

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

**CONCEPTUAL TOOLS FOR MANAGING TWO MONTEREY BAY
FISHERIES**

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Teresa Lin Ish

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The Thesis of Teresa Lin Ish
is approved:

Professor Marc Mangel, Chair

Professor Margaret McManus

Professor Baldo Marinovic

Frank Talamantes
Vice Provost and Dean of Graduate Studies

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Conceptual tools for managing two Monterey Bay fisheries

Teresa Lin Ish

Abstract

I developed two conceptual models addressing fishery questions in the Monterey Bay motivated by 1) the California Market Squid (*Loligo opalescens*) and 2) marine reserves as a recovery and management tool. The model for California Market Squid incorporates the close ties between environmental variability and squid life history. Inclusion of environmental factors in the model provides a biological mechanism contributing to the large fluctuations that occur in the fishery. Furthermore, I predict that removal of 30% of the unspawned SSB may drive the population to extinction within 30 generations.

Reserves are generally agreed to be good for habitat and ecosystem conservation; however, specific measures of success, such as increases in yield or size at age have been difficult to generalize across reserves. I identify density dependent body growth and displaced fishing effort as potential explanations for the variable outcomes. I predict that density dependent body growth will reduce length at age inside reserves, even if mean length in the reserve increases. I also predict that although reserves increase yield, nothing maximizes yield as well as conservative fishing practices, and that displaced fishing effort decreases benefits of reserves, indicating the need to reduce effort, as well as create reserves.

I would like to thank my advisor Dr. Marc Mangel and my committee, Dr. Margaret McManus and Dr. Baldo Marinovic for their wisdom and support. I would also like to thank the Mangel Lab for a number of comments and collaborations, as well as contributing to an enjoyable graduate career. Finally, I would like to thank my family, friends, and Eric Logue for the emotional support that they've given me during my entire education. It is also important for me to recognize Jennifer Ramsay and Stephanie Zabitz for dealing with me on a day-to-day basis while I was completing this project.

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Introduction

In this thesis I will model two biologically and commercially important species found in the Monterey Bay. Through the use of descriptive and conceptual models, I hope to provide insight into the biology and the management of the fisheries for the California Market Squid, *Loligo opalescens*, and lingcod, *Ophiodon elongatus*.

The work on the market squid focuses on some of the factors that may be influencing population dynamics both within a generation and across generations. *L. opalescens* is a semelparous, annual species, and individuals are spawned throughout the year. Harvest occurs inshore on the spawning grounds. Squid are highly sensitive to environmental fluctuations, with catch rates declining 6-fold in El Niño years compared to non-El Niño years. I develop a life history model that links squid growth and reproduction with environmental factors, particularly upwelling, temperature, and food abundance, in a consistent Darwinian framework. Using these factors, I analyze multigenerational dynamics and the effect of harvest of unspawned adults on population dynamics, and show that increasing removal of unspawned adults is predicted to result in a decline in population growth rate and lead to overfishing.

Marine reserves are gaining prominence as fisheries management tool. Moreover, there is a dearth of information that concretely proves or disproves their success in terms of improving fisheries yields, increasing abundance or

size, or protecting spawners, to name a few goals. Using lingcod as a model organism, I explore density dependent somatic growth as a mechanism for population regulation and growth inside and out of a marine reserve. I also explore the effect of displaced fishing effort (the movement of fishing mortality from the reserve to the area outside the reserve) on recovery and yield. I use this model to help explain the wide variety of results that have resulted from empirical studies. The model incorporates a variety of reserve sizes and fishing mortalities, and an analysis of displaced fishing effort. I predict that displaced fishing effort increases population recovery time, while density dependent growth decreases it. I also predict that, while yield increases after reserve creation, conservative fishing maximizes it.

These models serve as conceptual as opposed to calculational tools (sensu Mangel et al 2001), but their benefits to management are not diminished. While calculational tools are intrinsic to making predictions regarding stocks and making immediate management decisions, their accuracy is hinged on understanding and interpreting the biology and ecology of the fished species. Conceptual tools can help increase understanding and will allow fisheries scientists to gain insight into their system and improve their ability to manage the fisheries. Furthermore, they can be applied to a variety of species in a number of habitats.

Chapter 1: Environment, Krill and Squid: From Fisheries to Life Histories and Back Again

Introduction

The California market squid, *Loligo opalescens* Berry, has had an active fishery for over 150 years, yet remains almost completely unregulated (Vojkovich 1998). After maintaining an open access fishery during this time, permits were required in 1998 (Yaremko 2001). The most recent management recommendation by the California Department of Fish and Game (CDFG) includes 1) a yearly quota of 125,000 tons, 2) a reduction in the number of permits issued by 45% of current levels, 3) an expansion of the weekend fishing ban in place in Southern California to the Monterey Bay, and 4) the possible adoption of no-take spawning areas (Mangel et al. 2002).

Currently in California, the fishery for market squid is the largest in both value and tonnage, with 2000-2001 landings in Southern California reaching 115,670 mt and Central California landings at 7,730 mt, coming to a total of 123,401 mt, down slightly from a total high of 126,722 in 1999-2000 (CDFG 2002). With strong demand for squid, more participants enter the fishery from either out of state or other fisheries and landings have continued to rise (Pomeroy and Fitzsimmons 1998). Catch fluctuates dramatically in response to variable environmental conditions, such as El Niño-Southern Oscillation events (ENSO) (Vojkovich 1998; Rodhouse 2001) (Figure 1.1). For

example, the estimated maximum sustainable yield during ENSO events is often up to ten times less than the established yearly quota of 125,000 tons (CDFG 2002).

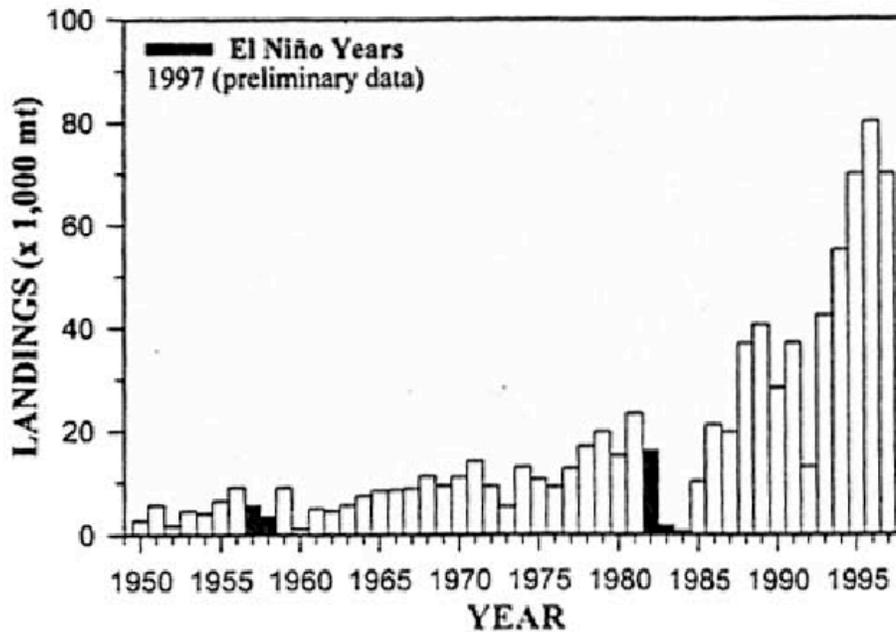


Figure 1.1 Annual catch for the state of California from 1950-1996. From Vojkovich 1998.

In 1984, 1993, and 1997 statewide landings plummeted during El Niño conditions (Figure 1.1; to 1996 only), despite an overall increasing trend in catches. In both the Southern California and Monterey Bay fishery, catches recovered after the declines, however squid landings have recovered more slowly in Monterey (Vojkovich 1998; Mangel et al. 2002). Important technological, capacity and regulatory changes that contribute to increases in catch per unit effort (CPUE), measured in tons per successful landing, that have occurred, beginning in the early 1980s, appears to have increased, for the

fishery as a whole. The increase in CPUE may reflect these changes more than an increase in the availability of squid (Mangel et al. 2002).

Fishing occurs primarily at night with purse seines, which surpassed lampara nets as the most common harvest method in 1989 following the removal of their ban in the Monterey Bay (CDFG 2002; Mangel et al. 2002). Squid are phototaxic and daytime visual predators, thus are attracted to high-powered lights hung over the edges of special light vessels. When many squid have aggregated, the seines encircle the squid, catching large quantities in a single netting (Vojkovich 1998). The fishery for adult squid occurs in the spawning grounds near shore. Peak catches occur during the fall and winter off southern California, and during late spring and summer in central California. From port samples collected, the average age of harvested market squid was 188 days (~27 weeks) (CDFG 2002).

L. opalescens also plays a crucial role in the California Current food web, acting as a major prey item for a number of marine mammals and birds, and a variety of commercially important fish species, such as rockfish, salmon, and sanddabs. All of these species feed on “market sized” squid, up to 180 mm mantle length (ML), and these squid often comprise a large percentage of the animals’ diets. In addition, squid feed heavily on krill (euphausiids), a potential fishery (although it is illegal to land or fish krill in state waters), and are in direct competition with commercially important species (Morejohn et al. 1978). Thus, squid form the penultimate link of a relatively simple, trophic system

consisting of upwelling-induced nutrient enrichment, phytoplankton, krill, squid and the various predators of squid (Mangel et al. 2002) (Figure 1.2).

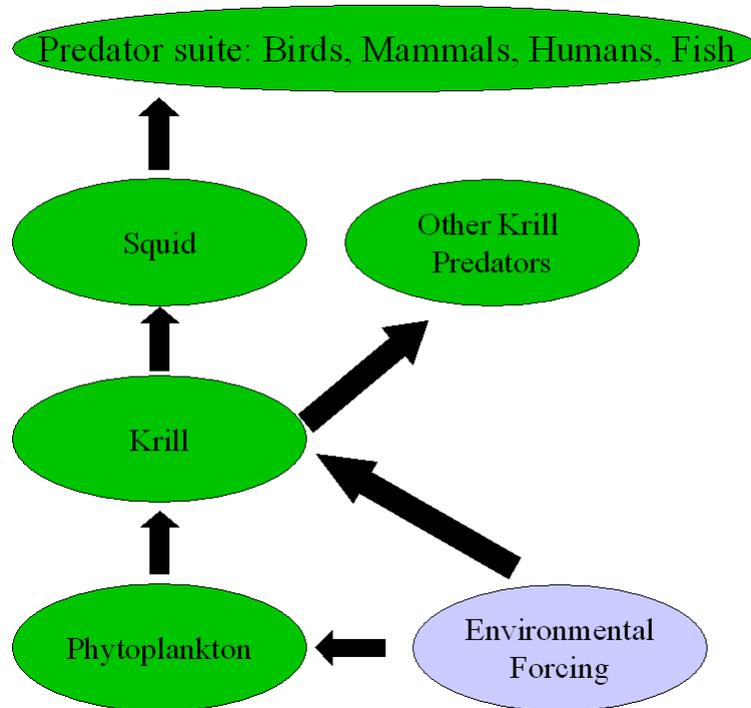


Figure 1.2 A simple foodweb linking the environment, krill, and squid.

The productivity of this linked system is strongly affected by inter-annual events such as El Niño. Large-scale declines in zooplankton (and especially krill) abundance occurred in the central California upwelling system during the 1997/98 El Niño (Marinovic et al. 2002), and similar observations were made off southern California during both the 1982/83 and 1997/98 El Niño events (McGowan et al. 1998). As described above, market squid landings in California declined dramatically following both these events. The abundance and spatial distribution of krill is also connected to environmental

conditions within a year (Figure 1.3; see Mangel 2002 for further details on calculation of the upwelling index). We are thus lead to consider the relationship between environmental forcing, krill availability and squid in the context of the fishery. More detailed food webs can be found in the literature (see, e.g. Morejohn et al. 1978). The Ecosystem Advisory Panel (Fluharty et al. 1999) recommended the development of such food webs for use in Ecosystem Management Plans that mimic Fishery Management Plans.

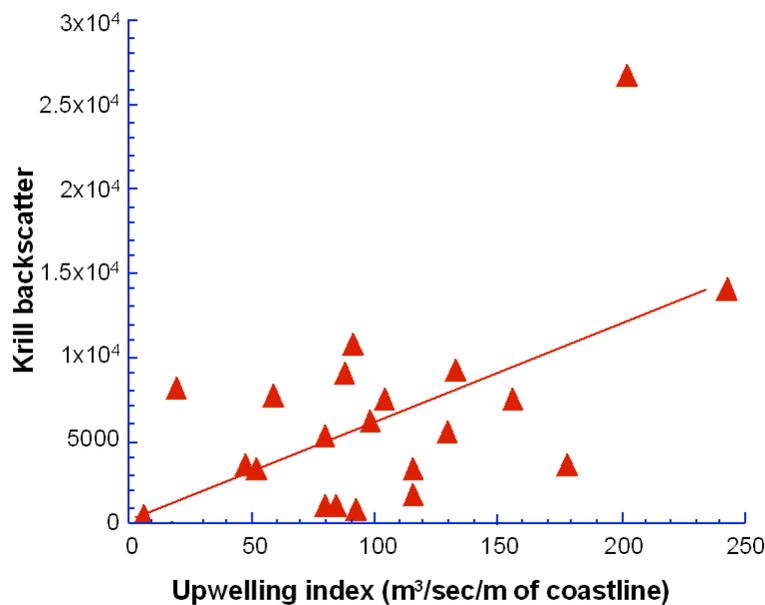


Figure 1.3 Krill backscatter, a proxy for krill abundance, in relation to upwelling from Mangel et al (2002).

Life history of Loligo opalescens (Berry)

The California Market Squid is an annual, semelparous species living a maximum of one year (CDFG 2002). Semelparity makes squid more prone to

environmental fluctuations (Rodhouse 2001), and makes management very difficult because there are large population fluctuations between years (Brodziak and Rosenberg 1993); (Anderson and Rodhouse 2001). In addition, if there is poor or no recruitment in a particular year, the local population may crash leaving no “safety” stock that can reproduce.

L. opalescens ranges from Baja California, Mexico to Alaska (Fields 1965; Wing and Mercer 1990), with spawning grounds located off of central and southern California. Squid spend most of their life offshore, until reproduction, when they move inshore to depths of 3 m to 180 m (Hixon 1983). Egg capsules are found year around in Monterey Bay, with the greatest concentrations inshore during the spring and summer (Fields 1965). Boyle (1995) found that *L. forbesi* carry a wide size range of eggs, indicating that squid may continuously spawn for several months. Females lay a cluster of capsules, each containing 180-300 eggs (Fields 1965; Okutani and McGowan 1969), which hatch in 3-5 wks. into larvae with a length of 2.5-3 mm, resembling adults (Yang et al. 1986). Larvae grow exponentially until they approach a juvenile stage, when their growth slows (Spratt 1979), until they reach an asymptotic size of 230 mm mantle length (O'Dor 1982) or 305 mm total length (TL) (Vojkovich 1998) and weigh 56-84g (Fields 1965).

Females mature at sizes ranging from 81 mm ML to 140 mm ML; mean size at maturation increases from April to November. Twenty-five to 50% of the total body weight in fully mature females constitutes reproductive organs

(Fields 1965). Yang et al (1986) reared *L. opalescens* in captivity from eggs to an age of 250 days (35.7 weeks), and spawning began on day 173 (week 24.7).

Understanding the life history of *L. opalescens*, and describing the mechanisms that drive squid behavior is crucial, if reasonable and effective management policy is to be made. There are already data that show the availability of squid to the fishery year round, with peaks in April and November. However, there has been little explanation of this phenomenon. We seek to provide insight into the life cycle of squid and the importance of that life cycle for the fishery, through analysis of environmental variation, prey variation, and life history variation.

Within-Season Analyses

The life history patterns just described suggest that we should consider within-season as well as between season information. Here, we report on two such analyses.

First, we analyzed the sizes of squid collected from surveys on the fishing grounds of the Channel Islands and Monterey Bay by our colleagues Baldo Marinovic and Nancy Gong (Figure 1.4). These data show a wide range of sizes at which squid enter the fishery (and consequently, a wide range of size at maturity). Then, we simulated 100 squid from early winter until all had died or moved inshore to reproduce. A fitness decision matrix determines movement inshore, with decision in the matrix set to maximize fitness. For example, it might be that squid use a time-based rule for moving inshore in

which after a certain length of time offshore, inshore movement occurs. They might use a size-based rule in which movement inshore occurs once a size threshold is crossed (although the wide range of inshore sizes suggests that this is unlikely). Finally, they might use a size and time based rule, in which the threshold for inshore movement varies according to time of year.

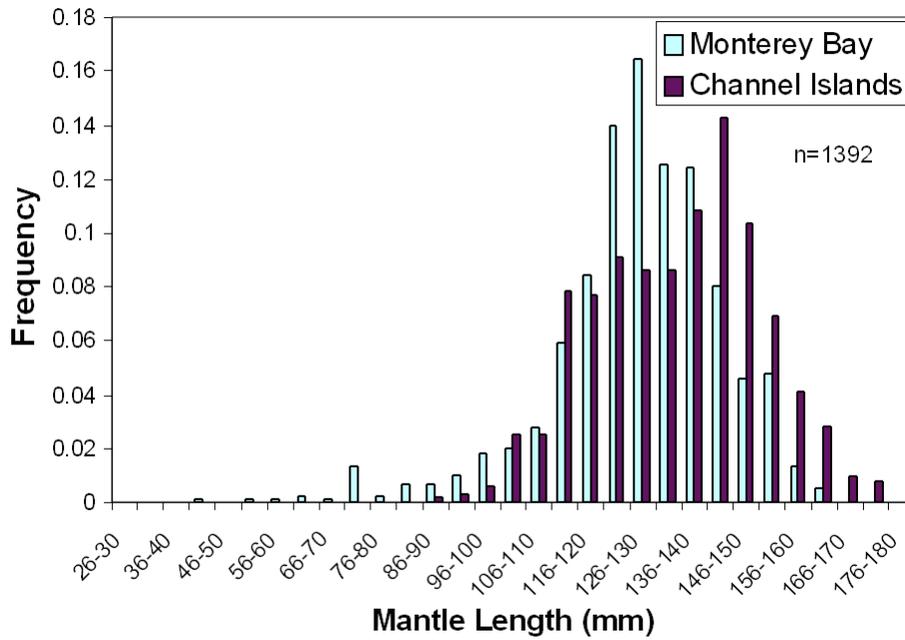


Figure 1.4 Size distribution of squid collected inshore from April to December of 2000 collected by our colleagues, Dr. Baldo Marinovic and Nancy Gong.

A Life History Model for Squid

In order to explain the mechanism behind the varying sizes and times at which squid are found inshore, we developed a life history model (Clark and Mangel 2000) for the squid, in which a genetic program of development and maturation is cued to environmental factors. We use the model to determine the

pattern of growth and maturation that maximizes a squid's reproductive fitness, and by doing this provide a possible explanation for the varying size and age distributions observed within the squid fishery, as well as the continuous movement of squid inshore.

The model includes components of adult growth, survival and reproduction and juvenile growth and survival. Darwinian fitness is a result of both survival and fecundity; we can incorporate inter-annual environmental fluctuations, such as El Niño events, through the inclusion of growth and survival.

Constructing the Dynamic Programming Equation

We assume that natural selection leads to patterns of growth, maturity and reproduction that maximize the long-term number of descendants (Houston and McNamara 1999; Clark and Mangel 2000). As a proxy for long-term number of descendants, we use the estimated number of grand-offspring (also see Mangel and Clark 1988; Clark and Mangel 2000). For this reason, the model covers a time span of 58 weeks, ranging from an arbitrary starting point, set to the end of March, and running a complete year, to the time at which the last laid eggs have hatched, given a five week incubation time in colder waters (Fields 1965). By completing a full lifecycle for a generation, we determine the survival and fecundity of the adult squid, and the size of the following generation as a proxy for their reproductive output.

Table 1.1 Parameter description and interpretation

Parameter	Interpretation
$E(y)$	Environment in year y
$L(E)$	Asymptotic size when environment is E
$W(t)$	Weight at week t within the year (determined allometrically from length)
$L(t)$	Length at week t within the year
$k(t,E)$	Growth rate at week t when environment is E ($=1, 2$)
m	Weekly mortality rate ($=.038$) from assumption that annual mortality is 0.2
g	Gonadal weight ($=25-50\%$ of body weight) (Hixon 1983)
W_0	Egg weight ($=0.0001$ g) calculated from $L(1)$
b	Estimated allometric exponent in fecundity-length relationship ($=3.9$)
$L_{bi}(t)$	Size of offspring laid in week t at the start of next year's fishery if the next year environment is normal ($i=1$) or El Niño ($i=2$)
$S_{bi}(t)$	Survival of offspring laid in week t to the start of next year's fishery if the next year environment is the same ($i=1$) or different ($i=2$) from the current environment
m_b	Size dependent mortality for juveniles
m_0	Size independent mortality for juveniles
M_R	Egg and juvenile mortality estimated so \square_{GM} in an unfished population is 1

We assume two general environments: a warm, low food availability environment, with higher growth rates but smaller asymptotic size and a cold, high food environment with a lower growth rate but larger asymptotic size (see Table 1 for symbols and interpretations). These represent El Niño years and non-El Niño years respectively.

Growth rate in a seasonally and annually fluctuating environment

The growth rate (k) of juvenile and adult squid in week, t , with environment, E , is determined by temperature (Grist and des Clers 1999).

Growth rate is given by

$$k(T(t), E) = 0.001\{0.916T(t) - 7.35\}, \quad (2)$$

where $T(t)$ is temperature ($^{\circ}\text{C}$). We used historical offshore sea surface temperature data, averaged by month, from around Monterey Bay, CA collected from NOAA-CIRES (http://www.cdc.noaa.gov/PublicData/data_faq.html) to calculate maximum and minimum temperatures, a summer and winter temperature. These temperatures allowed us to suppress the temperature component in Eqn 2. Assuming that local variation can be accounted by log-normally distributed process error (Hilborn and Mangel 1997), the growth rate becomes

$$k(t, E) = 0.02E + 0.015E + \cos\left(\frac{2\pi t}{52}\right) \exp\left[Z_{\sigma}(t) - \frac{1}{2}\sigma^2\right] \quad (3)$$

The resulting growth rate oscillates, reflective of the seasonal temperature variation, (Figure 1.5a).

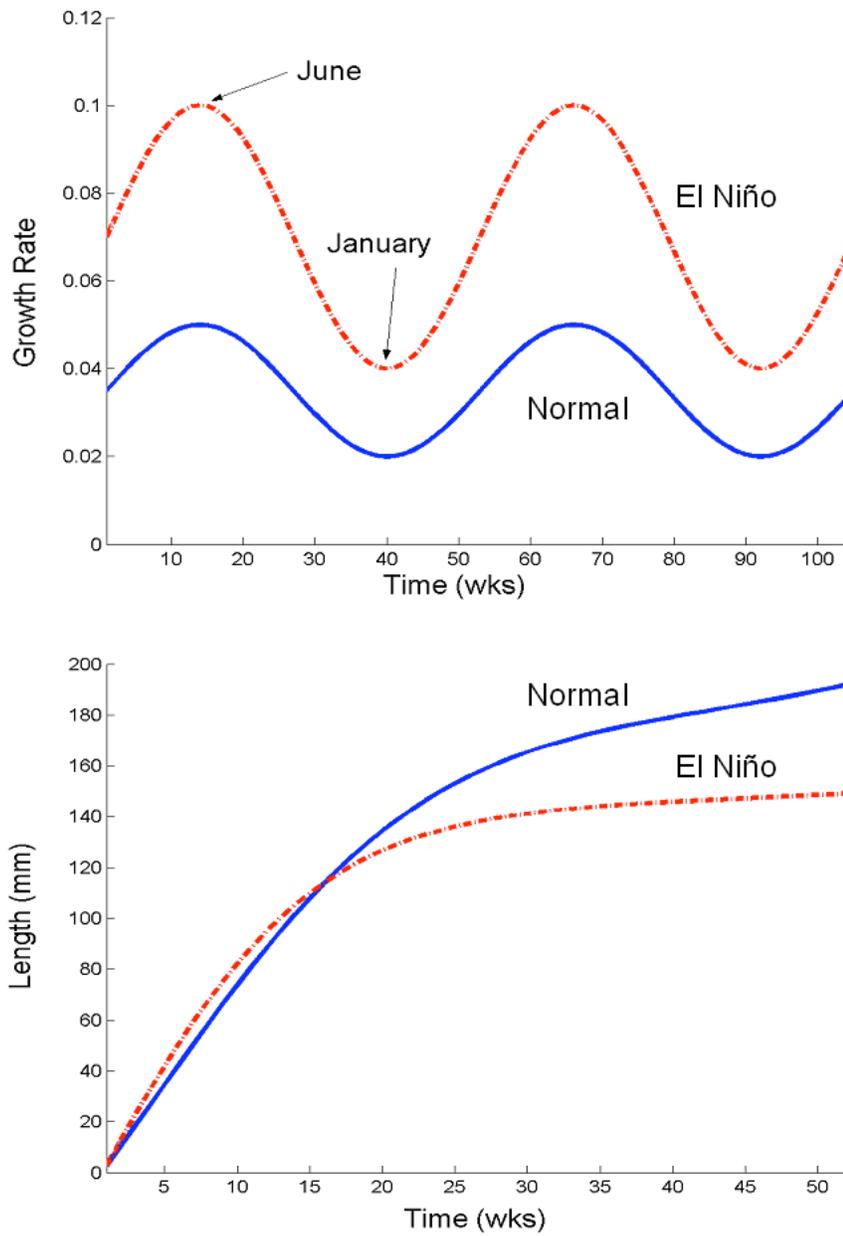


Figure 1.5 Growth rate (a) showing seasonality and the von Bertalanffy growth trajectory (b) for both environments.

We assume that growth follows von Bertalanffy equation (von Bertalanffy 1957) in which asymptotic size, $L(E)$, is a function of environment through the availability of krill;

$$\frac{dL}{dt} = k(t, E)(L(E) - L(t)). \quad (4)$$

Assuming that $k(t, E)$ is constant over each time step (=one week), equation 4 can be integrated and written in the discrete form

$$L(t+1) = L(t) \exp\left[-k(t, E) \exp\left[-\frac{1}{2} \Delta t^2\right]\right] + L(t) \exp\left[k(t, E) \exp\left[-\frac{1}{2} \Delta t^2\right]\right] \quad (5)$$

The length dynamics in the two environments are shown in Figure 1.5b.

Juvenile growth and survival with inter-annual environmental variability

Juveniles may experience a different environment than their parents. In the current version of the model, there are four possibilities: 1) normal conditions can remain normal, 2) normal conditions can turn to El Niño conditions, 3) an El Niño year can become normal, or 4) El Niño conditions can persist for 2 years. In each of these environmental regimes, squid have a different growth pattern due to changes in growth rate, because of the temperatures associated with each environment, and the asymptotic size, because of different levels of food availability. If outcome 1 or 4 occurs, the squid continue to grow on the same trajectory as their parents; however if outcomes 2 or 3 occur, the offspring squid change their growth pattern at the time that the environment changes, either shrinking due to decreases in food, in

the case of outcome 2, or approaching a larger asymptotic size, in the case of outcome 3 (Figure 1.6).

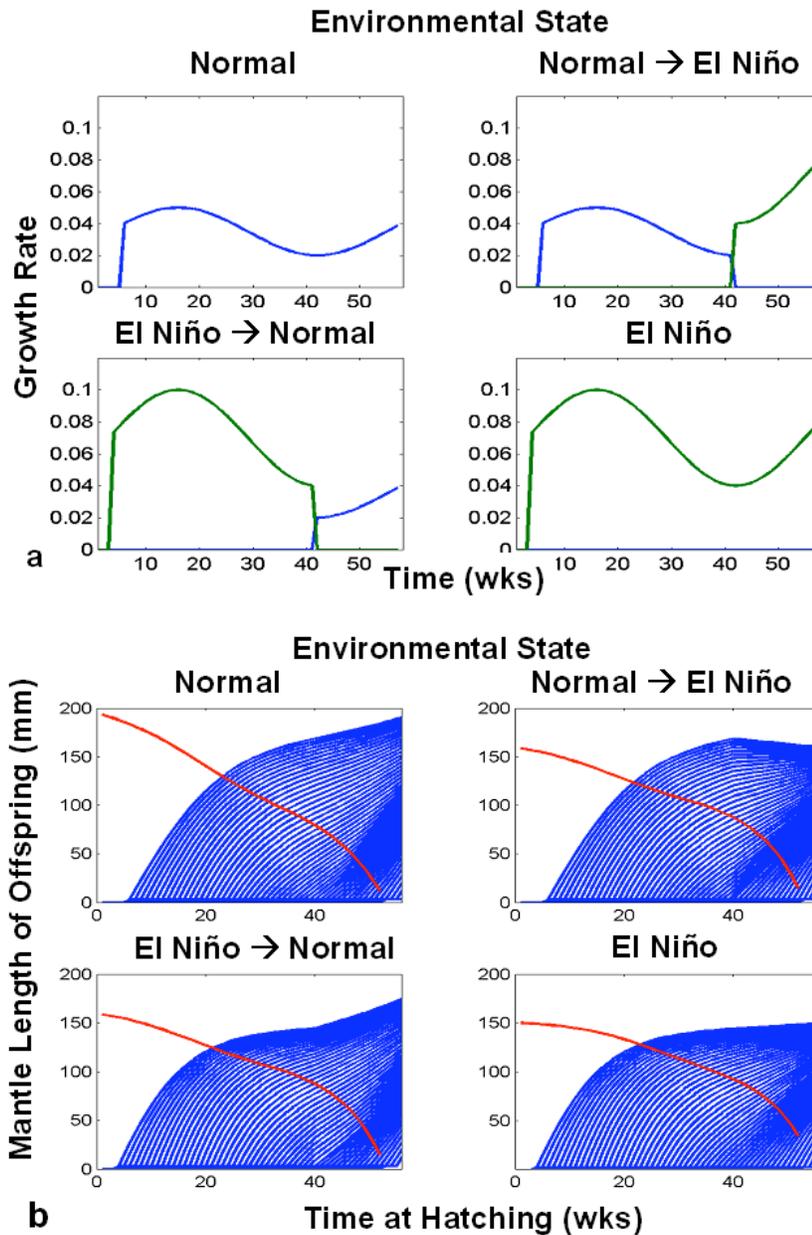


Figure 1.6 The growth rate (a) and growth trajectory (b) of juveniles in each of the possible environmental states. The red line in b shows the size of the juvenile at the time of analysis given it was laid in week, t .

We allow $L_{bi}(t,E)$ to denote the size of an offspring laid in week, t , six weeks after the start of the next year's fishery when the environment this year is E and next year is i . The growth rate and growth trajectory of the juvenile squid are the same as those of the parent squid, including the seasonally varying growth rate, until time at which the environment can change, at which time the juvenile squid growth rate and growth trajectory will change according to the new environment. We assume size dependent survival for juveniles (Hixon 1983), so that if $S_{bi}(t)$ denotes the survival of an offspring to week t after birth (suppressing the environment), where i can be environment 1 or 2, we have

$$S_{bi}(t + 1) = S_{bi}(t) \exp\left[-m_0 - \frac{m_b}{L_{bi}(t)}\right] \quad (6)$$

where m_0 is weekly juvenile survival and m_b is size dependent survival. Survival is computed from the time the parent goes inshore until the time at which juveniles are recruited to the fishery.

The sooner a parent squid moves inshore, the smaller the spawner, thus the lower the reproductive output, but the larger its offspring are at the beginning of the following year's fishery, and the greater the risk of juveniles dying. Combining these factors determines adult fitness.

Determining Fitness from Maturation

Reproductive output (fecundity) depends on length (Yang et al. 1986; Maxwell and Hanlon 2000), so the longer a squid remains offshore growing, the larger its reproductive output becomes. We let $\phi(l,t,E)$ denote the fitness from

maturation for a squid that moves inshore when the environment is E. If we assume that El Niño events occur about once every five years, then when the environment is normal (E=1), there is an 80% chance that it remains normal and a 20% chance that there are El Niño (E=2) the next year. Hence

$$\square(l, t, 1) = \frac{gl^b}{W_0} \left\{ 0.8S_{b1}(t)gL_{b1}^b(t) + 0.2S_{b2}(t)gL_{b2}^b(t) \right\} \quad (7a)$$

where g is gonadal mass, W_0 is egg weight, and b is the allometric measure of fecundity. If we assume that there is a 5% chance of an extended El Niño event, then the fitness for maturation in a El Niño environment becomes

$$\square(l, t, 2) = \frac{gl^b}{W_0} \left\{ 0.95S_{b1}(t)gL_{b1}^b(t) + 0.05S_{b2}(t)gL_{b2}^b(t) \right\} \quad (7b)$$

The first term on the right hand side of these equations denotes the expected number of eggs: it is the gonadal mass (determined allometrically from length) divided by the mass of a single egg. The term in brackets represents the expected number of offspring (i.e. grand-offspring) produced per juvenile at the time that the juveniles are recruited to the fishery in the next year.

Backward induction

While a squid is growing offshore, it also faces the risk of mortality before it has a chance to reproduce. As growth slows, the fecundity gained by increasing length when combined with the risk or mortality has less value than moving inshore to reproduce at a slightly smaller size. We evaluate this

tradeoff by stochastic dynamic programming (Mangel and Clark 1988; Clark and Mangel 2000). The timeline for our analysis is shown in (Figure 1.7).

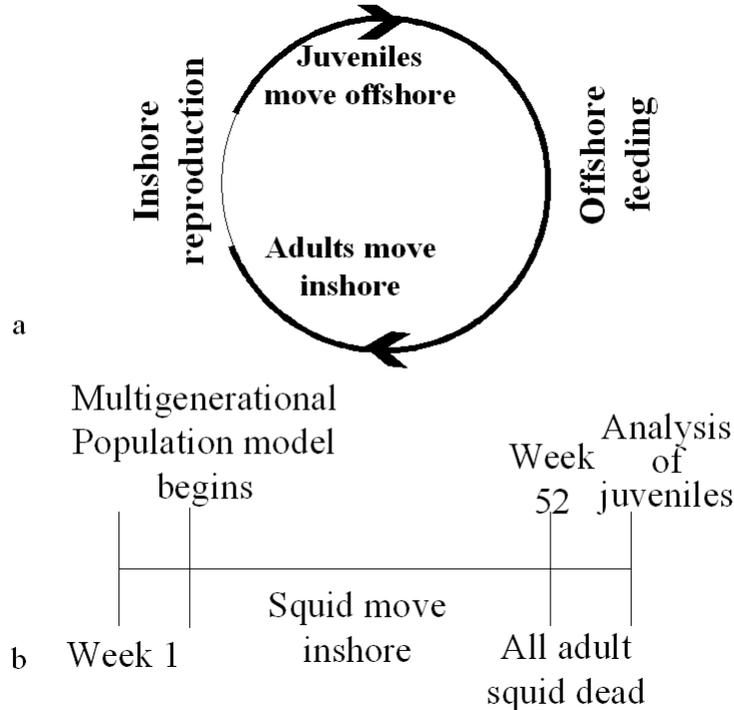


Figure 1.7 Circular (a) and linear (b) timelines for the model and squid lifecycles.

We let $F(l,t,E)$ denote the maximum fitness, measured in terms of expected offspring fecundity (ie number of grand offspring), given that $L(t)=l$ and the environment is E . Since squid are an annual species, they have a fixed lifespan, which we set as $t_{\max}+1$ weeks. Consequently, at week t_{\max} , a squid receives no fitness from remaining offshore and the fitness from going inshore is $F(l,t_{\max},E) = \square(l,t_{\max},E)$. For previous weeks, the life history decision is determined as the maximum of moving inshore, and reproducing, or remaining offshore for another week (thus growing and taking the risk of mortality). If

$l'(l,t,E,Z(t))$ denotes the length in week $t+1$, given that $L(t)=l$, the environment is E , and the local variation in growth rate takes the value $Z(t)$, we thus have

$$F(l,t,E) = \max \left\{ \begin{array}{l} \text{go inshore; remain offshore} \\ l'(l,t,E); e^{\square m} \square_{Z(t)} [F(l'(l,t,E,Z(t)), t+1, E)] \end{array} \right\} \quad (8)$$

where $\square_{Z(t)}$ denotes the average over the local variation $Z(t)$.

The solution of equation 8 generates a boundary curve (Figure 1.8) for the life history decision of remaining offshore and growing or going inshore and reproducing. The peak in the boundary curve for an El Niño environment

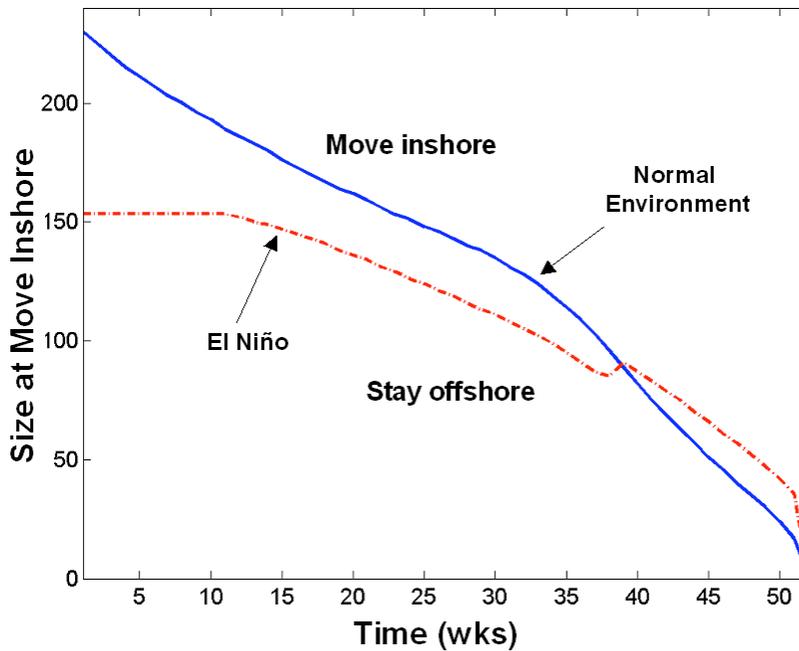


Figure 1.8 Size at which fitness is maximized by moving inshore to reproduce for a normal (blue) and El Niño (red) environment.

at week 40 is a result of the order of the expected size of juveniles (Figure 1.6b, red line) changing with the switch in environment that occurred at this time.

This peak follows the change in environmental state when the timing of the environmental switch is changed. The crossing of the boundary curves for the two environments is a result of an interaction between the fast growth of an El Niño environment, and the larger size achieved in a normal environment. If an individual is still offshore in week 40, when the environment changes, it can grow faster. However, by week 37 in either environment, an individual has a probability of $\ll 0.01$ of still being below the boundary curve.

Individual based model

To follow individual life histories, we simulated a population of 100 squid with initial size normally distributed squid around a mean size of 75 mm ML and standard deviation of 5 mm with randomized growth (equation 5), and followed their patterns of growth, maturation and inshore migration. This allowed us to generate a series of size frequency distributions while squid are offshore. As squid move inshore, they become available to the fishery for harvest. In order to relate the landing volume from the fisheries data to the simulated squid, we computed biomass inshore using an allometric length (cm) to weight (g) relationship for *Loligo pealei* (Alford and Jackson 1993; allometric exponent =2.15, coefficient =0.25). This allowed us to compute both the weekly values and the cumulative values for biomass inshore.

The size distribution for the offspring as they enter next year's fishery is a proxy for the reproductive potential of the next generation, which allows us to consider population dynamics and harvest strategies. The mean size of the

offspring is then used to calculate the initial size distribution for the following generation.

Multi-generational analysis

Population dynamics for annual species are often highly variable (Rosenberg et al. 1990; Anderson and Rodhouse 2001). Fishery yields for *L. opalescens* show highly variable annual catch that is, in part, driven by environmental state (Vojkovich 1998). Thus, recruitment must also be variable, as the biomass available to the fishery is reduced as shown in the first part of the model. In an effort to understand the population dynamics of this annual species, we created a multigenerational model based on the previous individual based model.

Environmental variability is a key regulator of squid population dynamics on a year-to-year basis, as predicted by the first individual based model. A series of bad years, without any fishing pressure, can possibly drive a population to extinction. This decline is exacerbated when portions of the spawning stock biomass are harvested before spawning. With as little as 20% of the spawners removed, the stocks could be depleted severely.

To make predictions about population dynamics in a changing environment, one cannot simply average the different population trajectories. Using Figure 1.9 as an example of different growth trajectories due to environmental variation, one sees that the arithmetic mean would steadily

increase, not truly reflecting the population dynamics through different simulations. Fortunately, use of the geometric mean for finding the growth rate of populations in variable environments is well established (Roughgarden 1998).

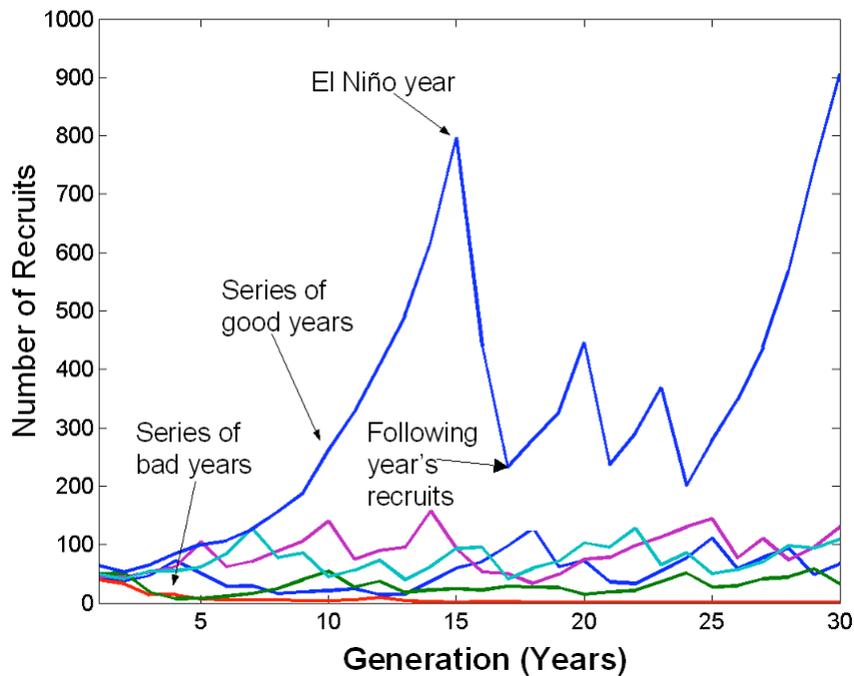


Figure 1.9 Examples of some growth trajectories after a series of good years, a series of bad years, or in variable environmental states.

Population Growth Rate

By analyzing multigenerational changes, population dynamics could be tracked over multiple years. We calculated the change in population size in two ways; measuring recruitment in year, i , $N_R(i)$, at each generation over the span of the simulation and calculating the geometric mean for the average annual per capita population growth. The annual average population growth rate, $\tilde{\lambda}_i$, is

$$\tilde{\lambda}_i = \frac{N_R(i)}{N_R(i-1)}. \quad (9)$$

Consequently, the growth rate for the population over the life of the simulation is

$$N(T) = N(1) \tilde{\lambda}_1 \tilde{\lambda}_2 \dots \tilde{\lambda}_{T-1}, \quad (10)$$

where $N(T)$ is the number of individuals recruited to the population in the last year of the simulation, time T . The geometric mean growth rate is defined by

$$N(T) = \lambda_{GM}^T N(1) \quad (11)$$

from which

$$\lambda_{GM}(T) = \left[\tilde{\lambda}_1 \tilde{\lambda}_2 \dots \tilde{\lambda}_{T-1} \right]^{\frac{1}{T}}. \quad (12)$$

From equation 9 we have

$$\lambda_{GM}(T) = \left[\frac{N_R(2)}{N_R(1)} \frac{N_R(3)}{N_R(2)} \dots \frac{N_R(T)}{N_R(T-1)} \right]^{\frac{1}{T}} \quad (13)$$

so that

$$\lambda_{GM}(T) = \left[\frac{N_R(T)}{N_R(1)} \right]^{\frac{1}{T}}. \quad (14)$$

We use $\lambda_{GM}(T)$ as the running geometric mean growth rate as $T \rightarrow \infty$. In our case, as $T=30$ years, which for an annual species, is an appropriate time horizon.

The mean population per capita growth rate, λ_{GM} , provides an excellent approximation to the overall health of the stocks. Assuming there is no density dependent regulation, any $\lambda_{GM} < 1$ ensures that a population will go extinct in

time. With no stock recruitment curve for squid established, the amount of spawning stock biomass that can be removed from the population is unknown. Because spawned individuals are taken with unspawned squid (CDFG 2002), it is possible that increased catch rates will reduce λ_{GM} enough to drive the population to extremely low levels (Figure 1.10).

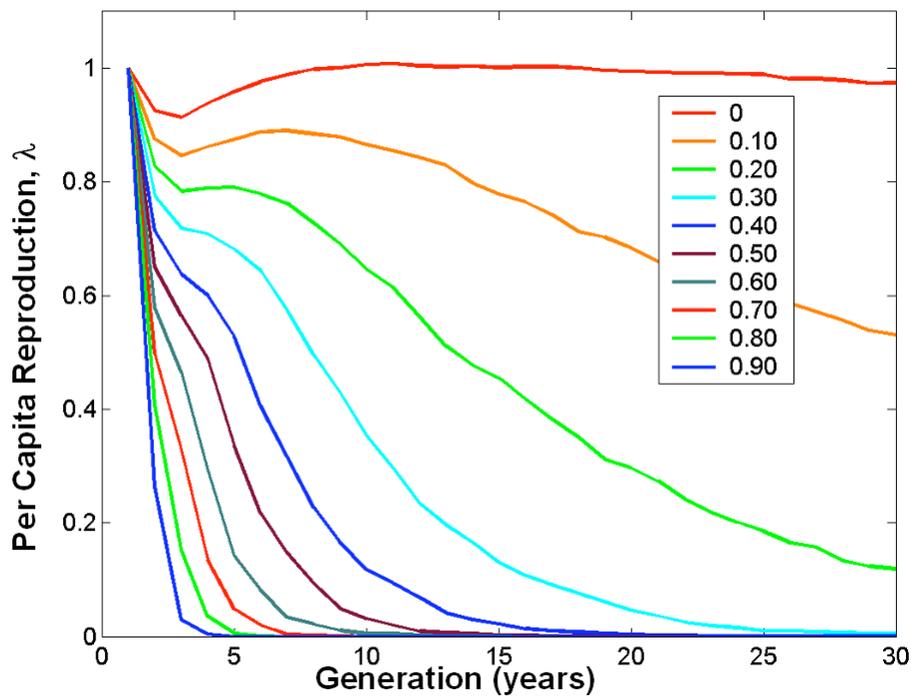


Figure 1.10 Change in λ over 30 generations (years) with increasing removal of unspawned individuals.

Population Dynamics

After calculating the reproductive output of individuals from the good-good scenario (outcome 1, Figure 1.6b) in the forward simulation, the number of recruits to the next generation is

$$N_R(i) = \frac{\prod_{t=1}^{52} B(t)S_{bi}(t)}{M_R} \quad (15)$$

where $B(t)$ is the reproductive output ($\frac{gl^b}{W_0}$ from equations 7a and b) for the biomass inshore, $S_{bi}(t)$ is the survival of recruits (equation 6), and M_R is an mortality constant that includes egg predation, unhatched eggs, and some juvenile mortality chosen so that $N_R(i)=N_R(i+1)$ for two normal environments. The initial size distribution for the next generation is normally distributed with

$$\square = \frac{\prod_{t=1}^{52} B(t)S_{bi}(t)L_{bi}(t)}{\prod_{t=1}^{52} B(t)} \quad (16)$$

and standard deviation of 5mm. The environment quality for the first year is a “good” year, and the following years’ environments, with the following years randomly determined by

$$\Pr\{E(t+1) = 1 \mid E(t) = 1\} = 0.80$$

$$\Pr\{E(t+1) = 2 \mid E(t) = 2\} = 0.05$$

This is an individual based model in which individuals have variable growth rate (equation 5) where $L_{bi}(t)$ is the size of the offspring six weeks after the start of the fishery, according to the decision curve calculation. The multigenerational simulation begins at week 6 because $L_{bi}(t)$ is the size at week 6. The multigenerational simulation continues as with the forward simulation.

We then use the model to predict reproductive output, spawning stock biomass, and mean size of offspring at start of the following year as individuals move inshore, and the process is repeated for 30 generations.

Harvest of unspawned individuals

We removed fractions of the spawning stock biomass to simulate harvest of unspawned individuals. Using equation 14, we calculated the geometric mean of the population with removal of SSB to establish the threshold of unspawned harvest that the population could support without crashing. We also used the geometric mean at each generation to predict the number of generations that the population could sustain removal of unspawned individuals before crashing. To establish confidence intervals, we ran the forward simulation 1000 times.

Predictions of the Model

Initial Forward Simulation

Early and late in the season, the values for the size at which a squid moves inshore to breed are near the asymptotic size, and very low, respectively (Figure 1.8). This is a manifestation of the timeline assigned to the model. Early in the season, the offspring have a longer time period until recruitment to the fishery. Thus, the benefit of going inshore decreases because of decreased survival. Late in the season, the squid are nearing the end of their lives, and there is less time for the offspring to grow, but the total survival is higher. The

maximum fitness is now achieved by sacrificing the number of offspring for the size of the offspring. Values between these two extremes are a balance of time and length, at the given time, which maximize fitness. Note that the life history decision is size-driven early in the season and time-driven late in the season. The forward iteration tracks the size distribution of the squid offshore in both environments (Figure 1.11). The number of squid in the population declines

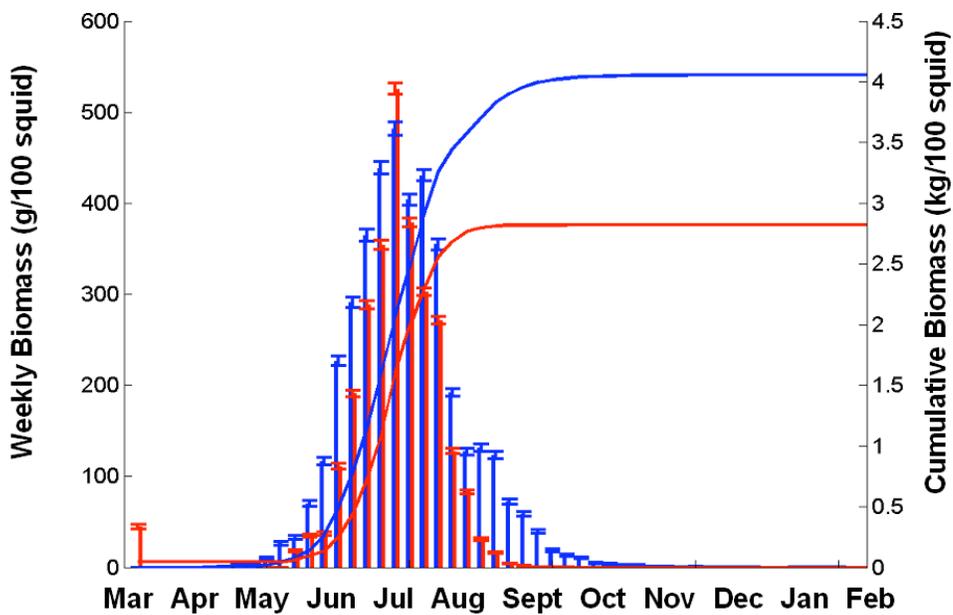


Figure 1.11 Cumulative and weekly biomass inshore and available to the fishery for a normal environment (blue) and an El Niño environment (red). due to mortality offshore and inshore migration, however for both environments, the offshore size distributed remained approximately normal. In addition, all squid were inshore by week 35 (week from model+10 week offset; early November), and biomass inshore peaks in week 19 (early July) in the normal environment and week 20 (mid-July) in the El Niño conditions.

Biomass inshore each week is predicted to be higher in a normal environment than in El Niño conditions, with the exception of week one (Figure 1.11). This pattern is due to high food availability in the normal environment, which allows the squid to grow larger. Cumulative biomass for the forward iteration shows a total biomass inshore to be almost 1.5 times higher in normal conditions than in El Niño conditions. The difference between environments in biomass available in is not as marked as the differences in fishery landings between El Niño and non-El Niño years, but this model does not account for the likely increased mortality during El Niño years, rather it only calculates the differences in food availability and growth rates. The general shape of the distribution in biomass over time remains the same, with fewer squid coming in early and late in the season, reflecting the tails of the size distribution, as well as the mid-sized squid from the initial distribution coming inshore at the midpoint between the other two groups. The peak in biomass for the El Niño environment occurs five weeks before the peak in biomass in the normal environment.

Predictions from the Multigenerational Simulation

We predict that even a 10% removal of SSB reduces λ to below one, and a 30% removal will drive the population extinct within the time frame of our analysis (Figure 1.12). While populations are predicted to still be viable

when up to 20% of SSB is harvested before spawning, however, this is simply due to a fairly short time horizon. If $\lambda < 1$, the population will decline.

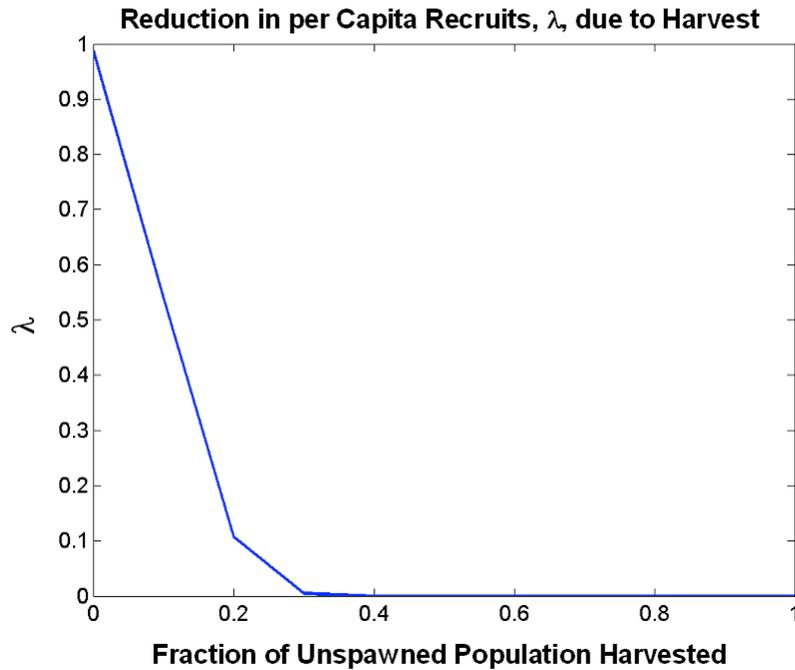


Figure 1.12 Reduction in per capita recruits (population growth rate), λ_{GM} , when a given fraction of the population is harvested before spawning.

If the market squid population shows compensatory recruitment, fraction of unspawned individuals that may be harvested without the population crashing will increase. Density dependent recruitment could be incorporated into this model by varying M_R with spawning stock biomass once more data regarding a stock-recruitment relationship is collected.

Sensitivity Analysis

Mortality rates affected the boundary curve the most. Increasing adult mortality, which increases the risk of remaining offshore, lowered the size at which squid are predicted to move inshore. Increasing juvenile mortality increased the size at which squid move inshore. To test the importance of fecundity in the boundary curve, we also varied the allometric exponent b . A low value for b causes a sharp decline in the size for the boundary curve. Including the weight or quantity of offspring (rather than fecundity) in the adult fitness function changed the shape of the boundary curve, by increasing the length when an individual moves inshore early in the season. When grand offspring are used as the measure of fitness, a squid trades both its own mortality with that of its offspring. Early in the season, when the size at which a squid moves inshore is high, it is because most of the fitness a squid would have gained by moving inshore would be lost with high offspring mortality at the beginning of next year's season. As this risk declines, the size of inshore migration declines.

Changing the gonadal to egg weight ratio, W_0 and g , had no effect on the boundary curve in either environment because they appear linearly in the equations. Furthermore, because the value of staying offshore is ultimately related to the value of moving inshore, and these changes affect both values similarly, resulting in no change in the fitness values. The choice of times used through out the model, whether deciding the starting point for the forward

iteration or choosing when to measure the size of the offspring, are arbitrary. Because offspring size affects fitness value, it is important to recognize the effects of when they are measured on the boundary curve. Changing the setpoints varying the quantitative but not the qualitative predictions of the model.

Our model currently lacks density dependent recruitment. Instead, we assume a power recruitment function (Needle 2001). Predictions of \square_{GM} would vary if the simulated population showed density dependence, most likely by increasing the rate at which unspawned biomass could be removed without reducing \square_{GM} to zero.

Discussion

Confronting the model with data.

The primary predictions of our model are that squid will come inshore year-round to reproduce, and that the timing and size of the inshore migration can be predicted from a combination of life history and environmental information such as temperature and food (krill) availability.

The peak in biomass inshore (Figure 1.11) corresponds well to the peaks in harvest for the Monterey Bay fishery, which occur in late spring and summer (CDFG 2002) (Figure 1.13). The summer spawners are thought to represent those squid born in the previous fall. Since the simulation that generated these figures was based on a normal distribution of sizes with a mean of 75 mm ML,

the mid-size and large squid could have been born as late as August. The spring spawners' offspring could be modeled, and because of increased summer growth rates, one would expect to see their biomass inshore peak in mid to late-fall. It is possible, of course, that some squid live more than one calendar year.

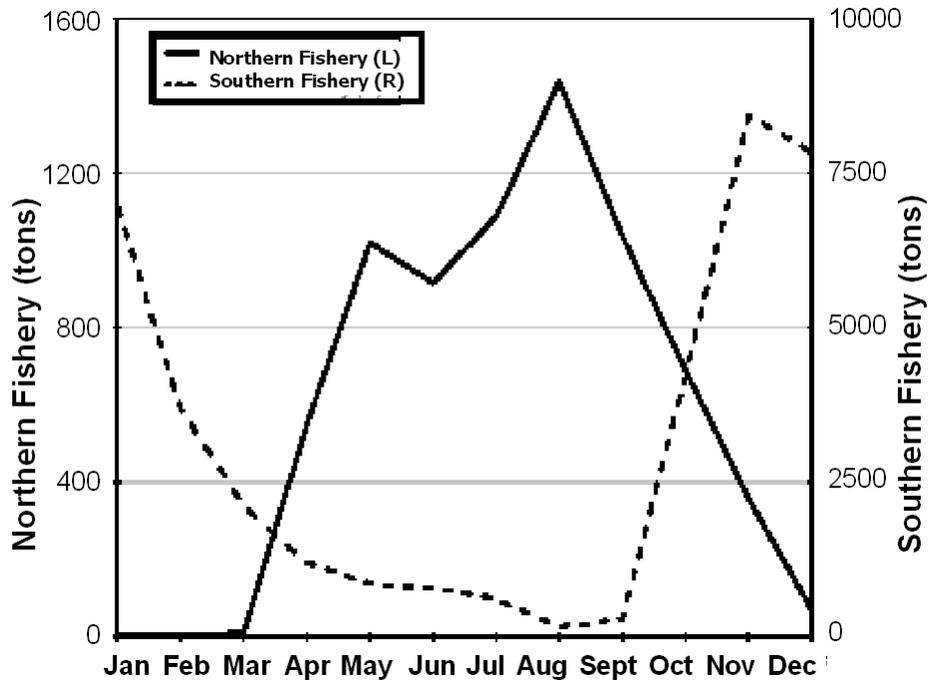


Figure 1.13 Average landings for the Northern (solid) and Southern (dashed) squid fisheries. From CDFG 2002.

The mean size for squid collected inshore in Monterey Bay is 127.5mm ML, and in the Channel Islands is 134.7 mm ML (Figure 1.4). These samples were collected from April to October of 2000, with additional Channel Island samples occurring in January and February 1999, as well as November and December 2000. In comparison to the model, the mean in Monterey Bay is slightly smaller than the mean size of squid inshore in El Niño conditions, and

much smaller than the mean in normal conditions, as predicted by the model. Predicted mean size of squid in El Niño conditions is 139.16 mm ML, and 168.86 mm ML in the normal environment. The size distributions predicted by the model in the normal environment are just outside the range of sizes found in Monterey Bay and the Channel Islands.

The model is not tuned to either location specifically, thus the difference in the predicted sizes, could be due to the extremely high asymptotic length associated with unlimited food resources that was used in the normal environment of the model. It could also be attributed to the fact that, while upwelling indices are similar between Monterey and the Channel Islands (Figure 1.14), temperatures, thus growth rates, are higher in the Channel Islands, resulting in larger individuals. Furthermore, the number of squid in the model is much smaller than from the sample data obtained. If the initial size distribution were larger and thus broader, we would see a larger spread in the inshore size distribution as the squid reach maturity at different lengths according to the boundary curve.

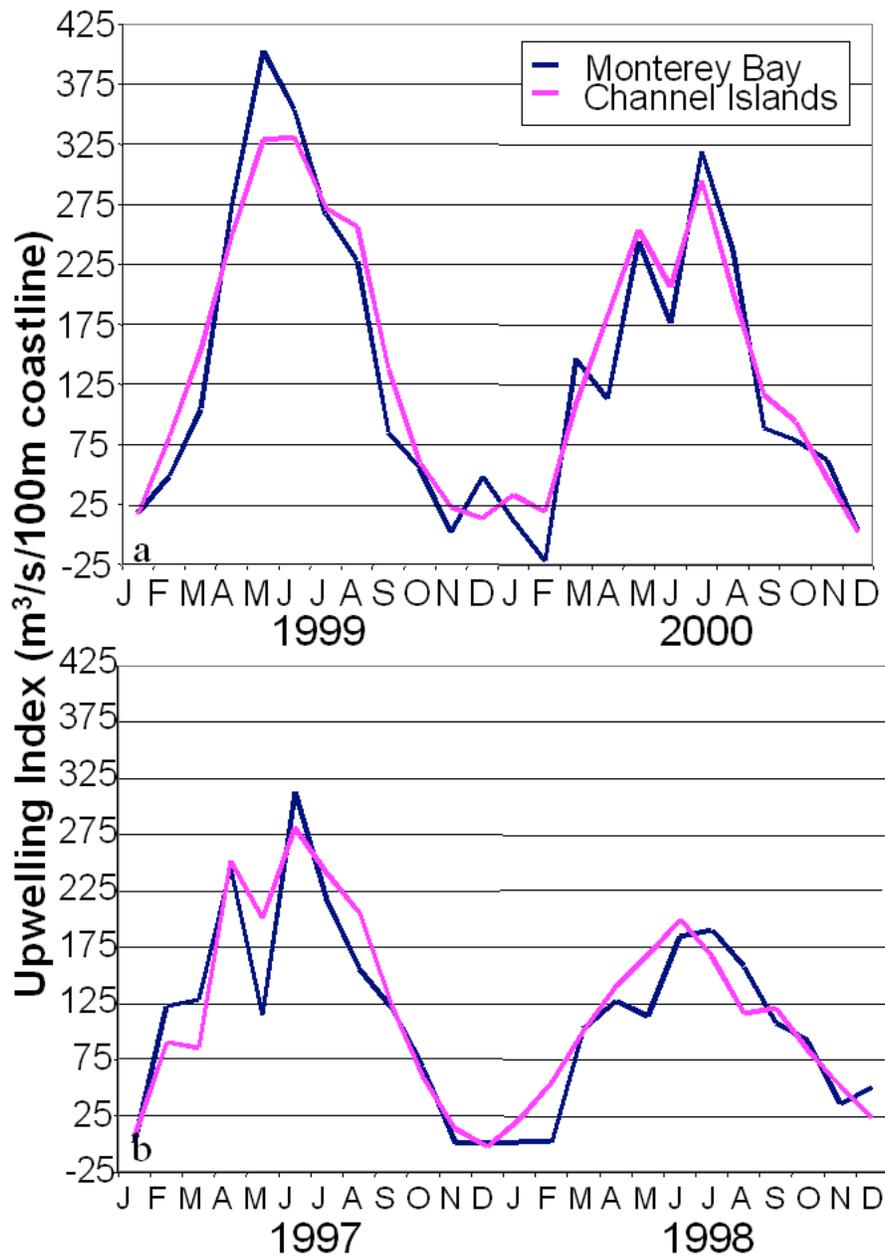


Figure 1.14 Upwelling indices for normal (a) and El Niño (b) environments for both the Channel Islands and Monterey Bay. Data from <http://las.pfeg.noaa.gov>.

We predict that populations will show fast recovery from a poor growth or El Niño years, providing that the following year is a high food availability year (Figure 1.9). Fishery data show that recovery of yields following an El

Niño year is swift, with yields often returning to the level of the last non-El Niño harvest (CDFG 2002). As long as poor quality environments do not persist, the population is expected to recover fully, which ultimately has little impact on the long term growth of the population, and as long as a minimum number of unspawned individuals are harvested, there should be little impact on long term harvests.

Implications for fishery management

The model developed here is a theoretical one, rather than an applied calculational tool (sensu Mangel et al. 2001). Indeed, our extremely simple formulation involves only two environmental states (“normal” and “El Niño”) in which there is a countervailing effect of temperature and food (low/high and high/low respectively). One could easily incorporate a broader set of environments, with more complicated correlations, into the model without changing the conceptual flavor.

However, we can draw a number of insights that have implications for fishery management because changes in environment, combined with semelparity and potential harvest before reproduction can cause large inter-annual variations in stock size (Anderson and Rodhouse 2001). First, understanding how environmental variations affect squid life history is essential to a well-managed fishery. The fundamental ecological science for doing this will be community, rather than population, ecology because of the need for understanding the linkages in the foodwebs. For example, asymptotic size

depends upon krill availability, which depends upon phytoplankton. Thus, factors that affect the distribution and abundance of phytoplankton will affect squid abundance. Second, there is no single stock of squid “sitting” on the fishing ground; rather there is a seasonal influx of individuals to the fishing ground. Thus, within season monitoring and management is crucial, to ensure that a sufficient number of individuals spawn.

Third it will be possible to overexploit the squid fishery even though squid are semelparous. If the fishery intercepts individuals between the offshore feeding grounds and the inshore breeding grounds, before reproduction, then the potential spawn of those individuals is lost to the population.

While the rapid lifecycle and fast growth of the California Market Squid make it an excellent candidate for a high yield, sustainable fishery, there are a number of biological reference points that must first be established, the most important being a stock recruitment relationship. Without this, our model presents the most cautious scenario of the harvest of unspawned individuals in high productivity years, thus minimizing risk in the absence of knowledge (Needle 2001). However, because environmental fluctuations alone can drive down populations, our model’s predictions of maximum unspawned biomass harvest must be tempered by the estimated population size.

Chapter 2: Density Dependent Growth and Marine Reserves

Introduction

Marine reserves and marine protected areas are generally agreed to provide certain benefits to the marine communities they encompass; biodiversity within the protected area increases (e.g. Jennings et al. 1996; Chiappone and Sealey 2000; Ward et al. 2001; Halpern and Warner 2002), and the number of individuals, especially for target species, also increases (e.g. Tupper and Juanes 1999; Kelly et al. 2000; Halpern and Warner 2002). The average sizes of target species within reserves are larger than those outside of the reserve (e.g. Dugan and Davis 1993; Beets and Friedlander 1999; Halpern and Warner 2002). Furthermore, reserves have additional benefits of protecting habitat from destructive fishing practices (such as trawling). This further increases the chance for population recovery, and the reserve serves as a control, per se, for comparison to the fished habitats around it. While it is clear that reserves are good for marine populations and the ecosystem as a whole, it is still unclear what benefit, if any, they have for fisheries.

Within both scientific literature and popular media, marine reserves are often promoted as the panacea for declining fisheries' yield and biodiversity. Spillover, adult migration across reserve borders into fishing grounds, is often the first explanation for an increase in fishery yields from marine reserves (e.g. Environmental News Network <http://www.enn.com/enn-news->

archive/1999/08/082599/mreserves_5239.asp; Ward et al. 2001; Roberts et al. 2001). The impact of spillover, however, is directly related to the size of the reserve and edge effects associated with the reserve (Guenette and Pitcher 1999).

A second proposed mechanism for increased yields results from increased larval production from protection of spawners and dispersal out of the reserve boundaries. A number of commercially important fish and invertebrate species (e.g. abalone, many crustaceans, rockfish) have pelagic larval stages. By protecting adult spawning populations within a reserve, the larvae may spread beyond the reserve borders. These dispersed larvae are then assumed to recruit to fishing grounds, thus becoming available to the fishery as adults. In this way, the reserve system may be responsible for repopulating depleted fished areas. It should be noted, however, that increased yields due to larval transport may not be seen for years after the creation of a reserve, especially for long lived, late maturing fish.

Some empirical studies show larger fish (Dugan and Davis 1993), and greater abundances of harvested fish in reserves (e.g. Acosta 2002; Roberts et al. 2001; Dugan and Davis 1993). However, little conclusive work has been done to address the issue of the effects of reserves on fisheries. There is anecdotal evidence of reserves increasing catch (e.g. Bennett and Atwood 1993; Dugan and Davis 1993; Roberts et al. 2001) however, there are also studies that show no effect on abundance in surrounding waters (Dugan and Davis 1993).

While the mechanisms behind increased catch (e.g. spillover effects, increased reproductive output, etc.) are hypothesized, few attempts have been made to explain the cases in which no increases in catch were observed.

Within a reserve, processes other than fishing serve to regulate the number of individuals. Natural mortality, growth and reproduction generally play a role in determining population size and structure (Beverton and Holt 1959; Rochet 1998). Density dependent survival of juvenile reef fish is important for population regulation (Hixon and Carr 1997; Steele 1997; Holbrook and Schmitt 2002), however only a handful of studies (Helser and Brodziak 1998; Lorenzen and Enberg 2002; Gardmark and Jonzen Draft: version 2002-06-20) have explored the effects of density dependent growth of adult fish on population regulation. In this paper, we will primarily focus on density dependent somatic growth, rather than density dependent mortality.

Density dependent somatic growth is a relatively unexplored aspect of population growth. Increased biomass or density of a population causes competition for food resources, assuming no competitive dominants within the population, this results in decreased food availability, which in turn decreases asymptotic size. Lorenzen and Engberg (2002) recently explored this phenomenon for a variety of marine and freshwater species and found a range of intensities of density dependent body growth between species.

Creation of a reserve closes down an area to fishing, though it is unlikely that fishermen stop fishing simply because there is some area closed.

Displaced fishing effort results, which essentially maintains fishing mortality over the entire population at what it was before the creation of a reserve. This places increased pressure on the stocks outside of the reserve, which in turn places increased pressure on the reserves to perform as projected.

A model that addresses the potential unintended effects of reserves, such as density dependent growth and displaced fishing effort, increases our understanding of reserves. Using lingcod as a motivation, we consider three different strengths of density dependent somatic growth effects on adults. Next, we consider how different fishing mortalities affect the population and size distribution of individuals in the different growth regimes. Finally, we examine how these density different levels of density dependent growth, as well as displaced fishing effort, affect the recovery of depleted populations with different reserve sizes. Through the consideration of these often-overlooked effects of reserves, we use this model to aid in the resolution of the debate surrounding marine reserves and fisheries. We predict that populations will recover more quickly with reserves than without, and more quickly with density dependent growth than without. Furthermore, we predict that exploited populations with density dependent growth will have higher asymptotic size than those that are not, and that after the creation of a reserve and recovery, this asymptotic size will decline.

Lingcod life history and fishery

Lingcod, *Ophiodon elongatus*, are a moderately long-lived teleost whose range extends from Central California to the Aleutian Islands in Alaska (Adams and Starr 2001). Their habitat consists of rocky reefs to 1,000 feet; these habitats are variable and depend on life stage. Lingcod are moderately mobile; females move up to 1km/day (Martell et al. 2000), while males are more sedentary (Love 1996). Spawning occurs annually; egg production ranges from 6,000 to 500,000 per female, and males guard the eggs in nests (Love 1996). Female lingcod mature later in life and live longer than males; female maximum age is 20 years, and age at maturity is about 5 years (Love 1996).

Current estimates of lingcod biomass indicate that in some areas populations may be as low as 10% of the unfished biomass (Martell et al. 2000). Commercial fishing in the southern part of the fishery is dominated by groundfish trawl fishery, and is predominantly hook and line in the north (Jagiello et al. 2000). Lingcod harvests in the United States and Canada have decreased from a high of 5,133 tons in 1980 to 807 tons in 1999. Exploitation rates (catch/total biomass) of lingcod, for the recreational and commercial fishery combined, declined from 0.67 in 1993 to 0.06 in 2000 in the northern area and declined from 0.51 in 1997 to 0.15 in 2000 (Jagiello et al. 2000), which correspond to fishing mortalities of 1.11, 0.06, 0.71, and 0.16, respectively.

Description of the Model

We used a deterministic age structured model, evaluated annually to predict the effects of density dependent body growth and displaced fishing effort on yield and population recovery in the context of marine reserves. We assume that food availability is constant and that larvae are distributed uniformly over the study area. Parameters were taken from the literature or estimated based on common values for species with similar traits to lingcod (Table 1). Ultimately, the parameter values are somewhat arbitrary since lingcod were chosen as a somewhat generic study organism.

Table 2.1 Model parameter descriptions, values, and sources.

Parameter	Interpretation
k	Growth rate ($=0.90=e^{-.11}$) from (Jagiello 1999)
L	Asymptotic Size ($=130\text{cm}$) from (Love 1996)
L(a,t)	Length in cm at age, a, and time, t
W(a,t)	Weight in kg at age, a, and time, t
a ₅₀	Age at maturity ($=5$ years) from (Love 1996)
P _m (a)	Probability of maturity at age, a
σ_m	Variance around a ₅₀ ($=0.4$)
F(L(a))	Fishing mortality = 44.2 cm from (Adams and Starr 2001)
B ₀	Estimated maximum biomass at which intraspecific competition has no effect ($= 1.7\text{mt}$)
M	Natural mortality = 0.2 from (Hilborn and Liermann 1998)
N(a,t)	Population size of age, a, at time, t
ρ	Estimated steepness of recruitment curve ($=0.25872$) selected to keep unfished population constant
ρ	Estimated asymptotic limit of recruits ($=.0052$) selected to keep unfished population constant
B(t)	Biomass at time, t
S(t)	Spawning stock biomass at time, t

General growth model

In the absence of density dependent effects, we assume that lingcod growth follows the von Bertalanffy (1957) growth equation

$$\frac{dL}{dt} = k(L_{\infty} - L) \quad (1)$$

where k is the growth rate, L_{∞} is the asymptotic size that can be achieved with unlimited resources, and L is the current length in cm. Weight (in kg) is calculated using the allometric relationship (Figure 2.1)

$$W(a) = 7 \times 10^{-7} L(a)^3 \quad (2)$$

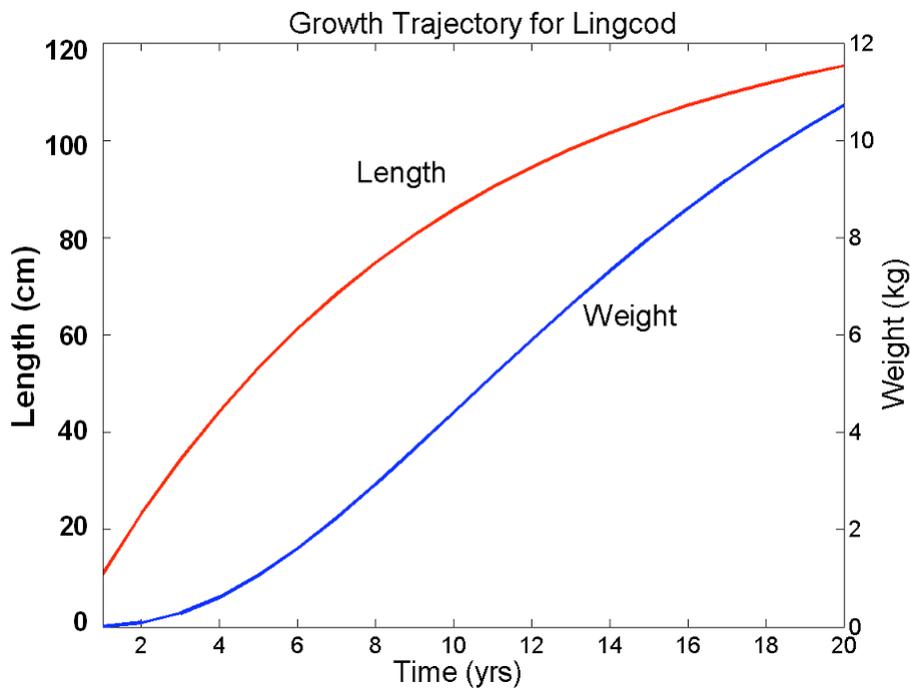


Figure 2.1 Von Bertalanffy growth trajectories for lingcod without density dependent growth.

Age-structured model

We use a general age-structured model, with Beverton-Holt (Beverton and Holt 1993) recruitment, to model the population dynamics. Fishing mortality is described by a knife-edge, length-based fishing mortality term. This is set for all individuals >44.2 cm (see equation 14). Fishing mortality was instantaneous for the year, and closed seasons were not included in the model. Thus, $N(a,t)$, the number of individuals of age, $a>1$, at time, t , follows

$$N(a+1,t+1) = N(a,t) \exp(-M - F), \quad (3)$$

where $N(a+1,t+1)$ is the number of individuals, of age $a+1$ in year $t+1$, M is instantaneous annual natural mortality (assumed to be $=0.2$; Hilborn and Liermann 1998), and F is instantaneous fishing mortality (varies; see below).

We assumed the probability of maturity at age a , $P_m(a)$ is

$$P_m(a) = \frac{\exp\left(\frac{a - a_{50}}{m}\right)}{1 + \exp\left(\frac{a - a_{50}}{m}\right)}. \quad (4)$$

Here, a_{50} is the age where 50% of females are mature, where $a_{50}=5$ (Love 1996).

The spawning stock biomass is

$$S(t) = \sum P_m(a)N(a,t)W(a,t) \quad (5)$$

and recruitment is

$$N(1, t + 1) = \frac{S(t)}{\square + \square S(t)}, \quad (6)$$

in which \square is rate at which recruitment reaches its maximum level (“steepness”), and \square determines the asymptotic limit of recruits (as $S(t) \rightarrow \infty$) to the population (then $N(1, t + 1) = \frac{1}{\square}$). Following the work of Brooks (2002) and Martell et al.

(2000), we set these values to maintain the unfished population size at 1000 individuals.

The Pacific Fishery Management Council’s recruitment data (Jagiello et al. 2000) suggest a steep recruitment curve (Figure 2.2). Because there is nest guarding, the number of recruits is limited by both nest sites and males to guard the nests, implying that there is some upper limit to recruitment. Arguments have been made for a linear stock recruitment curve for lingcod (MacCall 2002), which is conservative with regards to fishing, but may increase predictions of population recovery. This implies that all population regulation is post-settlement. Thus, density dependent body growth could be even more important in regulating population dynamics than this research shows.

A model for density dependent growth

In general, asymptotic size is a function of food availability (Beverton 1992). When limitation of food is due to competition, maximum size is thus related to the number of competitors. We assume that the main competitors are

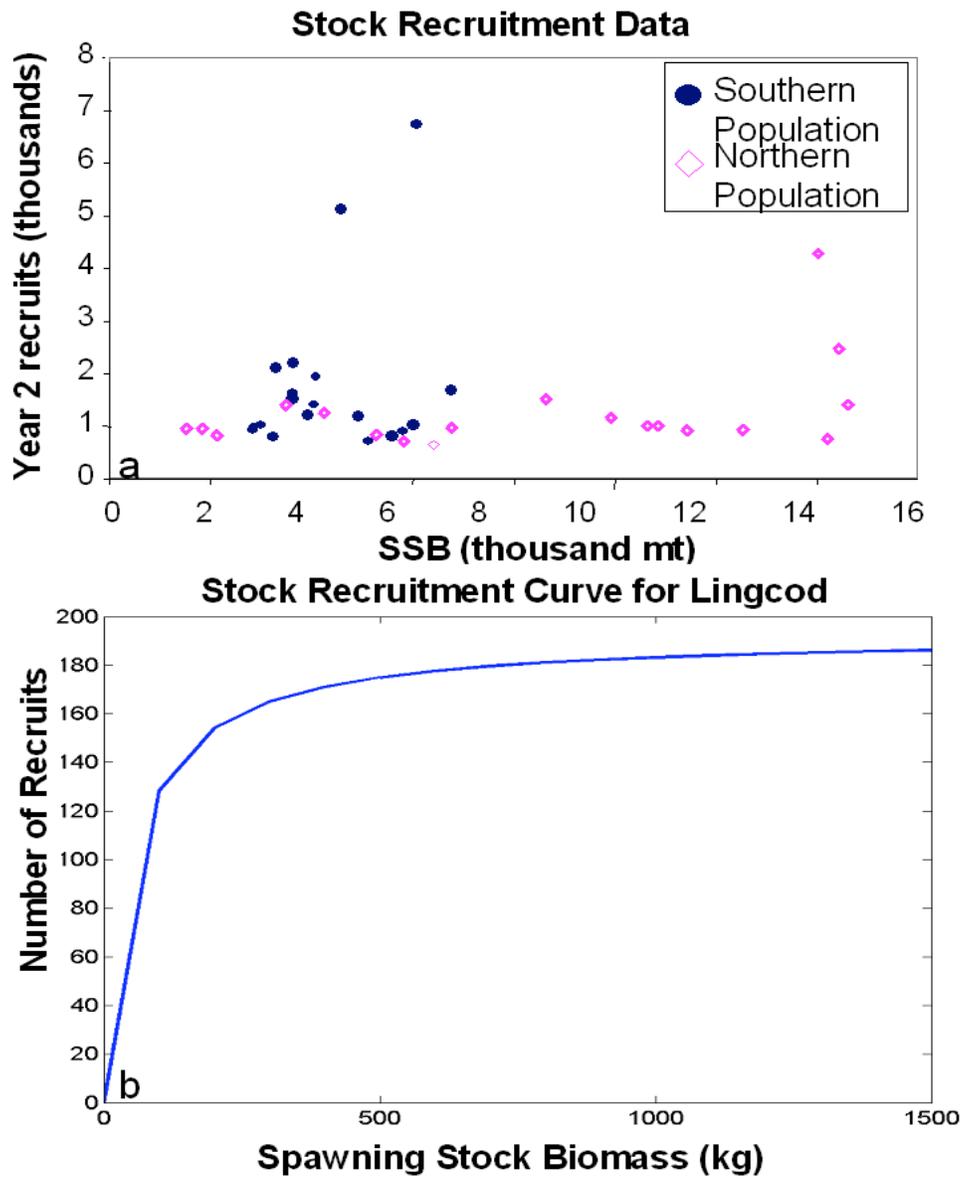


Figure 2.2 (a) Stock recruitment curve for year 2 individuals, data from Jiaglo et al 2000, (b) estimated stock recruitment curve used in the model.

intraspecific, all individuals compete equally, and the amount of food consumed by competitors is proportional to biomass

$$B(t) = \int N(a,t)W(a,t). \quad (7)$$

For a number of freshwater and marine species, Lorenzen and Engberg (2002) derived asymptotic size, $L'(B)$ as a function of biomass, B

$$L'(B) = L - \alpha B \quad (8)$$

where α determines the strength of density dependent growth. For 11 species of marine and freshwater fish, α ranged from about 0 to 3.9 (Lorenzen and Engberg 2002).

Equation (8), however, has two limitations. First, there is no biomass level at which density dependence has no effect on asymptotic size. Since individuals fed *ad libitum* do not consume all the food offered (Valiela 1995), there must be a population biomass at which there is no competition for food. Second, with a high biomass or α , it is possible to have negative linear growth rates or possibly, a negative asymptotic size.

To deal with these difficulties, we use

$$L'(B) = \frac{L}{1 + \alpha \left(\frac{B^2}{B^2 + B_0^2} \right)} \quad (9)$$

In equation 9, B_0 is the fraction of the steady state biomass, as calculated without density dependent growth, where density dependent growth has no effect on asymptotic size, set here to be 10% of the steady state. When B is much less than B_0 , individual growth rates are essentially biomass independent.

When $B \gg B_0$,

$$L'(B) = \frac{L}{1 + \frac{B}{L}} \approx L(1 - \frac{B}{L}) \quad (10)$$

Furthermore, when $\frac{B}{L} \ll 1$, equation 9 is approximately equal to equation 8 ($L' = L - \frac{B}{L}$).

Using equation 9 we have

$$\frac{dL}{dt} = k(L'(B) - L) \quad (11)$$

We use $\frac{B}{L} = 0$ (no density dependence), $\frac{B}{L} = 0.0006$ (moderate density dependence), and $\frac{B}{L} = \frac{2}{L}$ (high density dependence) strengths for density dependence.

These correspond to Lorenzen and Engberg's (2002) range of values for $\frac{B}{L}$. The effect of these different values of $\frac{B}{L}$ on asymptotic size is shown in Figure 2.3.

Density Dependent Growth on an Unfished Population

Density dependence and stock size

In an unfished population, density dependence alone can reduce the total number of individuals in a population by up to 10%, in case with the strong density dependence, compared to populations without density dependent growth. Despite the small difference in the number of individuals in the population, the total population biomass varied greatly between different values of $\frac{B}{L}$ (Figure 2.4). Thus, the population is maintained by a number of small individuals, which in turn reduces spawning stock biomass by creating a population that has a lower length at age.

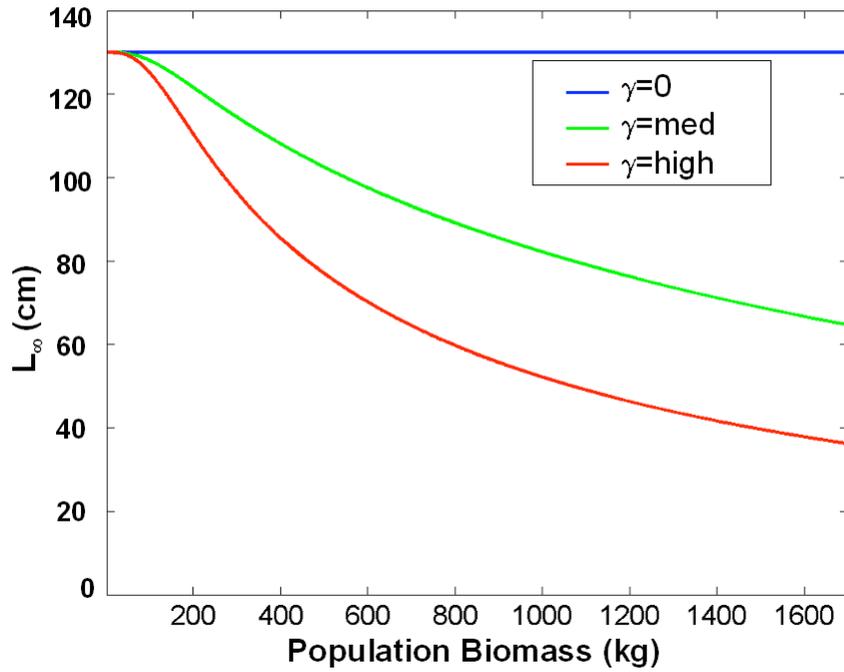


Figure 2.3 Change in asymptotic size with increasing biomass for no, medium, and high density dependence.

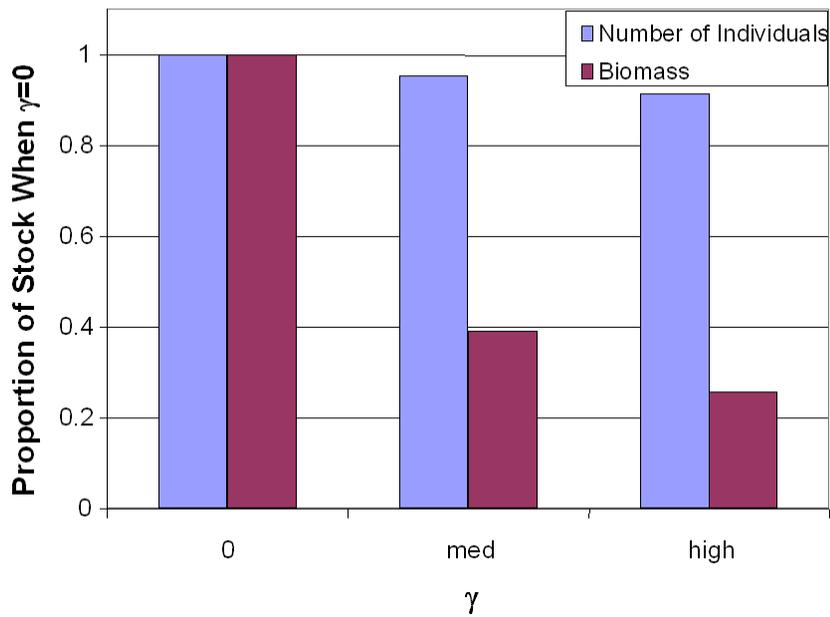


Figure 2.4 Proportion of individuals (blue) or biomass (purple) with density dependent somatic growth to without.

The number of individuals recruiting to the population however, changes little, despite the decrease in spawning stock biomass. This is due to the selection of a fairly flat recruitment curve. Thus, a reduced SSB due to density dependent growth can maintain the number of individuals at a level near that of populations without density dependent growth (Figure 2.2b).

Changes in size distribution

The size distribution of an unfished population varies with \square . As \square increases, the maximum size achieved in the unfished population decreases by 36% between no density dependence and $\square = \frac{2}{L}$ (Figure 2.5). Because asymptotic size is a function of food availability, one could make the prediction that if food were to become more available (either through changes in the environment or reduction of biomass) the upper size class of the largest fish would increase.

Spawning stock biomass and density dependence

Spawning stock biomass is a critical gauge for population health, fishery management, and for estimating recovery times of populations. If SSB varies in an unfished population due to density dependence, selecting an appropriate fishing level to achieve $F_{35\%}$, the fishing mortality that reduces SSB to 35% of its unfished biomass (Clark 1991), is more complicated. The large differences in biomass between populations with no density dependence and high-density

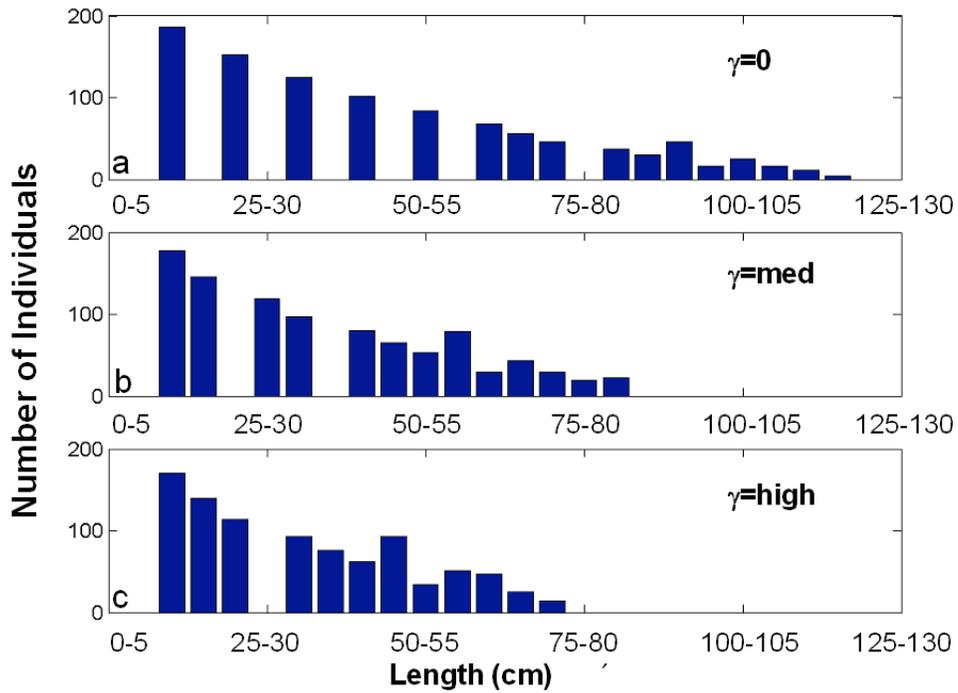


Figure 2.5 Change in size distribution of an unfished population for no (a), medium (b), and high (c) density dependent somatic growth.

dependent effects are reflected in the SSB (Figure 2.6). As the strength of density dependence increases, the fishing mortality order to achieve $F_{35\%}$ also increases (Figure 2.7). However, the yield and total population biomass are much lower.

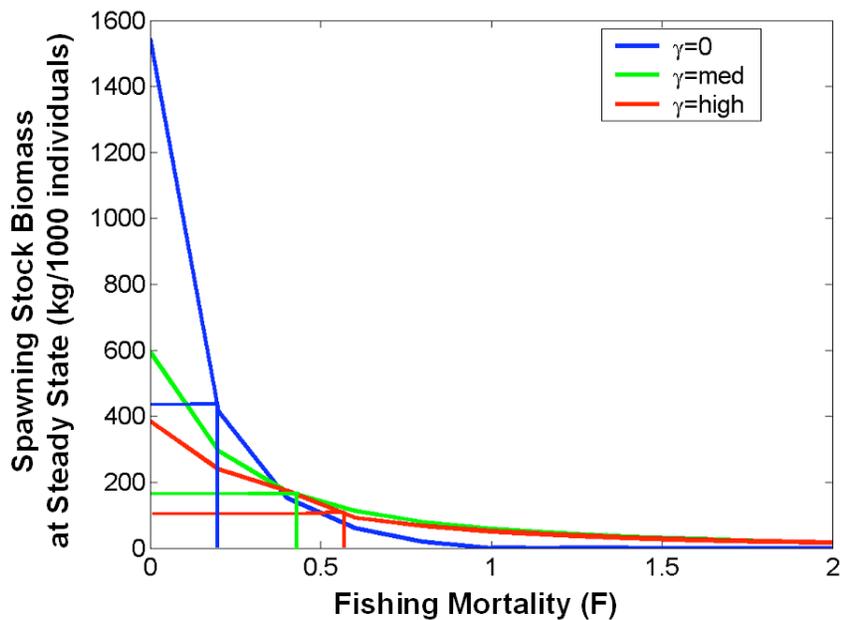


Figure 2. 6 Spawning stock biomass with no (blue), medium (green), and high (red) density dependent growth. The lines from the y-axis indicate 35% of unfished SSB, while the lines from the x-axis indicate the fishing mortality that achieves 35% of SSB.

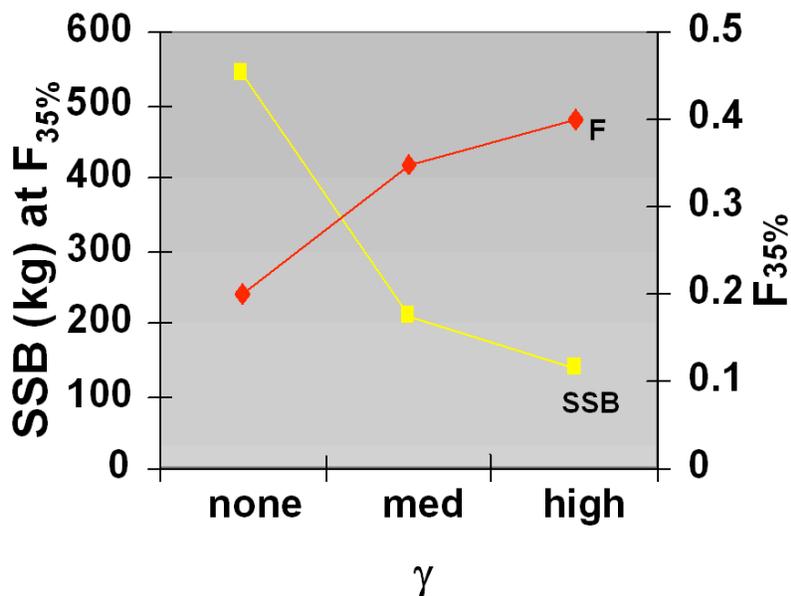


Figure 2.7 35% of unfished SSB (yellow) and $F_{35\%}$ (red) for each strength of density dependent growth.

Reserve Creation and Fishing Displacement

Age structured, population dynamics

We now consider the situation when a period of fishing without a reserve is followed by the creation of a reserve. We started the model with a population of 1000 individuals and fished down the population until it reached equilibrium determined by fishing mortality. We then created a no-harvest reserve 20 years after the populations were depleted and stable. Reserve size ranged from 0 to 50% of the population. The model analysis begins at the fished equilibrium and runs until all populations return to an equilibrium size.

We examine reserve fractions from 0 to 50% and $0 \leq F \leq 2$. For ease of presentation, results are shown for no reserve, a reserve fraction of 20%, and a reserve fraction of 50%. The population is uniformly distributed over an area that can support 1000 individuals. Furthermore, since lingcod are only moderately mobile, and larval transport likely contributes more than spillover to populations outside the reserve, we considered individual adult migration between reserve and non-reserve areas negligible.

We measured yield at steady state after reserve creation, calculated five years before the end of the simulation.

$$Yield = \sum_{a=1}^{a_{\max}} \frac{F(a)}{F(a) + M} (1 - \exp(-M - F(a))) N(a,t) W(a,t) \quad (13)$$

where

$$F(a) = \begin{cases} F & \text{if } L(a) \geq 44.2 \\ 0 & \text{otherwise} \end{cases} \quad (14)$$

Before the creation of a reserve, fishing mortality is homogenously distributed over the population. After creation, mortality is concentrated in the non-reserve area, and the effort from the reserve area is displaced. That is, fishing mortality is preserved at the same rate as it was before the creation of the reserve, but is now concentrated outside the reserve. We assume that fishers who once fished on the area set aside as the reserve move to the open grounds when the reserve is closed to fishing. This causes increased fishing mortality in the non-reserve areas to compensate for the closure of the reserve. With the (arbitrary) assumption that 5% of the total fishers leave the area, stop fishing, or change target species, the new fishing mortality is

$$F_{res} = F(1 + 0.95A) \quad (15)$$

where A is the fraction of the habitat protected by the reserve.

Reserve and Fishing Effects

In all cases explored, marine reserves are predicted to increase total population and biomass, and the greater the reserve size, the greater the equilibrium population. This, however, does not translate to a proportionate increase in yields with reserve size, nor a distinct benefit of reserves for low fishing effort. Recovery times for populations are predicted to vary due the

extent of depletion in the population before reserve recovery, mortality from fishing, density dependent effects, and reserve size.

Effects of Density Dependence on Yield

Density dependence growth decreases overall biomass, thus decreases yield when compared to populations without density dependence (Figure 2.8). Peak steady state harvest for all three growth regimes peaked at $F=0.2$. Note that, while the harvest for the no density dependent case crashed with high fishing mortality ($F=2$), the other two cases continued to provide yield. Density dependent somatic growth creates a size refuge, where more mature individuals were below the minimum harvest size because of decreased size at age.

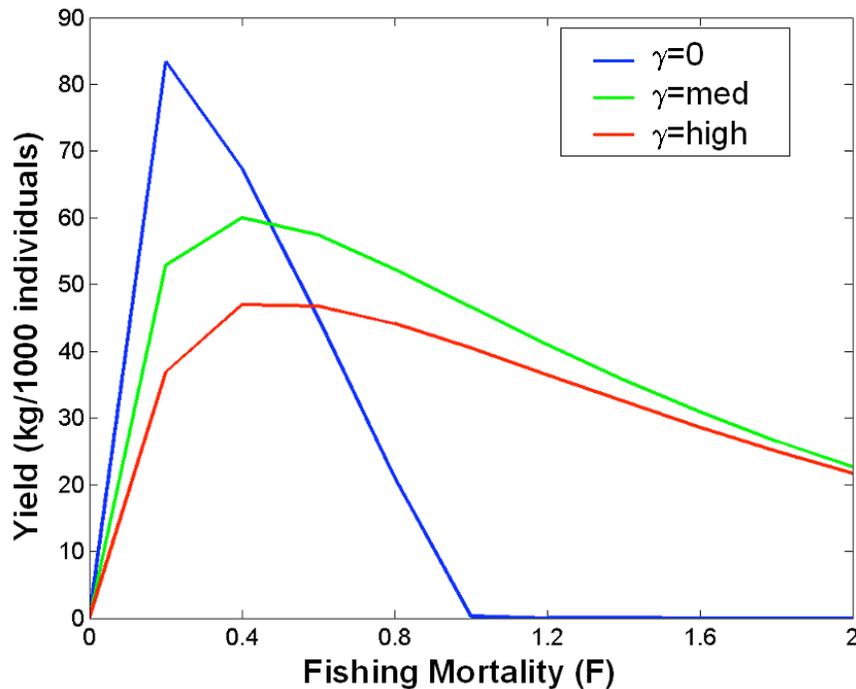


Figure 2.8 Yield at steady state without a reserve for no (blue), medium (green), and high (red) density dependent somatic growth.

Population recovery after the creation of a reserve

In populations with low fishing mortalities, recovery time of both individuals and biomass was lower for a 20% reserve than a 50% reserve regardless of density dependence. As fishing mortality increases, this pattern reverses for the recovery of individuals, as well as for biomass in populations without density dependent growth. Biomass recovery for populations with density dependence remains longer for the 50% reserve because asymptotic size is still fluctuating with the increasing biomass.

Table 2.2. Times to steady state from the creation of a reserve for biomass (a) and population in number of individuals (b) for each reserve fraction, γ strength, and fishing mortality.

a		$\gamma=0$		$\gamma=med$		$\gamma=high$	
		0.2	0.5	0.2	0.5	0.2	0.5
Fishing Mortality (F)	0.2	27	33	12	11	8	11
	0.4	34	37	14	19	16	12
	0.6	41	42	22	20	14	14
	0.8	50	46	23	21	20	19
	1	61	53	27	23	22	21
	1.2	80	56	26	28	23	22
	1.4	100	80	29	28	23	23
	1.6	120	89	31	30	26	23
	1.8	138	103	33	32	26	30
	2	156	115	35	32	26	33
	b		$\gamma=0$		$\gamma=med$		$\gamma=high$
0.2			0.5	0.2	0.5	0.2	0.5
Fishing Mortality (F)	0.2	24	29	17	24	12	14
	0.4	33	36	20	26	18	15
	0.6	41	39	25	28	16	17
	0.8	48	43	27	30	19	20
	1	63	51	29	33	24	22
	1.2	76	61	30	34	26	27
	1.4	98	77	31	35	29	30
	1.6	121	89	33	35	32	32
	1.8	137	99	35	36	32	34
	2	155	111	34	36	34	35

Recovery to steady state occurs more quickly with density dependent growth than without. Density dependent effects, as mentioned earlier, lower the

size at age of individuals, creating a harvest refuge for some mature individuals. Thus, once a reserve is created, there is a larger SSB at depleted levels available to rebuild the population. As with populations without density dependence, the recovery of individuals to a fraction of the unfished population in the steady state population exceeds that of biomass.

In order to quantify the benefit of reserves on the population as a whole, we compared the steady state biomass (population size) to the unfished biomass (population size) for the same density dependent strength, and reported this comparison in proportion of unfished biomass (population size). Recovery of biomass varies across β s, with the high β population returning to a higher portion of unfished biomass in both the 20% and 50% reserve scenarios than the other two cases. As we showed in Figure 3, strong density dependence results in a steeper relationship between asymptotic size and biomass. The combination of reduction in biomass from fishing thus increased asymptotic size, and the protection of the reserve is most likely the reason for the enhanced recovery of biomass with density dependent growth. Recovery leveled out with increased fishing effort, indicating that the reserve does good job in maintaining a desired minimum biomass (Figure 2.9).

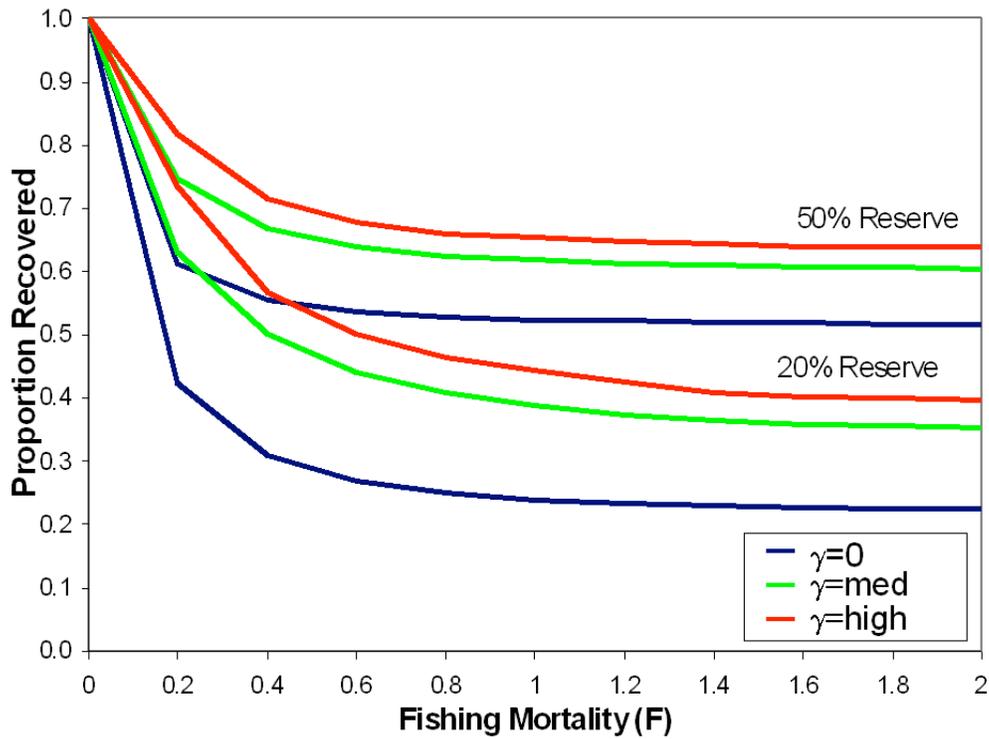


Figure 2.9 Proportion of biomass recovered after creation of a 20% or 50% reserve with no (blue), medium (green), and high (red) density dependent somatic growth.

Recovery of individuals showed less difference between the different strengths of density dependence than biomass showed, but retained the same patterns between reserve sizes and fishing mortality, with the exception of an outlying point (Figure 2.10). Strong density dependent growth affected the ability of the population to recover fully in number of individuals, however, since biomass recovered strongly, this could be an indication that individuals in the reserve are larger than they would be in an unfished population.

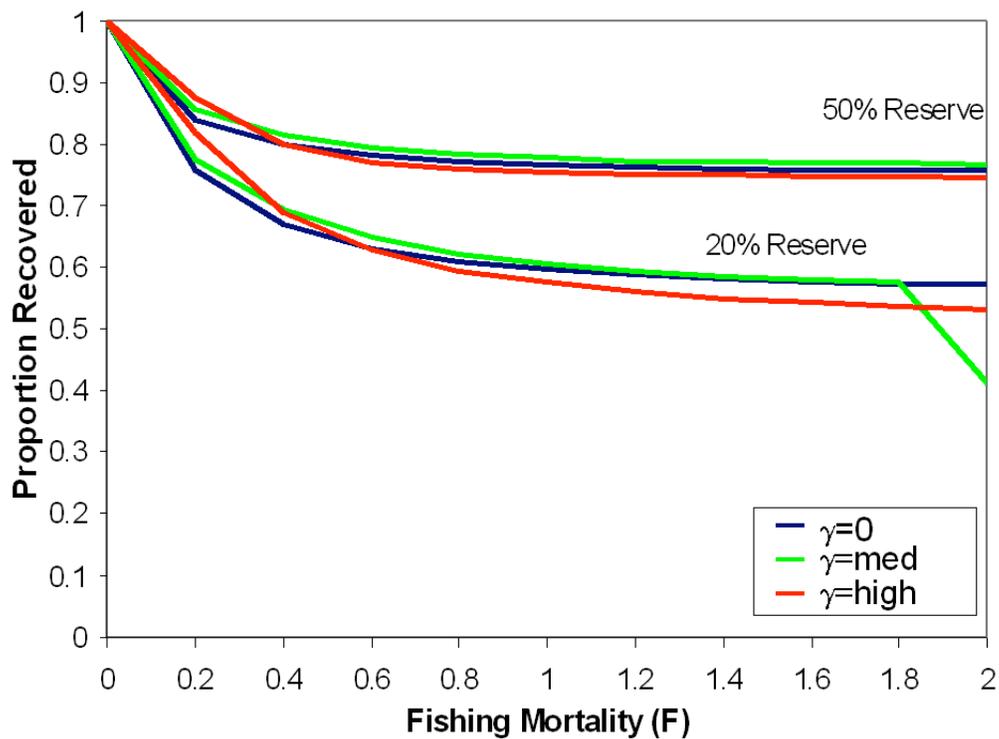


Figure 2.10 Proportion of individuals at steady state after reserve creation compared to steady state before reserve closure.

Effect of Reserves on Yield

As with the Figure 2.8, peak steady state harvest, evaluated at 200 years after the creation of a reserve, occurs in populations without density dependence for all reserve sizes at $F=0.2$. Harvest peaks in populations with density dependent growth are lower than those without, and occur at $F=0.4$ (Figure 2.11, Figure 2.12).

Reserves are predicted to increase yield, compared to no reserve, when fishing pressure is heavy (generally greater than $F \geq 0.5$ for the population without density dependent growth) for steady state yield, regardless of reserve

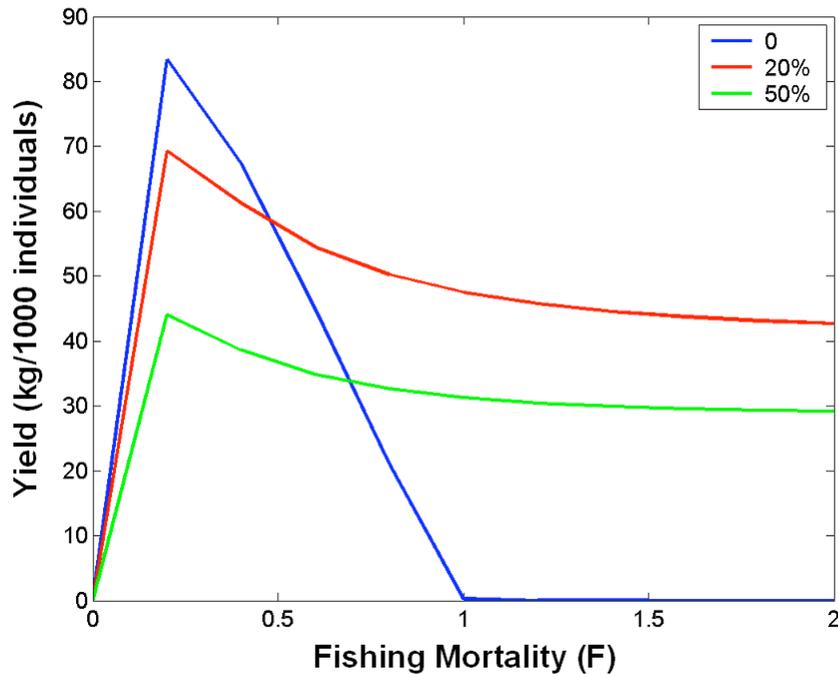


Figure 2.11 Steady state yield after reserve creation without density dependent growth with no reserve (blue), 20% reserve (red), and a 50% reserve (green).

size. This level of fishing pressure, however, is higher than $F_{35\%}$, meaning that even with or without reserves, the best way to maximize yield is to fish conservatively. Furthermore, reserves are predicted to stabilize yield, meaning that as fishing pressure increases, yields decline only slightly; like peak yield, this pattern was evident in all cases.

Yields are always higher with a reserve than without at $F > F_{35\%}$, but continually decline with increasing reserve size or fishing mortality. The ineffectiveness of reserves in the recovery of heavily exploited populations emphasize the fact that prudent recommendations for F are far more important

than reserves or reserve size, and that for some species, a 20% reserve may not be effective in achieving management goals (Mangel 2000).

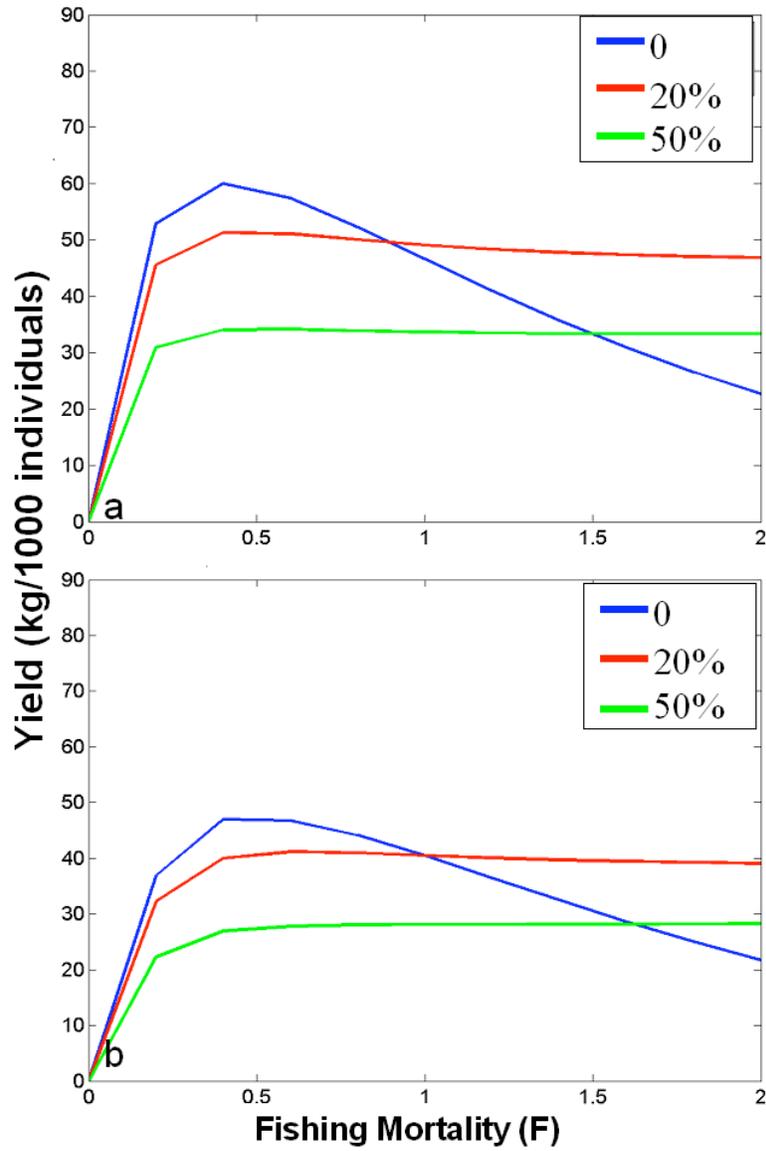


Figure 2.12 Steady state yield after reserve creation for β =med (a) and β =high (b) and three reserve sizes.

Change in asymptotic size after the creation of a reserve

Regardless of reserve size or fishing mortality, the size distribution for populations without density dependent growth recovered to the full size range (Figure 6a), although numbers of individuals were not fully recovered. In populations with density dependent growth, fishing mortality increased asymptotic size compared to the same populations without fishing or with lower fishing (Figure 2.13). The initial increase after reserve creation for $F \leq 0.8$ can be attributed to the increase in F because of displaced fishing effort, while the subsequent decline is associated with a build up in biomass due to the creation of a reserve. The middle fishing mortality, $F=0.4$, was never predicted to show the same decline because the recovery of biomass in the reserve is not as great when compared to recovery with higher fishing mortalities due to larger biomass from lower fishing.

Mean length for the population increased within the reserve, but not outside for all three density dependent strengths (shown for $\frac{2}{L}$ in Figure 2.14) because the number of larger individuals increases when fishing pressure is removed. Survival to a large size is diminished with fishing and we assume that larval dispersal is uniform over the population, so small individuals dominate the fished area, thus driving the mean length of the population down. An interaction between fraction protected (more protected, higher mean) and density dependent growth (higher $\frac{2}{L}$ lower L) occurs when comparing the

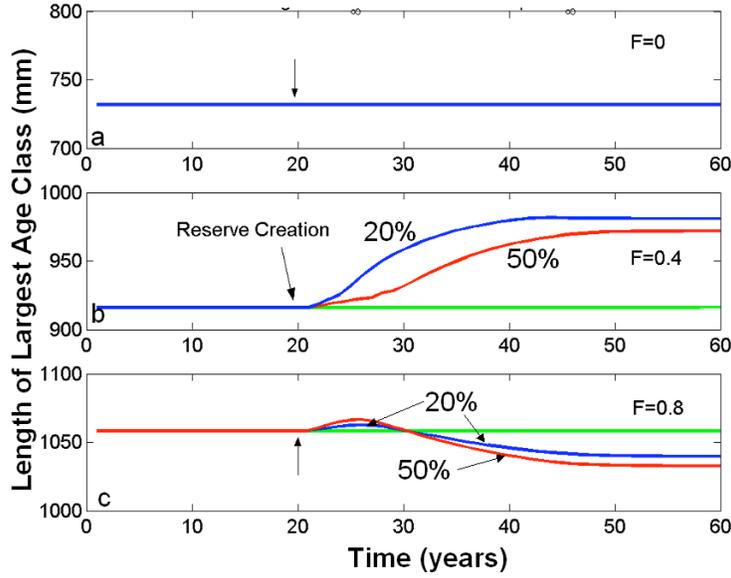


Figure 2.13 Asymptotic size after reserve creation when σ is high for three fishing mortalities and no reserve, 20% reserve and 50% reserve.

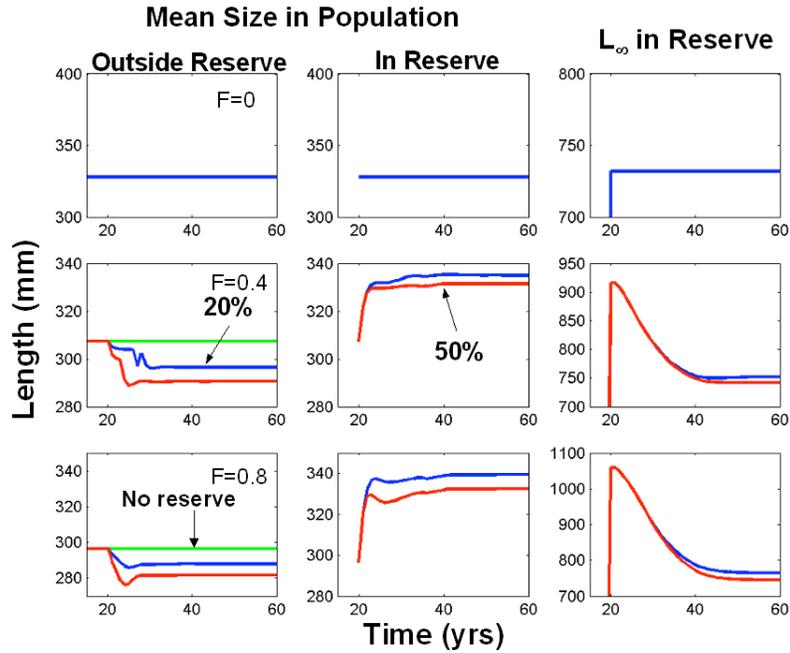


Figure 2.14 Changes in mean size outside (left) and inside (middle) of the reserve, and change in asymptotic size in the reserve (right) when σ is high. The top row is without fishing, the middle row shows $F=0.4$, and the bottom row shows $F=0.8$. Green lines represent no reserve, blue lines represent a 20% reserve, and red lines represent a 50% reserve.

mean size between the populations inside the 20% and 50% reserve, causing the 20% reserve to achieve a higher mean size than the 50% reserve despite fewer large fish.

Displaced fishing effort

We compared the difference between displaced fishing effort and a reduction of fishing effort proportional to the reserve size as it applied to spawning stock biomass and yield at all three density dependent strengths. SSB is predicted to be higher with reduced fishing effort than with displaced fishing effort, as would be expected due to decreased mortality. Furthermore, the differences between displaced and reduced fishing effort decreased with decreasing reserve size and increased fishing mortality (Table 2.3). Extrapolating from the data, we can predict that the recovery time of the population is lower without displaced fishing effort.

Table 2.3. Proportion of spawning stock biomass with displaced fishing effort to reduced fishing effort from reserve. A is the reserve fraction.

	$\gamma=0$		$\gamma=med$		$\gamma=high$	
	A=0.20	A=0.50	A=0.20	A=0.50	A=0.20	A=0.50
0.2	0.90	0.92	0.93	0.92	0.95	0.94
0.4	0.92	0.95	0.92	0.93	0.78	0.86
0.6	0.94	0.97	0.92	0.94	0.92	0.94
0.8	0.96	0.98	0.93	0.95	0.93	0.95
1	0.97	0.98	0.94	0.96	0.94	0.96
1.2	0.98	0.99	0.95	0.97	0.94	0.96
1.4	0.98	0.99	0.96	0.98	0.95	0.97
1.6	0.99	0.99	0.96	0.98	0.96	0.98
1.8	0.99	1.00	0.97	0.98	0.96	0.98
2	0.99	1.00	0.97	0.99	0.97	0.98

At low fishing effort without density dependence, yields differ little between the two harvest states and peak at a moderate fishing effort in favor of no displaced fishing effort. This may be attributed to a balance between overfishing with displaced fishing effort and lower total fishing mortality from reducing effort. Higher yield with displaced fishing effort for low fishing mortalities imply that reserves may allow for a slightly higher overall fishing effort to maximize yield (Table 2.4).

Table 2.4. Difference between yield with displaced fishing mortality compared to yield without with no density dependent growth. Numbers greater than 1 indicate that yield with displaced fishing mortality is greater than yield with reduced effort.

	$\gamma=0$		$\gamma=med$		$\gamma=high$	
	A=0.20	A=0.50	A=0.20	A=0.50	A=0.20	A=0.50
0.2	1.08	1.18	1.06	1.13	1.00	0.99
0.4	1.04	1.10	1.01	1.04	0.96	0.92
0.6	1.01	1.03	0.99	1.00	0.95	0.91
0.8	1.00	1.01	0.99	0.99	0.95	0.91
1	0.99	1.01	0.98	0.99	0.96	0.92
1.2	0.99	1.00	0.99	0.99	0.96	0.94
1.4	0.99	1.00	0.99	0.99	0.97	0.95
1.6	0.99	1.00	0.99	0.99	0.97	0.96
1.8	0.99	1.00	0.99	1.00	0.98	0.97
2	0.99	1.00	0.99	1.00	0.98	0.97

Displaced fishing effort interacts with the effect of density dependent growth on asymptotic size (Figure 2.14). Increasing the fishing pressure outside the reserve reduces biomass, allowing asymptotic size to increase. Increasing reserve size corresponds to a higher asymptotic size early after the creation of a reserve because of the higher mortality that occurs from density dependent growth. Once the biomass in the reserve builds, the asymptotic size

declines again. This decline does not occur at $F=0.4$ because the difference between the population outside the reserve, before and after creation, is minimal. Thus, the displaced fishing effort can be sufficient to maintain the increased asymptotic size. Additionally, the increase in fishing mortality on the fished area due to displaced fishing effort decreases the mean length of the population outside the reserve to a level lower than in the reserve. The work of Apostoloki et al (2002) generally agrees with our findings. They also found that this redistribution of effort is especially detrimental for population recovery when spawners are not protected.

Implications for marine reserves

Potential increases in yield from spillover or larval dispersion are often used as the measure of success of marine reserves to the fishing community and public (e.g. Dugan and Davis 1993; Mangel 2000; Roberts et al. 2001; Palumbi 2002). These statements are extremely difficult to make conclusively due to various aspects of the reserve and target species biology. In general, the size of the reserve is predicted to have minimal effects on stabilization of yield. Based on a reserve covering at least 10% of the habitat and moderate fishing mortality, we predict yields to be maintained over the lifetime of the fishery, and at steady state after recovery. However, no reserve size is predicted to increase yields to the level that they were at with no reserve and moderate fishing. Thus, while reserves may increase lingcod populations and ensure that there are some

yields, regardless of fishing mortality, nothing can match conservative fishing (at or near $F_{35\%}$) to maximize yields.

The most dramatic improvements after the reserve was closed to fishing are predicted to occur at heavy fishing efforts. When a certain fraction of the population is protected from fishing, there is a guarantee of that same fraction of SSB is contributing to new recruitment. Recovery took longer, but the recovery was a greater percentage of the total population; furthermore, at high fishing mortality, the reserve contained the largest fish in the population when there was no density dependence. This corresponds with the general observation that biomass, numbers, and size are higher within marine reserves when the species of concern is heavily exploited.

Biomass in depleted populations takes time to recover after the creation of a reserve, resulting in a higher asymptotic size in the early years of the reserve. This could contribute to claims of the reserve increasing sizes of individuals within reserve borders. However, as biomass increases in the reserve, density dependent growth causes decreased asymptotic size and eventually slowed to no increases in biomass. Since few reserves have been in existence for as long as this analysis runs, we may not see similar results in real reserves for a very long time. Halpern (2002) reviewed three case studies where the reserve did show no increase or a decline in biomass, average age, or length between the fished and reserve area, which could be an indication that density dependence has had an effect on the reserve.

Using mean length may not be an appropriate measure of reserve success. Simply by increasing the survival of larger fish, as reserves do, mean length is increased. This occurs regardless of density dependent growth. Thus, mean length decreasing outside the reserve could lead opponents of marine reserves to make claims of reserve failure. Likewise, asymptotic size increasing outside the reserve, as in the case with the catch of “trophy fish” (Roberts et al. 2001), could cause managers to proclaim success for a reserve. Abundance may be a better measure of reserve success. If the reserve increases abundance of targeted species and the age structure of the population is restored to a normal range, which may be enough of an indication that the reserve is successful in protecting a species.

When a narrow set of goals is chosen for a reserve, factors such as density dependent body growth can mar managers’ ability to evaluate the success of the reserve. Our work has shown that common goals such as increased yield outside the reserve, biomass, or average size, may not be the best ways to measure the success of a reserve. Instead, it may be helpful to think about how well the population as a whole, both inside and outside of the reserve, has responded to protection.

The effect of density dependence on spawning stock biomass is one of the most interesting aspects of adult density dependent growth. In order for fisheries scientists to accurately predict $F_{35\%}$, one must know the strength of adult density dependent growth. However, if the strength of density dependent

growth is under estimated because of long histories of exploitation, stocks may improve faster than predicted.

Lingcod are often predicted to have a fairly fast recovery time. Recovery to 40% of unfished female SSB using historical recruitment and reducing F by 25% of the 2000 level took less than 10 years (Jagiello et al. 2000) without a reserve. Martell (2000) predicted recovery to steady state (3 times the depleted biomass) with a 10% marine reserve or cutting F in half in approximately 60 years. Ensured maintenance of a given SSB can occur two ways. The first is fishing at a level that maintains SSB ($F_{35\%}$ or lower if the goal is 35% of SSB), and the second is to protect that fraction of spawners from fishing mortality. Our model predicted that regardless of fishing effort, recovery to 35% percent of SSB will eventually happen. However, with no reserve or a 20% reserve, this recovery only occurred for lower fishing mortalities for all density dependence strengths.

Alonzo and Mangel (in review) found similar results in the importance of reserve fraction for the California Sheephead, *Semicossyphus pulcher*, where increases in reserve size did not correspond to increases in reserve benefits in terms of yield. Displaced fishing effort may be depressing the benefit that increased reserve size may have on the population. Thus it is important to remember that reserves cannot be the only management tool, and must be combined with a reduction in fishing effort.

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