# Growth and Survival Responses to Experimental Fishing: models, experiments and lessons from the Northern pikeminnow of South Central British Columbia

by

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Abstract

# Abstract

The objective of this was study was to determine if species specific fishing could produce "cultivation-depensation effects" in an aquatic ecosystem with two predatory, competing fish species. I identified a unique stock of northern pikeminnow living in series of connected lakes that has obligatory rearing in specific nursery lakes; developed two novel likelihoods to measure the growth, movement and mortality responses; developed an ecosystem model to predict how the system would respond to fishing, and finally, compared the ecosystem modeling predictions to observed responses.

My research showed northern pikeminnow in South Central B.C. have obligatory rearing in specific nursery lakes then disperse to other lakes as adults. I argue that this large scale spatial ontogeny can be solely explained by temperature cues to spawn and that the distribution of adults is determined by density-dependent dispersal that equalize very large productivity and effective density differences between lakes.

I showed that in spite of being included in many stock assessments, and being used as proxies for natural mortality estimates and for exploitation rate targets, von Bertalanffy growth parameters are not generally estimated correctly. The data used to do so are virtually always biased due to: sizeselective gears, populations subjected to fishing and natural mortality and in some cases, size-dependent movement. I developed two new likelihoods to simultaneously estimate growth and mortality parameters: one for length-age data, and another for mark-recapture data. The first performs well across a range of recruitment anomalies and steady state fishing mortalities but fails when fishing rates have been variable (especially increasing) and when gear selectivity is dome-shaped. The second likelihood works well with simulated data but is not robust to assumptions of constant recruitment and measurement error being violated. I combined length-age and mark-recapture data to show using simulated sampling that it is possible to simultaneously estimate growth, mortality, and movement parameters where sufficient numbers of fish are observed moving. The assumptions required for these models to perform well are very restrictive.

I used a simple ecosystem model and compared the predictions to observed responses following depletion fishing in two-fish lake systems with rainbow trout and northern pikeminnow. Consistent with model predictions, growth was slower and mortality of juvenile rainbow trout higher relative to the control in lakes where northern pikeminnow were removed, while adult rainbow trout survival remained unchanged. Visual survey indices of northern pikeminnow fry indicated survival of 1+ fish worsened and 2+ improved following fishing. Consistent with model predictions, no obvious mortality or growth responses were observed in adult fish in either rainbow trout or northern pikeminnow removals. While the agreement between the model and observations was encouraging, field testing such complex predictions was fraught with difficulty. The probability distributions of the parameters of interest were very broad. Also, the model predicts that survival and behavioral dynamics producing the greatest differences in direction and magnitude of ecosystem response occur in size classes of fish and groups of zooplankton that are difficult to observe. It was not possible to conclude whether an alternate state was produced through cultivation-depensation effects. To do so would require longer term data on recruitment responses, vulnerability exchange processes and survival data of young age classes of fish.

This study identifies several shortcomings in our ability to predict and detect how ecosystems will respond to fishing. First, our ability to measure even simple response variables such as growth and mortality is not good. Secondly, even if we could, the direction and magnitude of these responses can be highly counter-intuitive. Finally, those processes with the most violent effects on our predictions are those for which we have very little information, namely dynamics determining the spatial distribution of the stock, the dynamics of young fish and behaviorally mediated predation rates.

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# **Prior Publications**

Taylor, N., Walters, C., and Martell, S. A new likelihood for simultaneously estimating the von Bertalanffy growth parameters, vulnerability, natural mortality and fishing mortality. *Canadian Journal of Fisheries and Aquatic Sciences.* 62:215-223

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While my supervisor frequently introduces me as a first experiment attempting to supervise a PhD student with only "don't screw up" as advice, nothing could be further from the truth. Much of the intellectual content of this thesis stems from conversations with Carl while carrying equipment, smoking outside the huts and sitting in on courses.

Finally none of this would have been possible without considerable financial and emotional support of my parents and loved ones.

# Chapter 1

# Introduction

Fisheries science typically assumes the relationship between the number of new juvenile fish produced and adult biomass to be density-dependent so that the number of juveniles produced per adult increases as adult population size decreases (called compensation). It is also earnestly hoped that this relationship is stationary, meaning parameters describing it do not vary with time. Explaining the failure of some fish stocks to recover following sustained fishing, notably Newfoundland cod (Gadus morhua) (Shelton and Harley, 1999; Rose et al., 2001), has led to the development of a new hypothesis called Cultivation-Depensation (Walters and Kitchell, 2001) that predicts how trophic interactions can cause juvenile fish survival to decline at low stock size (called depensation) in a pattern that may not be stationary. Here I review the traditional theory used to describe fish population dynamics, introduce the Cultivation-Depensation hypothesis and describe modeling and experimental research testing this hypothesis using lake ecosystems with only two fish species, rainbow trout and stunted northern pikeminnow Ptychocheilus oregonensis.

1

# 1.1 Review

## 1.1.1 Compensation in fish stocks

There has been considerable debate about density-dependent increases in stock productivity at low stock size, or compensation, but there is little debate that some resource will eventually limit the size of a fish population (Rose et al., 2001). The majority of the remaining debate is about the magnitude of compensation and processes that cause it (Rose et al., 2001). The processes that can produce compensation can be examined by looking at the following population dynamics tautology (Walters and Martell, 2004):

$$N_t = N_{t-1}S_a + FN_{t-1}S_j (1.1)$$

where  $N_t$  represents abundance at time t,  $S_a$  adult survival, F the mean fecundity of individuals, and  $S_j$  juvenile survival. If a population is at equilibrium, so that  $N_t = N_{t-1}$  then Eq. 1.1 reduces to the following:

$$1 = S_a + FS_i. \tag{1.2}$$

In order that this relationship be satisfied where harvesting has reduced  $S_a$  and/or  $S_j$ , at least one of the three rates must show compensatory change. Though density-dependent changes in fecundity have been reported (Rothchild et al., 1989) some authors doubt the whether changes in fecundity are sufficient to stabilize populations (Craig and Kipling, 1983; Koslow, 1992; Koslow et al., 1995) and in any case, harvesting fish typically reduces mean size hence F because in semelparous species increases in size often result in higher fecundities. However, the total fecundity of a population has been documented to change in response to changes in density, with younger individuals spawning earlier (Funakoshi, 1994) or with a greater proportion of females spawning (Koslow et al., 1995). Documented changes in adult survival as a function of density are relatively rare. The most compelling arguments about which rate is compensatory are those involving density dependent responses occurring in the early stages of life i.e. those processes that affect  $S_j$ .

Given the apparent stability and/or ambiguities in the relationship between fecundity, adult survival and adult density, it is reasonable to assume that most of the actual compensatory responses in fish stocks are occurring with the younger individuals. There are some excellent field examples of density dependent survival at various early life stages. Beverton and Iles (1992) document how the density dependent component of mortality changes over three time periods between settlement and the second year. They were able to show that the dramatic dampening effect of density dependent mortality of juveniles was sufficient to reduce the 200 fold variation in adult abundance to larval settlement to only a 4 fold variation in the second year. Using 14 populations of Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aieglefinus*), whiting (*Merlangius merlangus*), place (*Pleuronectes platessa*) and sole (*Solea vulgaris*) Myers and Cadigan (1993) showed both strong evidence of density-depended mortality within cohorts and relatively little interannual

variability in the density-independent component of juvenile mortality.

Juvenile survival is often related to the rate at which juvenile fish can reach sizes that make them invulnerable to predation. Post et al. (1999) showed using a series of experimental lakes stocked at different densities that at low density, age-1 growth increased and there was a corresponding increase in juvenile survival. Healey (1980) showed that exploited lakes of whitefish had a higher frequency of increased growth and recruitment than unexploited lakes. He also documented somewhat ambiguous changes in fecundity and proposed that adult suppression of young could be the result of adults confining juveniles to marginal habitats. Marshall and Frank (1999) also show empirical evidence that mean length of age-1 haddock were negatively related to the density of age-4 and older fish, that differences in age-1 length were persistent through life, and that recruitment was positively related to length at age-4.

# 1.1.2 Stock-Recruit Curve Analysis: Compensation Versus Depensation

Regardless of the mechanisms by which compensation is taking place, there is now a considerable amount of data from stock recruitment relationships to support such an assertion. The most important contribution comes from the work of Myers et al. (1995b) who analyzed over 700 spawner-recruitment series looking for parameters that were constant at the species level. Their work shows a remarkable result, that the standardized slope at the origin of a stock recruitment curve (or the maximum reproductive rate) is consistently between 1 and 5, i.e. juvenile survival rates at low density are 1 to 5 times higher than at natural "unfished" densities. Equally importantly, Myers et al. (1995a) show most (125/128) fish stocks do not show any evidence of depensation (or decreasing juvenile survival at low stock size).

Considerable work followed Myers et al. (1995a)'s analysis of stock-recruit data with particular attention devoted to determining whether or not models parameterized with depensation fit the data better than those without it (Liermann and Hilborn, 1997; Shelton and Harley, 1999; Liermann and Hilborn, 2001; Frank and Brickman, 2000). However, most studies concerned themselves with detecting a stationary depensatory relationship; that is, one with a domain on the stock recruitment curve where juvenile survival consistently and immediately decreases as adult density decreases resulting in a second low density equilibrium for the fished species.

# **1.2** Research Hypothesis and Experiment

## **1.2.1** The Cultivation Depensation Hypothesis

The main difference between the cultivation-depensation hypothesis and classical depensation is rooted in foraging arena theory (Walters and Juanes, 1993). In classical models of depensation such as that of Holling (1959), the proportion of prey consumed by a predator is limited by handling time or by Chapter 1. Introduction

satiation. Classical depensation (Holling, 1959) arises by assuming that the probability of prey encountering predator is a linear function of the densities of predators and prey (akin to first order chemical kinetics) but with predator searching times reduced at higher prey densities due to handling time effects, so that as prey density is reduced, the proportion of prey removed by predators increases. Foraging arena theory (Walters and Juanes, 1993) on the other hand predicts that risk-sensitive foraging on the part of the prey (juvenile fish in this case) mitigates their interaction with predators through exchange rates between the vulnerable prey pool (available to predators) and the non-vulnerable pool. It assumes that juveniles are confined to refuges away from predators (inshore shallow habitats, hiding places etc.) and that predation occurs mainly when juveniles are forced to enter risky states (the foraging arena, Walters and Juanes 1993; Walters and Kitchell 2001). In aquatic systems there is a growing body of evidence to support such a risk sensitive foraging structure (Tonn and Paszkowski, 1992; Tonn et al., 1994; Post et al., 1999).

Foraging arena theory predicts that a key factor determining the probability of an encounter of predator with prey is prey behavior, not overall prey density. At high densities, prey are forced to make more risky foraging trips in order to meet their energy demands because food density in the refuges is depressed. Foraging arena theory predicts that in the absence of other trophic effects, when adult density is reduced there is a corresponding decrease in the density of juveniles in the refuge areas meaning higher lo-

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cal food densities and hence fewer risky trips in the foraging arena to feed. One of the emergent properties of foraging arena theory is that it gives rise to the classic compensatory Beverton-Holt spawner-recruit model (Beverton and Holt, 1958; Walters and Korman 1999) and several testable hypotheses about how changes in behavior, productivity, and predation risk can alter the relationship between the number of recruits produced per spawner.

There are many hypotheses that explain the existence of alternate stable states in ecosystems (reviewed in Scheffer et al. 2001a). The Cultivation Depensation hypothesis (Walters and Kitchell, 2001) argues that fishing and juvenile dynamics can be the crucial elements in producing a 'flip' in the ecosystem state. Cultivation-depensation effects arise in Ecosim II (Walters et al., 2000) models though the following sequence of events (Walters and Kitchell 2001, represented in Fig. 1.1). Fishing reduces the adult population size of a "dominant" fish species and hence, the total number of juveniles in predation refuges. Juveniles reduce feeding time or time spent at body sizes small enough to be vulnerable to predation risk. Juvenile mortality then decreases so that the net number of recruits stays nearly constant even though fewer juveniles are being produced. However, if there is high predation by the adult fish on some smaller predator or competitor of the juveniles (a 'forage' fish) then as adult density is reduced, the forage fish is released to increase in abundance. Then one or two negative effects can occur. If the forage fish prev directly on juveniles, then predation mortality is directly increased. If the forage fish and juveniles are competitors, increased forage fish abundance leads to reduced food density and hence, increased juvenile foraging time and general predation risk.

Direct predation of forage fish on the juveniles of the dominant fish species is not necessary for cultivation-depensation. If the forage fish species is "released" to increase in abundance, the forage fish may directly prey on juveniles of the dominant species but if some foods are shared, then increased forage fish density means reduced food density and hence increased juvenile foraging time (Walters and Kitchell, 2001).

From a management perspective cultivation-depensation effects can have profound impacts. Firstly, they mean that excessive fishing can produce a permanent low density state of the target (or dominant predator) species. They also mean that ecosystem "flips" can happen in the opposite direction; ecosystems dominated by the forage species can be flipped back to the dominant predator state. Such transitions need not be solely the product of fishing either, since it is the ratio of risk to productivity that determines the number of recruits per spawner (Walters and Juanes, 1993). Whether concurrent with changes in productivity or not, cessation of fishing in a stock pushed into the forage fish dominated state will not recover without some additional management intervention (such as fishing the forage species).

## **1.2.2** Experimental depletions

The cultivation-depensation hypothesis is well suited to testing using experimental depletions since it makes specific predictions about how survival,



Figure 1.1: Trophic triangle describing where the survival of the juvenile of the dominant is negatively affected by the prey of the dominant species.

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growth and foraging time should change in response to density manipulations. In this study, I tested if cultivation-depensation effects described above could be produced in the field using depletion fishing. Specific predictions include (Walters and Kitchell, 2001):

- Increase in abundance of small forage fishes or invertebrates if predatory stock size decreases
- increasing rather than decreasing juvenile foraging time when adult abundance is low due to competition with forage fishes
- decreased juvenile survival rate at low adult population size due to increased foraging time and (or) direct predation by forage species.
- diet and habitat overlap between juvenile fish and the forage fish and/or direct evidence of predation by the forage fish on juveniles should be observed in stomach contents.

I conducted depletion fishing of northern pikmminow *Ptychocheilus oregonensis* in a series of lakes on Bonaparte Plateau in South Central B.C. having two predacious species: rainbow trout *Onchorhynchus mykiss* and stunted northern pikeminnow. The objectives of my study were a) to model the system to see under what parameter combinations cultivation-depensation effects could be observed, b) fish the system and c) measure how growth and survival variables of both species responded to depletion fishing. I first identified a unique system of lakes where northern pikeminnow have obligatory rearing in nursery lakes; I conducted depletion fishing; I developed new statistical methodologies to measure growth and survival responses to such fishing; I developed an ecosystem model of the study system to see what parameter combinations would produce cultivation-depensation (Walters and Kitchell, 2001) effects; and finally compared the predicted and observed responses to the experimental manipulations; 

# Chapter 2

# Ontogenetic Habitat Shifts Between Lakes by the Pygmy Pikeminnow

# Abstract

This is the first report of a freshwater fish population that has obligatory rearing in specific 'nursery' lakes. In two South Central British Columbia drainages, I identified two northern pikeminnow populations having either a single or multiple lake life-history type. I argue that such large scale spatial organization is controlled by temperature driven spawning cues and density-dependent migration from the nursery areas to outlying lakes. I used visual surveys and mark-recapture experiments to show the position of fry and apparent mortality rates in each drainage. I used bioenergetics modeling and showed it is physiologically possible to spawn and hatch in the headwater lakes, but considerable additional consumption would be required for fish rearing in non-nursery lakes to reach the same mass observed in nursery areas by the following year to compensate for delays in spawning. Using Chlorophyll A, I showed the nursery lakes to be more productive but that this advantage disappears once scaled to the effective density of northern pikeminnow between nursery and non-nursery areas.

keywords: unit stock, northern pikeminnow, ontogenetic shift

## 2.1 Introduction

Fisheries biologists typically treat lakes as unit stocks where little movement between lakes is assumed even where movement is possible and there are gradients in productivity and density between lakes. While it is understood that fish move between lakes over long time scales, the population dynamics of a typical lake population are assumed to be dominated by local birth and death processes. Following the research of Gerking (1959), many stream populations are also assumed to occupy only a small range of the stream in spite of the fact that many of the methods used to estimate the total displacement of fish population are biased against detecting larger scale dispersal in the first place (Gowen et al., 1994). However, at drainage scale, lakes are both connected to each other and have gradients of temperature, sediments, water, nutrients, and organic matter (Gomi et al., 2002) that animals could utilize over the course of their ontogeny provided that streams between lakes permit movement between them. Use of more than one lake has been observed in Arctic charr in response to productivity and temperature difference between lakes (Naslund, 1990). Ontogenetic movement can happen over very large scales in marine systems (Rooker et al., 2003).

Ecological theory has long predicted ontogenetic niche shifts in response to ontogenetic changes in resource and predation gradients (reviewed in Werner and Gilliam, 1984) and more recently in response to predation risk from larger sized fish of the same or different species (Persson and Eklov,

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1995). In fresh-water systems, habitat shifts in response to such gradients are observed, but the scale of these shifts and the experimental designs to detect them tend to be at small scale, for example, habitat refuges in small ponds or enclosures (Persson and Eklov, 1995; Olson, 1996; Osenberg et al., 1994). Fish in seasonal environments such as temperate lakes have only a short growing season to acquire sufficient energy to survive winter. Young fish face a very strong tradeoff between growing large enough to survive winter versus the predation risk associated with the additional feeding needed to do this (Post and Parkinson, 2001; Biro et al., 2005). Also, bioenergetics (Kerr, 1971; Kitchell et al., 1977) show strong dependence of swimming, consumption and digestion on temperature. The end of season length for age 0+ perch exhibit a nearly linear relationship between length and cumulative degree days (Power and van den Heuvel, 1999). Finally, the number of degree days for recruitment also seems to limit the northern edge of range for many species (Schuter and Post, 1990) when the growing season (as dictated by each species bioenergetics) is not long enough for species to reach sizes large enough to avoid being eaten, have sufficiently large lipid reserves to survive winter.

Northern pikeminnow *Ptychocheilus oregonensis* (Cyprindae) are distributed from Oregon to South Central British Columbia. They have been studied extensively as the target of predator removal programs in Idaho (Jeppson, 1959), British Columbia (Ricker, 1941) and most recently in the Columbia River (Rieman and Beamesderfer, 1990; Beamesderfer, 1992b; Friesen and Ward, 1999). In more temperate climes northern pikeminnow grow to asymptotic lengths of 350 - 450mm F.L. at which sizes they are prolific predators (Petersen and DeAngelis, 1992). At the northern limit of their distribution, they appear to be stunted growing only to approximately asymptotic lengths 200mm.

Here I document the first population of stunted northern pikeminnow that takes advantage of temperature, productivity and density gradients between lakes. I use bioenergetics modeling to show that large differences in consumption rates would be needed in order to compensate for delayed spawning caused by cooler temperatures, and argue that the distribution of adults is determined by the ratio of effective density to productivity.

# 2.2 Methods

#### 2.2.1 Study site

The study site was approximately 100 km North of Kamloops in South Central British Columbia, Canada. I studied northern pikeminnow in two separate sub-drainages of the Thompson River system. The western drainage (Fig. 2.1) includes Dad's Lake, with two 'head-end' lakes above it: Mom's and Nestor. In the eastern drainage I intensively studied Moose Pasture Lake, which also had two lakes above it called Cheryl and Wilderness (Fig. 2.1). The eastern lakes drain into the Deadman River and the western ones directly into the Thompson River. The other lakes in Fig. 2.1 were given cur-

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Table $2.1$ :	Table of lake areas	s, maximum depth	s and perimeters
Lake	Total Area (ha)	Max Depth $(m)$	Perimeter(m)
Cheryl	13.5	15	1563
Wilderness	11.9	11	1628
Moose Pasture	7.3	.10	1411
Dads	9.8	9	2044
Nestor	7.3	12	1531
Moms	7.1	15	1213

sorial visual surveys to check for the presence or absence of juvenile northern pikeminnow. Larger pikeminnow were abundant in all lakes. Since Moose Pasture and Dad's lakes were the only lakes where juveniles were found, I refer to them as 'nursery lakes' and the lakes above them as 'head-end' lakes. Evidence of the spatial organization of these two stocks came from two sources: visual surveys of fry (0+) and early juveniles (1-3+) in each lake, and the age structure of each lake estimated from population sizes at age. The area, depth and perimeters of the study lakes are listed in table 2.2.1.

## 2.2.2 Spawning and Visual Surveys

From mid-June to mid-July 2002, I observed the location of spawning in the inflow and outflow creeks of Wilderness, Moose Pasture, Cheryl, Dad's, Nestor and Mom's lakes. During this period I also pole seigned and electrofished in these same creeks every 2-3 days. In August of 2002 and 2003 I surveyed all the lakes included in figure 2.1 for the presence of absence of emerging fry. In August of that same year in Dad's and Moose Pasture lakes,



Figure 2.1: Map of study lakes. Arrows indicate the direction of stream flow and light grey colored lakes represent nursery lakes.

I enumerated the number of 0+, 1+ and 2+ and greater than 2+ fish visible around the perimeter of the lake. In every case I counted using polarized sunglasses and either walking the shoreline, or by boat between the hours of 10:00 and 14:00. The global positioning satellite (GPS) position of each aggregation of juveniles was recorded (virtually all juveniles observed were in schools of 5-200 individuals each).

## 2.2.3 Apparent mortality

I estimated the apparent mortality using length converted catch curves (Pauly, 1990). This was done because any migration from nursery lakes to head-end lakes would appear as higher apparent mortality (as fish leave). From June to September 2002, fish were continuously tagged using 5 or 15 mm Floy numbered tags during bouts of mark-recapture in each lake conducted at 1-2 week intervals. Fish as small as 55 mm were marked and only those fish released in perfect condition were included in this analysis. Summaries of marked, recaptured, unmarked and killed fish by date, length-converted-age, and lake are in section 2.5.

I converted observed lengths into ages using the von Bertalanffy growth parameter estimates fit to length-age data using the reduced likelihood with fishing model 4 (chapter 3, table 3.2) following Pauly (1990) but assuming no seasonal growth. While Pauly (1990) show that considerable bias can be produced in growth parameters by not including seasonality, I did not attempt to estimate the parameters to do so. Firstly, there were no length-

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age data collected during the colder months to provide any contrast between slow and fast growing periods. In winter months lakes are frozen and access is impossible. The bioenergetics data for the Columbia River indicated that growth in length below 4 C was effectively zero, I assumed that growth in length is assumed to be zero from November to end of April. Secondly, I was only interested in the relative comparisons of apparent mortality, so as long as growth parameter biases (and corresponding apparent mortality) can be assumed constant across lakes, then the absolute bias the apparent mortality estimates is irrelevant.

Northern pikeminnow depletions were conducted in 2001 in Cheryl and Mom's lakes (described in section 5.2.2). Therefore, catches-at-length from the depletion were also converted to ages, survived forward by one year at a rate of 0.7 (Rieman and Beamesderfer, 1990), and added to the estimated numbers at age in 2002 from the mark-recapture.

The apparent mortality Z was calculated as the slope of the log numbersat-age of fully recruited (5+) fish. I used a Peterson estimator to estimate numbers at age  $N_a$  where the negative log likelihood of both the marked and unmarked fish (Eq. 2.1) was:

$$\sum_{1}^{a} R_a \log(p_a) + U_a \log(1 - p_a)$$
(2.1)

where  $R_a$  is the number of recaptured fish at age a and  $p_a$  is the proportion of marked fish  $M_a$  to the estimated number at age  $N_a$  in that lake. While tag-loss and mortality were surely present, the purpose of this analysis was to compare across lakes so I implicitly assumed these to be constant across all lakes.

## 2.2.4 Hydrography and Productivity

I made contour maps of lake depth by measuring depth at 10 transects per lake at approximately 10 m intervals. The GPS position of each depth measurement was recorded and 1 m depth contour plots made. The proportion of the total lake area occupied by each depth contour was calculated using ArcView 3.0. As a measure of lake shallowness, I plotted the total proportion of lake area versus depth in meters (m).

At approximately two week intervals, I measured Chlorophyll A at fixed stations in the middle of each lake by filtering 50 ml of lake water through 2 400  $\mu$ m filter. Filters were then dissolved in acetone overnight and Chlorophyll A was measured using mass spectroscopy.

## 2.2.5 Bioenergetics modeling

The goal of the bioenergetics modeling was to compare, all other things being equal, what proportion P of the maximum physiological consumption rate an age 0+ fish would have to use in order to compensate for delays in hatching. In particular, given expected delays in spawning and hatching due to cooler water in inflows creeks (Beamesderfer, 1992a), I was interested in
determining whether or not northern pikeminnow could hatch and rear to age 1 in head-end streams/lakes and if so, how much additional consumption would be needed in order to make up for any delays in spawning produced by colder inflow creeks.

I lacked specific data on hatch time, weight at hatching and age 1 for northern pikeminnow, so a number of assumptions were needed. I set the hatch date (t = 0) in the outflow creeks to July 15. I used the von Bertalanffy growth model to predict weight-at-age 0 and 1, from lengths (model 4, chapter 3, table 3.2). I fit observed weight at length by fitting  $w = \alpha l^{\beta}$  to 1001 observations of length and weight in the Western drainage. I then converted predicted lengths to weights using the fit  $\alpha$  and  $\beta$  values. I estimated P by fitting the bioenergetics model to these 'observed weights' at age 0 and 1. I used the bioenergetic parameter set for northern pikeminnow developed by Petersen and Ward (1999). I assumed the diet composition of 0+ northern pikeminnow to be 100 % zooplankton. These parameter values are listed in table 2.2.5.

To simulate the effects of delayed hatching with inflow creek spawning in Mom's lake, I simply delayed spawning by increments of one day and compared the P value in Mom's lake that would have been needed to see the 'observed' size at of age 1 fish in Dad's lake. I compared the  $P_{head}$  from the simulations to the observed P of fish reared in the nursery area  $P_{hurs}$ .

I drove the bioenergetics model with observed temperatures integrated over the first meter of the water column in Dad's and Mom's lakes. Temper-

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Parameter description	Symbol	Value
Consumption parameters		
Allometric scaling parameter	Ac	0.278
slope of allometric mass function	Bc ·	-0.197
Temperature dependent growth function		
threshold T $1(C)$	te1	0
threshold T 2 (C)	te2	20.1
threshold T 3 (C)	<i>te3</i> .	22.7
threshold T 4 $(C)$	te4	27
proportion consumed at threshold temp 1	xk1	0.001
proportion consumed at threshold temp 2	xk2	0.98
proportion consumed at threshold temp 3	xk3	0.98
proportion consumed at threshold temp 4	xk4	0.01
Respiration Parameters		
Intercept of allometric mass function for respiration	Ar	0.00165
slope of allometric mass function for respiration	Br	-0.085
Q10 approximation	Cr	0.18
Coefficent of swim speed to metabolism	Dr	0.003
slope fo the function for temperature effect on respiration rate	tau	0.105
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Activity Parameters		
Intercept of allometric mass function	Aa	0.1
slope of allometric mass function	Ba	0.149
Q10 approximation	Ca	0.149
Diet Energy Density		
Zooplankton Energy Density Ed (J/gO2)	Ed	2500
Francism and Emanation		
Egestion and Excretion	A C	0.0
Proportion of consumption egested	AJ	0.2
Proportion of (consumption-egested)	Ae	0.07
Specific Dynamic Action	SDA	0.163

Table 2.2: Parameter values used in northern pikeminnow bioenergetics model from Petersen and Ward (1999)

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ature profiles were taken at mid-day from fixed stations at two-week intervals over the summer and the input temperatures for the simulations were integrated over the first meter of the water column. The choice of depth to measure temperature was consistent with observations of fry position and those of Barfoot et al. (1999) and Gadomski et al. (2001) showing fry preference for shallow warm water. Temperatures between observations were linear interpolations of the observed temperature.

A number of additional parameter assumptions were needed in order to completely parameterize the model. Lacking data on swimming speed of fry or any published functional relationship, I set swimming speeds of larvae in terms of body length per second to those of the northern squawfish's congener the Colorado pikeminnow *Ptychocheilus lucius*. Bainbridge (1958) measured the sustained swimming speed of 30, 43 and 52 mm TL for Colorado pikeminnow as 4.00 body lengths per second. Similar speeds for larval Colorado pikeminnow were measured more recently by Childs and Clarkson (1996) across a range of temperatures. I assumed the swimming speed of northern pikeminnow 0+ fish to be the same as Colorado pikeminnow in terms of body lengths per second and used the von Bertalanffy predictions of length-at-age (chapter 3, table 3.2) calculated over daily rather than annual time steps.



Figure 2.2: Mean temperature integrated from lake surface to 1 m in depth for Dad's Lake (squares) and Mom's Lake (diamonds). Lines represent linear interpolations between observed temperatures

# 2.2.6 Lake feeding load

Following Walters and Post (1993), I measured the effective density  $D_e$  of northern pikeminnow per hectare in each lake summed across ages a as

$$D_e \propto \sum_{a=1}^n l^2 h a^{-1} \tag{2.2}$$

This metric assumes the 'effective density' (Post et al., 1999; Walters and Post, 1993) of any age class in a size structured predator (or competitor) on the prey population is the product of two length-dependent factors: the predator gape size and swimming speed. Such a metric was necessary to compare the effective density of those lakes with many small fish versus those with fewer larger ones.

Since lakes differed in productivity, I scaled Eq. 2.2 to relative productive inputs as approximated by measured mean seasonal chlorophyll A in  $\mu g L^{-1}$ ,  $\mu g ChlAL^{-1}$  so that the standardized effective density  $D_s$  was calculated as

$$D_s \propto \sum_{a=1}^n l^2 h a^{-1} \mu g C h l A^{-1} L.$$
 (2.3)

# 2.3 Results

# 2.3.1 Spawning and Visual Surveys

I observed large spawning aggregations in the outflow creeks of Cheryl, Moose Pasture, Tasha, Nestor and Mom's lakes over large cobble. Even though suitable cobble and flow rates were available in the inflows of Cheryl, Mom's, Nestor and Wilderness lakes, no fish were ever observed or captured in fishing gear in these inflow creeks. I observed no fish spawning in the outflow creek of Dad's Lake although the outflow creek of this lake is dammed so it would not have been possible for large numbers of northern pikeminnow from Dad's lake to actually form spawning aggregations there.

Hatching northern pikeminnow are poor swimmers ?? and apparently unable to swim upstream into head-end lakes from outflow creek spawning areas. Hence the fry drift downstream to develop in the nursery lakes (Dad's, Moose Pasture).

There were fry and juvenile northern pikeminnow only in Dad's, Moose Pasture, North Island, Tasha and Estelle lakes (Fig. 2.1). Fry appeared in schools varying between 5-1000 individuals along the littoral area by early August. They preferred the very shallow margins of the lakes in water generally no deeper than 10 *cm*, with some plant cover. Such schools were only visible at mid-day and at warm temperatures. Fry were only present in those lakes where there was a lake upstream with northern pikeminnow. Both Mom's and Cheryl lakes have lakes upstream of them, but these upstream lakes have no northern pikeminnow. Northern pikeminnow in both cases have no access to the upstream lakes due to small waterfalls.

#### 2.3.2 Apparent mortality

The apparent M was similar in all lakes except for Wilderness. Since movement should appear as higher apparent mortality, represented by the slope of the length-converted-catch curve, population estimates in Fig. 2.3 showed that most fish must move before the age of 5+. There were very high numbers of 1-3+ age classes in the two nursery lakes, and correspondingly few or none estimated in the head-end lakes. If movement were occurring in fully recruited age classes, the apparent mortality would be significantly higher in the Moose Pasture and Dad's lakes.

# 2.3.3 Hydrography and Productivity

The two nursery lakes were both more productive with respect to their mean  $\mu gChlAL^{-1}$  values than the head-end lakes in their respective drainages (Fig. 2.4). The difference is particularly striking in the case of Dad's lake. Here the mean chlorophyll A was 23.59  $\mu gL^{-1}$  compared to values of 3.29 and 3.41  $\mu gL^{-1}$  in Mom's and Nestor lakes. In the case of the eastern drainage this difference was much smaller with the nursery lake (Moose Pasture) having a mean ChlA of 2.92  $\mu gL^{-1}$  compared to 2.29 and 2.12 in Wilderness and Cheryl lakes respectively. The effective density of fish in the nursery lakes



Figure 2.3: Maximum likelihood estimates of numbers at each length converted age. The pasted text is the slope of the fit line through the log numbers at age (log Na) representing the apparent mortality of fully recruited ages (5+)

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Figure 2.4: Chlorophyll A ( $\mu gChlAL^{-1}$ )measurements over time. Top panel is Western drainage: Dad's Lake (squares), Mom's Lake (diamonds) and Nestor Lake (triangles). Bottom panel is Eastern drainage: Moose Pasture (squares), Cheryl Lake (diamonds) and Wilderness Lake (triangles). is correspondingly very high (Fig. 2.5 top panel). So while the productivity of the nursery lakes is higher than the head-end lakes (Fig. 2.4), once it is partitioned among the greater number of mouths in Dad's and Moose Pasture, these lakes are on par or (in the case of Dad's), have even higher  $D_c$  that the headwater lakes (Fig. 2.5 bottom).

The nursery lakes also have a greater proportion of shallow littoral area, the preferred habitat of the northern pikeminnow juveniles. Greater than 60 % of the cumulative area of Dad's and Moose Pasture lakes is in water between 0 and 3 m (figure 2.6).

## 2.3.4 Bioenergetics predictions

The model showed that it was physiologically possible for fish to hatch as many as 50 days after the nursery hatch date and still be the same size the one year later. In order to do so however, very large increases in  $P_{head}$  were needed (Fig. 2.9 top). Interpreted in a behavioral sense, those fish hatched in inflow creeks would have to spend more time feeding relative to those hatched earlier in outflows (Fig. 2.9 bottom) in order to be the same size one year later and most of that feeding would have to take place before winter (Fig. 2.7).



Figure 2.5: Effective density per hectare as represented by the sum of squared fish lengths  $l^2ha^{-1}$  (top) Effective density per hectare per  $\mu gChlAL^{-1}$  as represented by the sum of squared fish lengths per hectare  $l^2ha^{-1}$  divided by mean ChlA ( $\mu gL^{-1}$  for Dad's (d), Moose Pasture (p), Mom's (m), Cheryl (c), Nestor (n) and Wilderness (w) lakes



Figure 2.6: Proportion of the total lake area by depth contour, Dad's open circles, Mom's open squares, Nestor, open diamonds, Moose Pasture closed circles, Cheryl closed squares, Wilderness closed diamonds



Figure 2.7: Predicted weights (in grams) of fit bioenergetics model to observed weight at age in the nursery area (open circles, P = 0.14) and the predicted weight at age of a fish hatched 15 days later in the head lake (solid line, P = 0.18)



Figure 2.8: Fit weight-length relationship of northern pikeminnow weight as a function of length.





Figure 2.9: Predicted proportion of maximum consumption rate  $P_{head}$  (top) required to reach observed size at age 1 and  $P_{head}/P_{nursery}$  (bottom) vs. delays in headwater lake hatch date.

# 2.4 Discussion

I show that fish undergo large-scale ontogenetic shifts between lakes. No fry were ever observed in non-nursery lakes. In addition, the differences in the age structures of the nursery lakes and head end lakes indicate migration occurs between the ages of 1 and 5+. The only distinctive feature of the nursery lakes is the presence of a lake containing northern pikeminnow above it. Note that both Cheryl and Mom's lake have lakes in the drainage above them (Fig. 2.1), but neither of these has northern pikeminnow. This pattern holds at a reasonably large scale and in two river drainages.

The ratio of effective density to  $ChlAL^{-1}$  as an index of the relative productivity of the lakes is very important for determining the distribution of the adults. Any advantage of the additional productivity of Dad's Lake or Moose Pasture is eliminated by the very high density of northern pikeminnow there. Dad's Lake is apparently much more productive than any of the other lakes but the benefits of such high productivity are completely neutralized by the higher density of fish there. While Moose Pasture Lake was not significantly more productive than any of the headwater lakes, the ratio of  $l^2ha^{-1}\mu gChlA^{-1}L$  makes that lake a much worse lake to rear in than those head-end lakes near it. Contrary to the situation with Dad's, the lakes above Moose Pasture are actually larger and support more adult fish, so that relative to its size and productivity, Moose Pasture receives many more fry than Dad's does.

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The bioenergetics modeling shows the most likely reason for the spatial distribution of fry is temperature dependent spawning behavior, rather than productivity and hydrographic differences between the lakes. While I did not have stream temperature data to support this argument directly, it is reasonable to assume that the inflow creeks temperature to be approximately the same as the mean annual air temperature (2-5 C) for this Montane Spruce biogeoclimatic Zone (?) and the outflow creek temperature to be the same as the lake temperature. If the proportion of the maximum consumption rate is interpreted in a behavioral sense (a higher proportion of the maximum consumption rate is equivalent to greater time spent in risky foraging behavior instead of hiding and growing) then delays in spawning are paid for by increasing predation risk. A delay of 25 days corresponds to doubling this risk. Natural selection predicts strong selection against such increased risk taking. Furthermore, the results are optimistic predictions of growth and spawning potential in the head-end systems. Inflow creeks go dry in low rain/snow years by the end of July. So while it might be possible to rear in a head-end lake and still reach the same size as in a nursery lake as late as fifty days after spawning in an outflow creek, there may be no inflow creek left to hatch/emerge from.

The bioenergetics predictions should be viewed with considerable caution. These predictions depend on two assumptions not tested and likely incorrect. The Petersen and Ward (1999) parameter values come from adult fish in the Columbia river system. Fish in the study system are very different to those

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in the Columbia. The fish in this study system are much smaller than in the Columbia, reaching asymptotic lengths of 200 mm, compared to the maximum size of 350 mm+ observed in the Columbia. Whether or not these differences are the result of phenotypic plasticity or genetic differences is not known. Local physiological adaptations have been shown to make large difference in the bioenergetics parameters (Munch and Conover, 2002). Secondly, the predictions rely on the assumption that the parameters are similar between adults and juveniles which is also incorrect (Post, 1990). That said, the purpose of the modeling exercise was to determine how much addition consumption would be required in order to compensate for later spawning. The temperature profiles in each lake were almost identical so any biases in P produced by incorrect parametrization would be consistent between nursery and head areas so the comparison between the two is still legitimate.

The number of growing degree days seems to limit the northern distribution of perch and bass species (Schuter and Post, 1990). Norther pikeminnow fry in the study area likely face a similar growth survival trade-off to that observed in rainbow trout studies 200 km South of the study area. Post and Parkinson (2001) show rainbow trout in small B.C. lakes face a tradeoff between allocating energy to somatic growth or to lipids. Energy allocated to somatic growth improves fitness of larger individuals by reducing sizedependent predation risk but at the expense of lower winter survival. Post and Parkinson (2001) showed that once fish reach a size large enough to reduce their predation risk, they allocate resources to lipid stores for winter survival rather than to somatic growth. For both reducing predation and for storing lipids to survive winter early hatching is critical for northern pikeminnow.

The spatial organization of these stocks of northern pikeminnow is similar to that observed in river systems with respect to the habitat preference for rearing areas. Gadomski et al. (2001) described a model of early life history in the Columbia River. In it, adults spawn in tributaries at 18-20 C, planktonic larvae drift into the mainstem and then rear in backwaters with fine sediment or sand substrates. Our observations are identical, except that the preferred areas for rearing are entire lakes, not river backwaters.

How unit stocks are defined spatially needs closer examination in lacustrine systems, especially where lakes are not isolated from each other. Theory predicts ontogenetic movement should be widespread in size-structured populations. In addition, there are both excellent theoretical and field examples of it in fish populations. In response to different resources gradients, shifts occur particularly in situations where adults present a predation risk to juveniles (Persson and Greenberg, 1990; Gowen et al., 1994; de Roos et al., 2002). However the scale of such modeling and field studies tends to be small, that is, within lakes. In the study systems there are productivity (*ChlA*) and temperature gradients between upper end and nursery lakes. Watershed systems in general have such gradients on larger (multi-lake) scales (Gomi et al., 2002), and in my watersheds fish should have no difficulty distributing themselves at such scales, provided streams are seasonally adequate to permit movement. Examples of fish movement at larger scale are appearing in the literature. Naslund (1990) showed spectacular density-dependent migrations between lakes of arctic char. Movement from streams to lakes has also been observed (Olsson and Greenberg, 2004). Contrary to the "restricted movement paradigm" (Gerking 1959), there is an increasing number of examples where movement in streams is significant (Gowen et al., 1994) and references therein) and many examples supposedly confirming the restricted movement paradigm use methods biased against detecting any such movement (Gowen et al., 1994).

Juvenile fish living in seasonal environments have to choose life-history strategies that allow them maximize their growth advantage while not exposing themselves to significant predation in order to do so. I show here that in addition to solving the small space/time scale problem of balancing growth with predation risk, northern pikeminnow must also solve a larger space/time scale problem of choosing life-history strategies that are physiologically favorable, in terms of allowing for the greatest amount of time to grow. Since there are large scale gradients in productivity and temperature between lakes, and in many cases relatively simple connections between them, the applied implication is that the initial survey effort in lacrustine systems should be distributed widely before assuming that lakes consist of individual stocks.

We typically assume that ontogenetic life-history movements are shaped

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by selections on a variety of phenological (timing), bioenergetic, and behavioral traits so as to maximize fitness given local environmental conditions. But in the stunted pikeminnow case, we may simply be seeing two key preadaptations, a minimum temperature for spawning, and a tendency to disperse upstream from crowded areas. Just the minimum temperature trait would lead to avoidance of inflow spawning in headwater lakes and hence to downstream fry dispersal. All that would be needed for the observed drainage wide organization is upstream return later in life.

# 2.5 Appendix

М	arked				10.4				00 4	00 5	10 5	17 6	05 5	
	age	04-Jul	31-Jul	U1-Aug	10-Aug	13-Aug	21-Aug	22-Aug	28-Aug	U6-Sep	TO-Sep	17-Sep	25-Sep	
		0	0	27	25	0	0	0	30	0	0	0	0	
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	4	ő	ŏ	8	49	õ	· 0	ŏ	8	õ	ō	ō	ō	
	5	70	0	25	69	0	0	0	9	0	0	0	0	
	6	90	0	22	41	0	0	0	3	0	0	0	0.	
	7	51	0	11	26	0	0	0	2	0	0	0	0	
	8	29	0	5	11	0	0	0	0	0	0	0	0	
	9	25	0	0	13	0	0	0	2	0	0	0	U	
	10	23	0	1	6	0	0	U	2	U	0	0	0	
	12	14	0	0	5	. 0	0	0	1	0	0	0	0	
	13	5	0	ő	5	ő	ő	ő	ô	ő	ŏ	õ	Ŭ	
	14	3	ŏ	ŏ	2	ö	õ	õ	0	0	0	0	Ō	
	15	7	0	0	6	0	0	0	Û	0	0	0	0	
	16+	24	0	1	15	0	Ú	0	1	1		0	0	
1	Killed													
	1	0	υ	Ű	0	0	Û	0	0	0	0	0	0	
	2	0	Û	0	υ	υ	Ũ	Û	U	0	0	0	0	
	3	0	0	0	0	0	Û	U	0	2	0	0	0	
	4	0	0	0	0	0	0	0	0	3	0	0	0	
	5	0	2	0	0	0	U	0	0	. 1	0	0	0	
	U 7	0	2	0	0	0	0	0	0	4	0	0	0	
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· .	11	0	2	υ	0	υ	0	υ	0	U	υ	0	0	
	12	0	1	υ	0	U	0	0	0	U	0	0	U	
	13	υ	υ	0	0	c	0	0	0	0	0	0	0	
	14	0	1	0	0	G	0	0	0	0	0	0	0	
	15	0	0	0	0	0	0	0	0	0	0	0	0	
	10+	U	0	0	0	0	0	0	0	U	U	U	U	
Recap	otured													
	1	0	0	0	0	0	0	0	0	0	0	0	0	
	2	0	0	0	0	0	ũ	0	1	0	0	0	0	
	3	0	0	0	0	0	0	0	4	4	0	0	0	
	4	0	1	0	5	0	0	0	0	13	1	. 0	1	
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· .	8	0	1	1	2	1	0	0	0	11	0	0	1	
	9	0	1	0	0	0	0	0	1	5	0	0	0	
	10	0	0	0	5	0	0	0	0	3	0	0	0	
	11	0	1	0	U	U	0	1	0	4	0	0	0	
	12	0	1	0	0	0	1	0	0	3	0	0	0	
	14	0	1	0	3	0	0	ő	0	1	0	0	ő	
	15	ŏ	ō	ŏ	1	Ŭ	õ	Ŭ	Ū	2	Ō	Ū	Ó	
	16+	ō	õ	0	1	0	2	υ	0	17	0	0	0	
T Tau and	a sultand													
Unm	1 1	0	0	0	1	0	0	0	0	Û	0	0	0	
	2	Ū	Ū	27	25	0	0	0	53	27	0	0	1	
•	3	Ū	Ū	65	103	0	0	0	218	374	υ	υ	22	
	4	2	0	8	93	Ο.	0	0	9	150	0	υ	4	
	5	74	50	25	163	U	16	0	9	235	υ	10	18	
· .	6	98	166	22	109	U	12	0	3	176	0	23	13	
	7	51	55	11	56	0	2	0	2	59	0	2	11	
	8	31	31	5	28	0	1	0	0	26	0	0	8	
	9	27	29	0	29	0	0	0	2	10	0	2	0 (1	
	11	24	13	1 0	13	-a	0	0	ő	7	0	0	0	
	12	10	9	0	10	Ŭ	ŏ	ŏ	1	5	Ŭ	Ű	5	
	13	5	2	ŭ	9	Ū	õ	Ū	Ū	3	Û	Û	2	
	14	5	6	υ	4	υ	0	U	U	2	0	0	Û	
	15	8	4	0	7	υ	0	0	U	3	U	1	2	
	16 +	33	27	1	26	υ	0	0	1	14	Û	2	13	

Table 2.3: Table of fish marked, marked fish killed during handling, recaptured, and unmarked by date and length-converted age in Dad's lake.

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Marked									
age	20-Jun	26-Jun	30-Jul	31-Jul	12-Aug	22-Aug	27-Aug	08-Sep	23-Sep
2	1	0	0	0	0	0	4	Ð	0
3	7	0	0	0	16	0	18	0	0
4	15	12	0	0	3	Û	0	0	0
5	8	36	0	0	1	0 Ó	1	0	0
. 6	5	12	0	0	0	0	0	0	0
· 7	3	8	0	Û	1	· 0	0	0	0
8	8	6	0	0	0	0	1	υ	0
9	. 5	6	0	Ű	0	0	0	0	0
10	1	2	0	υ	0	0	0	0	0
11	1	4	0	0	υ	Ü	0	υ	0
12	ī	i	Ū.	0	Ū	Ű	Ŭ	0	υ
13	ĩ	3	Ď	ŏ	õ	ē	Ū.	ō	Ő
14	ñ	1	ñ		ō	õ	1	ō	ō
14	n 0	1	0	0	ň	0 0		n o	ň
10	4	â	5	0	0	0	0	0	ő
10.4	-	5	.,	0	U	0	Ū	Ū	0
Recaptured									
2	0	0	0	0	0	0	0	0	0
3	U	2	U	0	0	0	1	10	U
4	0	6	1	0	0	0	0	0	0
5	U	7	2	U	0	0	0	4	0
6	0	3	3	υ	1	1	0	12	0
7	0	4	6	0	1	1	0	15	0
8	0	8	0	υ	U	0	υ	8	0
9	0	5	0	0	0	4	0	1	0
10	0	2	0	0	0	1	0	2	0
11	0	. 3	0	1	0	1	0	1	0
12	0	0	0	0	1	0	0	1	0
13	0	4	2	7	2	6	0	2	0
14	0	0	0	0	0	0	. 0	0	0
15	0	0	0	0	0	0	0	0	0
16+	0	1	0	0	0	0	0	0	0
Unmarked	-	_		-	21	~			
2	1	0	0	0	0	0 -	4	0	0
3	7	1	0	0	16	0	18	3	0
4	17	13	0	0	3	0	0	0	0
5	9	39	5	0	1	Ð ·	1	1	1
6	5	13	6	0	0	0	0	1	8
7	3	10	0	0	1	1	0	1	1
8	8	6	0	0	0	2	1	0	2
9	5	6	0	1	0	0	Û	0	2
10	1	3	1	0	υ	0	0	0	0
11	1	4	0	0	υ	U	0	0	0
12	1	1	0	1	υ	0	0	0	0
13	1	3	Ō	0	Ó	Û	0	0	0
14	0	1	0	Ō	0	0	1	0	0
15	ő	1	ŏ	ő	ő	0	Ū	Ū	0
16-	4	19	1	້ຳ	ň	1	ñ	30	1

Table 2.4: Table of fish marked, marked fish killed during handling, recaptured, and unmarked by date andlength-converted age for July, August and September 2002 in Mom's lake.

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Marking age	26-Jun	06-Jul	14-Jul	15-Jul	23-Jul	24-Jul	25-Jul	26-Jul
2	0	0	0	0	0	0	0	0
3	1	0	0	0	0	0	0	0
4	14	8	0	0	0	0	0	0
3	44	50		11	0	0	0	U
5	30	52	0	13	1	0	0	1
1	20	44	1	3	0	0	0	1
0	19	30	2	1	. 0	0	0	0
10	10	13	0	0	0	0	ő	0
10	9	10	0	0	ů.	ő	ő	0
12		<u><u></u></u>	0	ő	0	0 0	ŏ	1
13	2	5	0	0	ŭ	ŏ	ŏ	ō
14	3	6	ů	õ	ũ	ũ	Ū	Ū
15	Ũ	2	ō	Ū	Ū	0	0	0
16+	5	10	υ	1	U	U	0	1
Killed								
2	0	0	0	0	0	0	0	0
3	0	0	U	e	• 0	0	0	0
4	0	0	0	1	0	0	0	0
5	0	0	0	1	3	0	0	0
6	0	0	0	0	2	2	0	1
7	0	0	0	2	10	6	3	2
8	0	0	U U	U	15	8	3	1
9	U	0	U 0	0	14	U A	2	1
10	0	0	0	0	10	2	2	1
10	0	0	0	0		2	n	1
12	0	0 0	0	n	5	2	0	ó
14	0	0	0	ň	2	6	2	1
15	ŏ	ŏ	ŏ	ŏ	2	ŏ	0	1
16+	0	O	0	0	4	0	0	0
Recaptured								
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
4	0	0	0	1	0	0	0	0
5	4	8	0	1	2	0	U	0
0 -	6	6	0	3	4	0	0	0
1	1	4	2	2	16	4	2	1
8	U	4	0	2	10	4	2	2
10	0	3 7	0	0	14	4 2	6	1
11	ň	4	1	0	12	2	2	2
12	n	2	ń	0	12	ő	<u>n</u>	õ
13	0	ĩ	ŭ	ů Ú	16	š	. 0	ŏ
14	ŭ	2	õ	Ű	2	4	õ	õ
15	ŭ	Ū	Ū	Ū	4	$\overline{2}$	2	1
16+	U	1	U	0	16	10	2	5
Unmarked								
1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
3	1	0	0	0	0 ·	0	0	0
4	14	8	0	3	0	G	0	0
5	44	52	3	26	2	0	4	0
6	36	52	7	33	18	4	6	· 1
7	25	44	1	6	50	12	3	3
8	19	35	3	3	58	2	9	5
9	10	27	0	1	14	4	0	0,
10	9	13	U .,	U	16	12	U 7	1
11	8	12	ມ	U	14	U 1	2	2
12	2	9	U 0	0	4	9 6	<u>_</u>	0
13	23	с А	0	0	4	0	n	ő
15	0	2	0 0	ő	ŏ	ŏ	1	1
16+	5	11	õ	1	16	10	2	4

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Table 2.5: Table of fish marked, marked fish killed during handling, recaptured, and unmarked from Juneto August 2002 by length-converted age in Nestor lake.

Marking												
age	01-Aug	12-Aug	13-Aug	20-Aug	21-Aug	22-Aug	23-Aug	27-Aug	07-Sep	18-Sep	24-Sep	
2	U	U	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	U	0	0	0	0	0	0	
0	0	0	2	0	0	0	0	0	0	0	1	
0	0	0	19 18	0	0	0	0	0	0	0	0	
0	0	0	15	0	0	n 0	n n	0	o o	ŏ	ŏ	
0	0	ň	7	ň	0	ő	0	3	0	ŏ	ŏ	
0	ő	ŏ	. 4	ŏ	ŏ	ő	õ	Ŭ	ŏ	õ	ũ	
ő	ŏ	ŭ	i	õ	ů	õ	Ū	Ū	ō	Ū	0	
Ŭ	Ŭ	Ű	Ū	Ū	Ū	Ū	Ú	0	υ	υ	U	
Ū	Ū	Ű	2	υ	0	0	υ	0	υ	υ	Û	
0	υ	υ	υ	υ	U	0	υ	U	U	υ	0	
Û	υ	υ	0	υ	υ	0	U	0	υ	υ	υ	
0	0	υ	0	υ	υ	0	Û	0	0	υ	0	
0	14	U	1	0	0	υ	υ	0	0	0	U	
Killed												
2	0	0	0	0	0	0	0	0	0	0	0	
0	õ	õ	Ō	0	Õ	0	0	0	0	0	0	
ō	ō	Ō	0	0	0	0	0	0	0	0	2	
0	0	0	0	1	0	0	0	0	5	0	1	
0	0	0	0	2	3	1	0	0	1	0	1	
0	1	0	0	1	1	1	0	0	1	0	0	
0	0	0	0	7	1	1	0	0	0	0	1	
0	0	0	0	14	2	0	0	0	0	0	0	
0	0	0	0	5	1	0	n	· 0	0	0	0	
0	0	0	0	6	0	0.	0	0	0	0	0	
. 0	0	0	0	5	0	0	. 0	U	0	0	0	
0	0	0	0	0	0	U	0	0	0	0	U	
0	0	0	0	1	. 0	. 0	0	0	0	0	0	
10	0	0	0	1	0	0	0	0	0	0	0	
10+	U	0	0	1	0	0	U	0	0	0	0	
Recaptured												
• 2	0	0	0	0	0	θ,	0	υ	U	0	υ	
0	0	0	0	υ	0	0	U	o	0	Û	U	
0	0	0	0	0	0	U,	U	· 0	0	0	L	
1	2	1	3	0	0	0	Ű	O	2	1	3	
Ð	7	0	1	0	υ	. 0	, 0	0	G	υ	1	
0	4	U	5	2	2	1	0	0	4	U	3	
1	1	1	1	1	2	0	0	0	3	0	0	
U	2	0	1	3	1	1	0	0	1	U	2	
0	0	0	2	11	U	1	0	0	0	1	0	
0	0	0	2	8	2	0	0	0	0	0	U	
. 0	0	0	0	0	2	0	0	0	0	0	0	
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Unmarked						•						
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õ	ō	Ō	Ō	0	0	0	0	0	0	0	0	
ō	Ó	Ő	Ó	0	0	0	0	0	1	0	0	
0	0	0	2	0	0	0	0	0	3	0	1	
0	13	0	9	0	1	0	0	. 0	9	0	4	
0	15	0	18	4	3	1	· 2	. 1	16	1	15	
0	12	0	15	7	9	3	5	0	13	3	28	
0	3	0	7	14	14	0	9	1	9	1	6	
0	1	0	4	12	4	0	8	0	5	1	1	
0	0	0	1	20	3	0	4	0	1	0	2	
0	1	0	0	14	0	0	4	0	0	0	0	
0	0	0	2	5	1	1	1	0	0	0	0	
0	0	0	0	5	1	0	1	0	U	0	0	
0	U	0	0	1	1	1	1	0	0	0	0	
20	1	30	0	1	0	1	1	0	0	0	0	
30	1	30	1		0	1	-	0	0	0	0	

Table 2.6: Table of fish marked, marked fish killed during handling, recaptured, and unmarked from Augustto September 2002 by length-converted age in Nestor lake.

Marking 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16+	04-Jun 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0	18-Jun 0 3 32 14 16 17 21 13 7 5 1 4 2 1 12	27-Jun 0 4 2 2 3 1 0 1 2 0 0 0 0 0 1	08-Jul 0 4 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	10-Jul 6 3 1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0	02-Aug 1 2 0 0 0 0 0 0 0 0 0 0 0 0 0	07-Aug 0 8 5 71 13 8 4 10 2 4 1 2 2 1 1 10	08-Aug 4 145 28 12 4 2 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	16-Aug 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	18-Aug 0 19 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0	<b>19-Aug</b> 0 142 31 26 19 8 6 9 4 1 0 0 0 1 0 1 0 1	22-Aug 1 47 16 23 0 0 0 6 4 5 0 0 0 0 0 0 1	
Killed or Removed 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16+	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	· 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	
Recaptures 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16+	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 2 3 3 3 3 3 3 2 4 3 0 0 3 1 5	0 1 1 1 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 9 10 4 3 2 6 3 2 1 1 1 0 0 0 3	1     8     8     17     6     5     6     11     13     5     4     5     1     4     4     16     1	
Unmarked 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16+	19 7 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	$\begin{array}{c} 0 \\ 0 \\ 33 \\ 16 \\ 16 \\ 17 \\ 21 \\ 13 \\ 8 \\ 5 \\ 1 \\ 4 \\ 2 \\ 1 \\ 12 \\ \end{array}$	0 4 2 2 3 1 1 1 1 1 2 0 0 0 0 0 0 0 0 0 0 1	1 4 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	7 3 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	3 2 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0	0 14 190 206 42 28 19 26 10 10 7 3 6 3 2 19	4 148 28 12 4 2 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	7 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 24 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 147 51 52 28 11 6 9 5 1 2 2 0 0 1 2 0 0 1 0 4	16 509 50 12 6 5 16 4 8 4 2 3 3 0 17	

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Table 2.7: Table of fish marked, marked fish killed during handling, recaptured, and unmarked by length converted age from June to August 22 2002 in Moose Pasture Lake.

Marking 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16+	23-Aug 1 8 0 0 0 0 0 0 0 0 0 0 0 0 0	25-Aug 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	09-Sep 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	10-Sep 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	11-Sep 9 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	13-Sep 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	14-Sep 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	15-Sep 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	16-Sep 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	27-Sep 0 20 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	
Killed or Removed 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16+	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	$\begin{array}{c} 0\\ 7\\ 113\\ 134\\ 25\\ 23\\ 9\\ 19\\ 12\\ 3\\ 2\\ 1\\ 0\\ 0\\ 1\\ 6\end{array}$	$\begin{array}{c} 0 \\ 6 \\ 17 \\ 13 \\ 9 \\ 4 \\ 4 \\ 6 \\ 5 \\ 3 \\ 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ 5 \end{array}$	0 3 5 4 3 3 11 7 2 3 1 2 0 4	0 18 31 15 6 3 4 8 1 5 0 1 5 0 1 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0	0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	
Recaptures 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16+	0 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	$\begin{array}{c} 0 \\ 0 \\ 56 \\ 71 \\ 13 \\ 12 \\ 4 \\ 7 \\ 9 \\ 2 \\ 1 \\ 1 \\ 0 \\ 0 \\ 0 \\ 5 \end{array}$	$\begin{array}{c} 0 \\ 6 \\ 17 \\ 13 \\ 9 \\ 4 \\ 4 \\ 6 \\ 5 \\ 3 \\ 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ 5 \end{array}$	0 3 15 5 3 1 3 6 4 1 2 1 1 1 0 0 4	0 23 28 16 7 3 5 5 2 5 1 0 1 0 0 1 0 6	0 7 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 6 3 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 5 1 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 1	
Unmarked 1 2 3 4 5 6 7 7 8 9 10 11 12 13 14 15 16+	$egin{array}{c} 3\\ 26\\ 1\\ 1\\ 2\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\$	0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 26 258 143 27 15 8 6 1 0 0 0 0 1 0 0 1 1 2	6 42 43 25 6 6 5 3 0 0 0 4 0 2 1 1 4	$ \begin{array}{c} 11\\ 178\\ 81\\ 20\\ 8\\ 4\\ 0\\ 0\\ 1\\ 0\\ 0\\ 2\\ 1\\ 1\\ 4\\ \end{array} $	$egin{array}{c} 38\\ 725\\ 131\\ 46\\ 10\\ 4\\ 4\\ 0\\ 0\\ 1\\ 1\\ 1\\ 1\\ 0\\ 0\\ 2\\ 5 \end{array}$	11 425 34 6 1 0 1 1 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0	3 67 7 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	26 54 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	11 40 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	

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Table 2.8: Table of fish marked, marked fish killed or removed during handling, recaptured, and unmarkedby length converted age for August 23 to September 2002 in Moose Pasture Lake.

Marking										
age	19-Jun	25-Jun	26-Jun	07-Jul	09-Aug	23-Aug	25-Aug	05-Sep	16-Sep	26-Sep
ິ1	3	0	0	1	· 0	Ŭ	õ	Ō	Ū	ΰ
2	O	. U	U	4	υ	Ű	109	0	0	U
3	υ	U	36	1	31	U	74	0	Û	U
4	υ	1	60	0	57	0	27	U	υ	0
5	υ	1	13	Û	20	9	7	0	Û	· 0,
6	υ	U	U	Û	8	0	2	0	υ	0
7	υ	0	2	0	1	0	2	0	υ	. 0
8	υ	0	4	υ	4	υ	U	υ	0	U
9	0	0	1	υ	1	0	υ	Û	υ	U
10	0	0	0	0	1	0	1	υ	υ	U
11	0	0	1	0	υ	0	U	υ	υ	0
12+	1	0	2	0	0	0	1	0	0	0
<b>K</b> :11-4										
Killed										
a.ge 1	0	0	0	0	a	n	n	0	0	0
т Э	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	1	0	0	0	0
3	0	0	0	0	0	6	0	1	0	1
41 K	0	0	0	0	0	0	0	n 1	0	0
G A	0	0	0	0	0	0	0	1	0	0
7	. 0	0	0	0 0	0	0	0	n 1	0 n	0
8	0	Ő	0	ő	0	0	ů N	0	ň	ő
9	0	0	0	0	0	0	0	0	0	0
10	0	0	0	ů N	0	0	0	0	ň	0
11	0	0	0 0	õ	0	õ	0	0	ů N	0
12+	0	0	Ő	õ	0	. Õ	ő	0	n n	0 0
	Ū	Ŭ	°,	0	0		Ũ	0	U	0
Recaptures										
age										
1	0	0	0	0	0	U U	0	0	0	0
2	0	0	0	0	0	0	5	0	0	0
3	0	0	0	0	0	0	6	0	0	. 0
4	0	0	- 5	0	4	6	7	1	0	0
5	0	U	1	0	2	1	1	0	1	4
6	0	0	0	0	0	0	1	1	1	0
7	0	U	1	0	U	0	0	0	0	U C
8	0	0	0	0	1	0	2	0	0	0
	0	0	0	0	0	0	1	0	0	0
10	U	0	0	0	1	0	0	0	0	1
11	0	0	0	0	U	0	Ů,	0	1	0
12+	U	0	0	0	2	. 0	1	0	0	U
Unmarked										
age										
1	3	0	0	2	1	Ð	0	0	0	0
2	0	0	0	4	1	0	120	1	0	1
3	0	2	143	1	31	0	86	6	0	4
4	0	1	118	1	59	3	38	6	8	12
5	0	1	21	0	20	13	11	12	12	18
6	0	0	0	0	8	1	3	3	4	5
7	0	0	2	0	1	1	2	0	1	2
8	Ũ	0	4	0	4	1	1	1	0	0
9	0	0	1	0	1	1	0	0	0	1
10	0	0	0	0	ĩ	1	1	0	0	1
11	0	0	1	0	0	0	n	0	0	1
12+	1	0	6	0	0	0	2	0	1	0

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Table 2.9: Table of fish marked, marked fish killed or removed during handling, recaptured, and unmarked<br/>by length converted age from June to September in Cheryl Lake.

Marking													
age	16-Jun	18-Jun	19-Jun	13-Jul	14-Jul	27-Jul	07-Aug	26-Aug	04-Sep	14-Sep	16-Sep	28-Sep	
2	0	3	0	0	0	0	0	0	1	0	0	0	
3	0	70	1	0	0	0	23	0	0	0	. 9	0	
4	0	49	0	0	1	0	24	0	0	0	5	0	
5	0	24	0	0	0	0	6	0	1	0	1	0	
6	0	26	0	0	0	0	2	0	0	0	4	0	
7	0	6	0	0	Ű	0	$^{2}$	0	0	0	3	0	
8	0	12	0	0	0	0	2	0	0	0	1	0	
9	0	3	G	0	0	Ũ	2	0	0	0	0	0	
10	0	1	0	0	0	0	1	0	0	0	0	0	
11+	0	1	0	0	0	0	0	0	0	0	0	0	
Recaptures													
age													
2	0	0	0	0	0	0	0	0	0	0	D	0	
3	ō	ō	ō	ĩ	ñ	ō	ō	ō	ñ	0	0	õ	
4	ŏ	1	õ	ō	õ	õ	ī	ō	ō	ō	1	õ	
5	õ	1		ō	ō	ō	ī	2	2	ō	ō	1	
6	õ	ō	õ	õ	ĩ	õ	ō	1	ī	ō	0	ō	
7	ŏ	2	õ	õ	ō	õ	1	ō	ō	õ	0	ō	
8	ñ	0	ō	Ď	õ	õ	ĩ	ō	ĩ	ō	Ő	õ	
9	ŏ	õ	ũ	Ő	õ	ŏ	1	ĩ	ō	õ	Ö	õ	
10	õ	õ	ō	õ	1	õ	ā	ō.	ō	õ	Ő	ō	
11+	ő	ő	õ	ő		ŏ	ő	ő	ĭ	ő	ö	1	
(	U	5		0	0	U	0		•				
Unmarked													
age													
2	0	3	1	0	0	0	0	υ	5	0	0	24	
· 3	7	82	1	0	e	υ	. 25	υ	12	0	9	6	
4	5	53	0	0	1	U	24	12	18	1	5	1	
5	1	25.	0	0	5	U	6	17	10	2	1	1	
6	4	28	Û	U	Ó	6	. 2	10	1	0	4	0	
7	3	6	0	υ	1	4	2	6	2	0	3	0	
8	ĩ	13	ō	Ū	Ŭ	9	2	1	Ŭ	Ū	1	õ	
9	ō	3	õ	õ	Ŭ	1	2	1	ĩ	ĩ	ō	2	
10	ŏ	ĩ	õ	õ	ů.	ō	1	ō	ō	ō	ő	õ	
11+	õ	0	ő	ő	õ	č	ō	ŏ	ĩ	õ	õ	1	
	0	· ·			Ũ	0	, i i i i i i i i i i i i i i i i i i i		-	•	Ū	. *	

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Table 2.10: Table of fish marked, marked fish killed or removed during handling, recaptured, and unmarkedby length converted age from June to September in Wilderness Lake.

# Chapter 3

# Estimating Growth from Length At Age Data

# Abstract

Gear selectivity and cumulative effects of size-selective fishing bias lengthat-age samples used to estimate the von Bertalanffy growth parameters. In fished populations, fast growing young fish and slow growing old fish are over represented in size-age samples. To account for such effects, I treated sizeat-age observations as multinomial samples, with expected catches in each size-age category dependent on growth parameters, growth variation, size selectivity, abundance at age, and the history of exploitation. Using simulated data sets, estimated growth parameters using the multinomial likelihood were unbiased when fishing mortality was not too high and the shape of the vulnerability function was correct. In contrast, estimated growth parameters using a least squares approach over-estimated the metabolic growth coefficient (K) and under-estimated mean asymptotic length  $(L_{\infty})$ . I estimated growth parameters for the northern pikeminnow Ptychocheilus oregonensis as an example of the method and documented a stunted "pigmy" population with an  $L_{\infty}$  of 175 mm fork-length (FL), attributing its small size to effects of high density and/or a short growing season.

keywords: growth estimation, von Bertalanffy, size-selective fishing, gear

selection

# 3.1 Introduction

Estimating parameters for the von Bertalanffy growth model assumes a representative sample of lengths from each age class has been collected, then either fitting the growth function to length-age data directly or to data on changes in length between the time of marking and time of recapture such as Fabens (1965). This assumption can fail if the sampling process is size selective and there are cumulative effects of fishing on the distribution of size-at-age. Growth rates vary among individuals (Sainsbury, 1980; Burr and Doksum, 1980) and intensive size selective harvesting removes faster growing individuals. The result is that length-age samples are biased for larger fast growing young individuals, and biased for older slow growing individuals that avoided capture (Lee, 1912; Ricker, 1969; Sinclair et al., 2002a). Almost all length-age data sets collected for growth analysis involve size-selective capture methods that favor fast growing individuals. In addition, many come from populations that have historically been exposed to harvest so as to produce cumulative effects on size-structure at age (Hanson and Chouinard, 1992; Kristiansen and Svasand, 1998). In both cases, the result is a downward bias in estimation of mean asymptotic length  $(L_{\infty})$ , upward bias of the metabolic growth parameter (K) and upward bias in the apparent age where length is zero  $t_o$ .

Biased estimates of growth parameters will cause bias in mortality rate estimates (where length-age keys are used to convert length to age), bio-

 $t_{i,j}^{\ast}$ 

logical reference points for management such as yield per recruit (Ricker, 1969; Parma and Deriso, 1990), and management actions (quotas for example). Changes in size-selectivity over the course of a fishery complicate matters further, where size selectivity changes may be mis-interpreted as changes in growth rates. Sinclair et al. (2002b) documented changes in size selectivity for the Atlantic cod (*Gadus morhua*) fishery in the southern Gulf of St. Lawrence, and Sinclair et al. (2002a) noted that historical effects of temperature on measured annual growth increment and density-dependent increases in growth rate were relatively small in comparison to the effect of size selective mortality caused by the fishery.

In some cases, researchers wish to solely estimate growth parameters describing the age structure of the current population available to harvest with the understanding that these growth parameters represent the remaining fish that are targeted. In this case, the effects of size-selective fishing do not need to be accounted for. However growth parameters describing the harvested targeted population will change as vulnerability changes (as fishers target smaller fish for example). If a researcher wishes to estimate the potential growth under no harvesting or under managed selectivity changes (e.g. size limits), then growth parameters representing entire population are needed.

Recently, Laslett et al. (2002) derived a likelihood function for analysis of growth data from tagging experiments, that accounts for individual variation in growth through variation in individual asymptotic lengths  $L_{\infty}$ , measurement errors, and possible changes in the von Bertalanffy metabolic parameter

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K with fish age. Unfortunately, they follow previous workers (James, 1991; Palmer et al., 1991; Wang et al., 1995) in assuming away one of the most common sources of bias in growth data; they assume independence of sampled individual  $L_{\infty}$  and age despite much evidence that higher  $L_{\infty}$  (fast growing) individuals have a higher capture probability in fishing and sampling gear used to collect the length-age samples.

To deal with non-independence of age and individual  $L_{\infty}$ , likelihood functions for the analysis of length-age samples should include parameters representing probabilities of capture-at-age and probabilities of capture-at-length (i.e., size selectivity). Where applicable, the cumulative effects of size selective harvesting on apparent growth should also be considered. In this paper, I derive likelihood functions that include size selectivity, mortality, and growth parameters based on the assumption that size-age data are sampled from a multinomial distribution. I derive four likelihoods: (1) a full likelihood and (2) a "reduced" likelihood using the conditional maximum likelihood estimates for numbers at age instead of estimating total mortality, (3) a full likelihood that includes cumulative effects of F, and (4) a reduced likelihood with cumulative effects of F. I test the performance of these formulations with 100 simulated data sets, and show that they are better estimators of growth parameters than previous statistical models for growth data. Finally, I fit all four models to real length-at-age data from the pigmy northern pikeminnow (*Ptychocheilus oregonensis*) of south central British Columbia.

# 3.2 Methods

## 3.2.1 Likelihood derivation

I assume that the basic data available for analysis consists of a matrix  $n_{l,a}$ with elements numbers of fish sampled at (discrete) lengths l and ages a, and that this is a random sample of the number of vulnerable fish of length l and age a available in the population to be sampled. In this case, the general form of the likelihood for  $n_{l,a}$  given the parameter vector ( $\Theta$ ) used to predict  $n_{l,a}$  is multinomial, and the log likelihood is the product of the data  $n_l$ , a and the log of the predicted proportions  $p_{l,a}$  of length l and age a:

$$\ln L_1(n|\Theta) = \sum_l \sum_a n_{l,a} \ln(p_{l,a})$$
(3.1)

How the  $p_{l,a}$  term of the likelihood is computed depends on which of the four likelihoods presented below is being used.

## 3.2.2 Model 1 growth with no history of fishing

Where there has been no history of fishing, I calculate the predicted proportions in the matrix  $p_{l,a}$  as the proportion of vulnerable numbers of fish at age *a* and length *l* (in *mm* fork length (FL)) in the total population  $V_T$  of vulnerable fish.

$$p_{l,a} = V_{l,a}/V_T$$
, where  $V_T = \sum_l \sum_a V_{l,a}$ . (3.2)

I begin by assuming that  $V_{l,a}$  can be expressed as the product of three factors: a size dependent vulnerability  $\nu_l$  that depends on size l but not age, relative abundance  $N_a$  of age a fish, and the conditional probability P(l|a) of being in a discrete length interval l given age a:

$$V_{l,a} = v_l N_a P(l|a). \tag{3.3}$$

I assume that  $\nu_l$  has a functional form with increasing vulnerability at length

$$\nu(l) = \frac{1}{(1 + e^{-\gamma(l - l_h)})} \tag{3.4}$$

I describe the length at 50 % vulnerability  $(l_h)$  as a fraction of  $L_{\infty}$  and a shape parameter  $(\gamma)$  that describes the slope of the curve through  $l_h$  (Deriso et al., 1985). If I assume a stable recruitment in the population, then relative numbers-at-age  $(N_a)$  can be calculated using:

$$N_a = Re^{-M(a-1)}. (3.5)$$

Equation 3.5 computes the exponential decay of older cohorts relative to an arbitrary recruitment rate R of age 1 individuals. The natural mortality rate M is estimated with the growth and vulnerability parameters using Eq. 3.1. Where the assumption of a stable recruitment fails, it can be relaxed in the reduced likelihoods described below.

If I assume variation in growth among individuals of age a is caused

mainly by variation in individual asymptotic lengths  $L_{\infty,i}$  (Wang et al., 1995), then the von Bertalanffy prediction of size at age for any individual *i* is  $L_{\infty,i}f(a)$  where the basic age effect f(a) is shared by all individuals *i*. Using the von Bertalanffy growth model this shared effect is described by:

$$f(a) = 1 - e^{(-K(a-t_o))},$$
(3.6)

where K is the metabolic growth parameter and  $t_o$  is the theoretical time of zero length.

Assuming that individuals with  $L_{\infty,i}$  present at the start of cohort life are drawn from a normal distribution with mean  $L_{\infty}$ , and variance  $\sigma_{\infty}^2$ , any subcohort with a specific  $L_{\infty,i}$  will follow a growth trajectory determined by the  $L_{\infty,i}$  with which they were born. This implies that the integral defining P(l|a)for each age a should be evaluated with mean  $l_a = L_{\infty}f(a)$  and variance in mean length at age  $\sigma_a^2$ .

$$P(l|a) = \frac{1}{\sigma_a \sqrt{2\pi}} \int_{l-d}^{l+d} exp\left[-\frac{(l_a - l)^2}{2\sigma_a^2}\right] dl$$
(3.7)

where l is the length of the fish, d is half the length interval width,  $l_a$  is the mean length-at-age, and  $\sigma_a^2$  is the variance in length-at-age.

In most species of fish, the absolute value of  $\sigma_a^2$  increases with age ( $\sigma_a^2$  gets larger as *a* increases). In order to avoid estimating  $\sigma_a^2$  for each age, I assume that standard deviation at age  $\sigma_a$  can be expressed as a simple function of the mean length at age  $l_a$ . This function can be  $l_a$  multiplied by some coefficient
of variation (cv) which is assumed to be constant across all ages, or more complicated functions can be used. I chose to use equation 3.8 derived by Fournier and Sibert (1991).

$$\sigma_a = \lambda_1 e^{\lambda_2 \left(-1 + 2\frac{1-\rho^{a-1}}{1-\rho^{A-1}}\right)}$$
(3.8)

In this formulation  $\rho$  is the Brody growth coefficient ( $\rho = e^{(-K)}$ ), A, the number of ages,  $\lambda_1$  represents the magnitude of the standard deviations at age a and  $\lambda_2$  determines the length dependent trend in the standard deviations (if  $\lambda_2=0$ , the standard deviations are independent of length) (Fournier and Sibert, 1991). This formulation has the disadvantage of adding two parameters rather than one if  $\sigma_a^2$  is expressed as  $cv * l_a$ . The rationale for using it however, is that it makes a less restrictive assumption about how  $\sigma_a$  changes as fish grow older. It also reduces the covariation in the parameters by making the standard deviation of length-at-age depend on one growth parameter ( $\rho = e^K$ ) rather than all three as it would if it were expressed as  $l_a * cv$ .

### 3.2.3 Model 2 reduced likelihood

An option for avoiding the assumption of stable recruitment is to construct the model using the conditional maximum likelihood estimates for numbersat-age  $\hat{N}_a$  and using these in the predicted sample proportions at length and age  $(p_{l,a})$  instead of the  $N_a$  predicted by equation 3.5. This relaxes the assumption of stable age structure which would be violated with highly variable recruitment. Differentiating the log likelihood with respect to  $N_a$ , setting this derivative to zero and solving for  $N_a$  gives the conditional maximum likelihood estimates  $\hat{N}_a$ :

$$\hat{N}_a = \left(\frac{n_a}{n_T}\right) \left(\frac{V_T}{\bar{\nu}_a}\right) \tag{3.9}$$

where  $n_T$  is the total of the number aged in the sample,  $n_a$  is the total number in the sampled aged *a* years,  $V_T$  the total vulnerable numbers from equation 3.2. The value of  $\bar{\nu}_a$  must first be calculated from the product of vulnerability-at-length and the conditional probability of being in length interval *l* given age *a*:

$$\bar{\nu}_a = \sum_l \nu_l P(l|a). \tag{3.10}$$

which is the sum of the weighted mean vulnerability for age a, with vulnerabilities at length weighted by P(l|a).

If the prediction of  $N_a$  from total mortality rate (equation 3.5) is replaced in the likelihood by these conditional maximum likelihood  $\hat{N}_a$  estimates (allowing for any possible age structure in population being sampled), the multiplicative term  $\frac{n_a}{n_T}$  which does not vary with the parameters can be dropped (along with  $V_T$ ) and  $p_{l,a}$  expressed as:

$$p_{l,a} \propto \frac{\nu_l P(l|a)}{\bar{\nu}_a} \tag{3.11}$$

instead of equation 3.2, so the reduced likelihood  $(L_2)$  to be maximized with-

out M becomes:

$$\ln L_2 \propto \sum_l \sum_a n_{l,a} \ln \left( \frac{\nu_l P(l|a)}{\bar{\nu}_a} \right). \tag{3.12}$$

### 3.2.4 Model 3 growth under harvesting

To model the effects of growth under harvesting, I again take the approach that  $n_{l,a}$  is a random sample from a population where  $V_{l,a}$  is the total number of vulnerable fish of length l and age a. The same general form of the likelihood function (equation 3.1) applies but a historical fishing rate (F) must now be incorporated into the estimated sample proportions  $p_{l,a}$ . To do this I multiply each  $V_{l,a}$  element by a length and age specific survivorship  $\ell_{l,a}$  that accounts for a growth pattern that exposes each individual fish to a possibly unique history of the cumulative impact of fishing and natural mortality.

Absent temporal information on past variation in recruitment, natural mortality rate M, and overall (fully vulnerable ages) fishing mortality rate F, I treat these factors as having been stable for enough years to result in a stable age-size distribution. When a population has been subjected to a fishery, the numbers at each age cannot be described by equation 3.5 because each individual fish will be subject to a fishing mortality dependent on the growth trajectory of that individual. In this case, the  $N_a$  component of  $V_{l,a}$  in equation 3.3 becomes  $N_{l,a}$  which must be computed for each land a combination.  $N_{l,a}$  represents the survivors of fish that had individual  $L_{\infty,i}$  equal to l/f(a), i.e. followed a growth pattern that subjected them to cumulative instantaneous mortality (now including the fishing mortality F) at length and age:

$$Z_{l,a} = \sum_{\dot{a}} \left\{ M + \nu_l(\dot{a})F \right\}, \qquad (3.13)$$

to give

$$N_{l,a} = Re^{-Z_{l,a}}, (3.14)$$

where the sum (or integral) over  $\dot{a}$  represents mortality over ages up to age a and where  $\nu_{l(\dot{a})}$  represents the time sequence of  $v_l$  vulnerabilities seen by fish that followed the growth trajectory  $l_{\dot{a}} = L_{\infty,i}f(\dot{a}) = [l/f(a)]f(\dot{a})$  over ages  $\dot{a}$ . The initial recruitment can be set to R = 1 for convenience, since only the ratios of the  $V_{l,a}$  to total  $V_T$  appear in the likelihood function (the composition information  $n_{l,a}$  carry no direct information on total population size). For typical vulnerability functions  $\nu(l)$  describing  $v_l$ , there is no simple analytical solution for the sum or integral of  $\nu_{l(\dot{a})}$  values over ages  $\dot{a}$ , but these sums can be easily evaluated numerically given any assumed form for  $\nu(l)$ . This integral needs to be evaluated for all l, a combinations, since each such combination is assumed to have had a different  $L_{\infty,i}$  and hence a different exploitation history. With a history of exploitation, the vulnerable numbers at age and length  $V_{l,a}$  are calculated as:

$$V_{la} = v_l R e^{-Z_{l,a}} P(l|a)$$
(3.15)

 $p_{l,a}$  in equation 3.1 is now calculated with  $V_{la}$  calculated using equation

3.15:

$$p_{l,a} = \frac{V_{la}}{V_T} = \frac{v_l R e^{-Z_{l,a}} P(l|a)}{V_T}$$
(3.16)

so that the full likelihood  $(L_3)$  that includes size selective fishing mortality is:

$$\ln L_3(n|\Theta) = \sum_l \sum_a n_{l,a} \ln(\frac{v_l R e^{-Z_{l,a}} P(l|a)}{V_T}).$$
(3.17)

The only numerically complex part of this growth under fishing formulation is computing the length-age specific survivorship  $(e^{Z_{l,a}})$  for each l, a element. Consider for example, the function  $\nu(l)$  in equation 3.4. Representing  $l(\dot{a})$  as  $l(\dot{a}) = L_{\infty,i}f(\dot{a})$ , then this age function can be substituted for lengths in the vulnerability function for all length intervals l. For example, the substitution for the vulnerability function in equation 3.4 is:

$$\nu_l(\acute{a}) = \frac{1}{\left(1 + e^{-\gamma(f(\acute{a}) - l_h/L_{\infty,i})}\right)},$$
(3.18)

which then has to be integrated over  $\dot{a}$  and then multiplied by F in order to predict cumulative fishing mortality effects on the "subcohort" of fish that started life with asymptotic size  $L_{\infty,i}$ . For alternative vulnerability functions that are difficult to integrate (i.e. dome-shaped curves), I recommend simply summing the function over ages  $\dot{a}$  from 1 to a, using  $\dot{a}$  age steps of 1-year for long-lived fish and shorter steps (e.g. 0.5 year) for fish that live only a few years.

### 3.2.5 Model 4 Reduced likelihood with fishing

Calculating the reduced likelihood in the fishing case is essentially the same as in the non-fishing case in the sense that the  $N_a$ 's are replaced by their conditional maximum likelihood estimates. However, the cumulative effect of F on each l and a element must be included in the calculation Eq. 3.10 using Eq. 3.18 so that:

$$\bar{\nu}_{a} = \sum_{l} \nu_{l} e^{\nu_{l}(\dot{a})F} P(l|a).$$
(3.19)

Once this is done  $\bar{\nu}_a$  gets updates automatically with changes with F. The  $p_{l,a}$  matrix now is computed as:

$$p_{l,a} \propto \left(\frac{\nu_l e^{\nu_l(\hat{a})F} P(l|a)}{\bar{\nu}_a}\right) \tag{3.20}$$

and the reduced likelihood now including fishing becomes:

$$\ln L_4 \propto \sum_l \sum_a n_{l,a} \ln \left( \frac{\nu_l e^{\nu_l(\dot{a})F} P(l|a)}{\bar{\nu}_a} \right).$$
(3.21)

### 3.2.6 Simulations

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To test the derivations above I simulated data using known parameters (Table 3.2.6). Variation in past recruitment anomalies was included as log-normal process error with a mean of zero and standard deviation of 1 multiplied by a coefficient of variation  $CV_R$ .

I compared the performance of the standard Fabens (after Rothchild et al. (1989)) method that assumes a representative sample of numbers-at-age and minimizes the sum of squares difference between predicted and observed lengths-at-age to the four models I derive above using simulated data. I generated 100 data sets with no fishing (F = 0), with a sustainable fishery (F = K) and an overfished population (F = 1).

Fisheries where the fishing mortality has been stable for a long time are uncommon. Using the same parameters (Table 3.2.6) and a fully length-age structured simulation model, I tested models 3 and 4 with simulated data from stocks where F increased in increments of 0.1 per year for 5 years and where F was increased in increments of 0.1 per year for 10 years. For these cases, new recruits each year were assumed to have a fully representative distribution of individual asymptotic lengths (with mean  $L_{\infty,i}$  and variance  $\sigma_{\infty}$  computed with equation 3.8 evaluated at an infinite age ). Individuals of specific asymptotic lengths ( $L_{\infty,i}$ ) across all ages were then exposed to fishing mortality every year according to the size (and hence  $v_l$ ) they were in that year. As in the simulations with stable fishing mortality, natural mortality was assumed constant and  $CV_R$  was set to 0.5.

The sensitivity of all of the models to changes in parameters used to simulate data were tested by using extreme parameter values. I conducted simulations with: the length at half vulnerability  $l_h$  set to  $0.05^*L_{\infty}$  and  $0.9^*L_{\infty}$ , knife-edged vulnerability ( $\gamma = 0.9$  and with low variability in length at age ( $\lambda_1$  set to 5). Finally I tested the models with a short lived, fast

	Table 3.1:	Parame	ters use	d to gene	rate fal	ke dat	a.		
Parameter	Value	•							
$N_T$	1000					-		,	
$\ln L_{\infty}$	5								
K	0.15								
$t_o$ .	-0.25						•.		
Z	0.2						·		
$l_h$	0.6								
$\gamma$	0.1								
$\lambda_1$	16								
$\lambda_2$	0.5								
$CV_R$	0.5								

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growing population with K = 0.7, M = 0.7.

# 3.2.7 Growth parameter estimation for northern pikeminnow

I collected data for northern pikeminnow *Ptychocheilus oregonensis* from Moose Pasture lake located on the Bonaparte Plateau approximately 100 km north of Kamloops, British Columbia. I collected fish for ageing during a depletion experiment aimed at killing a high proportion of the population. Fish were captured during 6 bouts of fishing using four hoop nets. Three of these nets consisted of 6 m x 1 m fiberglass hoops covered in 1 cm mesh, 20 m center lead, and 15 m side leads. The other consisted of 6 m x 0.7 m steel hoops covered in 0.5 cm mesh, 15 m center lead, and 10 m side leads. Lapilli otoliths were taken from each fish and 945 were aged. I cut larger otoliths along the ventral/dorsal axis using an Isomet Bueller slow speed

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saw, burned and counted annuli. Otoliths too small to cut were burned and counted directly. For fish older than 5 years, failing to cut otoliths along the long axis sometimes resulted in significant underestimates of age.

During the three months preceding the depletion (9-15 September 2002), 1004 fish were tagged using 5 and 15 mm Floy numbered tags during four bouts of mark-recapture conducted at approximately 2 week intervals. Only those fish that were released in perfect condition are included in this analysis. Because the functional form of the vulnerability-at-length is unknown for fyke nets and northern pikeminnow, I used these tagging data to directly estimate vulnerabilities-at-length . I divided the fish into 5 mm size bins and estimated the gear selectivity for each bin using the likelihood described by Myers and Hoenig (1997). I include this analysis both to ensure that the functional form of the vulnerability-at-length has been specified correctly and to compare how well the vulnerability function estimated using only the length-at-age data and the multinomial likelihood(s) does relative to the direct estimates of vulnerability computed from the tagging experiment.

# 3.3 Results

For the simulated data with no fishing mortality K was overestimated and  $L_{\infty}$  underestimated using Fabens method (Fig. 3.1). These biases were small (0.20% for K and negligible for  $L_{\infty}$ ). There was still the common bias of a large negative *to* parameter which was underestimated by a factor

of two. With no fishing models 1,2,3 and 4 were unbiased for the growth, vulnerability parameters but slightly over-estimated M and in the case of model 3 F.

The parameter bias using Fabens, models 1 and 2 worsened with increasing F. With the Fabens method the bias was large and negative for to, small for K and negligible for  $L\infty$  (Fig. 3.1). Model 1 accounted for the fishing mortality by over-estimating the natural mortality (Fig. 3.2) but could not account for the selective mortality on higher  $L_{\infty,i}$  individuals caused by fishing and so underestimated  $L_{\infty}$ . Although model 2 suffered from the same bias in growth parameter estimates as model 1 did, models 3 and 4 were unbiased.

Biases in parameter estimates were much worse where F = 1.0 for all but models 3 and 4 (Fig. 3.3). The bias in K,  $L_{\infty}$  and  $t_o$  was less severe for models 1 and 2 but in the same direction as Fabens. When fishing mortality was low, the distortion in the sample caused by F was compensated for by high estimates of M (Fig. 3.2). This was not the case with high F (Fig. 3.3). Fishing mortality distorted the sample so much that the few older fish left were the small  $L_{\infty,i}$  (slow growing) individuals.

Models 3 and 4 correctly estimated the von Bertalanffy growth parameters (Fig. 1) at all levels of stable fishing mortality. Even with moderate recruitment anomalies used to simulate the data ( $CV_r=0.5$ ), F was over estimated. This was the case at low F (although it cannot been seen due to the scaling of Fig. 3.1 and 3.2) and much worse at higher F (Fig. 3.3).



Figure 3.1: Proportional error in parameter estimates for each likelihood formulation with F = 0. (a) Fabens, (b) model 1, (c) model 2, (d) model 3, and (e) model 4, (circles represent outliers).



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Figure 3.2: Proportional error in parameter estimates for each likelihood formulation with F = K. (a) Fabens, (b) model 1, (c) model 2, (d) model 3, and (e) model 4, (circles represent outliers).

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Figure 3.3: Proportional error in parameter estimates for each likelihood formulation with F = 1. (a) Fabens, (b) model 1, (c) model 2, (d) model 3, and (e) model 4, (circles represent outliers).

The performance of models 3 and 4 suffered with variable fishing. All the parameters were estimated well with 5 years of increased fishing (Fig. 3.4 a,c,e). But with 10 years of increased fishing, model 5 (Fig.3.4 f) performed as poorly was Fabens (Fig. 3.4 b) and model 4 was only slightly better (Fig. 3.4 d).

At all levels of fishing, the models 2 and 4 were less precise than models 1 and 3. Models 2 and 4 do not assume a stable age distribution and so admit that more parameter combinations can explain the data. The reduced likelihoods effectively estimated relative recruitment of each age a cohort  $R_t-a$ . This means a additional parameters are estimated. While there is loss in precision of the parameter estimates, models 2 and 4 allow a much more honest acknowledgement of the uncertainty caused by recruitment variation in cases where a stable age structure is doubtful or unknown.

All the models are sensitive to low values of  $l_h$ . A very slowly sloping vulnerability ( $\gamma = 0.05$ ) function had the same effect. Distortion in the data of younger age classes relative to fully represented ones needs to be present in the data for it to be possible to resolve the vulnerability parameters. For example, with no fishing, using the same growth parameters listed in Table 3.2.6 but with  $l_h$  is equal to 0.05 of  $L_{\infty}$ , the data do not contain any information about the vulnerability parameters and the result is mean biases of 300% for  $l_h$  and 500% for  $\gamma$ . M is confounded with the vulnerability parameters and it is under-estimated by 0.28. Fortunately the growth parameters K,  $L_{\infty}$  and to are well estimated with mean bias of less than 5% bias. As is



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Figure 3.4: Proportional error of Fabens (a,b), model 3 (c,d), model 4 (e,f), where F increases in increments of 0.1 to F = 0.5 (a,c,e) and to F = 1.0 (b,d,f). F over time was estimated but the proportional bias is not included here since the true F used to simulate the data changed annually.

expected where with little size selectivity, the Fabens method actually performs as well as likelihoods presented here because there is not significant distortion in length-age samples from either fishing or gear-selectivity.

With no fishing and parameters again set to those listed in Table 3.2.6 but making  $l_h = 0.9$ , the problem is that there are no fully represented ageclasses in the length-age sample. The parameters  $L_{\infty}$ , K,  $\lambda_1$ ,  $\lambda_2$  and lh are all well estimated with biases less than 8%, but to,  $\gamma$  and m are biased by 35, 21 and -40% respectively. As long as  $l_h$  is an intermediate value, then the model is robust to steeply sloping  $v_l$  ( $\gamma = 0.9$ )

The simulated estimates were robust to data simulated with faster growing (moderately high K = 0.5) and faster dying (higher M = 0.6) population. But in populations where K and M are greater than about 0.7, fractional ages (half or quarter year) ages need to be used or the model performs badly and either underestimates K or fails to converge at all.

These models break down when the shape of the vulnerability curve is not specified correctly, if fishing mortality is too large or if M is size or age-dependent, and with smaller length at age samples. If the actual vulnerability function is dome-shaped but an asymptotic function is assumed in the analysis, F is confounded with decreasing vulnerability of older/larger fish and becomes biased upward. Very high F is very destructive to the age structure of the population and no parameters can be estimated well. Where M is size or age dependent (where M decreases over age for example), there is severe confounding of M and F with the parameters that describe  $v_l$ . At low sample sizes it is possible to have no data by random chance from either the faster growing younger fish (that help resolve  $v_l$ ) or older fish (that resolve M and F). With 25 age classes these models worked very poorly with fewer than approximately 500 observations.

# 3.3.1 Northern pikeminnow growth parameter estimates

The five model fits to the northern pikeminnow data are plotted in Fig. 3.5. Parameters estimates are very similar for all of the models used. As they should, the likelihood formulations that include fishing (models 3 and 4) actually estimate a small fishing mortality in this population. Models 3 and 4 have a tendency to over-estimate the fishing mortality, but a non-zero value for this parameter is not as unreasonable as it might seem. The population is exposed to a small scale fishery from local lodge owners that have in the past conducted annual trapping programs during the spring spawn.

Parameter estimates from all four models are very similar (Table 3.3.1). Since this population was subject to some fishing in the past by fishing lodge owners in the area and because how stable recruitment has been is uncertain, the best model choice is the reduced likelihood with fishing.

The vulnerability curve estimated by model five (Fig.6) is very similar to that fit using the mark recapture data. Fitting with model 5 appears to over-estimate the vulnerability at length for smaller size classes (Fig. 3.6)

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Figure 3.5: Growth curves fit to northern pikeminnow data using all 5 models: solid=fabens, dashed=full likelihood, dotted=reduced likelihood, dotdash=full likelihood with fishing, longdash=reduced likelihood with fishing.

Т	able 3.2:	Estimated	parameter	values	for each	mode
		Model #				
Parameter	Fabens	1	2	3	4	
$L_{\infty}$	179.61	162.06	179.77	166.46	188.10	-
K	0.12	0.19	0.14	0.18	0.14	
to	-1.95	-0.41	-0.00	-0.38	-0.00	
$\lambda_1$	13.90	13.18	16.16	13.20	15.96	
$\lambda_2$	0.69	0.65	0.60	0.61	0.57	
$l_h$	-	0.45	0.49	0.44	0.47	
Г	-	0.21	0.20	0.19	0.19	
Z	-	0.38	-	0.26	-	
F	-	-	-	0.18	0.15	

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but otherwise seems a reasonable approximation (note that the parameter estimates for the vulnerability parameters in table 3.3.1 were similar for all models). Note that the vulnerability at length for the larger size classes is not well defined due to small sample sizes of tagged animals in those size bins.

# 3.4 Discussion

The estimated  $L_{\infty}$  of northern pikeminnow is small compared to other documented populations of this species. While the von Bertalanffy growth parameter (K) for this population of northern pikeminnow is similar to those published in the literature, the  $L_{\infty}$  is much smaller. Northern pikeminnow have been studied extensively due to their predation on juvenile salmonids in a variety of systems such as Cultus Lake British Columbia (Ricker, 1941; Steigenberger and Larkin, 1974) and they are presently managed in

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Figure 3.6: Plot of vulnerability curve (solid line) for northern pikeminnow estimated using likelihood 3 and direct estimates of vulnerability using mark-recapture.

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the Columbia basin to reduce their impact on juvenile salmon (Friesen and Ward, 1999). Typical  $L_{\infty}$  for this species are in the order of 400-600 mm FL (Parker et al., 1995) in the Columbia river basin and in Idaho lakes the average reported size of a sexually mature female approximately 440 mm TL (20 inches) for female and 300 mm (15 inches) for males Jeppson (1959). These values are well above even the maximum sizes observed in the study area. The reasons for their small size are presently unknown and could be density or environmental effects, but I hypothesize that it is mainly due to the short growing season (three months or so) that these fish experience.

The simulations shown here are not unusual in showing the biases in the von Bertalanffy growth parameters (and corresponding yield per recruit analyses) due to gear selectivity and size-selective mortality on the estimation of growth parameters. These problems are well known (Deriso et al., 1985; Parma and Deriso, 1990; Sinclair et al., 2002b). The methods I present are original in using simulation studies to show the biases in estimates of both the von Bertalanffy parameters, the parameters describing size-selectivity, natural and fishing mortality and in presenting likelihoods that model these effects. Unlike Parma and Deriso (1990) and Sinclair et al. (2002b), I make no effort to include environmental effects or in the case of Sinclair et al. (2002b), density dependent growth. Parma and Deriso (1990) show that increasing the contribution of environmental factors have little effect on the variance in size at age relative to size-selective harvesting, and that most fisheries data contain little information about such effects. Sinclair et al.

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(2002b) also determined that by far the largest effect on mean predicted  $L_{\infty}$  was size-selective mortality.

I have shown it possible under a restricted set of assumptions to estimate the von Bertalanffy growth parameters, M, F and the vulnerability parameters from only size-at-age data when other data from a fishery are not available. I caution that estimates of the vulnerability and mortality parameters should be considered very uncertain. Unfortunately, the sensitivity of the models to stable fishing mortality and known vulnerability shape restricts the applicability of these models. Recall that the models are robust to an increasing fishing rate as long as the fishing mortality has not grown too rapidly. While the Fabens method performed almost equally as well in the case of growing F it did not tell the researcher anything about M or the vulnerability function  $v_l$ . Of particular concern is the breakdown of the models following a very rapid increase in F. Having accurate assessment of the true growth parameters of the stock is particularly needed in order to assess the rebuilding potential of the stock in such situations.

Fortunately, in many cases the reason for estimating growth parameters in the first place is that it is part of a larger stock assessment where F (and sometimes  $v_l$  as in virtual population analysis ) is already estimated. This method could be applied in more complex stock assessments where  $n_{l,a}$  tables can be provided for a collection of sample years. For each such table, the stock assessment model provides additional information on time-varying recruitments  $R_{t-a}$  and fishing mortality rates F and in some cases (like virtual population analysis)  $v_l$ . Assuming the  $n_{l,a}$  data are collected independently each year, the log-likelihood term for each of these tables can simply be added to the overall log-likelihood for the assessment model. The accounting (sum or integration) calculations for each  $Z_{la}$  (cumulative mortality by size and age) are would require calculating the survival of those individuals growing along each  $L_{\infty,i}$  trajectory, but may carry valuable information on changes over time in F. A potentially important advantage of this approach would be to correct the problem that has plagued some past length-based stock assessment methods of ignoring cumulative effects of fishing on length distribution patterns. Mean length and variability of length at age are explicitly variable and dependent on  $F_t$  in method 3 only, due to variation in  $Z_{l,a}$ .

## 3.5 Acknowledgements

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# Chapter 4

# Estimating movement and growth parameters given size-dependent spatial ontogeny

# Abstract

I developed a likelihood to simultaneously estimate growth, natural mortality, and gear selectivity parameters using change in length from tagging data. I combined this likelihood with two others for mark-recapture and for length-age data to estimate the von Bertalanffy growth parameters, natural mortality, gear selectivity and in some cases length-dependent movement parameters. Using simulation studies I showed that if a stable recruitment can be assumed it is also possible to estimate tag loss but that the assumptions required to do so are very limiting. The combined likelihood was not robust to large recruitment variation, measurement or ageing error. The advantage of such an approach however is that it provides a framework to use all sources of data to measure population parameters.

# 4.1 Introduction

There are many tools at the disposal of stock assessment scientists to measure growth and mortality parameters provided sampling is done representatively. But representative sampling may be difficult to acheive, especially if fish move a lot. Fish movement is invisible and can contaminate sampling in a number of ways: the spatial distribution of the population may be unknown and sampling done from only a portion of the true range, if sampling is based on an agency's jurisdiction rather than the distribution of the fish; or the spatial distribution may be dynamic (a function of the stock's size or oceanographic conditions). The number of examples where fish are distributed over larger area than previously thought is increasing in both aquatic (Anras et al., 1999; Arnekleiv and Kraabol, 1996) and marine systems (Haist et al., 1999; McHich et al., 2002; Rooker et al., 2003; Block et al., 2005). Such biased sampling will contaminate estimates of population parameters such as growth and mortality, particularly if the movement is size dependent and the age or size composition differs between areas. If larger fish swim faster (and hence further) then sampling at the margins of a stock's distribution will be biased for faster growing fish, and sampling in the center of the distribution biased for slower growing fish. Finally, the center of a stock's distribution may also move as oceanographic conditions vary. Such dynamics are present for example in Pacific Hake (Benson et al., 2002). Even where sampling can be assumed representative in the spatial sense, Laslett et al. (2002) show growth parameters must be estimated simultaneously with natural mortality and measurement error for mark-recapture data. In Chapter 3, I showed using simulated length-age data that gear selectivity must also be considered. So in order to properly estimate growth parameters, in some cases it is also necessary to also estimate mortality, gear selectivity and in some cases movement must be included in the stock assessment.

The format of most mark-recapture data is convenient for estimating sur-

vival parameters at fine time scale (that of the mark-recapture experiment) and when size information is included with observed recaptures then it is also convenient for estimating growth parameters. Growth analysis only requires that the 1s and 0s typically used to denote observations of individually marked fish be replaced with size at time.

Regardless of technique, estimates of growth and survival parameters rely heavily on assumptions that can rarely be met, or shown to be met, in practice. With length-age data the principal concern is age validation, that is, showing that annuli counted on a structure represent actual years. Beamish and McFarlane (1983) found that only 3.4% of 500 studies conducted before 1982 were successfully able to validate ages across the full age range. There has been little recent improvement in this ratio, with only 15% of studies doing so since then (Campana and Thorrold, 2001). Measurement error is often not even considered in assessments or worse, assumed to be zero and used to check the validity of ageing (Paragamian and Beamesderfer, 2003). Finally mark-recapture experiments rely on assumptions of no tag-loss, no tagging mortality and all tags being reported. Studies that estimate tag-loss are in vogue (Ebener and Copes, 1982; Pierce and Tomcko, 1993; Swanson and Schram, 1996; McGlennon and Partington, 1997; Julliard et al., 2001; Feldman et al., 2002; Rikardsen et al., 2002; Brattey and Cadigan, 2004) but it is practically very difficult to do dual tag studies and using internal tags is expensive and limited to relatively large fish. Even if a dual tagging study can be done, it cannot be used to determine tagging mortality. Furthermore, dual tagging may actually increase the tagging mortality. It would be useful therefore to estimate a combined tag-loss, tag-mortality term without using such studies.

This study consists of three parts. First I develop a likelihood analogous to that developed in Chapter 3 that can be used to estimate growth parameters from mark-recapture data. Then I develop and explore the performance of combined likelihoods for length-age, change in length and mark-recapture data under two distinct situations, with and without length dependent movement similar to that described in Chapter 2. Using simulation studies, I test the performance of each at estimating the von Bertalanffy growth parameters, movement parameters, mortality and tag-loss in a range of scenarios that include measurement error, ageing error and tag loss. I find the performance of the combined likelihoods good but not robust to assumptions about stable historical recruitment, and measurement error.

# 4.2 Methods

### 4.2.1 Length-age likelihood

The details of the likelihood for the length-age data are discussed in chapter 3 so will be only briefly reviewed here. I assume the data available for analysis consists of a matrix  $n_{l,a}$  with elements of numbers of fish sampled at (discrete) lengths l and ages a, and that this is a random sample of the number of vulnerable fish of length l and age a available in the population to

be sampled. The general form of the likelihood for  $n_{l,a}$  given the parameter vector ( $\Theta$ ) is multinomial, and the log likelihood a product of the data  $n_{l,a}$ and the log of the predicted proportions  $p_{l,a}$  at length l and age a:

$$\log L_1(n|\Theta) = \sum_l \sum_a n_{l,a} \ln(p_{l,a}) \tag{4.1}$$

 $p_{l,a}$  is expressed as the product of three factors: a size dependent vulnerability to gear  $\nu_l$  that depends on size (but not age), relative abundance  $N_a$ of age *a* fish, and the conditional probability P(l|a) of being in a discrete length interval *l* given age *a* 

$$p_{l,a} = \frac{v_l N_a P(l|a)}{\sum_l \sum_a v_l N_a P(l|a)}.$$
(4.2)

I assume vulnerability at length  $\nu_l$  as an increasing function of length

$$\nu(l) = \frac{1}{(1 + e^{-\gamma(l-l_h)})}.$$
(4.3)

with parameters  $(l_h)$  as the length at 50 % vulnerability and a shape parameter  $(\gamma)$  that describes the slope of the curve through  $l_h$  (Deriso et al., 1985). Assuming stable recruitment  $N_0$ , then relative numbers-at-age  $(N_a)$  can be calculated using:

$$N_a = N_0 e^{-M(a-1)}. (4.4)$$

Equation 4.4 computes the exponential decay of older cohorts relative to  $N_0$ individuals. The natural mortality rate M is to be estimated along with the growth and vulnerability parameters using Eq. 4.1.

I assume variation in growth among individuals is caused variation in individual asymptotic lengths  $L_{\infty,i}$  (Wang et al., 1995), so that the von Bertalanffy prediction for any individual *i* is  $L_{\infty,i}f(a)$  where f(a) is shared by all individuals *i*. Using the von Bertalanffy growth model this shared effect is described by:

$$f(a) = 1 - e^{(-K(a-t_o))},$$
(4.5)

where K is the metabolic growth parameter and  $t_o$  is the theoretical time of zero length.

Assuming that individuals with  $L_{\infty,i}$  present at the start of cohort life are drawn from a normal distribution with mean  $L_{\infty}$ , and variance  $\sigma_{\infty}^2$ , an individual with a specific  $L_{\infty,i}$  will follow a growth trajectory determined by the  $L_{\infty,i}$  they were born with. This implies that the integral defining P(l|a)for each age a should be evaluated with mean  $l_a = L_{\infty}f(a)$  and variance in mean length at age  $\sigma_a^2$ .

$$P(l|a) = \frac{1}{\sigma_a \sqrt{2\pi}} \int_{l-d}^{l+d} exp\left[-\frac{(l_a - l)^2}{2\sigma_a^2}\right] dl$$
(4.6)

where l is the length of the fish, d is half the length interval width,  $l_a$  is the mean length-at-age, and  $\sigma_a^2$  is the variance in length-at-age.

In most fish species, the absolute value of  $\sigma_a^2$  increases with age ( $\sigma_a^2$  gets larger as *a* increases). To avoid estimating  $\sigma_a^2$  for each age, I assume that standard deviation at age  $\sigma_a$  can be expressed as a simple function of the mean length at age  $l_a$ . This function can be  $l_a$  multiplied by some coefficient of variation (CV) which is assumed to be constant across all ages, or more complicated functions can be used such as that of Fournier and Sibert (1991) as described in Eq. 4.7.

$$\sigma_a = \lambda_1 e^{\lambda_2 \left(-1 + 2\frac{1-\rho^{a-1}}{1-\rho^{A-1}}\right)}$$
(4.7)

In this formulation  $\rho$  is the Brody growth coefficient ( $\rho = e^{(-K)}$ ), A, the number of ages, age a,  $\lambda_1$  represents the magnitude of the standard deviations at age a = 1 and  $\lambda_2$  determines the length dependent trend in the standard deviations (if  $\lambda_2=0$ , the standard deviations are independent of length) (Fournier and Sibert, 1991). This formulation has the disadvantage of adding two parameters rather than one if  $\sigma_a^2$  is expressed as  $CV * l_a$ . The rationale for using it however, is that it makes a less restrictive assumption about how  $\sigma_a$  changes as fish grow (rather than assuming a fixed coefficient multiplied by length at age).

### 4.2.2 Mark-Recapture Data

I assume the data consist of marked cohorts R with individual fish of length l tagged and released at time t. Each individual i therefore has a capture history consisting of lengths  $l_{i,t}$  at marking and subsequent recapture. The recapture history of the cohort  $R_t$  then is a matrix with elements  $l_t$  if captured and 0 if not, rows of individual tag numbers and columns t when sampling

Cohort	tag	$t_1$	$t_2$	$t_3$		$ t_{k-1} $	$ t_k $	
$R_1$	xxx	$l_1$		$l_3$	—	-	—	
	xxx	$l_1$	$l_2$	-	$l_4$	$l_{k-1}$	-	
	xxx	$l_1$	_	$l_3$	—	$l_{k-1}$	-	
	xxx	$l_1$	-	-	$l_4$	-	$l_k$	
$R_2$	xxx		$l_2$	$l_3$	—	$l_{k-1}$	-	
	xxx		$l_2$	$l_3$			-	
	xxx		$l_2$	-	$l_4$		·	-
	xxx		$l_2$		—	$l_{k-1}$	-	
	xxx		$l_2$	$l_3$	$l_4$		_	]
Parameters		• • •					_` !•	_
							•	
capture probability	$p_t$	$p_1$	$p_2$	$p_3$	$p_4$	$p_5$	$p_6$	
survival	$\phi_t$	$\phi_1$	$\phi_2$	$\phi_3$	$\phi_4$	$\phi_5$	$\phi_6$	

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Table 4.1: Format of mark-recapture data by cohort R released and recaptured at times t and estimated parameters for survival  $\phi_t$  and capture probability  $p_t$ 

occurred (table 4.1).

Two likelihoods are used for the mark-recapture data: the probability of the observed sizes at capture and recapture given the predicted age structure as well as the probability of the capture history given predicted survival over the mark-recapture time period. The first depends on the growth, recruitment and vulnerability parameters that led to the size/age structure of observed marked and recaptured animals. The second depends only on mortality parameters over the course of the mark-recapture experiment. I discuss first the likelihood for growth and second that for survival.

#### 4.2.3 Mark-Recapture Likelihood for Growth

The general form of the likelihood for estimating growth parameters from mark-recapture data is an adaptation of Laslett et al. (2002)'s formulation to include the effects of gear selectivity. It is the product of two parts: the joint probability of being marked at length at time of first capture  $l_c$ ,  $pr_{l_c}$ and the joint probability  $h(l_c, l_r | a, l)$  of being measured to have lengths  $l_c$ at time of marking and at recapture  $l_r$  after some time increment  $\delta t$  later. Using discrete lengths l and ages a the likelihood is:

$$\log L_2 = \sum_{l_c} \sum_{l_r} n_{l_c, l_r} \log[\sum_l \sum_a pr_{l_c} h(l_c, l_r | a, l)]$$
(4.8)

where the data  $n_{l_c,l_r}$  are the lengths at capture and recapture,  $h(l_c, l_r | a, l)$  is the joint density of  $l_c$  and  $l_r$ . I assumed the probabilities of observed length at capture and recapture to be independent and normally distributed with the true mean length at marking  $l_1$  and length at recapture  $l_2$  respectively

$$h(l_c, l_r | a, l) = e^{\sigma_o^2 (l_c - l_1)^2 + (l_r - l_2)^2}$$
(4.9)

where  $\sigma_o^2$  is the measurement error variance,  $l_c$  and  $l_r$  the measured lengths at marking and recapture. I assumed each marked fish follows an average growth trajectory described by some function f(t), that allows for individual variation in each fish i so that its true length  $l_1$  at time t and true age A is

$$l_1(t) = L_{\infty,i} f(t, A, \theta) \tag{4.10}$$

I assumed that individual variation in length at age comes from normal distribution of individual  $L_{\infty,i}$  with mean  $\mu_{\infty}$  and variance  $\sigma_{\infty}^2$ , A the age of fish and  $\theta$  a vector of growth parameters. Using the von Bertalanffy model, we expect the lengths of fish marked at  $t_1$  and recovered at  $t_2$  to be functions f1 and f2 (respectively) of the metabolic growth parameter (K) and the amount of time  $\delta t$  after marking so that  $l_2$  is the predicted length at recapture computed as:

$$l_2 = L_{\infty,i} f(t, A + \delta_t, \theta) \tag{4.11}$$

Since the true age A was unknown, for each combination of age a and length l in Eq. 4.8 I computed the individual  $L_{\infty,i}$  that would have produced the observed length. I assumed this distribution was normal with the mean asymptotic length  $L_{\infty}$  and variance  $\sigma_{\infty}^2$ . Individual  $L_{\infty,i}$ 's were calculated for each length and age combination using f(a) (Eq. 4.5):

$$L_{\infty,i} = l/f(a) \tag{4.12}$$

The predicted proportions at length and age for the mark-recapture same

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ple have a similar form to the length-age data (Eq. 4.2):

$$pr_{l,c} = v_l N_a \frac{1}{f(a)\sqrt{2\pi\sigma_{\infty}^2}} e^{(L_{\infty,i} - \bar{L_{\infty}})/2\sigma_{\infty}^2}$$
 (4.13)

Additional recaptures are simply added to the log-likelihood of that individual's growth trajectory. The vulnerability parameters that predict  $v_l$ , the growth parameters that predict  $h(l_c, l_r | a, l)$  combined with M to predict  $pr_{l,c}$  are estimated in the likelihood.

I treated the observed lengths as coming from a distribution with a mean true length l and a measurement error term assumed normally distributed with mean zero and standard deviation  $\sigma_o^2$ . I assumed the distribution of measurement errors was the same for marking and recapture. For each observed length at either marking or recapture, I compute a range of possible true lengths  $l_{rng} = l_c$  or  $l_r \pm 2\sigma_o$ . This format does not permit estimating the measurement error. This must be assumed or done empirically where possible by querying the lengths of fish marked at short time intervals (say one day) apart and computing the mean difference between those two times.

# 4.2.4 Mark-Recapture Likelihood for Survival with no Movement

I used the method reviewed in Lebreton et al. (1992) for estimating survival. The data and parameters used are of the form described in table 4.1 but instead of 1's typically used to denote recaptured fish I use size observations  $l_t > 0$  where fish were observed and  $l_t = 0$  where not.

Calculating the likelihood of each individual *i* capture history involves three steps: determining the time when each fish was last observed alive  $\tau$ ; computing the probability of each  $l_t$  observation for time  $t \leq \tau$  given the fish was alive; and computing the probability the fish was not observed for time  $t > \tau$ . The probability of the data at all time points  $t \leq \tau$  is simply the product of survival  $\phi_t$  and the capture probability  $p_t$  if the fish was observed and if not, the product  $\phi_t$  and the compliment of the capture probability  $q_t = 1 - p_t$ :

$$Pr_{i} = \left\{ \begin{array}{c} l_{t} > 0 : \phi_{i}p_{i,t} \\ l_{t} = 0 : \phi_{i}q_{i,t} \end{array} \right\}$$
(4.14)

where  $p_{i,t} = v_l p_t$ .

The computation is more complex for the probability of observations at time  $t > \tau_t$ . Here the probability of each observation is the sum of the probabilities that could have led to the fish not being observed. Individual fish may not have been observed due to any combination of dying at any time  $t > \tau$  or not being detected even though alive.

Fortunately these probabilities can be calculated by backwards recursion. If  $\chi_t$  is the probability of not being observed again given release alive at  $t = \tau$ and the last sampling time point t = k then  $\chi_k$  is by definition 1. According to Cormack (1968)  $\chi_i$  is calculated as:

$$1 + \chi_i = \phi_i (1 - q_{i+1}\chi_{i+1}) \tag{4.15}$$
The log-likelihood of each capture history is multinomial with the predicted probability equal to the product of the probabilities of all the time tobservations. Suppose for example, an individual was marked at t = 1 at 120 mm, not observed at t = 2, measured again at t = 3 at 123 mm; then not observed again in two addition surveys conducted at times t = 4 and t = 5. Its capture history is: 120 0 123 0 0. The likelihood  $L_i$  of individual *i*'s capture history is the product of the probabilities of each of observation at time t:

$$L_i = \phi_2 q_2 \phi_3 p_3 \chi_3 \tag{4.16}$$

The total log-likelihood of all data then is the sum of the likelihoods of each individual of the individual capture histories i.

$$\log L_3 = \sum_i L_i \tag{4.17}$$

The capture probabilities  $p_t$  may be estimated in the likelihood but are given by the conditional maximum likelihood estimate:

$$p_t = \frac{\sum r_t}{\sum\limits_i v_{l,i} N_{l,i}} \tag{4.18}$$

where  $r_t$  is the recapture of individual *i* (either 1 or 0)  $v_{l,i}$  is the gear selectivity of individual *i* and  $N_{l,i}$  is the predicted survivorship of that individual. Using the conditional maximum likelihood estimates of the capture probabilities is convenient particularly if the capture probabilities are low, and/or if many animals are never observed again after marking (for such data there is very little information about the capture probabilities).

Calculating  $v_l$  requires predicting the length of each individual at time  $l_{i,t}$  and calculating its vulnerability  $v_{l,i}$  using Eq. 4.3. I predicted  $l_{i,t}$  at  $\Delta t$  time after first marking  $t_c$ ,  $l_{t_c+\Delta t}$  as

$$l_{i,t_c+\Delta t} = l_{c,i} + (L_{\infty} - l_{c,i})(1 - e^{-K(\Delta t)})$$
(4.19)

using the von Bertalanffy growth parameters estimated with Eqs. 4.8 and/or 4.1.

# 4.2.5 Mark-Recapture Likelihood for estimating survival parameters and movement

To estimate movement parameters I depart from the traditional mark-recapture method described above and instead adopt the state-space approach of De Valpine and Hastings (2002) to formulate a likelihood function. Here I suppose a time series consisting of length observations  $y_1, y_2, ... y_T$  until some maximum time T. I denote all observations Y until time t as  $Y_t$ .

The likelihood is calculated recursively with the probability of all the data at time t given the parameters  $P(Y_t)$  expressed as the product of the probability of the data through t-1 and the probability of the latest observation  $y_t$ .

$$P(Y_t) = P(Y_{t-1})P(y_t|Y_{t-1})$$
(4.20)

 $P(y_t|Y_{t-1})$  is expressed as:

$$P(y_t|Y_{t-1}) = \sum_{s_t} P(s_t|Y_{t-1}) P(y_t|s_t, Y_{t-1})$$
(4.21)

where  $s_t$  represents all possible fish states (alive in area 1, alive in area 2, etc. and dead).  $P(y_t|s_t, Y_{t-1})$  is the probability of the observation given the state, or simply the capture probability. For example, if a fish is observed in area 1 at time t then the probability of that observation is simply the capture probability in that state  $p_{s,t}$ . The probability of it being observed in any of the other states (alive in other areas, or dead) given it was captured in area 1 is therefore zero.  $P(s_t|Y_t)$  is updated at each time step using Bayes theorem so  $P(s_t|Y_t)$  is equal to the prior  $P(s_t|Y_{t-1})$  multiplied by the probability of the data given the state (the likelihood  $p(y_t|s_t)$ ) divided by the sum of all possible combinations of priors and likelihoods (the marginal).

$$P(s_t|Y_t) = P(s_t|Y_{t-1})p(y_t|s_t) / \sum_{s_t} P(s_t|Y_{t-1})p(y_t|s_t)$$
(4.22)

Where there is an observation in one of the location states, the posterior probability of being in that state is simply 1. The priors at the subsequent step  $P(s_{t+1}|Y_t)$  are the product of the posterior state probabilities  $P(s_t|Y_t)$ and the state transition matrix  $M_{s_t,s_{t+1}}$  which is a square matrix with rows





Figure 4.1: Movement model used to simulate data. Fish enter the movement pool at the length-dependent movement rate  $\mu_l$  from the nursery area then divide into areas 2 and 3 with the proportion  $\mu_2$  going to area 2,  $1 - \mu_2$  going to area 3, and  $1 - \mu_1$  staying in the nursery area.

 $s_{t+1}$  and columns  $s_t$  with elements survival rate  $\phi$  and movement probabilities  $\mu_s$ . Taking  $P(s_t|Y_t)$  as a column vector with rows for each state,

$$P(s_{t+1}|Y_t) = M_{s_t,s_{t+1}}P(s_t|Y_t).$$
(4.23)

The transition probability of going from any location state to the dead state is simply  $1 - \phi$ , and from the dead state to the dead state 1.

#### 4.2.6 Movement Model

There is considerable flexibility to model complicated movement patterns using the above methodology. Since the partial objective of this study was to simulate the estimation of growth and movement parameters for a stock with a spatial structure like that described in Chapter 2 and for simplicity, I simulate a stock with two life history types: a moving type which undergoes a single length-dependent movement from the nursery area, and a resident type that remains in the nursery area its entire life (Fig. 4.1). Fish are assumed not to return to nursery area after dispersing. For convenience I subscript each area according to Fig. 4.1. The proportion of fish at length l in site sis  $\psi_{l,s}$ . I assume this probability to be the product of the total proportion at length leaving the nursery area  $\mu_{l,1}$  and a length dependent movement probability function assumed to be normally distributed, with mean length at movement  $l_{\mu}$  and standard deviation  $\sigma_{\mu}$  so that the predicted proportion at length in the nursery area is:

$$\psi_{l,1} = (1 - \mu_1)(1 - \frac{1}{\sigma_\mu \sqrt{2\pi}} \int_0^{l_{max}} exp\left[-\frac{(l_\mu - l)^2}{2\sigma_\mu^2}\right] dl)$$
(4.24)

The proportion at length in site 2 is  $\psi_{l,2} = (1 - \psi_{l,1})\mu_2$  and  $\psi_{l,3} = \psi_{l,2}(1 - \mu_2)$  for site 3. For example, with the total proportion moving  $\mu_n$  set to 0.70 and  $\mu_2$  set to 0.5 the predicted proportion at length in all areas is illustrated in Fig. 4.2.

Because any length-dependent movement will also affect the length-age structure in each site,  $\psi_{l,s}$  terms for site must be included to the predicted proportions at length and age in Eq. 4.13 and Eq. 4.2.

In the movement case, Eq. 4.13 becomes

$$pr_{l_{c,s}} = \psi_{l,s} v_l N_a \frac{1}{f(a)\sqrt{2\pi\sigma_{\infty}^2}} e^{(L_{\infty,i} - L_{\infty})/2\sigma_{\infty}^2}$$
 (4.25)

and Eq. 4.2

$$p_{l,a,s} = \frac{\psi_{l,s} v_l N_a P(l|a)}{\sum_l \sum_a \sum_s \psi_s v_l N_a P(l|a)}.$$
(4.26)

so that the likelihood  $L_2$  (Eq. 4.8) becomes

$$\log L_{m2} = \sum_{s} \sum_{l_{c,s}} \sum_{l_{r,s}} n_{l_{c,s},l_{r,s}} log[\sum_{l} \sum_{c} \sum_{s} pr_{l_{c},s} h(l_{c,s},l_{r,s}|a,l,s)]$$
(4.27)





Figure 4.2: Proportion of the population in each area as a function of length  $\psi_1$ , in area 2 (red,  $\psi_2$ ) and 3 (green  $\psi_3$ ).

and  $L_1$  (Eq. 4.1) becomes

$$\log L_{m1}(n_{l,a,s}|\Theta) = \sum_{l} \sum_{a} \sum_{s} n_{l,a,s} \ln(p_{l,a,s})$$
(4.28)

#### 4.2.7 Combined Likelihoods

The way movement is modeled here requires that growth, mortality and movement likelihoods be combined. With practical sample sizes, length-age or size-at-capture and recapture data do not contain enough information to estimate the parameters of the movement probability function (Eq. 4.24). Also, the survival likelihoods (with or without movement) require either assumptions, or estimates of growth to estimate the capture probabilities using Eq. 4.18 (since  $v_l$ 's are needed) and obviously the length-dependent movement probability function (Eq. 4.24).

These formulations have considerable flexibility with respect to how survival and mortality are modeled. The estimate of M in the growth likelihoods (Eqs. 4.1 and 4.8) assumes stable recruitment. I test how robust Eq. 4.8) is to this assumption below. Survival and movement may be modeled as time dependent  $\phi_t = e^{-M\Delta t}$  at fine scale (at each time step in the mark-recapture experiment), as distinct for the marked cohort, or assumed the same as the historical M that gave rise to the age structure represented in Eqs. 4.1 and 4.8.

Since part of the purpose of this study was to explore if a combined tag-loss/tag-mortality parameter can be estimated without dual marking, I

assumed that the natural mortality experienced by the marking cohort(s) M was the same as the M that gave rise to the age structure so that the difference in the apparent mortality experienced by the marked cohort must be due to a combined tag-loss/tag-mortality term.

### 4.2.8 Simulation Stock-Assessment Using Combined Likelihoods with No Movement

I tested the performance of the likelihoods using simulated data. The likelihood used for the length-age data ( $L_1$  Eq. 4.1) was tested extensively in chapter 3;  $L_3$  for survival data has also been used and tested extensively (reviewed in Lebreton et al. (1992)) and Eq. 4.20 likewise for animal movement (Jonsen et al., 2003, 2005) so their individual performance was not evaluated here. I tested: the performance of the mark-recapture likelihood for growth increments (Eq. 4.8) across a range of recruitment and measurement error values; and the ability of the combined likelihoods (Eq. 4.1, 4.8, and 4.16) to capture tag-loss in simulated data with and without supplimentary length-age data. I explored the following scenarios:

- a) data generated with no tag loss and fit assuming no tag loss using only the growth increment likelihood  $L_2$  (Eq. 4.8)
- b) data generated with tag loss and fit assuming no tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17)

- c) data generated with tag loss and estimating this tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17)
- d) data generated with tag loss and estimating this tag loss using length-age (L<sub>1</sub>), growth increment (L<sub>2</sub>) and tag survival likelihoods (L<sub>3</sub>) (Eqs. 4.8, 4.17 and 4.1).

Parameter	Value	
sample size	$N_T$	1000
log asymptotic length	$\ln L_{\infty}$	$5.5 \ mm$
von Bertalanffy growth parameter	K	$0.15 \ yr^{-1}$
natural mortality	$\cdot M$	$0.2 \ yr^{-1}$
fraction of $L_{\infty}$ at half vulnerability	$l_h$	$0.5 \ mm$
selectivity slope	$\gamma$	0.1
standard deviation in length at age 1	$\lambda_1$	$16\ mm$
age standard deviation scalar	$\lambda_2$	0.5
tag loss	$t_l$	$0.3 \ yr^{-1}$
measurement error	$\sigma_m$	$5 \ mm$ .

Table 4.2: Parameters used to generate fake data for combined likelihoods

I ran three sets of simulations for the combined likelihoods with parameter values listed in table 4.2.8. For the first, recruitment variation was assumed to be 0, measurement and ageing error set to zero and tag loss set to 0.3. For the second set, I included variation in past recruitment anomalies as log-normal process error with a mean of zero and standard deviation of 1 multiplied by a coefficient of variation  $CV_R$  of 0.2, and measurement error of 5 mm. For the final series, ageing error was included in the simulated length-age data (see below).

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Ageing error may be either measurement error due to structures showing different numbers of annuli (Beamish and McFarlane, 1983) or error arising from the subjective assignment of rings on structures to annuli. The former is generally not normally distributed, and instead tends to be negatively biased, resulting in under-ageing of older fish (Campana and Thorrold 2001, Shayne MacClellan Department of Fisheries and Oceans. Nanaimo. Canada. *pers. comm.*). This error structure occurs because the first spawn often appears as a check on the otolith when fish stop growing. Under-ageing is very common. Since the amount of tissue laid down on each ear bone gets smaller with age, many annuli can be compressed together. If the otolith is sectioned along the short axis, these compressed rings may appear as a single ring. Furthermore, the preparation of otoliths for reading usually involves burning them so this same outer layer can be completely charred during this process.

I modeled the simulated ageing error accordingly, assuming readers correctly estimated ages with a certain probability C of being correct where the correct age is estimated and otherwise making a normally distributed error with mean size  $\alpha * a$  and standard deviation 0.1 \* a. I modeled  $\alpha$  as a sigmoidal function (Fig. 4.2.8) having a positive domain at ages under some inflection age  $a_i$  and a negative domain for older fish so that:

$$\alpha = e^{\frac{a_i - a_{..}}{1 + e^{a_i - a_{-0.5}}}} \tag{4.29}$$



Figure 4.3: Plot of  $\alpha$  used to simulate ageing error

and the estimated age  $\hat{a}$  in the simulated data:

$$\hat{a} = N \ (\alpha a, 0.1a) \tag{4.30}$$

where  $\hat{a}$  was a normally distributed random number with mean  $\alpha * a$  and standard deviation 0.1 \* a. For simulations C = 0.7 and  $a_i = 8$ .

I initially simulated data with 1000 length-age and mark-recapture samples. The capture probabilities at all time steps in the simulated data were set to 0.2. For subsequent simulations without varying annual recruitment (and hence estimates of growth and mortality), and with measurement and/or ageing error the simulated number of marked fish was 300. This was done to explore more realistic sample sizes, and also for computational efficiency. Calculating  $L_2$  is computationally intensive because of having to integrate across ages, lengths (Eq. 4.8) and measurement errors ( $\sigma_o$ )(Eq. 4.9). This issue is not trivial, the number of function evaluations of Eq. 4.8 needed for each simulation trial is a multiple of the number of observations, ages, length-bins, and the range of measurement errors.

# 4.2.9 Simulation of growth parameter estimates with length-dependent movement

Given the difficulty of marking small fish in mark-recapture programs, it is not practical to model, or even attempt to characterize any size-dependent movement process of juvenile fish. Nevertheless such movement will have an

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effect on the size-age structure where sampling is limited to either nursery or outlying areas. I explored potential biases from using the length-age likelihood (Eq. 4.1) when each area is treated as an independent stock having its own growth and mortality parameters. The main purpose of these simulations was to determine whether or not it is necessary to model all of the movement dynamics in order to correctly estimate growth and mortality parameters. For computational efficiency I chose Eq. 4.1 for these simulations.

# 4.2.10 Effects of Gear Selectivity and Capture Probability on Mortality and Movement Parameters

When there are mark-recapture data available, movement rates may be estimable. Two things are required to do so: fish must be captured and marked at sizes small enough that such movement can be detected (the ratio of the length at half selectivity to the gear to the mean length at which movement takes place  $l_h/l_{\mu}$  small), and they must be recaptured in sufficient numbers (high capture probability). I therefore tested the performance of Eq. 4.20 across a range of capture probabilities and ratios of mean length at movement  $l_{\mu}$  to the length at half selectivity to the gear  $l_h$  ( $l_{\mu}/l_h$ ). For these simulations I set the reference model  $l_{\mu} : l_h$  to 0.16, 1.16 and 1.83 and capture probabilities  $p_t$  at all time steps equal to 0.05, 0.35 and 0.55. I ran 100 simulations of for each combination of  $p_t$  and  $l_{\mu} : l_h$ .

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Growth parameters were estimated using Eq. 4.13 assuming no measurement error and variation in past recruitment anomalies was included as log-normal process error with a mean of zero and standard deviation of 1 multiplied by a coefficient of variation  $CV_R = 0.2$ . Each simulated dataset consisted of a single marked cohort of 1000 (the approximate total number marked in Dad's and Moose Pasture lakes over the summer of 2001) individuals marked in the nursery area, with recapture sampling occurring every 2 months for two years.

### 4.3 Results

#### 4.3.1 Estimation Trials with No Movement

Estimates of growth parameters were unbiased and with low variance when large datasets (1000 growth increment observations) were simulated with no recruitment variability, no tag loss and neither measurement nor ageing error (Fig. 4.4 (a)).

When data were generated with tag loss  $(t_l)$ , but it was not estimated, M was positively biased. The growth increment data predicted the correct M and the addition of the  $L_3$  term to the total likelihood dragged the estimate of M up by 15 % (Fig. 4.4 (b)).

The models were not robust to violations in the assumption of stable recruitment or to smaller mark-recapture cohorts. Even small annual variability in recruitment ( $CV_r = 0.2$ ) caused high variance in growth and mortality



Figure 4.4: Boxplots of proportional bias ((true - estimate)/true) of 100 growth and mortality parameter estimates for scenarios a) data generated with no tag loss and fit assuming no tag loss using only the growth increment likelihood  $L_2$  (Eq. 4.8), b) data generated with tag loss and fit assuming no tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17), c) data generated with tag loss and estimating this tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17), and d) data generated with tag loss and estimating this tag loss using length-age  $(L_1)$ , growth increment  $(L_2)$ and tag survival likelihoods  $(L_3)$  (Eqs. 4.8, 4.17 and 4.1) with  $CV_R = 0$ , no measurement or ageing error.

parameters when only the mark-recapture data were used (Fig. 4.5 panels a, b, and c). Due to high covariance of parameters, poor estimates of one resulted in poor estimates of the others. When tag loss was not fit (Fig. 4.4 (b)) but data generated with it, M was positively biased but the estimates of the growth parameters  $L_{\infty}$  and K were also biased. This bias was reduced when tag loss was fit (Fig. 4.5 c), but only marginally. The addition of length-age data reduced the bias and the variance of parameter estimates considerably (Fig. 4.5 d) but only when ageing error was zero.

The ability of the length-age data to compensate for measurement errors (in  $L_2$ ) in the combined likelihood was compromised when aging error was included. Because of the function that was used to generate the ageing error, (the tendency of young fish be over-aged and older fish to be under-aged) M was positively biased (there were few "observations" of old fish) and K negatively biased.

The parameters used to describe the variance in length at age ( $\lambda_1$  and  $\lambda_2$ ) were poorly estimated all scenarios except the first where there was no recruitment variation and large sample size. With few growth increment samples, there was little information about the distribution of lengths at each age.

In general  $\lambda_1$  and  $\lambda_2$  were the most sensitive to data simulated with measurement error. There were also the most poorly behaved during fitting, often resulting in the models failing to converge. This was also the case for estimates of  $CV_{la}$  when  $\sigma_a$  was defined more simply as a product of length at



Figure 4.5: Boxplots of proportional bias ((true - estimate)/true) of 100 growth and mortality parameter estimates for scenarios a) data generated with no tag loss and fit assuming no tag loss using only the growth increment likelihood  $L_2$  (Eq. 4.8), b) data generated with tag loss and fit assuming no tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17), c) data generated with tag loss and estimating this tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17), and d) data generated with tag loss and estimating this tag loss using length-age ( $L_1$ ), growth increment ( $L_2$ ) and tag survival likelihoods ( $L_3$ ) (Eqs. 4.8, 4.17 and 4.1) with  $CV_R = 0.2$ , no ageing error, measurement error= 5mm.



Figure 4.6: Boxplots of proportional bias ((true - estimate)/true) of 100 growth and mortality parameter estimates for scenarios a) data generated with no tag loss and fit assuming no tag loss using only the growth increment likelihood  $L_2$  (Eq. 4.8), b) data generated with tag loss and fit assuming no tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17), c) data generated with tag loss and estimating this tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17), c) data generated with tag loss and estimating this tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17), and d) data generated with tag loss and estimating this tag loss using length-age ( $L_1$ ), growth increment ( $L_2$ ) and tag survival likelihoods ( $L_3$ ) (Eqs. 4.8, 4.17 and 4.1) with  $CV_R = 0.2$ , ageing error, measurement error= 5mm.

age and a coefficient of variation in length at age  $(l_a C V_{la})$ . In some cases, the simulated data could best be explained by making the variance in length-atage very large. Though fixing these parameters always improved the stability of the model it only improved the bias in parameter estimates significantly for scenario d). (Fig. 4.7).

## 4.3.2 Simulation of growth parameter estimation with length-dependent movement

When each area was treated as a separate stock while the simulated data came from a stock with ontogenetic movement from area 1 to area 2, the main effect was that growth parameters were unbiased but gear selectivity parameters ( $l_h$  and  $\gamma$ ), and M were biased (Fig. 4.8). In areas 2 and 3 the model 'saw' the failure to observe small fish as a gear effect, so  $l_{h_2}$  and  $l_{h_3}$ had mean proportional biases of 200%. This was the 'correct' interpretation of gear selectivity in any case, since overall selectivity can be viewed as the product of both the gear effects and spatial distribution effects. The small fish did not appear vulnerable to the gear because they were not there. Movement out of area 1 (the nursery area) appears as a mean 50 % bias in estimates M.

The von Bertalanffy growth parameters were unbiased across a range of smaller  $l_{\mu}$  values but once  $l_{\mu}$  became large, the bias in M grew large or the model often could not converge at all. In the nursery area, M was confounded



Figure 4.7: Boxplots of proportional bias ((true - estimate)/true) of 100 growth and mortality parameter estimates for scenarios a) data generated with no tag loss and fit assuming no tag loss using only the growth increment likelihood  $L_2$  (Eq. 4.8), b) data generated with tag loss and fit assuming no tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17), c) data generated with tag loss and estimating this tag loss using the growth increment  $L_2$  and tag survival likelihoods  $L_3$  (Eqs. 4.8 and 4.17), and d) data generated with tag loss and estimating this tag loss using length-age  $(L_1)$ , growth increment  $(L_2)$ and tag survival likelihoods  $(L_3)$  (Eqs. 4.8, 4.17 and 4.1) with variance in length at age parameters ( $\lambda_1$  and  $\lambda_2$  fixed at their true values)

by an apparent dome-shaped gear selectivity process (due to movement).

M was over-estimated in the nursery area, where fish movement to outlying areas increased the apparent mortality. This bias decreased as the total proportion remaining in the nursery area  $\mu_n$  increased and as the ratio of  $l_h/l_\mu$  increased. When the total proportion moving  $\mu_1$  was high, the bias in the nursery  $M_1$  was also higher but it depended also on the ratio of  $l_h$  to  $l_\mu$ and on  $\sigma_{\mu}$ . If movement was complete at sizes smaller than the gear was capable of detecting (small  $l_\mu$  and  $\sigma_\mu$ ), then there was little bias in the samples taken from each area. When the simulated gear was able to capture smaller and smaller fish, the samples at young ages became increasingly distorted, and the bias in M grew proportionately larger in the nursery area.

## 4.3.3 Effects of Gear Selectivity and Capture Probability on Mortality and Movement Parameters

Across a range of capture probabilities and gear selectivity values, M was well estimated (Fig. 4.9) for models that included movement. Variance in estimates of M increased as capture probability decreased, but the bias was negligible (1-3 %) and negative. However, the parameters that defined movement were only well estimated in those cases where capture probabilities were relatively high (greater the 30 %) and where  $l_h/l_{h\mu}$  was approximately 1. ÷



Figure 4.8: Boxplots of proportional bias ((true - estimate)/true) of 100 growth  $(L_{\infty}, K, \lambda_1, \lambda_2)$ , mortality (M), length at half gear selectivity  $(l_h)$ , and gear selectivity function slope  $(\gamma)$  parameters when each area is assumed to be separate stock, while simulated data come from a stock with ontogenetic movement from area 1 to areas 2 and 3.

There are several important caveats. Even with relatively high capture probabilities,  $l_h/l_{h\mu}$  set to 0.16 and 1000 fish marked, the number of marked fish that actually move over a two year period is relatively small (approximately 160) and those tagged fish are distributed between two areas. So, even with relatively high capture probabilities, the number of observations that can be used to define the movement parameters is small even when a large proportion of the population is leaving the nursery area (70%). When  $l_h/l_{h\mu} = 1.16$ , the number of marked fish that are actually observed moving is much smaller (approx. 15-20). In the case of high  $l_h/l_{h\mu} = 1.83$ ,  $\mu_2$  is not estimable at all, or correctly estimated to be small, because there should typically be no observations of fish going to that area. Additionally, here again I assumed the same M for the marked cohort and the historical age structure sample so the estimated value of M is robust to lower capture probabilities in ways it would not otherwise be had the only information about M been from the mark-recapture data. Finally, regardless of whether or not parameters defining length-dependent movement can be estimated, admitting the possibility of movement in the model makes a big difference to variance of the estimate of M, since many combinations of capture probability and natural mortality can explain the observed data.



Figure 4.9: Boxplots of proportional bias ((true - estimate)/true) in 100 estimates of M and movement parameters with capture probability (rows) set to 0.05, 0.35, 0,55 and with ratio of length at half gear selectivity to the mean length at movement  $l_h/l_\mu$  set to 0.16, 1.16 and 1.83.

### 4.4 Discussion

The suite of growth, survival and movement likelihoods I presented here permit simultaneous analysis of several processes using data commonly collected in many applied ecology programs. This is particularly useful because these parameters are nearly always of interest in applied ecology but also because both biological and observation processes mean these parameters must be estimated together.

Consistent with the observations of Eveson et al. (2004), different types of data contain more information about some processes than others. For example, only with very large sample sizes (greater than 100 000) could the length-age data be used to estimate movement rates using simulated data. The problem is that using practical sample sizes, estimating M using lengthage data requires estimates of movement rates, and likewise, if movement rates are a function of size, then correct estimates of growth are also required. One potentially serious problem with combining all data together is that some data may bias parameter estimates due to improperly modeled effects (for example mark-recapture data with a lot of measurement error, assumed to have none). More data and more complicated likelihoods do not necessarily mean better parameter estimates, therefore the processes used to collect such data should be examined very carefully.

Rather than assume small measurement and ageing errors as well as convenient distributions for such errors, I have tried to simulate the performance of the likelihoods under the worst rather than best situations. The biases in parameter estimates shown here are therefore conservative, and worse than might be expected in many mark-recapture and/or ageing programs.

Measurement error tends to bias growth parameter estimates disproportionately in smaller, slower growing fish. In this analysis, measurement error was set at 5 mm because in the field large measurement errors occur when fish tails are damaged from spawning, or when larger rule increments are mis-read (fish length is recorded as 235 rather than 230 mm for example). It is instructive to think of the measurement error relative to the annual increment of the fish. In the simulations performed here a 5 mm measurement error is larger than the annual increment of fish greater than age 12, less than half the maximum age.

The magnitude and direction of the simulated ageing error was considerable. The choice of such a function to represent this error was based on the review of Campana (2001) who shows that very few ageing programs validate their ageing correctly or even at all. Much ageing can reasonably be assumed correct, or to have normally distributed error purely from counting. However, the reality of most stock assessment programs is that all these sources of error are present and there are systematic biases towards under-aging older fish.

It is unreasonable to assume mark-recapture programs for size and fish survival are not subject to some violation of assumptions about constant recruitment, lack of measurement error, no tag-loss etc. Therefore, the choice

of methods for estimating growth parameters using mark-recapture is a choice between the least of evils. On one hand, traditional methods ignore natural mortality, gear selectivity and measurement error altogether. Methods such as Laslett et al. (2002) and Eveson et al. (2004) do not account for sizeselectivity, so over-estimate K and  $L_{\infty}$  of the total population, an issue that is irrelevant if the stock assessment scientist wishes only to describe the growth of the population being harvested. On the other, the method I developed here is data intensive, means tolerating at least a 5 - 10% bias in K and poorly estimated parameters describing the variance in length-at-age. However, the direction of the bias in K and M is the most conservative. Stock assessments using underestimates of K and M predict smaller than actual yield-perrecruit and current biomass. Further, the bias does not matter if the objective is simply to compare the growth of one stock to another.

Combining length-age, growth increment and mark-recapture data can only be used to estimate of tag-loss when recruitment is reasonably constant over time. In cases where recruitment is variable, noise caused by the recruitment variation makes M unstable, hence unreliable as a resource base for detecting tag-loss. Also, since the M of the population is what is of interest in some cases, making such an assumption defeats the purpose of doing the mark-recapture in the first place. However there is a considerable literature developing for estimating tag-loss (Ebener and Copes, 1982; Pierce and Tomcko, 1993; Swanson and Schram, 1996; McGlennon and Partington, 1997; Julliard et al., 2001; Feldman et al., 2002; Rikardsen et al., 2002; Brattey and Cadigan, 2004) so such information could be used to generate priors for the tag-loss. But none of this literatures addresses problems with long-term tagging mortality or tag under-reporting. Admitting a range of possible tag-loss values is important for properly admitting uncertainty about mortality estimates since the trade-off between tag-loss and mortality is one-to-one and uncertainty about what the true tag-loss is propagates through the estimates of all the other parameters.

Assuming that constant recruitment so tag-loss can be estimated is obviously incorrect. Nevertheless with external tags it is better than making the still worse assumption of no tag-loss, no under-reporting, and no tagmortality. This is particularly true when external tags are used. Where the magnitude of the tag-loss/tag-mortality is large, the bias in M (and the corresponding positive bias in estimates of the population size where applicable) produced by such assumptions failing is considerable and also in the least conservative direction (over-estimating M and hence the population size). For example, tag-loss for dart tags has been reported by McGlennon and Partington (1997) at  $0.0006d^{-1}$  and for anchor tags at  $10 - 20\% yr^{-1}$ (Ebener and Copes, 1982). Even in the case of internal tags, passive induced transponder tag (PIT) failure has been reported in sharks as high as  $12\% yr^{-1}$ (Feldman et al., 2002). These biases are also in the least conservative direction with respect to exploitation rate predictions. Estimating higher that actual natural mortality means predicting higher than optimal exploitation rates.

The simulations were unrealistic in assigning fixed nursery and non-nursery boundaries. When stocks have such a spatial structure, fishing and survey sampling are likely to overlap each area to a certain extent. Nevertheless a number of fisheries are divided along similar lines with an onshore sector targeting younger fish and an offshore sector targeting different fishes, e.g. Pacific Hake or Yellowfin tuna. In such situations separate gear and spatial effects need to be considered for data coming from each fishing sector in any case (onshore, offshore etc.), because in addition to spatial effects, the gear used also differs.

This is not the first paper to use the state-space methods like De Valpine and Hastings (2002) with mark-recapture data. Rivot et al. (2004) used this method and mark-recapture data to estimate upstream migration of adults and downstream migration of juveniles in Atlantic salmon. Clark et al. (2005) use a hierarchical Bayesian model to estimate maturation age, survivorship, and population growth in simulated and real data, and Jonsen et al. (2003) used state space approaches to combine information from multiple individual movement trajectories with missing data. Finally state space methods have been used to estimate growth parameters for physiologically based individual growth models with size trajectory data (Fujiwara et al., 2005). The method used in this study is not fully a state space formulation because of the predicted growth trajectories are modeled deterministically using the von Bertalanffy growth model, but it is the first to combine growth information with movement data to estimate a size-dependent movement function. Unfor-

tunately the models presented here require a lot of data, (several 100 marked and recaptured fish, approximately 1000 length-age observations, and in the case of movement several marked fish observed to have moved) and are not robust to either measurement or ageing error.

Since datasets used to measure growth and mortality may not contain enough information to estimate parameters such as gear selectivity and mortality, integrating the information from all available data sources to estimate growth parameters should be expanded to the entire stock assessment process for many commercial fisheries. Stock assessments typically contain information about the fishing mortality and gear selectivity and often have many years of length-age, or length-frequency or mark-recapture data. Several years of this data could be incorporated into multiple length-age and markrecapture tables to track changes in natural mortality and growth over the time of a fishery.

# Chapter 5

# Predicted and Observed Ecosystem Responses to Fishing

### Abstract

I used a simple ecosystem model and compared the predictions to observed responses following experimental fishing in a two fish lake system with rainbow trout and northern pikeminnow. Consistent with the model's predictions, growth and mortality of juvenile rainbow trout was higher relative to the control in lakes where northern pikeminnow were removed while adult rainbow trout survival remained unchanged. Visual survey indices of northern pikeminnow fry indicated survival of 1+ fish worsened and 2+ improved following fishing. Consistent with the model's predictions no obvious mortality or growth responses were observed in northern pikeminnow. While the agreement between the model and observations was encouraging, field testing such a hypothesis was fraught with difficulty. The probability distributions of the parameters of interest were very broad and the model predicts many of the important dynamics, in particular behavior mediated vulnerability exchange rates, to occur in fish size classes and groups of zooplankton that are difficult to observe.

keywords: non-target species response to fishing, cultivation-depensation,

northern pikeminnow, movement mortality estimation

### 5.1 Introduction

Juvenile survival is usually assumed to improve at low stock size so as to make recruitment much more sensitive to stock size than would be the case if survival were constant. There is good evidence to support this assumption (Myers et al., 1999, 1995b). Given the failure of a number of overexploited stocks (Shelton and Harley, 1999) to recover following collapse, there has recently been considerable concern about whether or not recruitment decreases at low stock size (depensation). Myers et al. (1995b) concluded that only 3/128 stocks showed significant depensation. Nevertheless, considerable work followed their analysis with particular attention devoted to determining whether or not models parameterized with depensation fit the data better than those without it (Liermann and Hilborn, 1997, 2001) and if depensation could be detected at all in complexes of multiple 'sub-stocks', each with differing productivites (Frank and Brickman, 2000). In all these cases, the depensatory dynamics were assumed stationary in a statistical sense, where the parameters describing the relationship are assumed time-invariant.

Changes in ecosystem productivity and the process of fishing itself likely alter recruitment dynamics of fish stocks over time, since they alter food and predation regimes. Foraging arena theory (Walters and Juanes, 1993; Walters and Korman, 1999) predicts that as the ratio of predation risk to food production changes over time, then so too will recruitment. Abrupt ecosystems state transitions have been observed in aquatic systems (Scheffer

et al., 2001b; Scheffer and Carpenter, 2003). Walters and Kitchell (2001) postulate a specific hypothesis termed "Cultivation-Depensation" explaining how such shifts might happen in response to fishing, and what observations should be observed in the field if they are. If their explanation is correct, the cultivation-depensation hypothesis is that if a dominant stock is reduced, there will be a reduction in the extent to which it "cultivates" more favorable conditions for its juveniles by reducing abundance of competitors and predators.

Cultivation-depensation effects arise in Ecosim II (Walters et al., 2000) models though the following sequence of events (Walters and Kitchell, 2001). Fishing reduces the adult population size of a fish species and hence, the total number of juveniles in predation refuges. Juveniles reduce feeding time or time spent at body sizes small enough to be vulnerable to predation risk. Juvenile mortality then decreases so that the net number of recruits stays nearly constant even though fewer juveniles are being produced. However, if there is predation between the adult fish and a predator or competitor of the juveniles (a "forage" fish) then as adult density is reduced, the forage fish is released to increase in abundance. Then one or two negative effects can occur. If the forage fish prey directly on juveniles, then predation mortality is directly increased. If the forage fish and juveniles are competitors, increased forage fish abundance leads to reduced food density and hence, increased juvenile foraging time and general predation risk. These dynamics can be represented with a trophic triangle such as that in Fig. 1.1.

I used field data collected in 2001-2003 to constructed a simple ecosystem model of small lakes in northern British Columbia Canada (see Section 2.2.1) using Ecopath with Ecosim (Walters and Christensen, 2004). These lakes had two predatory fish species, rainbow trout (*Onchorhynchus mykiss*) and stunted northern pikeminnow (*Ptychocheilus oregonensis*). The study system had the foraging arena structure described above with juvenile rainbow trout and northern pikeminnow (in all age classes) confined to the margins of the lake during the day (Section 5.2.2), whereas adult rainbow trout were distributed mainly in the center of the lakes.

I sampled in the system and measured the growth and survival response of the two fish communities to depletion fishing (where a large proportion of the population was fished in a short series of fishing bouts) of both rainbow trout and northern pikeminnow. I found that consistent with model predictions, survival and growth of small rainbow trout decreased in lakes where northern pikeminnow were removed and that no changes in growth or survival for adult adult northern pikmeinnow could be detected and it was not possible to estimate growth and survival parameters due to low sample sizes for adult rainbow trout.

### 5.2 Methods

#### 5.2.1 Ecosim Model of Predicted Observations

The details of the Ecopath-Ecosim modeling approach are discussed extensively in Walters et al. (1997, 2000) and Walters and Christensen (2004) so will only be briefly discussed here. Ecopath is used to define the initial ecosystem biomass state that is mass-balanced, i.e. where estimated total biomass loss rates  $z_i$  for each modeled biomass group i are partitioned among assumed static predation rate components and unaccounted losses. In Ecosim models, these static flows are turned into dynamic, time-varying predictions by assuming that flows C from prey i to predator j groups are mediated by vulnerability exchange rates  $v_{i,j}$  between "vulnerable" and non-vulnerable prey pools (Walters et al., 2000):

$$C_{i,j} = \frac{v_{i,j}a_{i,j}B_iB_j}{v_{i,j} + v'_{i,j}a_{ij}B_j}$$
(5.1)

where  $a_i$  is the effective search rate of predators, B the biomass and  $v'_{i,j}$ the exchange rate from the vulnerable pool back to the non-vulnerable pool, assumed to be equal to  $v_{i,j}$ .

The vulnerability exchange rates  $v_{i,j}s$ 's determine the rate at which prey enter either a vulnerable state j (which is available to be eaten by predators) from an invulnerable state i (assumed not to be vulnerable to predators). These dynamics are assumed to occur on a much faster time scale than other
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population dynamics such as predation and mortality (Walters and Juanes, 1993; Abrams and Walters, 1996) and thus reach an equilibrium vulnerable pool of prey V that is available to predators (Walters et al., 1997). The behavioral interpretation of what  $v_{i,j}$ 's are can best be thought of as any behavior (avoidance, fish schooling, habitat refuges etc.) that limits the access of the prey to the predators. Small  $v_{i,j}$ 's mean that a lower proportion of the total prey population is in the vulnerable state at any given time, and vice versa. These rates therefore have a very large influence on the population dynamics predicted by Ecosim. Small  $v_{i,j}$ 's imply a lot of foraging arena structure (Walters and Juanes, 1993), whereas large rates imply classical type II (Holling 1959) predation dynamics.

Overall biomass was simulated for pelagic zooplankton, chaoborus larvae, benthos, phytoplankton and detritus since data to estimate these were unavailable. Simplification of the system into these groups was done to allow a focus on specific hypotheses about size-dependent predation and competition interactions involving the two fish species. Chaoborus larvae were singled out as a particularly important group because they are the main diet item of (70%) of pikeminnow but were virtually absent in rainbow trout stomach contents. Pikeminnow undergo daily offshore migrations that are concurrent with the nightly rise of chaoborus (Table 5.2.1, Dave O'Brien *unpublished data*). The diet matrix was parameterized using stomach content data collected over 2001 and 2002 (Dave Obrien *unpublished data*).

I used the multi-stanza approach (Walters and Christensen, 2004) for

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modeling fish species in the system, with parameters listed in Table 5.2.1. The multi-stanza version of Ecosim allows for the division of a species into age-size groups (stanzas) assumed to share similar mortality and diet composition. It assumes growth follows the von Bertalanffy (von Bertalanffy, 1934) growth curve. To initialize the population stanza age structure, it is assumed that recruitment and mortality have been stable for long enough for the population to be at a stable age distribution. Leading values for mortality are needed for all stanzas, while annual consumption per unit biomass Q/B and biomass are needed for one leading group. The biomass and Q/B of the remaining groups are calculated using age-dependent weight  $w_a$  and survivorship  $l_a$ . The initial population growth corrected proportion of a fish  $l_a$  is modeled in Ecopath as:

$$l_a = e^{-\sum_a Z_a - aBA/B} \tag{5.2}$$

where Z is this case is the instantaneous annual natural mortality (in years  $yr^{-1}$ ) The  $l_a$  for any given age is the sum of Zs is over all ages up to a, and BA/B term represents the effect on relative numbers at age of the population growth rate (Walters and Christensen, 2004).

The relative biomass of other stanzas relative to the leading stanza is initialized using relative biomass proportions  $b_s$ , where for any stanza s:

$$b_s = \frac{\sum_{a=a_{s,\min}}^{a_{s,\max}} l_a w_a}{\sum_{a=1}^{a_{\max}} l_a w_a}$$
(5.3)

(Walters and Christensen, 2004). The relative weights at age  $w_a$  are assumed to follow the von Bertalanffy prediction:

$$w_a = (1 - e^{Ka})^3. (5.4)$$

where K is the von Bertalanffy growth parameter estimated for both fish species using the methods described in Section 5.2.6. Q/B estimates for non-leading stanzas are calculated with a similar approach, assuming that feeding rates vary with age as the 2/3 power of body weight (Walters and Christensen, 2004). Consumption per unit biomass ratios for oldest stanza's were assumed to be 1.5 for northern pikeminnow and 5 for rainbow trout.

I divided northern pikeminnow (NPM) in age into 4 life-history stanzas denoted by the age a at which the stanza began. This stanza division was chosen since northern pikeminnow are markedly different in sizes for only the first four years. Rainbow trout (RBT) were divided into two stanzas, 0-1 and 2+ years.

Rather than parameterize the fish groups in absolute biomass, they were parameterized relative to each other. Where the biomass of the 4+ northern pikeminnow and the 2+ rainbow trout were assumed equal they were both set to 1. Ecopath was used to calculate invertebrate biomasses needed support the base estimated consumption rates caused by these relative biomasses, assuming reasonable ecotrophic efficiencies (Table 5.2.1, ecotrophic efficiency is proportion of  $Z_i$  explained by modeled predation).

Start Age $yr^{-1}$	Relative Biomass	Instantaneous Natural Mortality ( $Z yr^{-1}$ )	Consumption per unit biomass $yr^{-1}$
Northern pikeminnow			
1	0.002	3	13.033
2	0.009	0.5	5.362
3	0.022	0.3	3.5
4+	1	0.2	1.5
Rainbow trout			
0	0.061	3	16.491
2	. 1	0.7	5

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Table 5.1: Parametersformulti-stanzarepresentationofnorthernpikeminnow and rainbow trout populations

I predicted changes in mortality, body growth, population size and feeding time following a very short pulse of intense 'depletion' fishing F = 1applied for one year. I explored the sensitivity of the model to a range of vulnerability exchange rates  $(v_{i,j})$  for the fish and zooplankton groups. I explored how differences in relative fish biomass and vulnerability exchange rates the model would or would not produce Cultivation-Depensation effects, and in particular two equilibria with only one fish group dominant at each. In search for parameter combinations that would produce multiple equilibria, the two fish biomasses were set to 1.0, so as to represent a potentially unstable equilibrium point between the two stable equilibria. When two stable states exist, any fishing disturbance tends over time to one of the biomasses being dominant.

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рі	predator, as a proportion of total annual biomass food intake										
Prey Pred	RBT 2+	RBT 1	NPM $4+$	NPM 3	NPM 2	NPM 1	Chaob	$\operatorname{Ben}$	Zoo	Phyto	Det.
RBT 2+											
RBT 1			0.049	0.02	0.091						
NPM 4	0.00001	.·									
NPM 3	0.00005										
NPM 2	0.0001		0.00049								
NPM 1				0.0005	0.009						
Chaob			0.665	0.686	0.27						
Ben	0.909	0.1	0.19	0.196	0.27	0.1					
$\mathbf{Z}$ oo	0.091	0.9	0,095	0.098	0.36	0.9	1				
Phyto								0.05	1		
Det.								0.95			
		•									

Table 5.2: Diet composition matrix for Ecopath model. Each column is the diet composition of a particular

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	Biomass	Production per unit biomass	Consumption per unit biomass	Ecotrophic efficiency	Unassimilated Consumption
		$yr^{-1}$	$yr^{-1}$		
RBT 2+	1	0.7	5		0.2
RBT 1	0.0613	3	16.491		0.2
NPM 4	1	0.2	1.5		0.2
NPM 3	0.0219	0.3	3.5		0.2
NPM 2	$0.\dot{0}0865$	0.5	5.362		0.2
NPM 1	0.0019	3	13.033		0.2
Chaob		2	6	0.8	0.2
$\operatorname{Ben}$		3	15	0.3	0.2
Zoo		5	20	0.8	0.2
Phyto		30		0.4	
Det.	100				

# Table 5.3: Basic parameter inputs for Ecopath Model

## 5.2.2 Experimental fishing

In the summer of 2001 I depletion fished two lakes called Mom's and Cheryl (see Fig. 2.1) in two separate drainages on the Bonaparte Plateau north of Kamloops in south central British Columbia. I set one lake in each drainage aside as a control (Dad's and Moose Pasture). Early observations showed northern pikeminnow are confined to the shoreline during the day but perform crepuscular migrations offshore from nearshore hiding spots. This behavior was used to selectively remove them by setting gillnets along the entire shoreline of the experimental lakes. This same behaviour was used to selectively deplete rainbow trout in Wilderness and Nestor lakes in 2001 and 2002, by setting gillnets mid-lake rather than parallel to shore (O'Brien *unpublished data*).

During June and July of 2001 northern pikeminnow depletions were conducted in two or three bouts of several (3-5) consecutive nights fishing. During each bout, the length of gillnet used was sufficient to completely surround Mom's Lake and about 80% of the perimeter of Cheryl Lake. I rotated net panels with different bar meshes around each evening to ensure each area was exposed to all meshes. Summaries of the depletion effort by date and bar mesh are compiled in Table 5.4 for Cheryl Lake and in Table 5.2.2 with a plot of the proportion of mesh sizes used in figure 5.1.

I measured the fork-length (FL) of every fish captured and sacrificed 285 from Cheryl lake and 264 from Mom's Lake for ageing.

Given the nursery structure discussed in Chapter 2, I determined after

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		Prop	ortion	or par	mesn i	Jy Chi	
Date	Total $(m)$	1.25	1.5	1.9	2.5	3.1	3.75
26-Jun-01	1200	0.06	0.06	0.08	0.57	0.11	0.11
27-Jun-01	1200	0.06	0.06	0.08	0.57	0.11	0.11
28-Jun-01	1200	0.06	0.06	0.08	0.57	0.11	0.11
2-Jul-01	1300	0.06	0.06	0.10	0.57	0.10	0.10
3-Jul-01	1300	0.06	0.06	0.10	0.57	0.10	0.10
15-Jul-01	1300	0.06	0.06	0.10	0.57	0.10	0.10
16-Jul-01	1300	0.06	0.06	0.10	0.57	0.10	0.10
17-Jul-01	1300	0.06	0.06	0.10	0.57	0.10	0.10
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Table 5.4: Total length and proportions by bar length (cm) Cheryl Lake Proportion of bar mesh by cm

Table 5.5: Total length and proportions by bar length (cm) Mom's Lake

		Proportion of bar mesh by <i>cm</i> .						
Date	Total $(m)$	1.25	1.5	1.9	2.5	3.1	3.75	
18-Jun-01	1150	0.06	0.06	0.08	0.57	0.11	0.11	
19-Jun-01	1150	0.06	0.06	0.08	0.57	0.11	0.11	
20-Jun-01	1150	0.06	0.06	0.08	0.57	0.11	0.11	
9-Jul-01	1135	0.06	0.06	0.10	0.57	0.10	0.10	
10-Jul-01	1135	0.06	0.06	0.10	0.57	0.10	0.10	
11-Jul-01	1135	0.06	0.06	0.10	0.57	0.10	0.10	



Figure 5.1: Proportion of gillnet meshes used on all depletions.

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carrying out the Cheryl and Mom's Lake depletions that in order to observe a northern pikeminnow recruitment response, a nursery lake had to be manipulated as well. In late August and early September of 2002 I fished the eastern drainage nursery lake called Moose Pasture (Fig. 2.1). Fish were captured during 6 bouts of daily fishing using 4 hoop nets. Three of these nets consisted of  $6 \ge 1 m$  fiberglass hoops covered in 1 cm mesh, 24 m center lead, and 15 m side leads. The other consisted of  $6 \ge 0.7 m$  steel hoops covered in 0.5 cm mesh, 15 m center lead, and 10 m side leads. Lapilli otoliths were taken from each northern pikeminnow and 945 of these were aged of 3682 fish caught in Moose Pasture. Using the same gear, an additional 1082 northern pikeminnow were captured and aged from Dad's Lake in September 2003.

Additional depletion fishing of rainbow trout was conducted in Wilderness Lake in 2001 and Nestor Lake in the summer of 2002 (David O'brien *unpublished data*. A map showing the lakes, and what removals (either northern pikeminnow or rainbow trout) is shown in Fig. 5.2.

#### 5.2.3 Fish ageing

To age the fish I cut Lapilli otoliths along the ventral/dorsal axis using an Isomet Bueller slow speed saw, burned and counted annuli. Otoliths too small to cut were burned and counted directly. For fish older than 5 years, failing to cut otoliths along the long axis resulted in significant under-ageing.



Figure 5.2: Map of experimental lakes showing the location of rainbow trout density reductions (RBT depletion), and northern pikeminnow density reductions (NPM depletion).

#### 5.2.4 Depletion Experiments

Population sizes and percent removal were estimated using the method outlined in Schnute (1983). The analysis consists of a population model describing the numbers remaining  $(N_t)$  and an observation model describing the predicted number caught  $C_t$ .  $C_t$  was predicted as proportion of the population removed by the fishing gear each night (q) and the numbers remaining alive at time t  $(N_t)$ :

$$N_t = N_o - \sum_{t=0}^t C_t$$

$$C_t = qN_t$$
(5.5)

The observed catches at time t in length bin l were fit to the predicted catches in Eq. 5.5 using a Poisson log likelihood. Ignoring all constants that do not depend on the estimated parameters, the poisson log probability of the data  $(C_t)$  given the estimated parameters  $(q, N_o)$  is:

$$P(C_t|N_{o,l}, q_l) \propto C_{t,l} \ln (q_l N_{t,l}) - q_l N_{t,l}.$$
(5.6)

The parameter  $q_l$  was evaluated at its conditional maximum likelihood estimate:

$$q = \frac{\sum\limits_{t} C_t}{\sum\limits_{t} \hat{N}_t}.$$
(5.7)

I used 10 mm length bins.

Since there were tagged animals in Moose Pasture Lake when depletions were conducted it was possible to use these data to estimate depletion also. I used fish marked in the two weeks preceding removals to obtain a population estimate (assuming no tag loss or mortality in that time interval). The loglikelihood was calculated as:

$$L = R_l \log(Pr_l) + U_l \log(1 - Pr_l)$$

$$(5.8)$$

where  $R_l$  is the number of recaptures at length,  $U_l$  the number of marked animals and  $Pr_l$  the predicted probability of capturing a marked animal.  $Pr_l$ was the ratio of tagged recaptures to the number of tagged fish at risk to capture (or the ratio of total captures ( $M_lU_l$ ) to total N at risk,  $N_{o,l}$ ).

It is typical in depletion experiments for each bout of several days fishing to result in an underestimate of N, due to some fish not being vulnerable during any short-term bout. I hopefully corrected for this effect by using more than one bout on each lake, and the daily catches over all bouts (Fig. 5.11) support this hope.

### 5.2.5 Visual Surveys

I conducted visual fry surveys in all study and control lakes in 2002 to confirm the presence or absence of fry and to generate a quantitative index of fry abundance. A second series of visual observations was on approximately the same dates in 2003. Due to a nearby forest fire only one set of observations was possible in 2003. The surveys were conducted on sunny days between 9:00 A.M. and 3:00 P.M. by either walking or rowing as close as possible

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along the shoreline.

Where fry were present (in Moose Pasture and Dad's lake) I recorded estimates of the number of 0+ fry, age 1+, and age 2+ northern pikeminnow observed along with the GPS positions of each school spotted. I calculated crude survival rates by calculating the ratio of the 2+ index in 2003 to the 1+ index in the previous year, and likewise the 1+ index in 2003 to the 0+index in 2002. These survival estimates are plotted for the manipulated lake (Moose Pasture) and the unmanipulated lake (Dad's) in Fig. 5.15.

### 5.2.6 Estimation of Survival and Growth Parameters

For northern pikeminnow growth, I used mark-recapture methods to measure the growth and survival responses following manipulations. At approximately weekly intervals, I surveyed all the lakes using the gear described in Section 5.2.2, recorded the fork length of all marked and unmarked animals, and marked new animals. Since the overwhelming majority of northern pikeminnow marked were greater than 90 mmFL (or approximately 4+), they are treated as a single adult "stanza" and assumed to be subject to same natural mortality. I divided marked rainbow trout into two groups: those greater or smaller than 200 mm. All data used for this analysis come from fish captured in fyke nets and marked following experimental depletions in each lake.

I estimated northern pikeminnow survival and movement parameters in the eastern and western drainage lakes using the combined likelihoods de-

Table 5.6:	Total number of marked an	d recaptured northern	pikeminnow b	y drainage,	lake and	treatment.
	NPM=northern pikeminnov	v, RBT=rainbow trout	t and dep=dep	letion		

		Number of	Total number	Total recaptures from	Treatment
Drainage	Lake	marked cohorts	marked	all cohorts/times	
	Moose	. 7	343	153	NPM dep
$\mathbf{East}$	` Cheryl	10	613	216	NPM dep
	Wilderness	. 7	580	143	RBT dep
	Dad's	11	2024	667	Control
$\mathbf{West}$	Mom 's	. 11	597	428	NPM dep
	Nestor	9	629	155	RBT dep

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roup and lake		> 200 mm	28	13	19	22	22	٥
r trout by size g otal number recaptury	in all cohorts/times	< 200 mm	60	33	53	4	67	13
red rainbow		> 200 mm	121	58	54	91	69	68
and recaptu <sup>Total number</sup>	narked by stanza	< 200 mm	210	204	388	49	278	61
of marked		> 200 mm	17	16	7	15	16	7
Total number Number of marked	cohorts by stanza	< 200 mm	18	16	30	13	14	ລ
Table 5.7:	Lake		Mocse	Cheryl	Wilderness	Dad's	Mom's	Nestor
	Drainage	size		East		-	West	

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scribed in Section 4.2.5 (Eqs. 4.20, 4.27 and 4.28). Fish marked following experimental manipulations were marked and recaptured in approximately weekly intervals, with the number of marked cohorts (groups of animals marked in any particular sampling bout), the number of fish marked in each cohort and the total number of recaptures from all cohorts at all times in each lake summarized in tables 5.2.6 and 5.2.6.

I did not assume a normal distribution of mean length at movement (Eq. 4.24) since it is restrictive about the shape of movement probability density. Instead, I represented the cumulative probability of moving at length l as the product of the maximum proportion moving from the nursery area  $u_1$  and an incomplete beta distribution. The length dependent cumulative movement probability function became:

$$\psi_{l,n} = \mu_n \int_0^l l^{\alpha-1} (1-l)^{\beta-1} dl$$
(5.9)

where  $\alpha$  and  $\beta$  are the shape parameters and  $\mu_n$  the maximum proportion moving. I set a lower bound on the parameter  $\alpha$  of 2 for fitting since at values approaching 1 it was possible for the curve to predict 100 % of fish moved before 50 mm FL.

Gear selectivity parameters (Eq. 4.3) were fixed with  $l_h = 0.45$  and  $\gamma = 0.2$  for all areas and both fish since they were not estimable. The assumed gear selectivity parameters are basically the same as those estimated by the length-age likelihood (Chapter 3 Table 3.3.1).

For rainbow trout, I assumed no structured ontogenetic movement and estimated the rainbow trout growth and survival parameters using the combined likelihoods described in Section 4.2.4. It was not possible to estimate the historical natural mortality for rainbow trout < 200 mm so I fixed these values at the mean value of the prior for natural mortality for juvenile rainbow trout where M = 1.78 (see Section 5.2.7 below).

#### 5.2.7 Prior Distributions

In all estimation procedures for both fish species I used Bayesian priors for all mortality, growth and tag-loss parameters. In the case of rainbow trout, the tag loss was a hyper-parameter and assumed shared across all the study lakes. Analysis of the northern pikeminnow data was too memory-intensive to allow parameter estimates for all six study lakes to be run at once. The analysis was done instead by drainage where tag-loss was assumed equal across the drainage.

The prior on northern pikeminnow natural mortality M and the mortality of the tagged cohorts by lake  $M_t$  was normal  $N^{\sim}(\mu = 0.30, \sigma = 0.19)$  and built from 7 estimates of natural mortality in the Columbia River (Rieman and Beamesderfer, 1990). Growth parameter priors come from 2 observations in Montana lakes and streams (Carlander, 1969; Peters, 1964) and from Rieman and Beamesderfer (1990). For  $log(L_{\infty})$  the prior was  $N^{\sim}(\mu = 6.23, \sigma = 0.1)$ and for the von Bertalanffy K parameter  $N^{\sim}(\mu = 0.14, \sigma = 0.08)$ .

The prior for age 1 rainbow trout natural mortality come from Post et al.

(1999)'s 47 observations of age 1 rainbow trout survival across a range of rainbow trout densities. This prior was normal  $N \,\tilde{}\,(\mu = 1.78, \sigma = 1.95)$ . Priors for the rainbow trout von Bertalanffy growth parameters and for adult mortality come from 7 estimates in (Ruiz-Campos et al., 1997; Pidgeon, 1981; Kwain, 1981). For K this prior was  $N \,\tilde{}\,(\mu = 0.53, \sigma = 0.1)$ , for  $L_{\infty}$  it was  $N \,\tilde{}\,(\mu = 6.0, \sigma = 0.2)$  lacking information on M, the prior for M was set to the same as for K.

The prior for anchor tag loss for both species comes from studies that estimated the tag-loss rates for fish of comparable sizes using Floy type anchor tags (Ebener and Copes, 1982; Ebener, 1982; Muoneke, 1992; Pierce and Tomcko, 1993; Swanson and Schram, 1996; McGlennon and Partington, 1997; Julliard et al., 2001; Rikardsen et al., 2002; Brattey and Cadigan, 2004). This prior was again assumed to be normally distributed  $N^{\sim}$  ( $\mu = 0.33, \sigma = 0.27$ )

# 5.2.8 Markov Chain Monte Carlo Sampling for parameter uncertainty

I expressed parameter uncertainty by sampling the posterior probability distributions of each estimated parameter using the *MCMC* algorithm built into AD Model Builder (a C++ software, Otter Research Ltd. Sidney, B.C., Canada), which allows fast maximization of the likelihoods of complex models because analytic derivatives are automatically calculated. Four Markov chains were run for each analysis (adult northern pikeminnow, rainbow trout smaller than 200 mm) until the multivariate potential scale reduction factor (Gelman et al., 1995) was smaller than 1.05. 30 000 samples of the posterior were taken from each chain following convergence. Convergence diagnostics were performed using the *CODA* with the *R* statistical software package (*http://www.r-project.org*).

# 5.3 Results

# 5.3.1 Predicted responses to experimental fishing of using Ecosim

The model showed that it is possible to produce cultivation-depensation effects in the experimental system and that it was possible to produce a flip from either a rainbow trout dominated system to a northern pikeminnow dominated one and vice-versa (Figs. 5.4 through 5.10). These predictions were very sensitive to changes in the vulnerability exchange rates. Flips were not predicted when all vulnerability exchange rates between prey and predators were set to 2 (implying a maximum mortality rate on prey at very high predator abundance of 2x the Ecopath base rate) for all groups. In order to produce flips by northern pikeminnow depletion fishing, the vulnerability exchange rates between zooplankton and their predators, as well as chaoborus and 2+, 3+, 4+ northern pikeminnow had to be 3 or greater and the vulnerability exchange rate between zooplankton and chaoborus greater than 10.

When vulnerable exchange rates were high enough to produce flips, the main predicted changes in the system following northern pikeminnow biomass reduction (Fig. 5.4) operated through the chaoborus and zooplankton dynamics. As 4+ northern pikeminnow declined, chaoborus was released from predation. While its total predation mortality declined (Fig. 5.4), the biomass of chaoborus did not increase (Fig. 5.3) significantly since at the same time its own food supply, zooplankton, was decreasing because of increases in rainbow trout 2+ density and large increases in growth by the remaining 2, 3, and 4+ northern pikeminnow and 2+ rainbow trout (Fig. 5.5). Because of decreased zooplankton density, predicted relative feeding time of both the juvenile rainbow trout and northern pikeminnow increased. Interestingly, the predicted response of the rainbow trout population was for the total biomass to increase and be comprised of fewer, but larger fish. While the mortality of the juveniles increased, the adults were larger (Fig. 5.5) and so the predicted biomass of rainbow trout higher.

Producing flips by rainbow trout depletion fishing occurred only when vulnerability exchange rates between 2+,3+ and 4+ northern pikeminnow and 2+ rainbow trout were 5 (Figs. 5.8 to 5.10) or greater. As was the case in producing flips with northern pikeminnow depletions above, the vulnerability exchange rates of zooplankton to chaoborus needed also had to be greater than 10 in order to produce flips.

The models were relatively insensitive to changes in the relative fish start-

ing biomasses and would still produce a flip from one dominated state to another in both cases where rainbow trout biomass is half the northern pikeminnow biomass and vice-versa. In general, you could move the unstable starting point around a lot, without eliminating the two stable points where alternate equilibria exist at all.

## 5.3.2 Estimated Depletion

The depletion estimates here are those of the vulnerable (active) population. The depletion estimates in Fig. 5.12 and the upper panel of Fig. 5.13 are very high, i.e. are optimistic about the impact of the removal fishing. Gillnets are passive gear and so fish must be active in order to be captured in them. Furthermore, incomplete depletions in a particular gear type may be due to learned gear avoidance (after an unsuccessful capture encounter). The depletion estimates based on the tagged animals (Fig.5.13) showed the depletion to be on average 70% across size classes rather than the 100% estimated using Eq. 5.6.

Bycatch mortality of rainbow trout was negligible during depletions in Moose Pasture (since trap gear was used) and Mom's Lake. However, there was considerable bycatch in Cheryl Lake of rainbow trout where 1257 mainly small (< 200 mm) were captured.



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Figure 5.3: Predicted relative biomass (B) changes after depletion fishing of 4+ northern pikeminnow. The biomass of 2+ RBT and 4+ NPM have been arbitarily set to 1 and the other groups scaled accordingly.



Figure 5.4: Predicted changes in M after simulated depletion fishing of 4+ northern pikeminnow.



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Figure 5.5: Predicted body weight changes (kg) after 4+ northern pikeminnow depletion fishing.

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Figure 5.6: Predicted changes in relative feeding time after 4+ northern mikeminnow depletion fishing.



Figure 5.7: Predicted relative changes in biomass B following 2+ rainbow trout depletion fishing. The biomass of 2+ RBT and 4+ NPM have been arbitarily set to 1 and the other groups scaled accordingly.



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Figure 5.8: Predicted changes in M following 2+ rainbow trout depletion fishing.



Figure 5.9: Predicted changes in weight (in kg) after rainbow trout depletion fishing.



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Figure 5.10: Predicted relative changes in feeding time after rainbow trout depletion fishing.



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Figure 5.11: Depletion catches of northern pikeminnow(in numbers) by date for Cheryl lake in 2001 (top), Mom's lake in 2001 (middle) and Moose Pasture lake in 2002 (bottom).



Figure 5.12: Estimated northern pikeminnow vulnerable numbers (N) and percent depletion estimates by length for Cheryl and Mom's lake.

FL (mm)

FL (mm)



Figure 5.13: Northern pikeminnow population and percent depletion estimates by length,  $\nabla$  represent 95 percent CI.



Figure 5.14: Fit of proportion northern pikeminnow leaving the nursery area function by length for each drainage.

### 5.3.3 Visual Surveys

The change in the visual survey index shows that survival of fish from 0+ to 1+ was better in the unfished lake than the fished one (0.06 in Dad's lake but only 0.03 in Moose Pasture) following experimental fishing (Fig. 5.15). In contrast, the survival rate from 1+ to 2+ was much improved following fishing of adults in Moose Pasture relative to the unfished lake (Fig. 5.15). A serious problem with interpreting these result however, is that they come from a single pair of observations so are not reliable.

# 5.3.4 Northern pikeminnow growth, mortality and movement parameter estimates

The northern pikeminnow in each drainage have approximately the same growth curves (Fig. 5.16). In both drainages, the observed lengths at age in the non-nursery lakes tended to be higher than the nursery lakes suggesting either that larger fish move upstream to the head-end lakes, or that growth is better in these lakes.

Northern pikeminnow movement differed between the eastern and western drainages in two ways. In the eastern drainage, there was a tendency for fish to migrate into the headwater lakes at smaller sizes (Fig. 5.14). For example, age 2+ NPM were absent from the western drainage (Fig. 5.16 upper panel) but present in the eastern drainage (Fig. 5.16 lower panel). This observation was also consistent with the population estimates (Fig. 2.3) showing the



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Figure 5.15: Percent change in visual survey index in Dad's (blue) and Moose Pasture (red).


Figure 5.16: Fit of von Bertalanffy growth curve through length-age data in western (top) and eastern (bottom) data. Jitter added to better see overlay.

presence of 1 and 2+ fish in Cheryl lake, but not in Mom's or Nestor lakes. Also, the total proportion moving from the nursery area  $\mu_n$  appeared to be lower in eastern drainage than in the western (Fig. 5.18).

The broad posterior probability distributions meant there were no clear differences in growth or survival parameters in northern pikeminnow greater than 90 mm between the eastern and western drainage(Fig. 5.17).

### 5.3.5 Rainbow trout growth and mortality estimates

It was not possible to estimate growth parameters for rainbow trout > 200 mm. There were very few data, so the growth likelihood would not converge and only  $M_t$  was estimable using only Eq. 4.17. In addition, no fish marked following the experimental manipulations in Nestor Lake were recaptured so it was not possible to estimate  $M_t$  in that lake at all.

There did appear to be some effect of the rainbow trout depletion fishing in Wilderness lake and to the combined northern pikeminnow (and accidental) rainbow trout depletion in Cheryl lake (Fig. 5.20). However, while the posterior modes of these distributions are a different, the posteriors are too broad to confidently argue a difference was observed.

The estimated von Bertalanffy K for juvenile rainbow trout was the same between all treated and untreated lakes. There were differences in the  $log(L_{\infty})$  between treated and untreated lakes, (Fig. 5.21), with fish appearing to be stunted in those lakes where northern pikeminnow were removed (Moose Pasture, Cheryl and Mom's).



Figure 5.17: Posterior samples of growth parameters  $(log(L_{\infty}), K)$ , historical natural motality M, and tag loss tl for unfished western (left column) and fished eastern drainage (right column).



Figure 5.18: Posterior samples of movement parameters (maximum proportion leaving the nursery area  $\mu_n$ , proportion of the moving pool going to lake 2  $\mu_2$  (Cheryl and Mom's), and the beta distribution parameter  $\beta$  for the unfished western (left column) and fished eastern drainage.



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Figure 5.19: Posterior samples of northern squawfish tagged cohort mortality  $M_t$  by lake.



Figure 5.20: Posterior samples of  $M_t$  for rainbow trout greater than 200 mm by lake.



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Figure 5.21: Posterior samples of the log asymptotic length  $log(L_{\infty}$  for rainbow trout smaller than 200 mm by lake.

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Figure 5.22: Posterior samples of the von Bertalanffy K for rainbow trout smaller than 200 mm by lake.

In spite of the very large posterior probability intervals,  $M_t$  for the rainbow trout was higher in those lakes where northern pikeminnow were fished (Moose Pasture, Cheryl, and Mom's Fig. 5.23). The lowest mortality was observed in Dad's lake, where there was very high northern pikeminnow density.

## 5.4 Discussion

I cannot say whether or not the experimental manipulations of either rainbow trout or northern pikeminnow will eventually result in alternate stable states. There is some agreement between the observed results and from model predictions with parameter combinations implying strong cultivation-depensation effects. But, to make a case that the experimental fishing produced an alternate stable state through cultivation-depensation effects would require a) observed changes in relative feeding time of 1+ northern pikeminnow and 1+ rainbow trout; b) observed changes in zooplankton and chaoborus densities; and c) a long series of observations following the manipulations showing that any recruitment responses were not transitory. Even in the case of mortality and particularly growth of 1+ rainbow trout, the posterior probability distributions for growth and mortality parameters showed the data can be explained by a large range of parameter combinations, including some contrary that would not imply strong cultivation-depensation effects according to Ecosim.



Figure 5.23: Posterior samples of the instantaneous annual mortality of tagged fish by lake for rainbow trout smaller than 200 mm.

Measuring the northern pikeminnow response to experimental removal to either rainbow trout or northern pikeminnow was much more problematic than simply wide probability distributions for response parameters. Because of dispersal among lakes of northern pikeminnow in the study system, the experimental unit was effectively a drainage. Therefore, the only relevant comparison for northern pikeminnow responses to northern pikeminnow fishing were between the fished and unfished nursery lakes (Moose Pasture and Dad's respectively). Even ignoring the problem that sample size for the manipulations was one lake, the flow of fry from lakes above the treated (Moose Pasture) and control lake (Dad's) could have been affected by fishing conducted in those upstream lakes. Fortunately, the manipulations in lakes above Dad's and Moose Pasture were identical, offering the possibility of long term comparisons.

In the case of measuring the effects of rainbow trout removal, no 1+ and 2+ northern pikeminnow parameters could have been measured, since there are no fish of those size classes in those lakes. The non-nursery lakes were probably reasonable experimental units insofar as measuring the response of rainbow trout to fishing of northern pikeminnow since little interaction between 1 and 2+ northern pikeminnow and rainbow trout recruits was either predicted in the model here or observed in the field.

There was a trade-off between northern pikeminnow density and rainbow trout growth and mortality (Figs. 5.23 and 5.21 (Post et al., 1999). In Ecosim, this trade-off operates through the effects of northern pikeminnow on

chaoborus which in turn affects the density of rainbow trout food supply (the zooplankton and benthos Figs 5.21, 5.22, and 5.5). However, since rainbow trout were not marked until they were at least 100 mm, changes occurring in growth and survival of these fish before that point were invisible. Where northern pikeminnow were fished, juvenile rainbow trout density could have increased for example if northern pikeminnow predation was reduced resulting in slower growth and higher mortality similar to the pattern observed by Post et al. (1999). Distinguishing between the two hypothesis is simply a matter of observing the system over a few more years. The important thing to measure is how recruitment (in biomass) has changed before and since the manipulations.

Ontogenetic movement of northern pikeminnow severely confounds any measurement of mortality and growth response. Implicit in the analysis shown here was a large and unlikely assumption that movement rates remained constant over time. Recall in chapter 4.3.3 that I combined the length-age and tagging data to simultaneously estimate growth and movement parameters. This approach implicitly assumes that the historical movement rates leading to the observed length-age structure (in this case collected before any manipulations) was the same following experimental removals. This was necessary in order to accurately estimate the growth parameters in the nursery lakes needed to predict growth trajectories of the marked fish (used in turn to predict the probability of movement). This assumption would be violated in the likely case that movement being density-dependent.

The very high effective densities of northern pikeminnow in the nursery lakes (chapter 2, Fig. 2.5) suggest these lakes are very crowded. If the cue for fish to move upstream is very high density in the nursery area, then density reductions in the nursery area would result in less migration and possibly no change in mortality rates. An additional problem is that movement of northern pikeminnow could have occurred to lakes where no sampling could have detected. In the eastern lakes, fish could leave Moose Pasture lake by the outflow creek, and in the case of Dad's, to both Tasha lake above it and the outflow creek below it (Fig. 2.1).

The estimates of any movement parameters could be grossly incorrect. The simulation studies in chapter 4.3.3 show that in cases with low capture probabilities and where movement occurs at sizes smaller than the selectivity of the gear (low  $l_h/l_{h\mu}$ ), the total proportion of the population leaving the nursery area ( $\mu_1$ ) is over-estimated. While the movement probability function used in the analysis of the field data was different, the estimated movement functions show that movement likely occurs in size classes too small to be captured with standard hoop nets, meaning we should expect a positive bias in estimates of the total proportion leaving the nursery area  $\mu_1$ . However, these same simulation studies showed that the estimate of mortality of the tagged cohort  $M_t$  was still unbiased.

Ontogenetic movement does present an interesting opportunity for northern pikeminnow control in this system. By preventing northern pikeminnow from returning to head-end lakes using dams, populations in those lakes

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would eventually decline. Since the jumping ability of rainbow trout is much greater than northern pikeminnow, such barriers need not prevent their access to headwater lakes. Only a single construction event would be needed to build these barriers with regular maintenance to prevent streams cutting around the stream banks around them. This would be considerably less effort than large-scale predator removal. Unfortunately, the effect of the dams might take several years to be felt since northern pikeminnow are relatively long lived, and have been known to spawn in the margins of lakes (Jeppson, 1959). On the other hand, efforts to eradicate northern pikeminnow in any lake lower in the drainage will be almost entirely fruitless since there will be a constant flow of fry from lakes upstream.

Comparing measured and predicted experimental responses of ecosystem to fishing has several advantages. First, it gets away from attempting to intuit ecosystem responses to fishing. There is little dispute that fishing will have community wide effects and that the interactions effects are not likely simple. It is optimistic to think any "expected" (as discussed by Sih et al. (1985)) effects of such removals could come from anything other than an ecosystem model. Ecosystem responses to fishing may occur in several different species, at several different trophic levels and have dynamics mediated by change in prey behavior (vulnerability exchanges rates). In addition, some of the expected response variables such as juvenile rainbow trout survival respond are likely to change in highly counter intuitive ways (survival decreasing but overall biomass of adult rainbow trout increasing over time). That said, the Ecosim model I used here might require a more detailed description of the population dynamics (more groups to describe zooplankton for example) to realistically describe population dynamics.

My results were similar to those of Vander Zanden et al. (2005) in identifying the potential importance of the benthic-zooplankton linkage in predicting the outcome of predator removal from lakes. The modeling approach used here is significantly different in that I assumed the dynamics were mitigated by behavior (vulnerability exchange processes) and, that model predictions were very sensitive to assumptions about those dynamics. Even though simple predator prey models are known to produce paradoxical behavior (Abrams and Walters, 1996), larger scale ecosystem models with the same flaws are still being produced (Vander Zanden et al., 2005; Mangel and Levin, 2005) with apparent disregard to the problems of the simple models.

This study identifies some daunting practical challenges with measuring how ecosystems might respond to fishing (experimentally or otherwise). The major problems were firstly the spatial organization of the stock and secondly, that dynamics predicted to be the most important to the response to fishing are those occurring in size classes too small to measure. In the case of marine fisheries these difficulties are likely to be worse. Spatial dynamics in marine systems are arguably much more complex, and more poorly understood than lakes. Many marine systems are also likely to by already affected by fishing (Fisher and Frank, 2004), and data on non-target species at any size or trophic level are even more limited for most marine ecosystems. The model predictions and the field experience shows the most important dynamics are those that occur in precisely those young age groups and/or small size classes for which there is very poor information even for the target species of most fisheries.

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## Chapter 6

## **General Conclusions**

# 6.1 The difficulty of properly estimating growth and mortality parameters

Growth and mortality should be relatively simple parameters to measure in response to harvesting but I have shown here that it is not easy to estimate these parameters correctly even with likelihoods that correctly account for the sampling process. This is a serious concern since growth parameters are used in virtually every stock assessment to predict size at age, yield per recruit, and often even as proxies for natural mortality itself (Pauly, 1980; Jensen, 1997). Traditional methods, such as the Fabens method are biased in the worst possible direction (over-estimating the metabolic growth parameter K and natural mortality M). This bias will lead to over-estimating the optimal exploitation rate.

The biases in traditional method for estimating growth parameters have been known for some time (Parma and Deriso, 1990) but solving the problem has proven very difficult even with techniques developed in this thesis and elsewhere Laslett et al. (2002); Eveson et al. (2004). The likelihoods developed here (Chapters 4 and 3) are not very robust to their assumptions and could not be used in many fisheries. Consider for example that the length-age likelihood fails to estimate parameters correctly when the historical fishing rate has been variable (chap. 3, Fig. 3.4) meaning that these methods could only be applied in a very restricted number of cases. Of particular concern is that growth parameters bias is worst in the common situation where exploitation rate increases rapidly before a collapse. Unfortunately, this is when it is most important to be able to estimate the correct target exploitation rate, and to correctly project the biomass for rebuilding.

Estimating growth parameters needs to be included in the stock assessment itself, rather than treating growth parameters as 'known' values external to the models, their estimation could be included with parameters (such as productivity, etc.) that are usually estimated in such models. Natural mortality, gear selectivity and fishing mortality are often already modeled in most stock assessment models so predicting a matrix of vulnerable numbers at length and age (pl, a Eq. 4.6) for every year would be relatively simple. When there are time series of length-age data, mark-recapture data many years of such tables could be included as time series to estimate the effects of fishing on the size and age structure of the stock. Many such tables could potentially provide information about time-varying growth and recruitment.

## 6.2 Evaluating Ecosystem Impacts of Fishing

The dynamics Ecosim predicted to have the greatest effect on an ecosystem's response to fishing are also those most challenging to study: the vulnerability exchange rates, and juvenile fish survival. Methods to estimate survival at least exist but there are considerable difficulties catching small fish and marking them once captured. The vulnerability exchange rates have the greatest effect on predicted direction and magnitude of the response to fishing. Estimating vulnerability exchange rates is typically done in Ecosim by fitting time series; analysis of change in prey mortality with changes in predator abundance; examination of long-term changes in predator abundance and calculations based on movement/exchange-rate data (Walters and Martell, 2004). Since I did not have multiple years of data only direct calculation of movement and exchange rate data would have been possible. Since the most important dynamics occur in small fish, the challenge here is to develop methods measure this exchange rate directly or indirectly in juvenile fish.

If this study is carried forward for several years it will be possible to estimate the recruitment in the years that following depletion fishing once those recruits become fully vulnerable to fishing year using a standard stockassessment model. However, without observations of changes in the vulnerability exchange rates (or some proxy of foraging time) it will not be possible to say anything about whether Cultivation-Dependent effects were pro-

#### Chapter 6. General Conclusions

duced. While agreement between observed and predicted response variables were encouraging, the true test of whether or not cultivation-depensation was produced will be to actually observe an alternate stable state with lower recruitment over several years and the changes in foraging behavior that produced that state.

While Mangel and Levin (2005) may be right saying we have no excuse for not shifting to a community paradigm in fisheries, the data requirements to practically do so may be considerable. Consider the study system. To monitor and manage the community effects of fishing in this case I had to consider the dynamics of one species with two life-history types; one with large-scale density dependent spatial dynamics (northern pikeminnow) and rainbow trout on a more localized scale. Considering the relatively closed nature of this system and the large quantity of data - measuring growth and mortality responses should have been relatively simple. In many (especially marine) fisheries the data are poorer; the spatial dynamics are more complex; and the dynamics are further complicated by fast changing variables such as fishing effort.

My study shows that simple growth and mortality variables may respond to fishing in very counter-intuitive directions. Consider for example, our modeling and field results showed that juvenile rainbow trout mortality was actually higher following northern pikeminnow removals. The model predicts this response but at the same time predicts an overall increase in rainbow biomass related to improved growth. The number of juvenile rainbow trout surviving might have indeed been lower in numbers, but the fewer remaining rainbow trout could have grown better, lived longer and produce more recruits that many smaller fishes would have. Without considering such effects, the data from other predator control programs might be ambiguous. Bibliography

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