizon

We turn our attention to the finite time horizon. This case is particularly interesting because 'real-world' managers often have fixed time horizons over which to manage a resource. The finite time horizon case also facilitates comparison to my later analysis in which there is a trend in the vital rates over time.

I show that, for a broad class of models, the optimal escapement at time t depends on the stock size x_t only in through constraint $y_t \leq x_t$. That is, it is not optimal to take advantage of unusually large or small stock sizes to gain information.

To solve for the optimal harvest policy, I reformulate the problem (equation 6.5) as a sequence of single decisions that capture the payoff from the current decision plus the result of the optimal choices going forward in time (see Chapter 5 also). It will be convenient to define an immediate harvest value (*à la* Reed, 1979) as

$$Q(x) = p(x - y_\infty) - \int_{y_\infty}^{x} c(s)ds. \tag{6.6}$$

y_∞ is the lowest economically viable escapement or 'zero profit level' where $p = c(y_\infty)$; harvesting below y_∞ costs more than it it is worth. When $p > c(0)$, $y_\infty = 0$.

The value from harvesting the stock at time t down to y_t is simply $Q(x_t) - Q(y_t)$. To this value, I add the future value from harvesting y_t or its progeny later; we define this future value as $V(x_{t+1}, \mathscr{I}_{t+1})$, as the value also depends on the belief state. The right side of equation 6.5 is thus $V(x_0, \mathscr{I}_0)$. However, this recursive approach is more useful when we

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[3] The finite profit or yield per stage is guaranteed by the concavity of growth function and the finite support of the shocks.

start at the end of the time horizon. At the ultimate time T the value function is

$$V(x_T, \mathscr{I}_t) = Q(x_T); \tag{6.7}$$

future harvests have no value to us.

At time $T-1$ it is thus

$$\begin{aligned}
V(x_{T-1}, \mathscr{I}_{T-1}) = \max_{0 \leq y_{T-1} \leq x_{T-1}} & \left\{ Q(x_{T-1}) - Q(y_{T-1}) + \delta \underset{Z_{T-1}, \Theta_{T-1}}{E} (V(X_T)) \right\} && (6.8) \\
= \max_{y_{T-1}} & \left\{ Q(x_{T-1}) - Q(y_{T-1}) + \delta \underset{Z_{T-1}, \Theta_{T-1}}{E} (Q(X_T)) \right\} && (6.9) \\
= Q(x_{T-1}) + \max_{y_{T-1}} & \left\{ -Q(y_{T-1}) + \delta \underset{Z_{T-1}, \Theta_{T-1}}{E} \left[Q(f(y_{T-1}, Z_{T-1}, \hat{\theta})) \right] \right\} && (6.10) \\
= Q(x_{T-1}) - Q(y^*_{T-1}) & + \delta \underset{Z_{T-1}, \Theta_{T-1}}{E} \left\{ Q(f(y^*_{T-1}, Z_{T-1}, \hat{\theta})) \right\}, && (6.11)
\end{aligned}$$

where y^*_t is the optimal value of the escapement at time t.

A candidate for y^*_t is the interior optimum that satisfies the first-order conditions:

$$0 = -\frac{\partial Q(y_{T-1})}{\partial y_{T-1}} + \delta \frac{\partial E_{Z_{T-1}, \Theta_{T-1}} \left[Q(f(y_{T-1}, Z_{T-1}, \hat{\theta})) \right]}{\partial y_{T-1}} \Bigg|_{y_{T-1} = y^*_{T-1}} . \tag{6.12}$$

Note that equation 6.12 is independent of the value of x_{T-1}; unless y^*_{T-1} is less than x_{T-1} it is the optimal escapement at $T-1$.

Stepping back one more time period, we have

$$\begin{aligned}
V(x_{T-2}, \mathscr{I}_{T-2}) &= \max_{0 \leq y_{T-2} \leq x_{T-2}} \left\{ Q(x_{T-2}) - Q(y_{T-2}) + \delta \underset{Z_{T-2}, \Theta_{T-2}}{E} \left[V(x_{T-1}, \mathscr{I}_{T-1}) \right] \right\} && (6.13) \\
&= \max_{y_{T-2}} \Bigg\{ Q(x_{T-2}) - Q(y_{T-2}) + \delta \underset{Z_{T-2}, \Theta_{T-2}}{E} \Bigg[Q(f(y_{T-2}, Z_{T-2}, \hat{\theta})) - Q(y^*_{T-1}) \\
&\quad + \delta \underset{Z_{T-1}, \Theta_{T-1}}{E} \left[Q(f(y^*_{T-1}, Z_{T-1}, \hat{\theta})) \right] \Bigg] \Bigg\} && (6.14) \\
& && (6.15)
\end{aligned}$$

In the last line, note that the distribution of Θ_{T-1} will be modelled using $g(\mathscr{I}_{T-2}, y_{T-2}, x_{T-2},$

where $x_{T-1} = f(y_{T-2}, Z_{T-2}, \hat{\theta})$.

The first order conditions for a maximum for this time-period are more complicated– there is now a term representing the control's influence on the future information state:

$$\begin{aligned} 0 &= \left\{ -\frac{\partial Q(y_{T-2})}{\partial y_{T-2}} + \delta \frac{\partial\, E_{Z_{T-2},\Theta_{T-2}} \left[Q(f(y_{T-2}, z_{T-2}, \hat{\theta}))\right]}{\partial y_{T-2}} \right. \\ &+ \left. \delta^2 \frac{\partial\, E_{Z_{T-2},\Theta_{T-2}}\, E_{Z_{T-2},\Theta_{T-1}} [Q[f(y^*_{T-1}, z_{T-1}, \hat{\theta})]]}{\partial y_{T-2}} \right\} \Bigg|_{y_{T-2}=y^*_{T-2}} \qquad (6.16) \end{aligned}$$

As we go further back in time, each information state over which we take the expectation will depend on the current control and its projected influence multiple time steps into the future on the belief state (e.g., at time $T-3$, $\mathscr{I}_{T-1}$ will be $g_{T-2}(g_{T-3}(\mathscr{I}_{T-3}, y_{T-3}), y^*_{T-2})$. However, we note that none of these terms depend on the current stock; the optimal (interior) solution is independent of the size of the stock.

Passive versus Active Adaptive Management

In passive adaptive management, we do not model the impact of the control (y_t) on the future information state, so the expectation of the future information state is always the current information state; that is, the first-order conditions for a maximum are equivalent (for all time) to those for $T-1$ for the active case. In general, the passive and active policies are equivalent at other times if the expectation of the future information state is independent of the control. In equation (6.16), we can see that if this is the case, the δ^2 term will be zero, reducing the first-order conditions to that of the passive management.

Thus, we expect the active and passive strategies to be identical always in the penultimate period, while they typically will differ earlier. In the special case when the pre-posterior is not a function of the control, the policies are the same. This is particularly relevant because it is (much) computationally easier to calculate the passive adaptive management strategy.

6.3 Yield Maximizing Beverton-Holt Growth with Uniform, Multiplicative Shocks

Let us develop a simple model that is relatively tractable so that we may gain insight into its optimal harvesting policy. Because adaptive management solutions typically are solved exclusively numerically, gaining an intuition about them can be difficult. To this end, I make several simplifying assumptions that make our task easier: (1) we will maximize yield (so, $p = 1$, $c(x) = 0$ for all x), (2) the shock is uniform, (3) it multiplies a growth function as in Reed (1979), and (4) the uncertain parameter has only two candidate values. Taken together, these assumptions create a fishery with an adaptive management policy that is fairly tractable to calculate.

Let us imagine that the stock grows according to a Beverton-Holt stock-recruitment curve ($f(y_t, b) = y_t/(b + ay_t)$). I introduce environmental stochasticity by assuming that population is perturbed by a multiplicative, uniform shock; that is,

$$X_{t+1} = f(y_t, b)Z_t, \tag{6.17}$$

where Z_t are independent, identically distributed uniform random variables with lower bound $1 - w$ and upper bound $1 + w$ (with $0 < w < 1$). We consider uncertainty about the value of the parameter b, which is the inverse of the growth rate at low density (i.e., $f'(0) = 1/b$). We are unsure whether b takes one of two candidate values b_1 and b_2. Let us assume, without loss of generality, that $1/b_1 < 1/b_2$ so that b_1 represents the low-productivity model. For this simple form of uncertainty, we can then fully describe the information state with a single variable, ρ_t, which is the probability at time t that b_1 is the true value, b, i.e., $\Theta_t \sim \text{Bernoulli}(\rho_t)$.

At T, the optimal escapement y_T^* is 0; future fish have no value, so, since $c = 0$ and therefore $y_\infty = 0$, we harvest all remaining fish. Thus $V(x_T, \rho_T) = x_T$. We then step backwards, to time $T-1$, and find:

$$V(x_{T-1}, \rho_{T-1}) = \max_{0 \le y_{T-1} \le x_{T-1}} \left\{ x_{T-1} - y_{T-1} + \delta \underset{Z_{T-1}, \Theta_{T-1}}{E} V(x_T, \rho_T) \right\} \tag{6.18}$$

$$= \max_{0 \le y_{T-1} \le x_{T-1}} \left\{ x_{T-1} - y_{T-1} + \delta \underset{Z_{T-1}, \Theta_{T-1}}{E} x_T \right\} \tag{6.19}$$

$$\begin{aligned} = \max_{0 \le y_{T-1} \le x_{T-1}} \Bigg\{ & x_{T-1} - y_{T-1} \\ & + \delta \underset{Z_{T-1}}{E} \left[\rho_{T-1} f(y_{T-1}, b_1) z_{T-1} + (1 - \rho_{T-1}) f(y_{T-1}, b_2) z_{T-1} \right] \Bigg\} \end{aligned} \tag{6.20}$$

$$\begin{aligned} = \max_{0 \le y_{T-1} \le x_{T-1}} \Big\{ & x_{T-1} - y_{T-1} \\ & + \delta \left[\rho_{T-1} f(y_{T-1}, b_1) + (1 - \rho_{T-1}) f(y_{T-1}, b_2) \right] \Big\} \end{aligned} \tag{6.21}$$

$$= x_{T-1} - y^*_{T-1} + \delta \left[\rho_{T-1} f(y^*_{T-1}, b_1) + (1 - \rho_{T-1}) f(y^*_{T-1}, b_2) \right]. \tag{6.22}$$

To find y^*_{T-1}, we differentiate the maximand of (6.21) with respect to y_{T-1} to obtain the first-order conditions for a maximum:

$$\frac{1}{\delta} = \left[\rho_{T-1} \frac{\partial f(y_{T-1}, b_1)}{\partial y_{T-1}} + (1 - \rho_{T-1}) \frac{\partial f(y_{T-1}, b_2)}{\partial y_{T-1}} \right] \Bigg|_{y^*_{T-1}}. \tag{6.23}$$

We then turn to time $T-2$ when the value function is

$$V(x_{T-2}, \rho_{T-2}) = \max_{0 \le y_{T-2} \le x_{T-2}} \left\{ x_{T-2} - y_{T-2} + \delta \underset{Z_{T-2}, \Theta_{T-2}}{E} V(x_{T-1}, \rho_{T-2}) \right\} \tag{6.24}$$

$$\begin{aligned} = \max_{0 \le y_{T-2} \le x_{T-2}} \Bigg\{ & x_{T-2} - y_{T-2} + \delta \underset{Z_{T-2}, \Theta_{T-2}}{E} \Big[x_{T-1} - y^*_{T-1} + \\ & \delta \left(\rho_{T-1} f(y^*_{T-1}, b_1) + (1 - \rho_{T-1}) f(y^*_{T-1}, b_2) \right) \Big] \Bigg\} \end{aligned} \tag{6.25}$$

$$\begin{aligned} = \max_{0 \le y_{T-2} \le x_{T-2}} \Bigg\{ & x_{T-2} - y_{T-2} + \delta \Bigg[\rho_{T-2} f(y^*_{T-2}, b_1) + (1 - \rho_{T-2}) f(y^*_{T-2}, b_2) - y^*_{T-1} + \\ & \delta \Bigg(\underset{Z_{T-1}, \Theta_{T-1}}{E} g(\rho_{T-1}, y_{T-1}, f(y_{T-1}, b_i) Z_{T-1}) f(y^*_{T-1}, b_1) + \\ & \left(1 - \underset{Z_{T-2}, \Theta_{T-1}}{E} g(\rho_{T-1}, y_{T-1}, f(y_{T-1}, b_i) Z_{T-1}) \right) f(y^*_{T-1}, b_2) \Bigg) \Bigg] \Bigg\}. \end{aligned} \tag{6.26}$$

Now, we need to know the expectation of ρ_{T-1} in period $T-2$. We can use Bayes

Theorem to update ρ_t;

$$\rho_{t+1} = g(\rho_t, y_t, x_{t+1}) \tag{6.27}$$

$$= \frac{\Pr(x_{t+1}|b_1)\rho_t}{\Pr(x_{t+1}|b_1)\rho_t + \Pr(x_{t+1}|b_2)(1-\rho_t)}. \tag{6.28}$$

The expectation of the posterior distribution, $E_{Z_t,\Theta_t}(\rho_{t+1})$ is called the 'pre-posterior' and is a critical component of active adaptive management, because it maps the expected effect of a management action onto the information state.

From equation (6.28) and (6.17), the pre-posterior can be written as:

$$\underset{Z_t,\Theta_t}{E}(\rho_{t+1}|y_t) = \int_{1-w}^{1+w} \sum_{b_i} \frac{\Pr(f(y_t,b_i)z_t|b_1)\rho_t}{\Pr(f(y_t,b_i)z_t|b_1)\rho_t + \Pr(f(y_t,b_i)z_t|b_2)(1-\rho_t)} \Pr(b_i)\frac{1}{2w}dz. \tag{6.29}$$

Let us start assembling the pieces to calculate this pre-posterior. First, the probability that we achieve a given population size is calculated as follows:

$$\Pr(X_{t+1} \leq x_{t+1}|b_i) = \Pr\left(\frac{y_t Z_t}{b_i + a y_t}\right) \tag{6.30}$$

$$= \Pr\left(Z_t \leq \frac{x_{t+1}(b_i + a y_t)}{y_t}\right) \tag{6.31}$$

$$= \int_{1-w}^{\frac{x_{t+1}(b_i+ay_t)}{y_t}} \frac{1}{2w} dz \tag{6.32}$$

$$= \frac{1}{2w}\left[\frac{x_{t+1}(b_i + a y_t)}{y_t} - (1-w)\right] \tag{6.33}$$

and

$$\Pr(X_{T+1} = x_{t+1}|b_i) = \frac{d\Pr(X_{t+1} \leq x_{t+1}|b_i)}{dx_{t+1}} \tag{6.34}$$

$$= \frac{1}{2w}\frac{b_i + a y_t}{y_t}. \tag{6.35}$$

Combining (6.35) with the bounds on X_{t+1} that it inherits from the bounds on Z_t, we have

$$\Pr(X_{t+1} = x_{t+1}|b_i) = \begin{cases} \frac{b_i + a y_t}{2 w y_t}, & \text{if } \frac{(1-w)y_t}{b_i + a y_t} \leq x \leq \frac{(1+w)y_t}{b_i + a y_t} \\ 0, & \text{otherwise.} \end{cases} \tag{6.36}$$

Some values of the shock will drive the population to extreme sizes that are only consistent with one model. In this case, we immediately learn which model is true. [4]

The probability of being in the region where only b_1 is consistent is $\frac{\rho_t(1-w)}{2w}\frac{b_1-b_2}{b2+ay}$; the probability of being in the region where only b_2 is consistent is $\frac{(1-\rho_t)(1+w)}{2w}\frac{b_1-b_2}{b1+ay}$. The expectation of ρ_{t+1} is thus

$$\underset{Z_t,\Theta_t}{E}(\rho_{t+1}) = \frac{\rho_t(1-w)}{2w}\frac{b_1-b_2}{b_2+ay_t}+ \tag{6.37}$$

$$\left(1-\frac{b_1-b_2}{2w}\left[\frac{\rho_t(1-w)}{b_2+ay_t}+\frac{(1-\rho_t)(1+w)}{b_1+ay_t}\right]\right)\left(\frac{\frac{b_1+ay_t}{2wy_t}\rho_t}{\frac{b_1+ay_t}{2wy_t}\rho_t+\frac{b_2+ay_t}{2wy_t}(1-\rho_t)}\right)$$

$$= \quad \rho_t. \tag{6.38}$$

Now, we return to equation 6.24 by substituting (6.38) for $E_{Z_{T-1},\Theta_{T-1}}\rho_{T-1}$:

$$V(x_{T-2},\rho_{T-2}) = \max_{0\leq y_{T-2}\leq x_{T-2}}\Bigg\{x_{T-2}-y_{T-2}+ \tag{6.39}$$

$$\delta\Bigg[\rho_{T-2}f(y^*_{T-2},b_1)+(1-\rho_{T-2})f(y^*_{T-2},b_2)-y^*_{T-1}+$$

$$\delta\Bigg(\rho_{T-2}f(y^*_{T-1},b_1)+(1-\rho_{T-2})\,f(y^*_{T-1},b_2)\Bigg)\Bigg]\Bigg\}. \tag{6.40}$$

The derivative of the pre-posterior with respect to the control is 0, so the first-order conditions are equivalent to equation 6.23 (with updated time subscripts). Now, we not only have our optimal threshold escapement, but also know that the active and passive adaptive management policies are equivalent (recall section 6.2.1). We can repeat this procedure backwards in time and will find the same first-order conditions each period.

In figures 6-2 and 6-3, I show a single realization of how these optimal policies perform when either b_1 or b_2 is true. Note that, when b_2 is the correct parameter value, the value of the belief state may not be monotonic 6-3. This is because any value of the recruitment that is consistent with both b_1 and b_2 is more likely to have come from b_1's being true, since–by

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[4] Note that for some small w and y_t, it is possible that the bounds of these two distributions will not intersect. In that special case, the probability that x_{t+1} is consistent with b_1 is equivalent to our belief that b_1 is the true value (i.e., ρ_t).

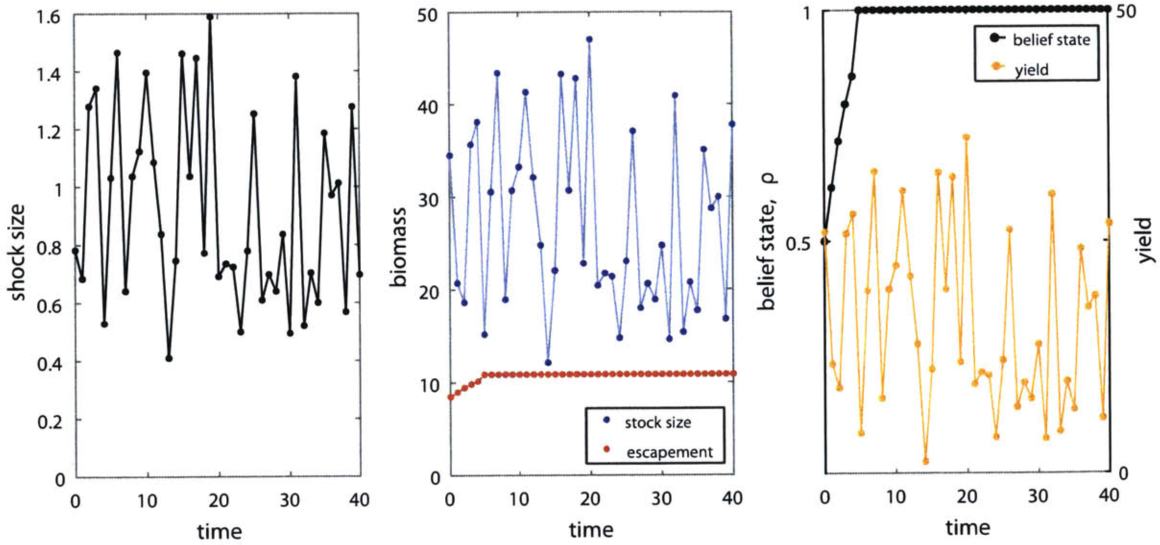

Figure 6-2: A single realization of the optimal policy and its outcomes through time when $b = b_1$. The first panel shows the shocks that occurred in each time period. In the next panel, red circles show the optimal escapement, while blue dots show the population size. The black line shows the belief state, while the orange line shows yield. Note that at $t = 5$, a sufficiently large shock occurred that fell outside the range of recruitments consistent with b_2, causing a slight 'jump' in the information state and optimal policy. Parameter values are $a = 0.02$, $b_1 = 0.15$, $b_2 = 0.03$, $w = 0.6$, $\delta = 0.9$, $x_0 = 31.51$.

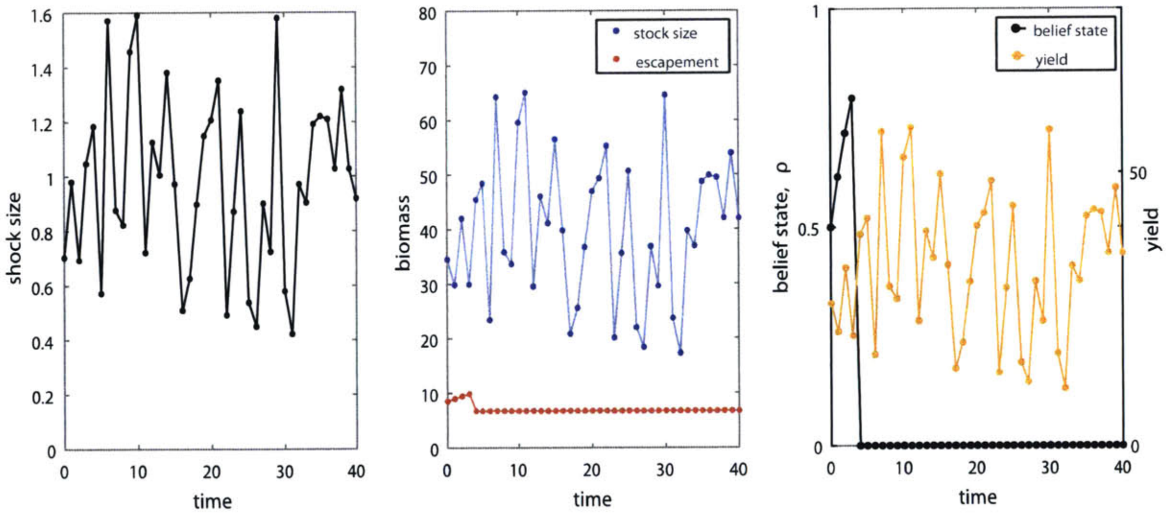

Figure 6-3: A single realization of the optimal policy and its outcomes through time when $b = b_2$. The first panel shows the shocks that occurred in each time period. In the next panel, red circles show the optimal escapement, while blue dots show the population size. The black line shows the belief state, while the orange line shows yield. Note that at $t = 4$, a sufficiently large shock occurred that fell outside the range of recruitments consistent with b_2, causing a 'jump' in the information state and optimal policy. Parameter values are the same as in figure 6-2.

construction–b_1 has higher probability density over the smaller range of recruitment values that are possible for it. This is interesting, since the manager is essentially being 'mislead' by the data she collects for a period of time!

I ran 500 simulations and aggregated the results in terms of stock and yield sizes. The initial population size was assigned as the expected recruitment from choosing the optimal escapement associated with $\rho_0 = 0.5$. While having perfect information does outperform the adaptive management policy (see figures 6-4 and 6-5), once the parameter is well known, the performance is equal. For these parameter values, the correct model only narrowly outperforms the adaptive management case, while the 'average' policy only underperforms slightly. However, managing as if the incorrect model is true does markedly worse.

Since the passive and active adaptive management policies are identical, there is no experimentation. In this case, note that we learn rather quickly; within 10-15 time steps, we have close to perfect knowledge regardless of the true underlying model.

6.4 Sustainable or not? Yield Maximizing Piecewise Linear Growth Function with Multiplicative, Uniform Shocks

An interesting case is one in which we are unsure if a stock is sufficiently productive to sustainably harvest, or, on the other hand, would be optimally extirpated (e.g., Clark (1973)). If we are unsure which type of stock we are managing, how should we proceed? To investigate this, I chose a simple piecewise linear growth function (Figure 6-6). Let α_i be the growth rate at low densities and k be the carrying capacity k, which is reached at an escapement of η_i. The growth is thus

$$X_{t+1} = f(y, \alpha_i) Z_t = \begin{cases} \alpha_i y_t z_t \text{ if } y_t < \eta_i \\ k z_t \text{ if } y_t > \eta_i . \end{cases} \tag{6.41}$$

Z_t is a uniformly distribution iid shock, with lower bound $1 - w$ and upper bound $1 + w$.

Without loss of generality, we assume that $\alpha_1 > \alpha_2$, such that $\alpha_1 > 1/\delta$ (i.e., it is viable to harvest) and $\alpha_2 < 1/\delta$ (i.e., it is optimal to fish out the stock). If α_1 is the true

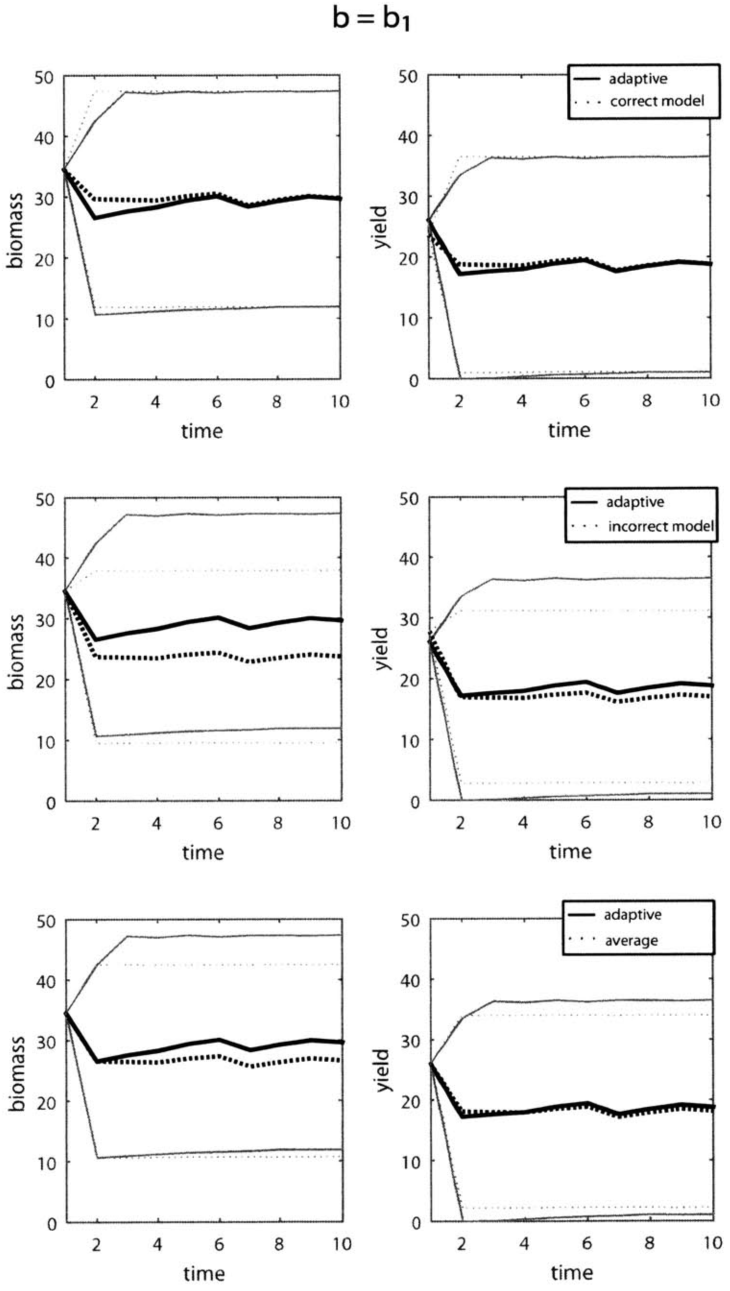

Figure 6-4: Performance of adaptive and non-adaptive management strategies when $b = b_1$. The top panel shows the adaptive policy's performance in terms of stock size (left) and yield (right) versus perfect information. The black lines show average results; the grey lines show the minimum and maximum values. The middle panels contain the results for the adaptive and 'incorrect' model. Finally, I show the performance of the adaptive model and a model that assigns equal weight to each model and does not update this weight. Parameter values are $a = 0.02$, $b_1 = 0.15$, $b_2 = 0.03$, $w = 0.6$, $\delta = 0.9$, $x_0 = 31.51$, as in figure 6-2.

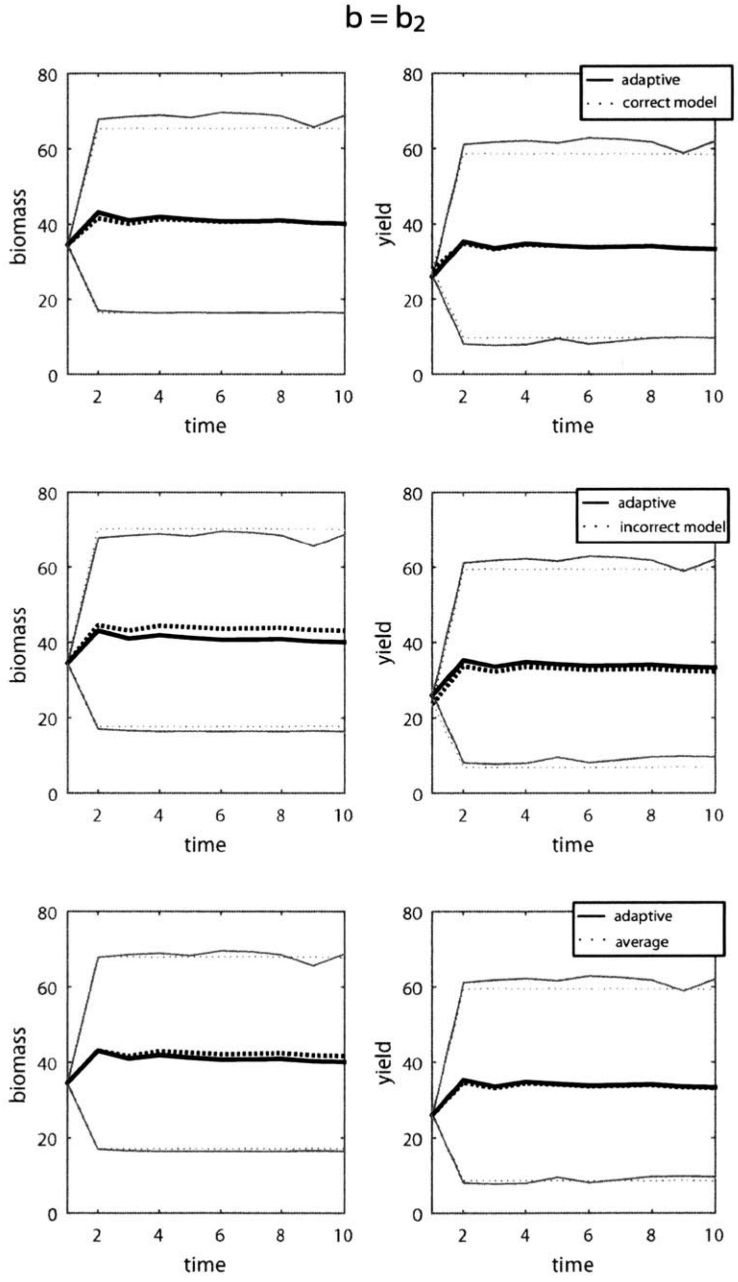

Figure 6-5: Performance of adaptive and non-adaptive management strategies when $b = b_2$. The top panel shows the adaptive policy's performance in terms of stock size (left) and yield (right) versus perfect information. The black lines show average results; the grey lines show the minimum and maximum values. The middle panels contain the results for the adaptive and 'incorrect' model. Finally, I show the performance of the adaptive model and a model that assigns equal weight to each model and does not update this weight. Parameter values are as in figure 6-4.

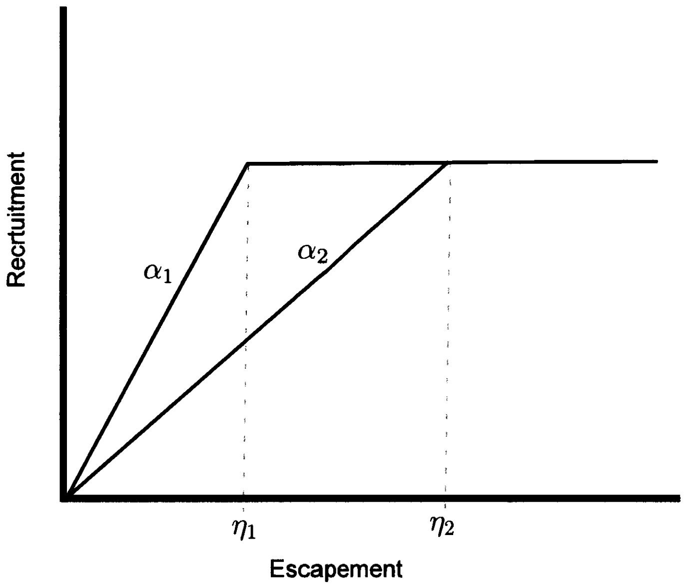

Figure 6-6: A schematic of the potential growth functions (Equation 6.41). Option 1 (growth rate α_1) is an economically viable stock ($\alpha_1 > 1/\delta$), while option 2 (growth rate α_2) is not. The onset of density dependence is at an escapement of η_1 and η_2 respectively.

growth rate at low density, then the optimal escapement in each period is η_1. (To see why, consider harvesting–even for a single period–above η_1; we forgo harvest to do so, but there is no expected gain, since the expected recruitment is still k. Harvesting at lower levels is similarly disadvantageous, but because we are havesting too hard.)

Now let us consider the case in which we are unsure which parameter is correct. Let ρ_t be our belief at time t that α_1 is the correct model. Note that it will never be optimal to leave an escapement larger than η_1; if α_1 is the true value, then we will gain no more fish by sacrificing harvest, while if α_2 is the correct value, we want to escape no fish. Thus, we may restrict our attention to a truncated range of escapements ($y < \eta_1$).

We find that the optimal policy is to harvest either down to η_1 or to 0, depending on the value of the belief state[5] The following section shows how we determined this.

Let us consider a stock of size x_0. If it is fished down to a level y, the expected recruitment in the next period is $\rho_0\alpha_1 y + (1 - \rho_0)\alpha_2 y$. Because the environmental shock is again uniform and our uncertainty constrained to two values, the expectation of $\rho_1 = \rho_0$. So, if we again harvest down to an escapement of y, the expected yield is again $\delta(\rho_0\alpha_1 y +$

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[5] If the stock size is below η_1, no harvest occurs.

$(1-\rho_0)\alpha_2 y - y)$. The expected yield from harvesting at y is then

$$\pi = (x_0 - y) + \frac{\delta}{1-\delta}\left(\rho_0\alpha_1 y + (1-\rho_0)\alpha_2 y - y\right). \tag{6.42}$$

We may then compare the yield of a policy with an escapement of η_1 and one with an arbitrarily smaller y_1:

$$\pi_{\eta_1} = (x_0 - \eta_1) + \frac{\delta}{1-\delta}\eta_1\left(\rho_0\alpha_1 + (1-\rho_0)\alpha_2 - 1\right), \tag{6.43}$$

versus

$$\pi_{y_1} = (x_0 - y1) + \frac{\delta}{1-\delta}y_1\left(\rho_0\alpha_1 + (1-\rho_0)\alpha_2 - 1\right). \tag{6.44}$$

The difference in yield is

$$(\eta_1 - y_1)\left[-1 + \frac{\delta}{1-\delta}\left(\rho_0\alpha_1 + (1-\rho_0)\alpha_2 - 1\right)\right]. \tag{6.45}$$

The policy of harvesting at η_1 is greater if

$$\rho_0 > \frac{1/\delta - \alpha_2}{\alpha_1 - \alpha_2}; \tag{6.46}$$

since we considering an infinite time horizon, this calculate holds for any starting ρ_0, so if at any time our updated belief state falls below that threshold, an arbitrarily smaller escapement is optimal. In fact, we should harvest all the fish at that point, as the expected value of all future harvest is less than the value of fishing down immediately.

6.5 Non-stationary case

Now we turn our attention to adaptive management in a deteriorating environment. The distinguishing feature here is that the growth function, f, changes through time. In Chapter 5 we considered this problem under the assumption that we had perfect information. Here, we relax this assumption, instead assuming that one of the parameters is imperfectly known.

As environmental conditions vary outside the range observed in the historical record, we are likely to see a different type of parametric uncertainty: uncertainty as to how the vital rates depend on these environmental variables. For concreteness, I will focus on temperature as the driver of changing vital rates. For fisheries, this is a sensible choice, because fish are poikilothermic, meaning their internal temperature varies with ambient conditions. The vital rates of fish have been shown to be be strongly temperature dependent (e.g., Munday et al., 2008; Houde, 1989; Donelson et al., 2010; Tanasichuk and Ware, 1987; Reist et al., 2006). However, species respond to temperature changes idiosyncratically (Persson, 1986, e.g.,). For a specific stock, under specific historical and future conditions, we are unlikely to know precisely the dependence of its vital rates on the temperature changes.

The application of adaptive management to populations impacted by climate change is expected to be a complicated task, as climatic changes occur over long time-scales and may involve a high degree of uncertainty from sources other than the parameter of interest (Gregory et al., 2006). On the other hand, as Conroy et al. (2011) emphasizes, adaptive management holds promise for better management in the face of conditions managers have yet to encounter. In this chapter, I attempt to investigate how deteriorating conditions impact adaptive management policies. To this end, I construct a simple example to try to build our intuition about how adding this temporally changing component alters the intuition we built earlier in this chapter. However, note that the logic we used to determine when the active and passive strategies are equivalent still holds–those strategies are equivalent when the preposterior of the belief state does not depend on the control.

The reader may not be surprised to learn that the optimal policy in a changing environment is no longer stationary; this makes sense because we expect that it will be optimal to respond to changes in stock dynamics. Second, building on the results of Chapter 5, we expect that at some time, the optimal action will be to fish the stock down to a low level, perhaps even to extirpation.

6.6 Non-stationary Yield Maximizing Beverton-Holt Model

Here, I extend the simple Beverton-Holt model I developed in section 6.3 to include a vital rate that varies over time. In particular, b, the inverse of the growth rate at low-density,

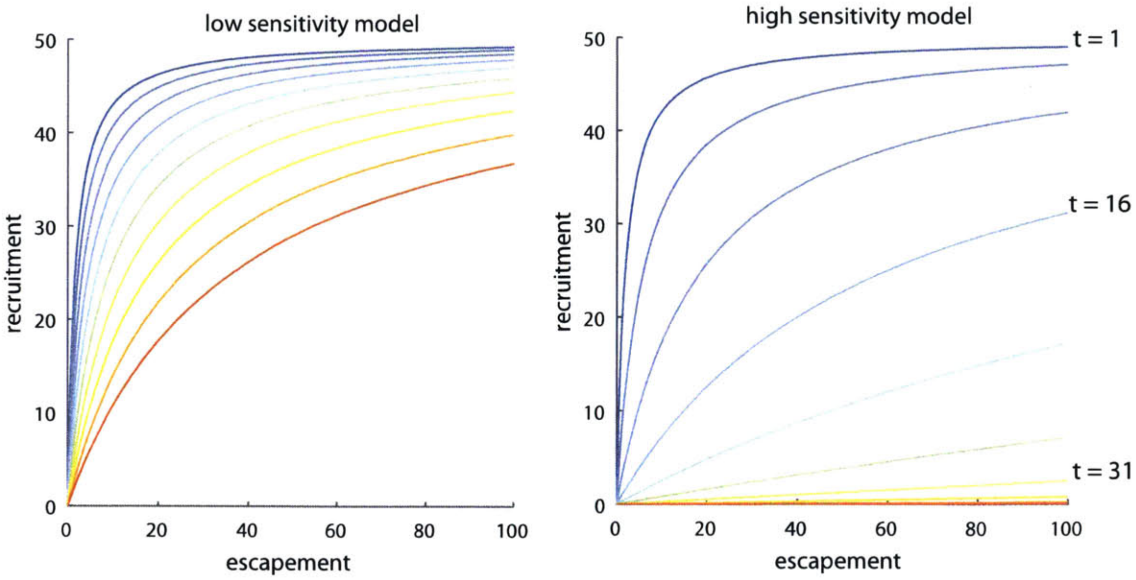

Figure 6-7: The average stock recruitment function over time for two different values of θ. In the first case, θ is 1.26; in the second, it is 1.07. Other parameters are $a = 0.02$, and $b_0 = 0.03$. Cool colors indicate early times, while warm colors indicate recruitment at later times.

varies over time so that the growth rate decreases over time. I specify that $b = b_0\theta^t$, so that as time (which I assume, for simplicity, is correlated perfectly to temperature) goes on, the growth rate decreases. Figure 6-7 shows how how such recruitment curves may look for different parameter values (without stochasticity).

Again, we imagine a Beverton-Holt recruitment function is multiplied by an iid uniform shock (with bounds $1 - w$ and $1 + w$):

$$X_{t+1} = f(y_t, \theta, t)Z_t = \frac{y_t}{b_0\theta^t + ay_t}Z_t. \tag{6.47}$$

Let us consider uncertainty about the sensitivity, θ, of the low-density growth rate to the temperature. We have two candidate values–θ_1 and θ_2. ρ_t will describe our confidence at time t that θ_1 is the correct value. Without loss of generality, let us assume that $\theta_1 > \theta_2$, so that θ_1 is the 'high sensitivity' model.

At the ultimate time-step, the optimal action is to harvest whatever fish remain, as they have no value to us in the future. Note that the value functions and first order conditions that we derive here are similar to those in the stationary case, excepting that the growth function now has a time-dependent term.

$$\begin{aligned} V(x_{T-1}, \rho_{T-1}) &= \max_{0 \leq y_{T-1} \leq x_{T-1}} \Big\{ x_{T-1} - y_{T-1} + \\ &\quad \delta \mathop{E}_{Z_{T-1}, \Theta_{T-1}} \left[f(y_{T-1}, \theta_i, T-1) z_{T-1} \right] \Big\} \qquad (6.48) \\ &= \max_{0 \leq y_{T-1} \leq x_{T-1}} \Big\{ x_{T-1} - y_{T-1} + \\ &\quad \delta \left[\rho_{T-1} f(y_{T-1}, \theta_1, T-1) + (1 - \rho_{T-1}) f(y_{T-1}, \theta_2, T-1) \right] \Big\} \qquad (6.49) \end{aligned}$$

The first-order conditions for a maximum are

$$\frac{1}{\delta} = \rho_{T-1} \frac{\partial f(y_{T-1}, \theta_1, T-1)}{\partial y_{T-1}} + (1 - \rho_{T-1}) \frac{\partial f(y_{T-1}, \theta_2, T-1)}{\partial y_{T-1}}. \qquad (6.50)$$

Going back on period in time, the value function is

$$\begin{aligned} V(x_{T-2}, \rho_{T-2}) &= \max_{0 \leq y_{T-2} \leq x_{T-2}} \Big\{ x_{T-2} - y_{T-2} + \\ &\quad \delta \mathop{E}_{Z_{T-2}, \Theta_{T-2}} \left[V(x_{T-1}, \rho_{T-1}) \right] \Big\} \qquad (6.51) \\ &= \max_{0 \leq y_{T-1} \leq x_{T-1}} \Big\{ x_{T-1} - y_{T-1} + \\ &\quad \delta \left[\rho_{T-1} f(y_{T-1}, \theta_1, T-1) + (1 - \rho_{T-1}) f(y_{T-1}, \theta_2, T-1) \right] \Big\}. \qquad (6.52) \end{aligned}$$

As in the stationary analog, the expectation of the ρ_{t+1} is ρ_t, which allowed us to simplify equation 6.52 so easily. The lack of dependence of the pre-posterior on the control also implies that the passive and active adaptive management policies are identical. If we repeat this procedure backwards in time, we find that the first-order conditions from $T-1$ are repeated at each time step (with their respective growth values at that time).

Figure 6-8 shows the optimal policy over time and over different information states; at a given time, if a stock associated with a particular information state is larger than this value, the stock is fished down to this level, otherwise no harvest occurs. Note that if we are confident (ρ close to 1) that the high sensitivity parameter is true, we fish hard early; the more confident that we are that the low sensitivity model is true, the longer we delay fishing out the stock.

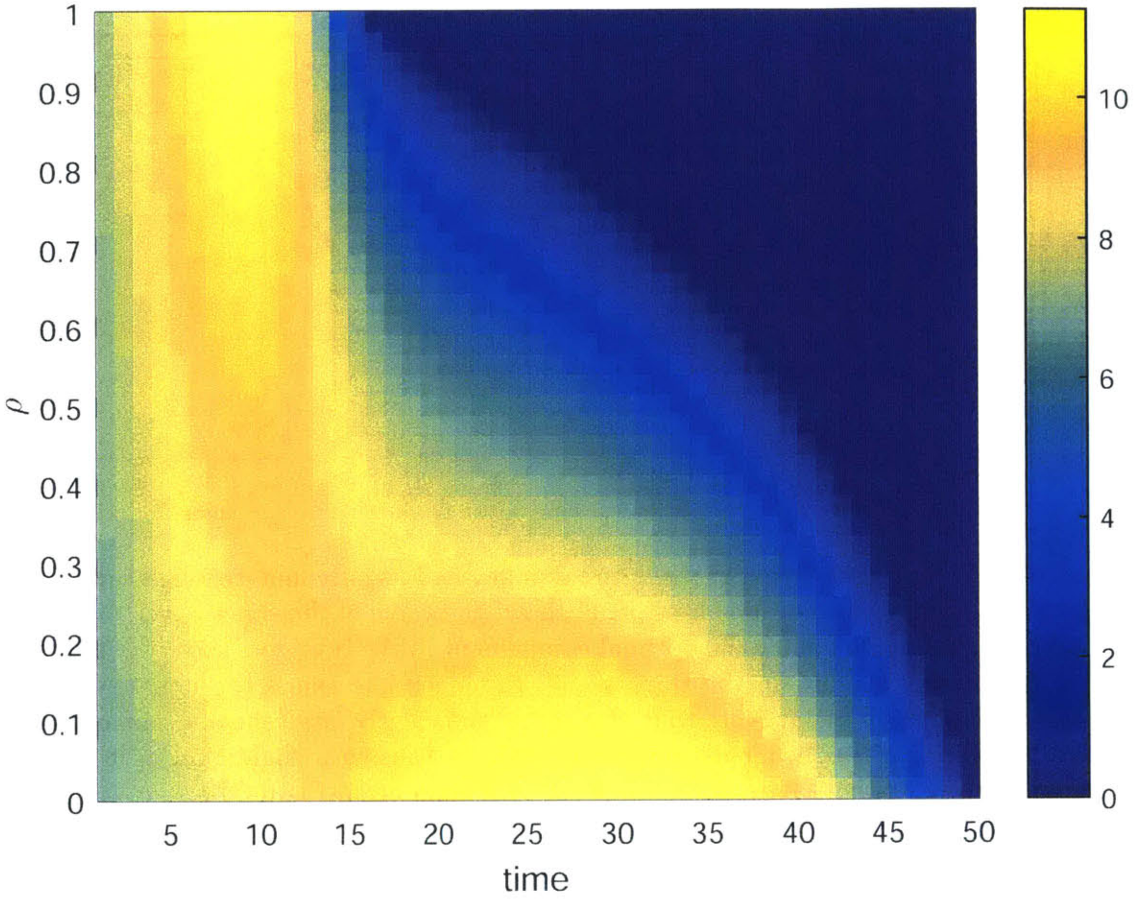

Figure 6-8: Optimal escapement over time and information state. The white area corresponds to the area where the first-order conditions for an optimum no longer exist; optimal escapement is 0. Parameter values $a = 0.02$, $b_0 = 0.03$, $\theta_1 = 0.1$, $\theta_2 = 0.05$, $\gamma = 0.1$, $w = 0.6$, and $\delta = 0.9$.

In figures 6-9 and 6-10 I show the realizations of this policy forward in time under the high and low sensitivity models respectively. As in the stationary model, the information state often changes abruptly, as a sufficiently large (or small shock) reveals the true parameter value instantaneously.

As in the stationary case, I compare the performance of the adaptive policy to a variety of non-learning policies (figures 6-11 and 6-12). When the high-sensitivity model ($\theta_1 = \theta$) is true, the adaptive policy does not differ greatly in performance from the non-learning policies (either incorrect or average). However, when the low-sensitivity model is true, the adaptive policy far outperforms the incorrect and average models in both population size and yield, because the harvester does not anticipate a population decline that is not

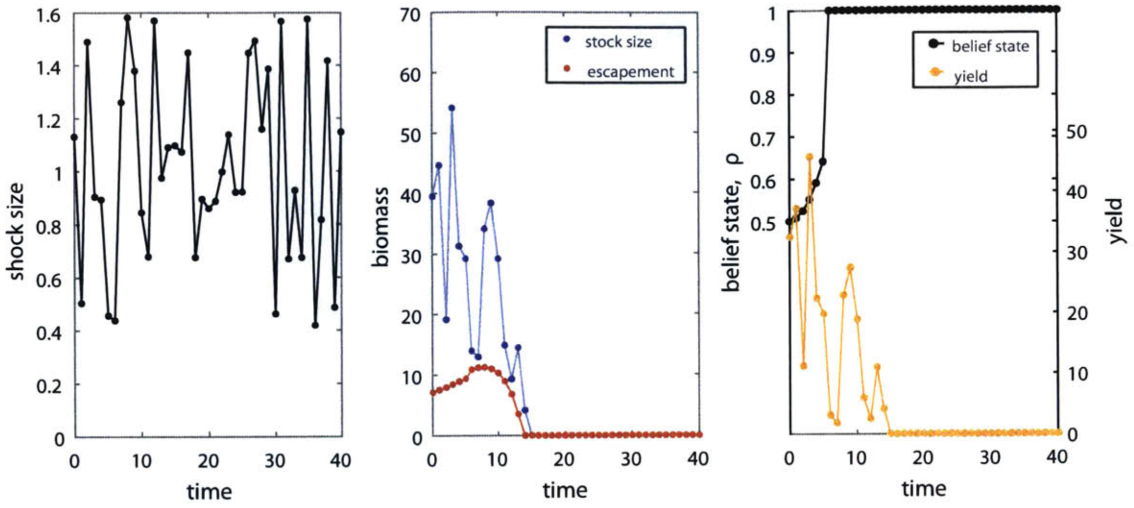

Figure 6-9: A single realization of the optimal policy and its outcomes through time when θ_1 is the true parameter value. The first panel shows the value of the shocks over time. In the second panel, red circles show the optimal escapement, while blue dots show the population size at that time. Finally, in the third panel, the black line shows the belief state, while the orange line shows yield. Note that at $t = 6$, a sufficiently large shock occurred that fell outside the range of recruitments consistent with θ_2, causing a slight 'jump' in the belief state and optimal policy. Parameter values are the same as in Figure 6-8.

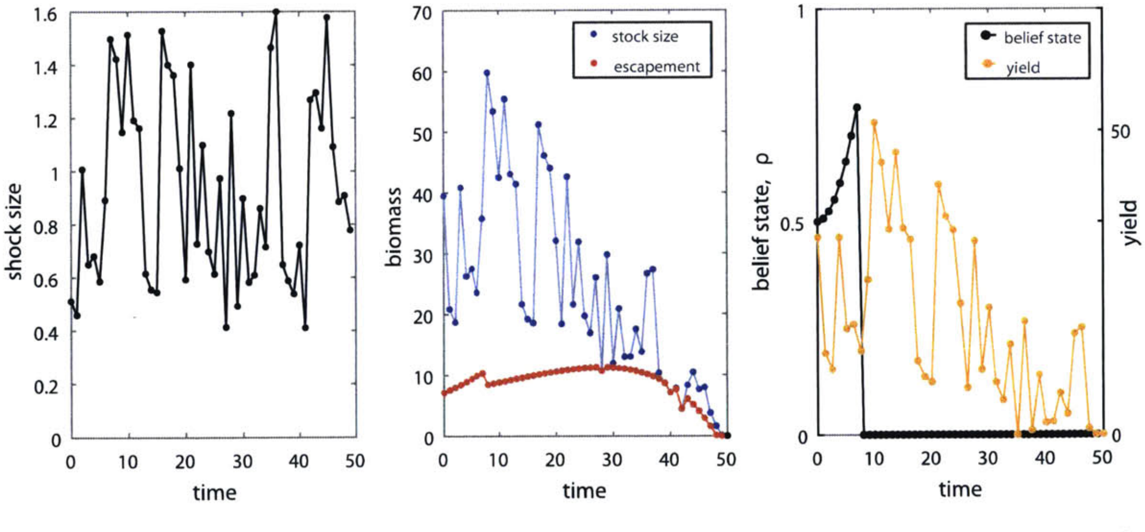

Figure 6-10: A single realization of the optimal policy and its outcomes through time when θ_2 is the true parameter value. The first panel shows the value of the shocks over time. In the second panel, red circles show the optimal escapement, while blue dots show the population size at that time. Finally, in the third panel, the black line shows the belief state, while the orange line shows yield. Note that at $t = 8$, a sufficiently large shock occurred that fell outside the range of recruitments consistent with θ_1, causing a large 'jump' in the belief state and optimal policy. Parameter values are the same as in Figure 6-8.

occuring.

6.7 Conclusion

In this chapter, I outline a few basic properties of adaptive management policies applied to simple, classic bioeconomic fisheries models. In particular, my results highlight that policies should often be pseudo-independent of the initial stock size and highlights cases (in particular, when the shock is uniform) in which the passive and active adaptive management policies are the same. We also extended these analyses to include a trend in time, which is an area that deserves more attention, given its relevance to management in the face of climate change.

The use of a uniform shock significantly simplified calculations such that I could solve for first-order conditions for the optimal policy rather than numerically calculating the entire policy using stochastic dynamic programming. This simplification also comes at a cost–the passive and active policies are equivalent. Changing the functional form of the stock recruitment function (e.g., to a Ricker model) or allowing the shock to multiply a parameter (e.g., $f = yZ/(b + ayZ)$) did not change the preposterior's independence from the escapement. When the active and passive policies differ, the analytical solution does not decouple between periods as it does in this case; the dependence of the belief state on past states creates a sort-of serial dependence among periods. Ignoring this dependence and only forecasting the belief state one-period ahead tends to create very poorly performing policies (the examples I tried had much lower yields than the passive adaptive management policy). Analytical and computational difficulties aside, calculating the active adaptive policy (when it differs from the passive policy) is attractive because it allows us to tackle questions about optimal experimentation, which I was unable to do in this chapter.

In doing this work, I found that the computation of optimal policies was quite sensitive to how finely discretized the state space was. This sensitivity became more pronounced when parameter uncertainty was added. One difficulty that this highlights is that when analytical results are not available to compare–as is most often the case–it is difficult to tell if a complicated policy is a numerical artifact or if it is reflective of the true policy. I

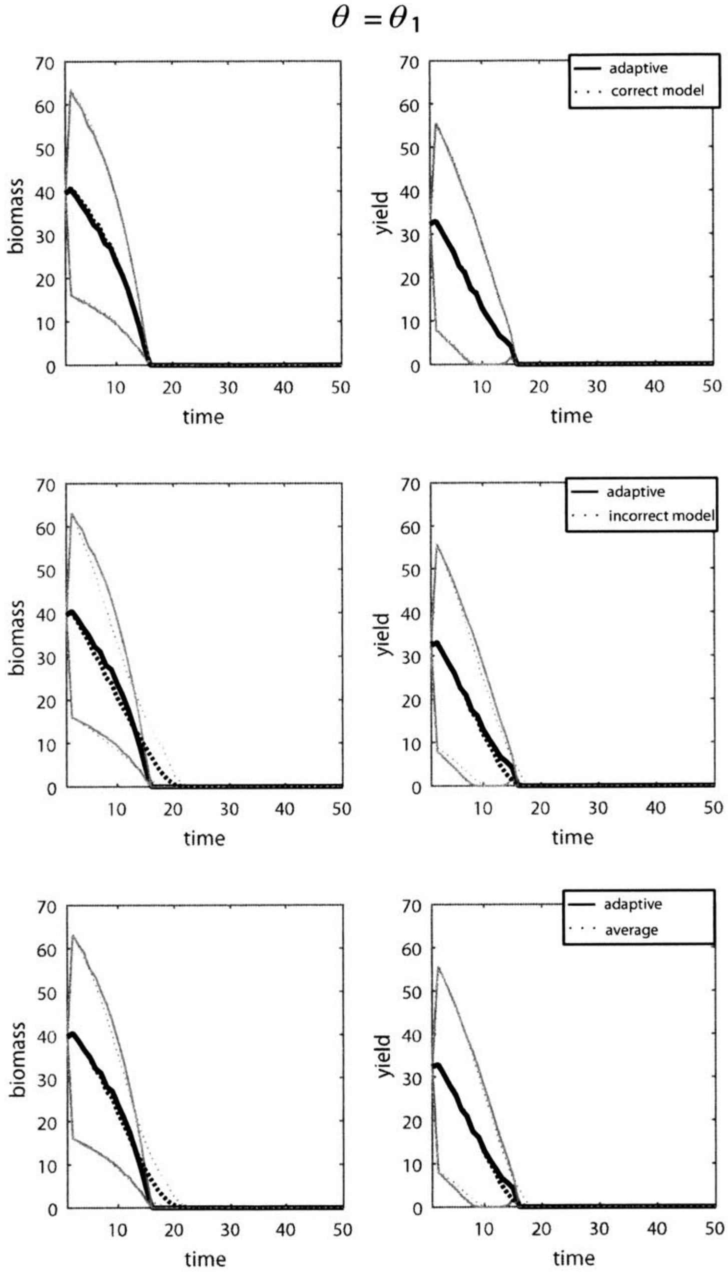

Figure 6-11: Performance of adaptive and non-adaptive management strategies when $\theta = \theta_1$. The top panel shows the adaptive policy's performance in terms of stock size (left) and yield (right) versus perfect information. The black lines show average results; the grey lines show the minimum and maximum values. The middle panels contain the results for the adaptive and 'incorrect' model. Finally, I show the performance of the adaptive model and a model that assigns equal weight to each model and does not update this weight. Parameter values are as in Figure 6-8.

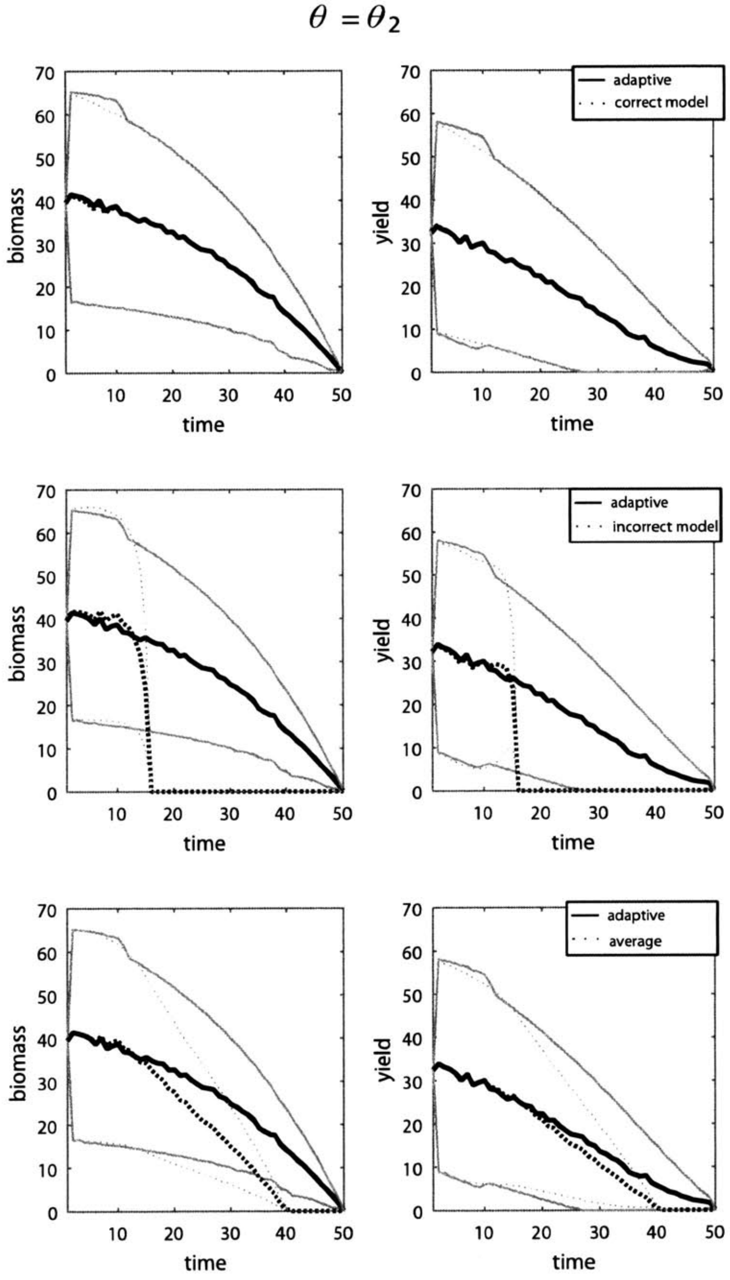

Figure 6-12: Performance of adaptive and non-adaptive management strategies when $\theta = \theta_2$. The top panel shows the adaptive policy's performance in terms of stock size (left) and yield (right) versus perfect information. The black lines show average results; the grey lines show the minimum and maximum values. The middle panels contain the results for the adaptive and 'incorrect' model. Finally, I show the performance of the adaptive model and a model that assigns equal weight to each model and does not update this weight. Parameter values are as in Figure 6-8.

believe that this mismatch is another reason to push in the direction I've been working, so that we may build better intuition as to when this is the case.

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Chapter 7

Discussion

Charles E. Fryer noted that "it is difficult, but who shall say that it is impossible, to discover...the causes of these fluctuations and occasional failures of a fishery..." (Fryer, 1883). Now technologies have improved our ability to monitor both fish and their environments (underwater vehicles, satellites, etc.), and sophisticated models have helped uncover the processes that influence population dynamics. Moreover, the scientific community has moved beyond simply seeking to understand 'the causes' of stock fluctuations towards controlling them and optimally managing wild fish stocks.

In this thesis, I have created and analyzed a collection of models concerning the management of fish stocks undergoing change. As a whole, my work suggests that accounting for change in fisheries fundamentally alters optimal management. Thus, the identification of fisheries that are impacted by, for example, habitat damaging harvest or rising temperatures is critical to optimal management. Here, I briefly summarize key findings from each chapter and suggest some promising directions for further investigation.

In Chapters 2 and 3, I developed models in which the changes result directly from harvesting.

In Chapter 2, I found that including harvest-induced habitat damage in a spatially-implicit patch-occupancy model did not incentivize the creation of no-take marine reserves as part of a profit-maximizing harvesting strategy. Reserves were, however, a relatively low-cost way to protect biodiversity. The approach I took is novel in its coupling of a patch-occupancy model to an economic model, which allowed me to include multiple species in a spatial context. This approach could be used to study other multispecies systems with different trophic interactions (see, for example, competition, in Hastings (1980), who studied an unharvested multispecies competition model) or objective functions. In addition, I studied the equilibrium dynamics and harvest rates, all in a spatially implicit framework. An investigation of the transient dynamics or explicit spatial interactions (e.g., with a cellular automaton model) would provide additional insight. For example, we could ask how long after the establishment of marine reserves would diversity benefits be realized. Or, does the spatial arrangement of patches and the dispersal ability of species change the general results I found in the spatially implicit model? Given the paucity of studies on the optimal management of multi-species fisheries (especially using spatial models), I believe there are many attractive, open questions that can be fruitfully addressed with a similar methodology.

Next, in Chapter 3, I constructed a two-patch model and included the rapid evolution of dispersal in response to harvest pressure. The evolution of dispersal essentially decoupled the two patches so the closure of a patch as a marine reserve ceased to be part of the profit maximizing strategy. However, I found that the evolutionary stable optimal harvesting strategy is not economically stable over shorter time scales, since such a strategy is sub-optimal between rare mutation events. To my knowledge, this is the only work that couples the optimal harvest of a stock with the evolution of dispersal.

To start, my co-authors and I made several simplifying assumptions. We investigated the optimal harvest at equilibrium and assumed that the evolution of dispersal was very rapid. We also did not treat dispersal or its evolution mechanistically. An investigation of optimal harvesting dynamics over time, when the rate of evolution–depending on rare mutations–is slow, might produce different optimal harvesting strategies. In contrast, allowing selection over the existing phenotypes may produce different results.

In Chapters 4 through 6, I considered climate change as example of an exogenous (to the harvester) source of change to the fishery.

I first describe in (Chapter 4) a statistical test for detecting unambiguous shifts of populations in space. The extension of the concept of stochastic dominance into distribution ecology promises to useful. If a later distribution is stochastically dominant to an earlier one, the population distribution moved only in the direction of interest, making stochastic dominance a stronger condition than the shift of the centroid or tail of the distribution alone. Applications of this methodology are particularly promising. A comparison of the results of studies using other metrics of change (e.g., movement of the centroid) with the results of my stochastic dominance test, would reveal the circumstances under which the methods produce contradictory conclusions.

In Chapter 5, I investigated the impacts of a continuously deteriorating environment on the optimal harvest of a fish stock. This work demonstrated how complicated the optimal response to changing vital rates may be; I found a non-monotonic optimal escapement schedule was optimal when fecundity declined over time, while monotonically decreasing escapement was optimal when mortality increased. I showed that density dependent dynamics are particularly important in structuring the shape of the optimal response. My results also suggest that the extirpation of a stock may be economically optimal, which highlights the importance of specifying the management goals for a fishery as well as the management time scale. My general results hold for a large class of growth and cost functions, but extending these analyses to more complicated growth functions would be useful. In addition, the objective I analyzed was profit (or yield) maximization. This objective is one of many potential objectives; one can imagine placing value on the size of stock for conservation, for tourism, or for other ecosystem services. Changing the objective function to account for such "existence value" may qualitatively change the optimal harvest (e.g. Kellner et al., 2011). The alteration of the objective function may be particularly interesting in the deteriorating habitat cases, valuing because the existence value would offset the eroding in situ value derived only from future harvest.

Finally (in Chapter 6), I extended the models I described in Chapter 5 to include uncertainty about the parameters. I attempted to characterize basic properties of optimal harvest policies for unchanging stocks and to contrast these with the properties for stocks that change over time. I focused on very simple models that were relatively analytically tractable to attempt to understand how the optimal adaptive management policy arises. Even small complicating additions (e.g., non-uniform shocks, maximizing profit instead of yield) necessitate numerical methods. Given the analytical and computational challenges associated with adaptive management, this work merely scratches the surface of the questions we might pose. In particular, further attention to the relative impacts of different types of uncertainty (e.g., parameter versus state uncertainty) on the form of optimal harvest policy. Investigation of a broader range of examples and case studies may also help highlight qualitative differences among optimal policies and the the systems that give rise to those policies. As others have suggested (e.g., Chades et al., 2012), adaptive management problems are computationally difficult, and improvements in numerical methods, including heuristics, are needed.

I have incorporated single sources of change in analyses. In reality, fish stocks are subjected to multiple stressors operating simultaneously. For example, a stock experiencing warming temperatures may be also impacted by trawling that damages spawning habitat. Analysis of singe stressors is foundational to further understanding, which may include modeling the interactions among these stressors or the comparison of more complicated management tools to achieve different objectives. We continue to accumulate longer-term data on fish stocks and gain more knowledge about the dependence of fishes' life-histories on environmental stressors. It is important to couple these observations with models that will help us determine which stressors are likely to impact management and what management changes might result.

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