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UNIVERSITY OF CALGARY

Understanding Dynamic Interactions Between Angler Behaviour and Fish Populations in

Spatially Structured Recreational Fisheries

by

Hillary G. M. Ward

A THESIS

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Abstract

Recreational fisheries are characterized by complex interactions between the biological processes governing fish production, and the social processes influencing angler behavior. For the most part, social and ecological components of recreational fisheries are studied independently and the outcomes of the research are rarely integrated in developing management strategies. This thesis attempts to integrate social and ecological processes operating in spatially structured fisheries. In order to understand the dynamic interactions across many sampling units, I developed a method to estimate fish density and demonstrate that gillnet catchability varies as a function of lake-basin characteristics and water temperature. Using this information, I conducted an analysis of angler characteristics to determine how anglers interact with the fishery. The results suggest a diverse group of anglers that varied in their spatial behaviour, harvest behaviour and catchability. The impact of heterogeneity in angler characteristics on fish populations was further explored by examining mechanisms resulting in hyperstability. Angler characteristics had strong interactions with the fishery: anglers who fished at low density lakes were more experienced than anglers at high density lakes. This segregation of angler experience across lakes appeared to explain the observed hyperstability. In spatially structured fisheries, it is also important to understand how the tradeoffs between environmental productivity and competition influence somatic growth rates and plasticity in life-history traits. Using experimental populations of Rainbow Trout to empirically test predictions from life-history theory, immature growth rates were best explained by climatic and density dependent competition effects, and age at maturity and the proportion of surplus energy invested into reproduction are dependent on juvenile growth

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conditions. Finally, integrating social and ecological processes operating in spatially structured fisheries requires understanding how feedbacks between anglers, fish populations and fisheries managers influence system outcomes. Using a conceptual analysis, I demonstrate that understanding behavioural-mediated interactions and the scale at which these processes operate is critical for managing for the sustainability of recreational fisheries. Together, this research suggests a way to improve the management of spatially-structured fisheries by integrating the dynamic interaction between social and ecological processes.

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Chapter One: Introduction

Recreational fisheries have increased in popularity over the last several decades and in some instances, harvest from recreational fisheries has resulted in overfishing and population collapse (Post et al. 2002; Schroeder 2002; Coleman et al. 2004). Management strategies for recreational fisheries are moving away from the traditional single-stock paradigm and shifting towards the idea that individual fisheries are nested within a broader landscape of angling opportunities (Carpenter and Brock 2004; Post et al. 2008; Post and Parkinson 2012). Across the landscape, individual stocks (e.g. lakes, rivers) vary dramatically in characteristics relating to the productivity of the stock (e.g. growing conditions, species composition) and the attractiveness of a site to anglers (including catch and non-catch related factors) (Shuter et al. 1998; Hunt et al. 2013). Most recreational fishing opportunities across North America are unregulated (although certain lakes have bag limits or catch and release regulations) and several authors have suggested that this open-access fishery results in a predator-prey system between anglers and fish populations, where mobile anglers link fish populations across the landscape (Cox and Walters 2002; Parkinson et al. 2004; Post et al. 2008). Therefore, recreational fisheries must be researched and managed at the landscape scale.

Research in recreational fisheries is often focused on developing optimal management strategies through two parallel approaches. Historically, fisheries management was based only on a biological component. A second approach to fisheries management is becoming increasingly widespread and is based on understanding the social component of fisheries. These two approaches differ fundamentally in their management view: human dimensions research often attempts to maximize the social

benefits from angling where-as biological research is often focused on evaluating the sustainability of fish populations. However, it has recently been suggested that management of recreational fisheries needs to focus on linking these biological and social processes in order to achieve both social and ecological goals (Fenichel et al. 2012; Hunt et al. 2013; Post 2013).

Management of the biological component in recreational fisheries aims to estimate targets for sustainable harvest and requires a detailed understanding of the interaction between biological and harvest processes. We have witnessed the collapse of many of the world's commercially fished stocks and increasing evidence is suggesting that similar outcomes could be seen for recreational fisheries (Post et al. 2002; Cooke and Cowx 2004; Coleman et al. 2004). This conservation concern has resulted in a considerable amount of research focused on describing the complex details of a fishery using population dynamics models so that managers are better able to understand factors that influence fish growth, survival and vulnerability to angling (Hilborn and Walters 2002). This approach assumes that by understanding the fine-scale details of factors influencing fish production (growth, survival and recruitment), optimal management strategies can be developed for a fishery. Often these strategies involve setting catch targets and implementing harvest-control measures to achieve some identified level of stock status (Walters and Martell 2002).

In addition, it is widely recognized that management of recreational fisheries needs to consider the social component, which is focused on the quality of the angling experience, because of the direct social and economic benefits associated with sport fishing (Cooke and Cowx 2004; Oh et al. 2005; Hutt and Bettoli 2007). A substantial

amount of research has focused on understanding and modeling angler behaviours in response to resource conditions. Fisheries research in this area often aims to answer important questions regarding angler behaviour (i.e. what influences anglers decision to fish?) and preference for resource attributes (i.e. how do anglers choose where to fish?) (Fedler and Ditton 1994; Fisher 1997; Hunt 2005). This type of human dimensions research gives managers a broad understanding of factors influencing angler behaviour and more recently, there is an increasing interest to better understand how angler behaviours interact with fish population dynamics (Johnston et al. 2010; Fenichel et al. 2012; Post 2013).

There is a dynamic interaction between the biological processes that determine fish production and the social and economic processes that influence angler behavior. At the core of this interaction there are three main processes that determine outcomes of the system: 1) biological response of fish populations to harvest; 2) variation in angler catchability with stock size; and 3) the behavioural response of anglers to variations in resource conditions. It is critical to understand how these components interact and influence our predictions about managing for sustainable recreational fisheries. For the most part, social and ecological components of recreational fisheries are researched independently and the outcomes of the research are rarely integrated into management strategies. This thesis attempts to integrate social and ecological processes operating in a multi-stock, spatially structured fishery to better understand the interaction between anglers and fish populations.

The research in this thesis used the Rainbow Trout *Oncorhynchus mykiss* fishery of British Columbia as an example study system. This fishery is considered a multi-stock,

spatially structured, open-access and put-and-take fishery (although some lakes have harvest limits or catch and release regulations) (Cox and Walters 2002; Parkinson et al. 2004; Post et al. 2008). The recreational fisheries sector in British Columbia contributes \$475 million to the provincial economy and provides approximately 3.9 million angler days per year (Fisheries and Oceans Canada 2005). In order to accommodate these demands, supplementing natural fish stocks (and originally fish-less lakes) with hatchery fish has become an important part in maintaining the recreational fishing industry. The widespread prevalence of monoculture lakes in this fishery (where populations are maintained solely through stocking) is an ideal study system for this research. Stocking allows for fish population densities to be manipulated in an experimental manner without the conservation concerns associated with wild fish stocks (Post et al. 2008). Although the research in this thesis is conducted on a single landscape, the results can be applied in a more general framework to other fisheries.

The objective of the research conducted in this thesis is to use experiments and observations to test hypotheses that describe the dynamic interaction between anglers and fish populations and understand corresponding sources of uncertainty. This thesis is composed of four experimental and data-driven chapters (Chapters 2-5) that are each focused on understanding a single component of the interaction between anglers and fish populations across a landscape. In Chapter 6, the research focus is broadened and I develop a conceptual framework for understanding interactions between anglers, fish populations and fisheries managers. In the final chapter (7), I summarize information learned from this thesis and suggest directions for future research of spatially-structured recreational fisheries.

The research in Chapter 2 focuses on developing a resource-effective method to assess fish population densities across a large number of lakes. I conduct an analysis using mark-recapture data to demonstrate how lake-basin characteristics and water temperature influence gillnet catchability, and I develop a method to estimate fish population density in the absence of mark-recapture information. In Chapter 3, I quantify the spatial behaviour, harvest behaviour and catch efficiency of anglers and examine how the composition of anglers varies across a spatial gradient. Chapter 4 integrates information on fish population densities and angler characteristics to understand how heterogeneity in angler behaviour across a spatially-structured fishery interacts with fish population dynamics. This analysis contrasts the relationship between angler catch-perunit-effort and fish density in an open-access recreational fishery with an experimental fishery (a set of lakes that had restricted access, standardized fishing methods and no heterogeneity in angler experience). In Chapter 5, I determine how the trade-off between environmental productivity and competition influences somatic growth rates and plasticity in life-history characteristics related to growth. In Chapter 6, I conduct a broad review of how the interaction of anglers, fish populations and managers can influence social-ecological outcomes. Using this information, I identify factors, behaviours and antecedents to behaviours most important to the outcomes of a coupled social-ecological system and provide information on how to reduce uncertainty and identify data gaps to improve management of recreational fisheries.

The research conducted in Chapters 2-4 has been published before the submission of this thesis and the full citations are given in Appendix C.

Chapter Two: Basin Characteristics and Temperature Improve Abundance Estimates from Standard Index Netting of Rainbow Trout (Oncorhynchus mykiss) in Small Lakes

2.1 Introduction

Index netting using standard multimesh gillnets is a common method for sampling fish populations (Willis 1987; Schaner et al. 1999; Appelberg 2000; Morgan 2002). The primary goal of index netting is to translate an observed catch-per-unit-effort (CPUE) into an estimate of total fish density. Index netting has many practical advantages for assessing populations, such as the ability to catch a wide range of fish sizes and species, and easy operation in a variety of habitats.

Gillnet CPUE is used as a measure of relative abundance, by assuming that

(1)
$$CPUE = qN$$
,

where *q* is a catchability coefficient and *N* is fish density (Hilborn and Walters 1992). This relationship assumes that catchability for a given sampling method is constant in a given body of water. However, many studies have shown that catchability varies with fish density (in addition to other factors) (Newby et al. 2000; Hansen et al, 2005; Jiao et al. 2006). A considerable amount of research has focused on understanding how catchability from index netting varies across multiple sampling units (Askey et al. 2007; Lauridsen et al. 2008; Pierce et al. 2010; Prchalová et al. 2011). In particular, catchability has been shown to vary as a function of water-body characteristics and fish density (Lauridsen et al. 2008; Pierce et al. 2010). It is common practice to estimate catchability as the ratio of CPUE to fish density (scaled for vulnerability) and model how catchability varies as a function of water-body characteristics (Pierce et al. 2010). However, this method has a high probability of artificially detecting density-dependent catchability and is prone to large error in the estimate of N (Shardlow et al. 1985). Therefore, in order to examine how catchability varies across multiple sampling units, it is necessary to estimate catchability directly through mark-recapture studies. For example, using a simple Peterson mark-recapture,

(2)
$$\frac{R}{C} = \frac{M}{N}$$

where M is the number of marked fish, C is the number of captured fish in the second sampling period, R is the number of recaptured fish and N is the total number of fish alive, catchability can be expressed as

$$(3) \qquad q = \frac{c}{N} = \frac{R}{M}$$

by combining Equations (1) and (2), assuming one unit of effort.

Understanding how catchability varies among sampling units may be useful for developing analysis methods for index netting, since knowledge of this variation could help improve the reliability of abundance estimates (Askey et al. 2007). Catchability of fully vulnerable fish is the product of capture efficiency and size-dependent processes and these processes are well studied for most fishing gears (Rudstam et al. 1984; Millar and Walsh 1992; Millar and Fryer 1999). Capture efficiency is defined as the number of fish captured per unit of sampling effort divided by the number of fish actually present in an area and is influenced by fish behavior and/or habitat preference. Size-selectivity is a result of extrinsic factors (gear construction and method of operation) that affect vulnerability of fish to gear (Bagenal 1978) and size-selectivity is assumed to be constant across sampling units for a single species (Askey et al. 2007). However, few studies have examined how catchability varies with water body characteristics (Lauridsen et al. 2008; Pierce et al. 2010).

Rainbow Trout (*Oncorhynchus mykiss*) are an economically important fish species in many lakes in North America. However, a standard index netting procedure to assess the status of the Rainbow Trout populations in these lakes has not been developed. Several studies have used an intensive gillnet design to estimate population abundance in small experimental lakes (Post et al. 1999; Askey et al. 2007). For larger lakes with established recreational fisheries, this high intensity of gillnets kills a large portion of the population and is therefore an unacceptable method for monitoring populations. The objective of our study is to develop a protocol to assess the status of Rainbow Trout in lakes where the gillnet catch represents a small proportion of the population. We assess how gillnet catchability varies with lake characteristics, and we use mark-recapture techniques to develop a method to estimate fish abundance from index netting using multimesh gillnets.

2.2 Methods

2.2.1 Study Design

This study examined gillnet capture patterns using mark-recapture data from 12 lakes in the south-central region of British Columbia, Canada. All study lakes were monocultures of Rainbow Trout, except Kentucky Lake, which also contained a population of Redside Shiner (*Richardsonius balteatus*). Lakes ranged from 5.7 to 44.7 ha in surface area and varied in the amount of littoral area, perimeter and depth (Table 2.1).

Gillnetting occurred between September 21 and October 7, 2011 and consisted of one floating and one sinking net, set overnight in each lake. Each net was made up of seven equal panels that varied in mesh size (25, 76, 51, 38, 89, 64, 32 mm). Each panel was 15.25 m long and 2.3 m deep, and panels were sewn together at the top and bottom so that a small gap existed between the panels. The sinking net sampled the littoral zone and was set approximately parallel to shore in 1-6 m of water, where as the floating net was set over deeper water to sample pelagic fish. Nets were quasi-randomly placed in areas of suitable net locations (areas without large woody debris). Sampling is traditionally conducted at this time of year, as decreasing water temperatures optimize net catches and the majority of the fishing effort is completed for the year (providing an assessment of the population following the angling season). This is the standard provincial government gillnet protocol for sampling Rainbow Trout lakes (<50 ha) in British Columbia (a detailed description of this method is available at http://archive.ilmb.gov.bc.ca/risc/pubs/aquatic/fishcol/index.htm).

Approximately one week prior to gillnetting, marked Rainbow Trout (adipose finclipped) were released into the study lakes. A sample of 30 fish from the marked population was measured, and the length distribution of the marked population was reconstructed by sampling with replacement from the sub-sample of 30 fish. The number of iterations corresponded to the number of marked fish in each lake. The mean length and standard deviation of the marked population was 123.3 mm and σ =17.4 respectively and approximately 11 fish/ha were released into each lake. These fish were assumed to be fully recruited to the sampling gear (Askey et al. 2007).

The key feature of this sampling design is that a standard amount of net-effort is required, which allows efficient sampling of many lakes during the fall season. However, in lakes where these methods are used, lake-basin characteristics vary considerably and it is hypothesized that this impacts the relative efficiency of gillnets. Therefore, we describe how gillnet catchability varies with lake-basin characteristics, so that these standard lakeassessment methods provide a reliable estimate of fish abundance when mark-recapture data are unavailable.

2.2.2 Model Development

In this sample design, gillnet effort remained constant (one floating and one sinking net per lake). The expectation is that the proportion of the population captured with the standard gear (herein termed Q_{max}) is a function of gillnet density (number of nets per hectare) and lake-basin characteristics. Lake-basin characteristics will determine how fish use habitats and the relative density of fish in these habitats. As lakes deviate from circular, the perimeter to surface area ratio increases. This variation in the perimeter to area ratio (herein lake complexity), coupled with variation in depth, creates a variation in spatial habitat use across lake.

Littoral area is potentially an important parameter influencing gillnet efficiency as a result of the spatial behavior of fish (Rainbow Trout feed primarily in shoal areas) and gillnet placement (sinking nets are set in littoral areas). But, many of our study lakes lacked empirical measures of littoral area, so we developed a model to predict littoral area based on lake-basin characteristics. We obtained information on these characteristics for all lakes in British Columbia that were less than 100 ha (data available online at

http://a100.gov.bc.ca/pub/fidq/main.do). We developed several candidate models to predict littoral area based on covariates such as lake area (A_T), lake complexity (C) and maximum depth (D). We estimated parameters using linear and exponential models, and models were fitted to observed data assuming normally distributed residuals and exponential models were log-transformed prior to fitting. The best fit model was used to predict littoral area for our study lakes where data were not available.

Askey et al. (2007) examined gillnet efficiency and selectivity for the same range of gillnet mesh sizes used in this study. However, in their study, they used an intensive gillnetting approach that was intended to deplete a substantial proportion of the population. Askey et al. (2007) used a sampling design with a net effort of 457 m²ha⁻ ¹night⁻¹ over three net-nights on lakes that were approximately 5 ha in size. However, because high densities of gillnets are known to interfere with each other (Prchalová et al., 2011), we are unable to scale their estimates of gillnet efficiency for our study design. Gillnet interference occurs when a fish caught in one net is less likely to be caught in a second net, so that setting twice the number of gillnets does not equal twice the catch (i.e., net sets were not independent). We assume the size-selectivity parameters estimated in Askey et al. (2007) are valid for our study. They estimated selectivity using a logistic function, for 10 mm length-bins, where the selectivity of fish in length-bin *i* is

(4)
$$S_i = \frac{e^{\alpha + \beta l_i}}{1 + e^{\alpha + \beta l_i}}$$

and *l* corresponds to the mid-point of the length-bin *i*. Parameter estimates for α and β were obtained using a hierarchical Bayesian model. Mean estimate of α and β from the

posterior predictive distribution were -7.579 (σ =0.824) and 0.0753 (σ =0.0192) respectively.

We used a Peterson mark-recapture to estimate gillnet efficiency, where the number of marked fish recaptured in each size bin (r_i) was modeled using the binomial distribution,

(5)
$$r_i \sim bin(m_i, p_i)$$

which is based on the number of marked fish (m_i) and the probability of capture (p_i) in size bin *i*. The probability of selecting a fish in size bin *i* is assumed to be a function of the gillnet catchability (Q_{max}) and selectivity parameters (as shown in Askey et al. 2007), where

$$(6) \qquad p_i = Q_{max} S_i$$

and the population size (N) is estimated as

(7)
$$N = \sum N_i = \frac{c_i}{p_i}$$

where c_i represents the total catch in length bin *i*.

We developed a model to describe how gillnet catchability (Q_{max}) varies with lake characteristics. In this sample design, a constant net effort is used (one floating and one sinking net gang per lake), and therefore catchability (q) must be adjusted for changes in effort density across lakes (E),

$$(8) \qquad Q_{max} = qE$$

where Q_{max} is similar to an exploitation rate of a fishery.

We then determined if adding covariates to the model could better explain the observed variation in Q_{max} . The first covariate tested was water temperature (*T*). Effects

of water temperature on swimming performance of Rainbow Trout is well studied and several studies have shown a quadratic relationship between swimming speed and temperature for salmonids (Brett 1967). This relationship likely occurs due to low levels of dissolved oxygen at low temperatures (Matthews and Berg 1997) and cardiac stress at high temperatures (Farrell et al. 1996). Chifamba (2000) also found that a quadratic equation best described the relationship between CPUE and water temperature for freshwater sardin (*Limnothrissa miodon*) in Lake Kariba, Zimbabwe. Therefore, we assume that variation in temperature will directly affect activity rates, and thus the *q* parameter from Equation (8),

(9)
$$q = e^{\left[-a(T-T_{max})^2 - q_0\right]},$$

where *a* determines the width of the quadratic, T_{max} is the temperature at which catchability is maximized and q_0 is a scaling parameter. The base quadratic equation was modified by the exponential relationship, to ensure that *q* remained positive. Although all our study lakes were netted within a two week period, the lakes varied substantially in elevation, and resulted in a large variation in water temperature at the time of gillnetting (mean and standard deviation of water temperature was 11.6 °C and 1.93 respectively). Therefore, we hypothesize that incorporating variation in water temperature will improve the fit of our model.

The second covariate tested was littoral area. Littoral area is also a potentially important parameter influencing catchability for reasons described above. As the proportion of littoral area (P_{Lit}) approaches one, the total fish density in the lake and the fish density in the littoral area become equal and should result in a decrease in catchability, and a corresponding decrease in Q_{max} (as shoal oriented fish becomes less

concentrated). Therefore, we hypothesize that littoral area will directly affect the catchability parameter (q) from Equation (8), in the form,

(10)
$$q = \frac{q_1}{P_{Lit} + x(1 - P_{Lit})}.$$

We also tested a model that included both temperature and littoral area effects on catchability. This model combines Equations (9) and (10), by substituting Equation (9) in for q_1 in Equation (10),

(11)
$$q = \frac{e^{[-a(T-T_{max})^2 - q_0]}}{P_{Lit} + x(1 - P_{Lit})}.$$

We logit-transformed all models so that Q_{max} was defined on the interval [0,1]. Therefore, the logit-transformed point estimate of Q_{max} from the mark-recapture data is described by normal distribution with an unknown mean (μ) and precision (τ), (from the logittransformed model) where

(12)
$$\operatorname{logit}(Q_{\max}) \sim N(\mu, \tau).$$

Estimates of Q_{max} can then be used with Equation (7) to estimate population abundance. We conducted a sensitivity analysis on the priors and probability model for the data. We used the best fit model, and fit this model to the data assuming log-normal error and different vague prior distributions (Table 2.2).

We explored how uncertainty in the estimated parameters leads to uncertainty in the estimated population size for variation in covariate values (assuming a constant neteffort density and catch). We used the posterior distribution from the best fit model and compared the coefficient of variation in the population estimate for the various covariate combinations. Fish density (and uncertainty in the estimate) was calculated using the binomial distribution,

(13)
$$C_j \sim bin(Q_{max,j}, N_j)$$

where *C* represents the catch in lake-*j* and *N* is fish density. Similarly, we also examined how changes in net-effort density (lake size) affect the uncertainty in the population estimate. We estimated fish density (and uncertainty in the estimate) across a variety of lake sizes and assumed constant values for the other covariates in the best fit model. We assumed that catch declines as a function of Area^{-1} .

2.2.3 Bayesian Implementation

Both analyses (littoral area and gillnet efficiency) were conducted using Bayesian techniques as we were interested in exploring the probability distributions of the estimated parameters. The analysis was run using openBUGS (Bayesian Inference Using Gibbs Sampling) software, version 3.2.1 (available at http://www.openbugs.info/w/). This software implements a Monte Carlo Markov Chain (MCMC) (based on the Gibbs sampler) to obtain a representation of the posterior probability density function (Thomas et al. 1992). Vague priors were used for each model (Table 2.2). For each model, we ran the MCMC for 200,000 iterations, and discarded the first 50,000 to remove any "burn-in" effects. Chains were initialized from two different starting points. Convergence of the chains was visually assessed by monitoring trace plots of the Markov chains as well as examining the Gelman-Rubin convergence diagnostics (provided in the BRugs package for the R programming environment).

We compared candidate models in a Bayesian framework using the DIC statistic (Spiegelhalter et al. 2002). The DIC statistic combines goodness-of-fit measure, $\overline{D(\theta)}$ (the posterior mean of the deviance) with a measure of model complexity (p_D),

(14)
$$DIC = \overline{D(\theta)} - p_D$$

where p_D is the effective number of parameters, which is defined as

(15)
$$p_D = \overline{D(\theta)} - D(\hat{\theta})$$

where $D(\hat{\theta})$ is the point estimate of the deviance at the posterior means. For models with vague prior information, p_D should be approximately equal to the number of true parameters. We calculated a Δ DIC, and models with Δ DIC values between 0 and 5 are considered to have a substantial level of empirical support, and those with Δ DIC values greater than 10 are thought to have essentially no support.

2.3 Results

We used mark-recapture data to estimate gear efficiency for a standard method index netting in 12 lakes. Combined net catches ranged from 53 to 268 fish per lake (Table 2.1). The study lakes exhibited a large variation in catchability (Q_{max}) which can be described by changes in lakes size (as a result of changes in gillnet effort density) and we found that efficiency was linearly related to effort density for log-transformed data (R²=0.6445; F=18.13_{1,10}; p<0.05). The study lakes varied substantially in their characteristics. The proportion of littoral area varied between 25% and 81% and water temperature varied between 8.8°C and 15.4°C across the study lakes (Table 2.1).

Littoral area was best predicted by total surface area, maximum depth and lake complexity (Table A.1),

(16)
$$A_{Lit} = \alpha A_T^{\ \beta} e^{(\gamma D + \delta C)}.$$

Parameter estimates for the best fit model were α =0.7882, β =1.0490, δ =0.001295 and γ =-0.03689 (R² = 0.8602). This model was used to estimate littoral area for study lakes where measurements were unavailable (Table 2.1).

We compared four candidate models to determine whether lake-basin covariates could predict Q_{max} . Including water temperature as a covariate resulted in a substantial decrease in the DIC statistic (2.19 vs. 22.39), in comparison with the null model (Equation 8). A model that included only P_{Lit} lead to no improvement in the fit in comparison the null model. Once variation in temperature was accounted for, adding P_{Lit} as second covariate resulted in a further decrease in the DIC. The difference in the DIC statistics between a model that only included temperature and one that included temperature and proportion littoral area was 8.49. In general, it is suggested that a difference of 5 is necessary to distinguish between models in the traditional AIC approach, and given the extra error associated with more parameters p_D , it is suggested that this difference should be greater (Burnham and Anderson 2002). Therefore, adding proportion littoral area to the model leads to an improvement over a model with only temperature, and we selected this as the optimal model,

(17)
$$Q_{max} = \frac{e^{[-a(T-T_{max})^2 - q_0]}}{P_{Lit} + x(1 - P_{Lit})} E.$$

The mean and standard deviations of the posterior probability density function for parameters in Equation (17) are given in Table 2.3, and the fit of the model to the data is shown in Figure 2.1.

There was no indication that the chains for the estimated parameters did not converge and we observed a less than 1% change in the estimates of the posterior for all parameters when the prior precision was reduced and modeled assuming log-normal error. Estimate of the 95% probability interval for x (coefficient for littoral area) did not overlap with 1, indicating a significant relationship (Table 2.3). This further suggests that including the proportion of littoral area (in addition to temperature and effort) best describes our data, even though the improvement based on the DIC statistic was considered to be only moderate.

Using the estimated parameters from the best fit model we examined how variation in temperature and the proportion of littoral area affects the estimate of q (Figure 2.2). This model predicts a seven-fold variation in q with temperature and declining q with increasing proportion of littoral area. We also examined how the uncertainty in the estimated parameters leads to uncertainty in the estimated population size (coefficient of variation) with variation in the proportion littoral area and temperature for the best-fit model. We found that the uncertainty in the population estimate is minimized when lakes are sampled between 10 and 14°C and that the uncertainty decreases as the proportion of littoral area increase (Figure 2.3). Similarly, we also examined how variation in lake size (net-effort density) contributes to uncertainty in the estimated parameters. We found that the uncertainty in the population estimate and the coefficient of variation increase with increasing lake size (Figure 2.4).

2.4 Discussion

Fisheries managers often require efficient methods for assessing populations across a variety of lake types. Here we present an analysis of how gillnet capture efficiency varies with lake characteristics and demonstrate how using a fixed number of gillnets can provide estimates of population size. Once we accounted for variation in lake-size (net-effort density), we found that gillnet catchability was driven by temperature and lake-basin characteristics (proportion of littoral area). This analysis suggests that in the absence of mark-recapture data, these three factors can be used to predict population size.

We observed a substantial improvement in the fit of the model to the data when temperature was added as a covariate. Our results complement several other studies that have linked gillnet CPUE to water temperature (Chifamba 2000; Linløkken and Haugen 2006). We estimated that maximum gillnet catchability occurs at 12.0°C and that there is a 7-fold increase in catchability with variation in water temperature (once lake size has been accounted for). Similarly, McMichael and Kaya (1991) demonstrated that Rainbow Trout catch rates via angling are also maximized at about 12°C.

The fit of a model to our data was further improved when the proportion of littoral area was included as a covariate. The estimate for the coefficient of P_{Lit} was 0.37, indicating that q decreases as P_{Lit} increases (Figure 2.2). The posterior probability density for x did not overlap with 0 and this suggests a significant relationship with P_{Lit} and implies that the proportion of the population in the pelagic habitat varies with the amount of littoral area. This observed relationship supports other results that demonstrate how littoral area affects the distribution of Rainbow Trout in lakes (see Swales 2006 for a review). This relationship suggests a density-dependent change in fish behavior that varies with the amount of littoral area. This behavioral flexibility makes sampling only one habitat not representative of the entire population and therefore, it is important to sample both littoral and pelagic habitats.

Understanding how habitat influences the distribution of fish species has important implications for sample design and analysis. Other studies have documented strong relationships between habitat and catch rates for a variety of species (James 1995; Myers et al. 1997; Pierce et al. 2010; Schmalz and Staples 2011). For example, Pierce et al. (2010) found that gillnet catchability was strongly related to lake-basin characteristics when fish density was calculated using total area. However, when they calculated fish density using littoral area, all relationships with lake characteristics disappeared. This suggests that understanding habitat use is important in estimating catchability. It is not surprising that we found a strong relationship between gillnet catchability and lake characteristics for Rainbow Trout as the biology of Rainbow Trout differs substantially from pike (Esox lucius). Pierce et al. (2010) also detected density-dependent catchability when the total lake area was used to calculate fish density. Hyperstability in Equation (1) results in density-dependent catchability (CPUE remains high as fish density decreases) and is hypothesized to be a result of several mechanisms, such as spawning aggregations, gear saturation, behavioral stimulation (bait-based capture), selective targeting (Walters and Martell 2004). It is unlikely that any of these mechanisms affect catchability in this gillnet design, since fish are sampled in the fall (Rainbow Trout spawn in the spring), nets are placed in areas that represent the general habitat of the lake and a small number of fish caught in each net (40-200 fish / 7-panels of net), making saturation effects unlikely.

We assume that the extrinsic factors affecting the catch (size-selectivity) remain constant across sampling units, but the intrinsic factors vary. This variation in intrinsic factors (fish behavior and habitat preference) are accounted for in our efficiency model.

Size-structure and intra-cohort interactions are well known to influence Rainbow Trout behavior through either density-mediated or behaviorally-mediated effects (Walters and Post 1993; Post et al. 1999). These density-dependent processes may impact the foraging behavior of Rainbow Trout, and thus impact exploitation rates observed in index netting. For example, Biro and Post (2008) demonstrate a large variation in capture vulnerability between domestic and wild Rainbow Trout strains. The majority of the study lakes consisted of a single strain (Pennask) of stocked Rainbow Trout and had no known natural recruitment. Kentucky and Pat Lake were also stocked with a domestic strain of Rainbow Trout from the Fraser Valley Trout Hatchery. Accounting for variation in efficiency between strains could potentially improve the fit of our model. However, no obvious patterns were detected by examining the residuals of the fit for Kentucky and Pat Lake in comparison with the other study lakes.

2.4.1 Bayesian Implementation and Uncertainty Analysis

Our study adds to the growing body of literature using Bayesian techniques for relatively simple statistical analyses. Bayesian techniques are now considered a standard approach in fisheries stock assessment and this has allowed for population and management parameters to be described by probability distributions, rather than traditional point estimates (McAllister et al. 1994; Punt and Hilborn 1997; Forrest et al. 2008; Robb and Peterman 2011). Although our analysis could have been completed using likelihood methods, we used a Bayesian approach to fully explore the uncertainty in the estimated parameters. The application of Bayesian techniques for fisheries management has been limited in the past due to computational intensive methods required to produce posterior distributions. However, the development of MCMC software such as OpenBUGS has increased the computational efficiency in this type of analysis. As with all Bayesian analysis, it is well known that errors in data, prior mis-specification and an inappropriate probability model for the data may result in unreliable posterior distributions (McAllister and Kirkwood 1998; Berger 1994). However, in our analyses, we used vague prior distributions and conducted a sensitivity analyses on the priors and probability model for the data and this indicated that our choice of distributions had little impact on the posterior probability density function of the estimated model parameters. We used a log-normal distribution in the sensitivity analysis and although we recognize that this distribution is inappropriate for our data (as a log-normal distribution allows Q_{max} to take on values greater than 1), we chose this distribution as a good comparison to the logit model as our estimates for Q_{max} are extremely low (maximum estimated value for Q_{max} was 0.12).

We used Bayesian statistics to demonstrate the importance of understanding sources of error in estimated parameters when developing sampling protocols for assessing the status of populations using index gillnetting. Our results indicate that estimates of fish density is the most precise when lakes are sampled around 12°C (and lakes with a large proportion of littoral area). We also show that lake area (or net-effort density) has a large impact on the coefficient of variation in the population estimate. Population estimates are most precise for high net-effort density and increasing net-effort density in large lakes will increase the precision in the population estimate. This analysis provides a simple method to incorporate uncertainty in the estimated parameters into uncertainty in the population estimate. This can be accomplished by randomly drawing

values (with replacement) from the posterior PDF for each of the estimated parameters, and then using these values, calculate *N* using the binomial distribution based on the observed catch (Equation 13). This process is also easily implemented in the OpenBUGS software package.

2.4.2 Management Implications and Future Directions

Management agencies often have insufficient capacity to use mark-recapture or depletion methods to assess fish populations. This sampling protocol and analysis allows for efficient sampling of many populations. However, management agencies need to consider what level of precision in population estimates is required for making management decisions. If the desired level of precision is not achieved through this approach, then mark-recapture studies or a more detailed population assessment model, based on life history and recruitment data is needed. There is always an underlying tradeoff between precision, resources needed and fishing mortality in choosing a netting intensity. Askey et al. (2007) showed results for intensively netted experimental lakes, but this level of fishing mortality would not be acceptable to the public in open fisheries. The results of our analysis show high variability in the population estimates with this sample design, but we also demonstrate that fishing mortality can exceed 10% on small lakes. The objective of our study was to estimate the efficiency of methods currently deemed acceptable in open fisheries in British Columbia in order to interpret current and historical data.

This study also demonstrates the importance of understanding fish behavior when designing sampling protocols. It is likely that several other covariates (for example,
depth, habitat structure, size-structure of the fish population and water quality) may also impact the distribution of fish within a lake. Future studies for developing methods for index netting should focus on quantitatively describing how these factors affect catchability. Additionally, future research could be directed to increasing the precision in the population estimates by analyzing the variation in net catches over multiple years, since recruitment (stocking rate) can be held constant on many lakes in British Columbia.

Lake	Area	Perimeter	% Littoral	Elevation	Temperature	Fish	UTM	UTM	UTM
	(ha)	(m)	Area	(m)	(°C)	Caught	Zone	Easting	Northing
Doreen	44.7	4404	51.6	1358	12.0	227	11	347334	5553943
Flyfish West	29.2	2800	66.4	1354	11.3	104	11	346908	5551011
Idleback	11.6	1830	74.3	1400	10.0	101	11	334147	5486617
Jackpine	42.9	3720	24.7*	1300	10.0	189	11	298681	5533393
Kentucky	36.0	5259	29.4	1000	8.8	53	10	674856	5531067
Leonard	11.9	2711	78.9	1344	13.8	66	10	684606	5522059
Loon	8.5	1100	56.7	1355	12.0	59	11	347264	5552363
McConnell	32.4	3100	51.9*	1285	10.1	81	10	680409	5600241
Ripley	5.7	1143	63.2*	923	15.4	152	11	308362	5457645
Six Mile	8.1	1900	80.1	602	12.2	116	10	659571	5623033
Stake	23.1	2736	78.0*	1320	9.8	268	10	678610	5598917
Vinson	20.5	2484	66.3	1374	13.2	89	10	684270	5519611

Table 2.1 Characteristics and total net catches for the study lakes. Measured values for % littoral area are indicated by an *.

Table 2.2 Prior distributions used in the analysis. B indicates a beta distribution with parameters (alpha, beta); LN: log-normal distribution (mean, log precision) and G: gamma distribution (shape 1, shape 2). Sensitivity analysis was only conducted on best-fit model

Parameter	Prior	Prior for Sensitivity Analysis
q	B(1,1)	N/A
q_0	LN(0.5,0.5)	N(1,0.01)
q_1	B(1,1)	N/A
а	LN(0.1,0.5)	N(1,0.01)
T_{max}	LN(12,0.5)	N(12,0.01)
x	LN(0.3,0.5)	LN(0.2,0.1)
τ	G(0.01,0.01)	G(0.01,0.01)
α	N(0.6,0.01)	N/A
eta	N(1.1,0.01)	N/A
γ	N(-0.03,0.01)	N/A
δ	N(0.003,0.01)	N/A

Table 2.3 Sample statistics from posterior probability density function for best fitmodel. PI corresponds to probability interval.

Parameter	Mean	Standard Deviation	Lower 2.5% PI	Upper 97.5% PI
а	0.1549	0.0170	0.1205	0.1880
T_{max}	12.02	0.1165	11.78	12.24
q_0	0.4873	0.0908	0.2962	0.6628
x	0.3702	0.1622	0.1105	0.7444

Figure 2.1 (a) Variation in gillnet catchability (Qmax) as a function of lake area. Observed (solid circles) and model predicted (open circles) values from best fit model. Model predicted values are horizontally offset for presentation. (b) Variation in residuals (observed - predicted values) of from graph (a) across lakes.



Figure 2.2 Model predicted effects of (a) temperature and (b) proportion of littoral area on q for best fit model. Figures were generated assuming $P_{Lit}=1$ for (a) and $T=T_{max}$ in (b) for a 20 ha lake.



Figure 2.3 Coefficient of variation in population estimates as a function of the proportion littoral and temperature.



Figure 2.4 (a) Variation in the uncertainty in the estimate of fish density with lake size (or net density). Error bars represent 95% probability intervals. (b) Variation in the coefficient of variation in the estimate of fish density as a function of lake size. Figures were generated assuming T=12°C and $P_{Lit} = 0.5$ and net density was calculated as 1 net combination (floating and sinking gang) per hectare.



Chapter Three: Angler Characteristics and Management Implications in a Large Multi-Stock Spatially Structured Recreational Fishery

3.1 Introduction

Recreational fisheries are complex systems governed by the interaction of ecological and social processes. Ecological processes such as recruitment dynamics, growth and survival are responsible for determining fish supply and production (Shuter et al. 1998; Parkinson et al. 2004), whereas social processes influence angler behavior and corresponding impacts on the fishery (Hunt et al. 2011). A substantial amount of research has been conducted on modelling the ecological component of fisheries (Hilborn and Walters 1992; Walters and Martell 2004) and these concepts have been more recently applied to the management of recreational fisheries (Radomski 2003; Allen et al. 2009). Similarly, human dimensions research of recreational fisheries often aims to answer questions regarding angling behavior; specifically to understand where, when and how much anglers fish and factors influencing harvest decisions among anglers (Fedler and Ditton 1994; Hunt 2005). However, these social and ecological processes do not operate independently, and recently several authors have suggested that the management of recreational fisheries needs to focus on understanding and quantifying the dynamic interactions within this social-ecological system (Johnston et al. 2010; Hunt et al. 2011; Fenichel et al. 2012; van Poorten et al. 2011).

Management strategies for recreational fisheries are moving away from the conventional single-stock paradigm and shifting towards the idea that individual fisheries are nested within a broader geographical landscape of angling opportunities (Shuter et al.

1998; Lester et al. 2003; Carpenter and Brock 2004; Post et al. 2008; Post and Parkinson 2012). Across a spatially-structured fishery, it is likely that anglers vary in skill level and harvest behaviors; and these anglers are not randomly distributed across the landscape. Hunt (2005) suggested that fishing site and participation choices vary across the angler population and involve six general attributes: costs, fishing quality, environmental quality, facility development, encounters with other anglers and regulations. Similarly, it is well understood that anglers' impacts on stocks vary greatly (Jones et al. 1995); angler experience varies substantially across the angler population and angler skill level is strongly correlated with catch rates (Bannerot and Austin 1983; Fisher 1997). Exploitation results from not only the intensity of angling effort, but also the efficiency of the effort. Additionally, the propensity of anglers to harvest fish varies across the population of anglers and is often correlated with angling specialization (Bryan 1977; Ditton et al. 1992; Johnston et al. 2010; Beardmore et al. 2011). This heterogeneity in angler characteristics results in the need to quantify the source (spatial distribution), efficiency and behavior of effort in order to develop empirically-based management strategies for a fishery.

The Rainbow Trout *Onchorhynchus mykiss* fishery of British Columbia is an example of a multi-stock, spatially structured, open-access fishery (Cox and Walters 2002; Parkinson et al. 2004; Post et al. 2008). There is a substantial amount of information on ecological processes that delimit the availability of resources in this system (Walters and Post 1993; Post et al. 1999; Parkinson et al. 2004) but a more limited understanding of the spatial distribution of anglers, the efficiency of angling effort and the resultant harvest mortality for this fishery. Our goal for this research was to assess the

spatial behavior, harvest behavior and catch efficiency of anglers across this large spatially structured fishery to understand the strengths of interactions in this socialecological system.

3.2 Methods

3.2.1 Study Design and Data Collection

We examined anglers and fish populations from 21 lakes within three management regions in the interior of British Columbia, Canada (Figure 3.1). We selected lakes to represent the range of physical characteristics and management conditions (i.e. bag limits) that exist within this fishery (Table 3.1). All study lakes were monocultures of Rainbow Trout and were annually stocked with age-0 or age-1 fish. Cobb, Eena and Vivian Lakes were also stocked annually with brook trout *Salvelinus fontinalis*.

Angler surveys were conducted at each lake between 1000 and 1800 hours from April 1 to August 31 in either 2010 or 2011. Survey days were randomly stratified among lakes between weekends and weekdays, and more intense survey effort occurred in the spring when angling pressure was greatest. All study lakes had single access points and no private housing (with the exception of Vivian and Eena Lakes), ensuring that all anglers had an equal opportunity of being interviewed. Anglers 18 years of age and older were interviewed before their trip and were asked questions relating to demographics and catch expectations. The same anglers were then interviewed after their trip and asked to report on catch success (Table 3.2). All anglers that completed a fishing trip within the

duration of the survey day were approached for an interview and if there was more than one angler in a party, each angler was interviewed separately.

Fish density was estimated in each lake using a standard gillnet sampling protocol in the fall following the angler survey. Two multi-mesh gangs of gillnets were set overnight in the littoral and pelagic habitat of each lake. This gillnet design is highly sizeselective against small fish, and essentially non-size-selective for larger fish (Askey et al. 2007). Fork length of all captured fish was measured and recorded. Estimates of fish density were adjusted to account for angling vulnerability. Cox (2000) demonstrated that Rainbow Trout in similar lakes within this same area exhibit the length-at-50% vulnerability (L_{50}) between 214 and 330 mm. We used an average value for L_{50} of 264 mm in this analysis. Captured fish from gillnets were grouped into 10 mm size classes and vulnerability-at-length (v_t) for the mid-point of the size bin was calculated as

(1)
$$v_l = \frac{l^m}{l^m + L_{50} m}$$

where m = 7 (Cox 2000). Fish density for each lake (D_L) was calculated as

(2)
$$D_L = \sum_l^{l_{max}} v_l N_l$$

where N_l is the population estimate in length-bin *l*. Additional sampling details are described in Ward et al. (2012).

3.2.2 Angler Characteristics

It is well known that recreational anglers have diverse characteristics and behaviors which affect optimal management strategies (Fedler and Ditton 1994; Fisher 1997; Johnston et al. 2010). We conducted an exploratory analysis of angler characteristics in this fishery. Specifically, we chose to focus the majority of our analysis on characteristics of anglers that directly impact the dynamic interaction of anglers with the fishery: the source (spatial distribution of anglers), efficiency (angler catchability) and behavior (propensity of anglers to harvest fish) of effort. The spatial distribution of anglers in this fishery was explored by calculating the distance the interviewed anglers travelled from their home to the lake (based on their postal codes). Catchability (q) is analogous to the capture efficiency of the angler and we used catchability as a measure of an individual's success as it is a better assessment than CPUE across lakes that vary in fish density. Catchability is the parameter that links catch-per-unit-effort (CPUE) to fish abundance (N) in the form CPUE = qN. Individual angler catchability was calculated as a measure of an anglers' success rate

(3)
$$q_{i,L} = \frac{CPUE_{i,L}}{D_L}$$

where $q_{i,L}$ is the relative catchability of angler-*i* in lake-*L*. Harvest behavior of anglers was explored by calculating the ratio between observed harvest and catch. In addition to understanding how harvest behavior varies with other angler characteristics in this fishery, we also developed a linear model to relate the proportion of the catch that is harvested to the bag limit and CPUE across lakes.

We used multivariate techniques to assign individual anglers to groups (clusters) based on the three variables: distance travelled to the lake, the proportion of the catch that was harvested and catchability. Assigning anglers to specific groups using this method creates clusters of individuals that are more similar to each other than to individuals in other clusters. We used a similar analysis to Chipman and Helfrich (1988) to assess the

existence of discrete angler groups. Each of the three variables was transformed to be between 0 and 1, and scaled across variables to ensure similar weighting in the analysis. These variables were then used in a hierarchical cluster analysis based on a Euclidean distance matrix and Ward's method to classify anglers (R package *hclust*). The optimal number of clusters to extract was determined by comparing the Dunn index, normalized gamma coefficient, average silhouette width and within cluster sum of squares across a range of cluster sizes (Halkidi and Batistakis 2001; Meila 2007). Optimal solutions for the Dunn index, normalized gamma coefficient and average silhouette width are considered to be the number of clusters that corresponds to the maximum value. The optimal number of clusters for the within cluster sum of squares is identified by a rapid decrease in the slope.

We explored how the mean and statistical significance of characteristics of anglers varies among these discrete groups and tested for differences in the distance anglers travelled to the lake, catchability and the proportion of the catch that is harvested between groups using ANOVA followed by a Tukey test for multiple comparisons. In addition to comparing differences in the three variables used in the cluster analysis, we also compared three other descriptive variables of anglers. We used two variables to describe frequency of fishing: angler avidity (the number of days fished per year) and the proportion of days fished in the previous year that were overnight trips. Additionally, we compared angler CPUE between groups. We chose not to include these three variables (days fished per year, proportion of overnight trips and CPUE) in the cluster analysis as they are descriptive variables of the anglers and do not directly affect the interaction of anglers with the fishery.

We also compared angler characteristics and the distribution of anglers within the identified groups among three management regions. A chi-square analysis was used to test the hypothesis that the proportion of anglers within groups differed across the three different management regions. All statistical analyses were conducted in R (2.13.1) and stated packages.

3.3 Results

We interviewed 2,498 anglers across 21 lakes to quantitatively assess the interaction of anglers with the Rainbow Trout fishery in three regions in British Columbia. Incomplete interviews were discarded from the dataset and the analysis was conducted on the remaining 1,956 interviews. Univariate analyses of the data showed that the spatial distribution (distance travelled to the lake), harvest behavior (proportion of the catch that was harvested) and catch efficiency (catchability) varied substantially across the interviewed anglers (Figure 3.2).

The distribution of the distance travelled by anglers to the lake was bimodal (Figure 3.2a), suggesting that the angler population was composed of both local and non-local anglers. A split of the angler population into non-local and local anglers (defined arbitrarily as anglers travelling greater or less than 200 km to the lake respectively) revealed dramatic differences in catch efficiency and harvest behavior among anglers. Catchability differed between local and non-local anglers ($t_s = -3.68$; df = 789, p = 2.48 x 10⁻⁴) with local anglers having lower mean catchability ($\mu = 9.41 \times 10^{-3}$; $\sigma = 0.024$) than non-local anglers ($\mu = 14.83 \times 10^{-3}$; $\sigma = 0.031$). The proportion of the catch that was harvested also varied between local and non-local anglers ($t_s = -2.98$; df = 1105, p = 2.95

x 10⁻³) and local anglers harvested a greater proportion of their catch ($\mu = 0.18$; $\sigma = 0.34$) in comparison with non-local anglers ($\mu = 0.13$; $\sigma = 0.30$).

The distribution of the proportion of the catch that was harvested (Figure 3.2b) suggests that most anglers harvested a low proportion of their catch ($\mu = 0.17$; $\sigma = 0.33$). Across lakes, the proportion of the catch that was harvested (ρ) was found to be a linear function of the mean CPUE and the bag limit (B_L) on a lake (R² = 0.9249),

(4)
$$\rho = -2.023 \times 10^{-3} CPUE + 5.18 \times 10^{-2} B_L$$

suggesting that decreases in CPUE and bag limits corresponded to an increase in the proportion of the catch that is harvested. Catch efficiency (catchability) also varied among anglers (Figure 3.2c), and approximately 88% of anglers had catchabilities less than 0.02 ha \cdot h⁻¹ (or less than 2 fish \cdot h⁻¹ in a lake with 100 fish \cdot h⁻¹).

We used multivariate techniques to determine if sub-classes of anglers exist within the total sample of anglers interviewed based on variables that describe how anglers interact with the fishery. Cluster validation statistics suggested that the optimal number of clusters to extract from the data was four. The Dunn Index and average silhouette width were maximized at four clusters and the normalized gamma coefficient was maximized at eight clusters. The within groups sum of squares had a rapid decrease in the slope at four clusters. Based on these results, four discrete groups of anglers were identified by the cluster analysis based on the cluster validation statistics provided by the Dunn Index, average silhouette width, normalized gamma coefficient and the within cluster sum of squares.

The four angler groups identified by the cluster analysis varied substantially in their quantitative characteristics and differed in their proportion within the sample of

anglers interviewed (Table 3.3). Angler Group 1 was characterized as having the lowest average travel distance to the lake (69.1 km), lowest catchability (3.22 ha \cdot h⁻¹ x 10⁻³) and lowest proportion of catch harvested (0.00) among the four angler groups. Angler Group 2 was characterized by the greatest travel distance to the lake where they were interviewed (381.1 km), Angler Group 3 was characterized by a ten-fold higher catchability (75.35 ha \cdot h⁻¹ x 10⁻³) whereas Angler Group 4 harvested the highest proportion of their catch (0.66) in comparison to other groups. The four discrete groups also differed in a series of other descriptive characteristics not used in the cluster analysis (Table 3.3). For example, Angler Group 3 was composed of the most avid anglers (fishing an average of 37.2 days per year) and Angler Group 2 took the highest proportion of overnight trips for the purpose of fishing (0.44). CPUE varied significantly among the angler groups, and was strongly correlated with catchability. Angler Groups 2 and 4 had non-statistically different catchabilities, but angler Group 4 had approximately two times higher average CPUE than angler Group 2, suggesting that Angler Group 4 fishes most often in lakes with approximately double the fish density.

The variables describing the quantitative interaction of anglers with the resource, and others descriptive variables, also differed among the three management regions stratified within the survey design (Table 3.4). Anglers in the Omineca region travelled the shortest distances to fish, anglers in the Okanagan region harvested the lowest proportion of their catch and had the highest catchabilities. Anglers in the Thompson region were the most avid anglers (fished the most days on average per year) and had the highest CPUE, and anglers in the Okanagan region took the highest proportion of overnight trips in contrast to the other regions. The proportion of anglers within the four

angler groups identified by the cluster analysis varied significantly among management regions ($X^2 = 125.4$; df = 6; $p < 2.2 \times 10^{-16}$). Angler Group 1 was the most numerous in all regions. In the Okanagan region, anglers were distributed roughly evenly between Angler Groups 2, 3 and 4. In contrast, anglers in the Omineca region mainly belonged to groups 1 and 4.

3.4 Discussion

Anglers who fish stocked Rainbow Trout lakes across a broad landscape in British Columbia varied substantially in characteristics that determine quantitatively how anglers interact with the fishery. Spatial distribution, efficiency and propensity to harvest varied among anglers. Angler efficiency (catchability) and harvest behavior were strongly correlated with distance travelled to the lake. Anglers who travelled short distances to the lake (local anglers) had lower catchabilities and harvested a higher proportion of their catch in comparison with anglers who travelled long distances to fish (non-local anglers). This suggests that the angler population does not interact homogeneously within this spatially structured fishery, and therefore it is useful to understand and quantify how different angler types affect the fishery.

Our observation of the existence of multiple discrete groups of anglers complements other studies that have described diversity in angler characteristics using similar multi-dimensional approaches (Chipman and Helfrich 1988; Fisher 1997). The theory of recreational specialization, first proposed by Bryan (1977), provides a conceptual framework for understanding the multi-dimensional aspects of anglers' behaviors and attitudes. Recreational specialization is now thought to include three main

dimensions: a behavioral dimension measured by the frequency of participation, a cognitive dimension measured by knowledge and skill, and an affective component measured by commitment to the activity (Scott and Shafer 2001). In North American based studies of angler specialization, least specialized anglers emphasized the important of non-catch related factors as motivations for fishing, but were still likely to harvest fish, and the most specialized anglers were motivated by resource-related factors (trophy fish) and were most likely to demonstrate catch and release behavior (Byran 1977; Chipman and Helfrich 1988; Fisher 1997; Hutt and Bettoli 2007).

The characteristics of the four groups identified by the cluster analysis align well with other studies that have identified several groups of anglers that represent the continuum of specialization (Graefe 1980; Chipman and Helfrich 1988; Hutt and Bettoli 2007). For example, Chipman and Helfrich (1988) identified six groups of anglers and found that the frequency of fishing, investment in the resource and consumptive habits best described variation among anglers in their study. Similarly, Hutt and Bettoli (2007) identified five groups of anglers and the groups differed in their attitudes towards harvesting trout and catching trophy fish. The variation in behavior of anglers in our study within the discrete groups is consistent with the literature surrounding the theory of recreational specialization. For example, anglers in Group 2 could be characterized as most specialized: these anglers travelled the furthest to fish, harvested a low proportion of their catch, and fished frequently. Similarly, several authors have found that most specialized anglers travelled greater distances, fish more frequently and attached a greater emphasis on angling as a recreational activity than anglers with lower levels of specialization (Salz et al. 2001; Oh et al. 2005; Hutt and Bettoli 2007; Carlin et al. 2012).

In contrast, anglers in Group 4 share similarities to low specialization groups as described by Chipman and Helfrich (1988). They identified that least specialized anglers were motivated by family-oriented recreation, were satisfied with catching small fish and placed greater emphasis on harvesting fish. In our study, anglers in Group 4 harvested the highest proportion of their catch, fished the lowest number of days per year and travelled a relatively short distance to fish. The characteristics of anglers in Group 1 tended to align best with low specialized anglers, except these anglers did not harvest fish. Similarly, anglers in Group 3 appeared to be closely related to the most specialized anglers as they fished the most frequently (and had the highest catchabilities) but travelled shorter distances on average in comparison with anglers in Group 2.

The relative proportion of the four angler groups differed among regions within the British Columbia Rainbow Trout fishery. This implies that region-specific management strategies could be developed to better reflect to the distribution of angler types. For example, Anglers in Group 2 appeared the most specialized and travelled the furthest to reach fishing opportunities. Arlinghaus and Mehner (2004) found that more specialized anglers were willing to travel further to access fishing opportunities, in comparison with lower specialized anglers. Management strategies aimed at maximizing utility across all anglers could consider optimizing management for highly specialized anglers by using restrictive regulations aimed at creating trophy-type fisheries at the least accessible lakes (see Johnston et al. 2010 for an example). In general, more specialized anglers are often more receptive of restrictive regulations in comparison with lower specialized anglers, and highly specialized anglers are more likely to follow restrictive regulations and even impose voluntary regulations to preserve fish stocks with high

angling quality (Ditton et al. 1992; Oh and Ditton 2006; Dorow et al. 2009). In contrast to managing lakes for highly specialized anglers, easily accessible lakes would likely derive the maximum utility by optimizing management based on the demands of least specialized anglers (such as family-oriented settings with liberal bag limits).

Anglers in Group 1 (low specialized anglers who did not tend to harvest fish) were the most common across all regions. Since least specialized anglers are motivated by family-oriented recreation and are satisfied with catching small fish, all regions could focus on managing easily accessible lakes with high stocking densities and liberal bag limits for these anglers. The proportion of anglers within the other three groups varied across regions. The Thompson region had the highest proportion of the most specialized anglers (Angler Group 2) and fisheries with restrictive regulations and low stocking densities would be optimal for this is group, since highly specialized anglers tend to prefer to fish at trophy fisheries which are enhanced by these management actions (Byran 1977; Chipman and Helfrich 1988; Fisher 1997; Hutt and Bettoli 2007). In contrast, the Omineca region was almost entirely composed of low specialized anglers and this suggests that most lakes in this region could be managed to maximize the utility of these low specialized anglers by having high stocking densities and liberal bag limits. The proportion of anglers among angler groups in the Okanagan region was more uniform than in the other regions. This suggests that lakes in this region could be managed for both highly specialized and least specialized anglers. By including this diversity in angler characteristics in predictive models, managers' abilities to predict the ecological impacts of fishing and strategies for optimizing management will be improved (Johnston et al. 2010).

Anglers in groups 4 represented 24% of all anglers interviewed. These anglers were characterized by travelling short distances to the lake, harvesting a high proportion of the catch, and having moderate catchabilities and CPUE. Across all anglers, the propensity to harvest fish at lake was negatively related to mean CPUE and positively related to the bag-limit. This suggests that as resources get scarcer, anglers are more likely to harvest fish, and similar trends have been noted for Walleye in Alberta, Canada (Sullivan 2002). In stocked fisheries, population collapse is not a concern, but neighboring wild populations may be at risk for overfishing. Specifically, if wild Rainbow Trout populations in close proximity to population centers attract least specialized anglers, these anglers are more likely to harvest fish and can have impacts on sustainability. Therefore, it is useful to understand the impacts and relative effort of such anglers across the landscape to highlight potential management concerns for neighboring wild populations.

We recognize that we have conducted our study on a relatively small and nonrandom subset of lakes within three management regions across the broad landscape of the Rainbow Trout fishery in British Columbia. Although non-random, these lakes do provide fisheries that are reasonably representative of those in the regions with moderately high effort, variable travel distance from primary residences and a range of fish abundances and therefore we suggest that the inferences we draw effectively describe how anglers interact within the fishery through their spatial distribution, efficiency and harvest behavior. Our approach differs from that used by researchers who simply want to study specialization, such as in Oh and Ditton (2006); our goal was to understand and

quantify the processes that translate angler behavior into harvest impacts over a spatiallystructured recreational fishery.

The occurrence of discrete angler groups, variation in the behavioral characteristics of these groups and variation in the proportion of these groups across regions demonstrates the potential for complex interplay of the ecological-social systems of recreational fisheries (Fenichel et al. 2012). Management of recreational fisheries that integrates both social and ecological components has been repeatedly called for (Arlinghaus 2006; Hunt et al. 2007; Post et al. 2008) but not often carried out at the scale of spatially complex fisheries (for an exception see Hunt et al. 2011). Effective integration requires quantitative relationships describing both social and ecological processes over space. Our work represents the first attempt to simultaneously quantify variation in angler characteristics among groups, characteristics that directly link to interactions with fish populations (such as catchability and propensity to harvest) and spatial behavior over a spatially distributed fishery. This understanding will provide the processes necessary to develop predictive process models to examine optimal management actions for this valuable fishery.

Lake	Area	Elevation	Management	Bag	Year
	(ha)	(m)	Region	Limit	Sampled
Burnell	12.7	730	Okanagan	0	2011
Cobb	215.0	771	Omineca	5	2011
Crown	7.6	807	Thompson	5	2010
Doreen	44.7	1358	Okanagan	5	2011
Eena	51.0	762	Omineca	5	2011
Flyfish	29.2	1354	Okanagan	5	2011
Gypsum	14.0	1458	Thompson	5	2010
Idleback	11.6	1440	Okanagan	1	2011
Jackpine	42.9	1200	Okanagan	5	2011
Kentucky	36.0	1000	Okanagan	5	2011
Kidd	18.8	1058	Okanagan	0	2011
Leonard	11.9	1344	Okanagan	2	2011
Loon	8.5	1355	Okanagan	5	2011
McConnell	32.4	1285	Thompson	5	2011
Pat	8.1	602	Thompson	2	2011
Ripley	5.7	923	Okanagan	5	2011
Stake	23.1	1320	Thompson	5	2011
Turquoise	6.5	808	Thompson	5	2010
Tyner	18.1	1332	Thompson	5	2010
Vinson	20.5	1374	Okanagan	1	2011
Vivian	45.0	779	Omineca	5	2011

Table 3.1 Physical characteristics, bag limit and sampling year for the study lakes.

1 Table 3.2 Angler Survey Questions

2	Pre-tri	p Questions
3	1.	How many days did you go fishing in the previous 2 years?
4	2.	What percentage of days fished in the previous 2 years were overnight trips?
5	3.	What is your postal code?
6	4.	How many fish do you expect to catch?
7	5.	How many fish do you expect to keep?
8	Post-tr	ip Questions
9	1.	How long did you fish for?
10	2.	How many fish did you catch?
11	3.	How many fish did you keep?
12		

- 13 **Table 3.3 Characteristics of angler groups identified by the cluster analysis.**
- 14 Variable means are presented for each angler group. Superscripts indicate variables
- 15 that are not significantly different at p<0.05 as indicated by Tukey's test for
- 16 multiple comparisons.

		Angler Group				ANOVA Results		
	Cluster Variable	1	2	3	4	DF	F	р
ables	Distance Travelled to Lake (km)	69.1	381.1	165.3	102.6	3	739.9	< 0.05
ıster Var	Proportion of Catch that was Harvested	0.0 ^{a,b}	0.02 ^{a,c}	0.04 ^{b,c}	0.66	3	1654	< 0.05
Clr	Catchability (ha·h ⁻¹ × 10 ⁻³)	3.22	6.43 ^a	75.35	6.45 ^a	3	964.7	< 0.05
Other Variables	Days Fished Per Year	26.8 ^{a,b}	30.4 ^{a,c}	37.2 ^c	24.4 ^b	3	7.4	< 0.05
	Proportion of Overnight Trips	0.34 ^{a,b}	0.44 ^c	0.40 ^{a,c}	0.30 ^b	3	13.1	< 0.05
	CPUE (fish \cdot h ⁻¹)	0.49	0.69	2.48	1.23	3	147.8	< 0.05
	Number of Anglers	945	371	171	469			
	% of Sample	48.3	19.0	8.7	24.0			

18 Table 3.4 Mean values for angler characteristics and the percentage of anglers for 19 each angler groups within the three management regions. Superscripts indicate 20 variables that are not significantly different at p<0.05 as indicated by Tukey's test</p>

		Management Region				ANOVA Results		
		Okanagan	Thompson	Omineca	DF	F	р	
		(8)	(3)	(7)				
able	Distance Travelled to Lake (km)	138.9	175.7	86.3	2	24.52	< 0.05	
uster Vari	Proportion of Catch that was Harvested	0.13	0.2^{a}	0.25 ^a	2	14.52	<0.05	
Clı	Catchability (ha·h ⁻¹ × 10 ⁻³)	13.0	9.7 ^a	1.9 ^a	2	16.22	< 0.05	
ables	Days Fished Per Year	26.6	32.7	19.7	2	15.12	< 0.05	
ıer Varia	Proportion of Overnight Trips	0.42	0.26 ^a	0.26 ^a	2	53.03	< 0.05	
Ō	CPUE (fish $\cdot h^{-1}$)	0.83 ^a	1.01	0.76 ^a	2	6.87	< 0.05	
	1	49.8	39.8	64.9				
Group	2	17.5	26.8	4.2				
Angler (3	12.3	4.3	0.0				
	4	20.4	29.1	30.9				
	Number of Anglers	1187	578	191				
	% of Sample	60.7	29.5	9.8				

21 for multiple comparisons.

Figure 3.1 Location of management regions included in this study in British Columbia, Canada. Region 3, 7 and 8 correspond to Thompson, Omineca and Okanagan respectively.



Figure 3.2 Frequency distributions (expressed as proportion of interviewed anglers) for (a) distance travelled from an angler's home to the study lake, (b) the proportion of the catch that was harvested and (c) catchability. The x-axis on graphs (a) is on a log scale and the axis labels have been back transformed for interpretation



Chapter Four: A Mechanistic Understanding of Hyperstability in Catch-Per-Unit-Effort and Density-Dependent Catchability in a Multi-Stock Recreational Fishery

4.1 Introduction

Catch per unit effort (CPUE) data is commonly used in both recreational and commercial fisheries to assess the status of fish populations under the assumption that the catch from a fishing vessel is proportional to stock size (Hilborn and Walters 1992; Quinn and Deriso 1999). CPUE is commonly assumed to be a linear function of fish density, where CPUE is linked to fish density (*N*) using the model

(1)
$$CPUE = qN$$

where q is a catchability coefficient. However, it has been recognized for more than 50 years that changes in CPUE may not accurately reflect changes in fish abundance (Beverton and Holt 1957). Many non-linear versions of this model have been suggested, the simplest being a power function,

(2)
$$CPUE = \alpha N^{\beta}$$

so that when $\beta \neq 1$, CPUE is not linearly related to fish density and α is an estimate of q when CPUE and N are near the origin. A CPUE index is defined to be hyperstable when $\beta < 1$ and hyperdeplete when $\beta > 1$ (Hilborn and Walters 1992). Dividing equation (2) by N demonstrates the relationship between catchability (q) and fish density,

(3)
$$q = \frac{CPUE}{N} = \alpha N^{(\beta-1)}$$

where catchability is constant across fish density when $\beta = 1$, and density-dependent when $\beta \neq 1$ (catchability decreases with fish density when $\beta < 1$ and increases with fish density when $\beta > 1$). Hyperstability in CPUE has been documented in many commercial fisheries, and a few recreational fisheries (Shuter et al. 1998; Rose and Kulka 1999; Erisman et al. 2011). Processes that are responsible for hyperstability in commercial fisheries include: gear improvements, technological advances and fish aggregation (Crecco and Overholtz 1990; Rose and Kulka 1999). However, in open-access recreational fisheries, mechanisms resulting in hyperstability remain largely unknown. Hyperstability results in the 'illusion of plenty' where the stock is presumed to be abundant as a result of high CPUE, and no management action is taken until both the fishery and fish population collapses (Post et al. 2002; Erisman et al. 2011). Therefore, catchability is a key variable driving the dynamic interaction between angler effort and fish density, and the need to better understand catchability in recreational fisheries is well recognized (Hunt et al. 2011a; Fenichel et al. 2012; Post 2013).

Three competing mechanisms have been proposed to explain the observed patterns of hyperstability in recreational fisheries. First, it is hypothesized that behavioral aggregations or heterogeneity in habitat quality results in non-uniform distributions of fish and creates areas with high catch rates. If fish continually move into areas of preferred fish habitat as other fish are removed through harvest, CPUE will remain high as stock size declines and exhibit hyperstability (Shuter et al. 1998; Post et al. 2002; Post 2013). This mechanism that results in hyperstability has been documented in a few commercial and recreational fisheries, and is especially prevalent in species that form spawning aggregations (Clark 2001; Harley et al. 2001; Erisman et al. 2011). In fact, this mechanism is presumed to be one of the main processes that led to the collapse of the Atlantic cod (*Gadus morhau*) fishery off eastern Canada (Hutchings 1996; Rose and

Kulka 1999). The second mechanism that may result in hyperstability is variation in angler behavior. Less experienced anglers (who have lower proficiency in capturing fish, resulting in lower individual catchability) may abandon low-density fisheries that do not produce sufficient CPUE to satisfy their expectations (Post 2013). Conversely, human dimensions research has suggested that experienced anglers may actually be attracted to low density fisheries because low density fisheries are often correlated with more restrictive regulations and larger fish size (Chipman and Helfrich 1988; Hutt and Bettoli 2007). Therefore, as the composition of anglers shifts to more experienced anglers in low-density fisheries, the net catchability of anglers' is higher than would be expected if angler experience was independent of fish density, leading to hyperstability in CPUE. Third, hyperstability may arise due to the interaction between angler effort density and fish behaviour at the individual level. This hypothesis postulates that the fish community is composed of individuals that vary in their vulnerability to anglers, and as fish are caught, the most vulnerable individuals are removed or enter an invulnerable state (if fish are caught and released) for a certain period of time (Cox and Walters 2002; Askey et al. 2006). As angler effort increases, the number of fish that are vulnerable to anglers at any given time is reduced and catchability (measured as a function of the total stock size rather than the vulnerable stock size) will decrease with increases in fish density and result in hyperstability.

Separating mechanisms resulting in hyperstability in open-access recreational fisheries is difficult since density-dependent mechanisms related to fish and angler behaviour are confounded. Furthermore, it is well recognized that inappropriate statistical methods are expected to falsely detect hyperstability (Shardlow et al. 1985; Richards and

Schnute 1986). We evaluated the relationship between angler CPUE and fish density to determine if hyperstability exists in the Rainbow Trout (*Onchorhynchus mykiss*) lake fishery of British Columbia. We contrasted the relationship between CPUE and fish density in an open-access recreational fishery with an experimental fishery (a set of lakes that had restricted access, standardized fishing methods and no heterogeneity in angler experience) to test whether hyperstability is primarily a function of fish or angler behaviour.

4.2 Materials and Methods

4.2.1 Study Design and Species Information

In order to separate mechanisms hypothesized to produce density-dependent catchability in recreational fisheries, we gathered CPUE data and assessed fish population densities in two separate fisheries using 28 lake-years of data, derived from 24 individual lakes across 4 years (Table 4.1). We examined the relationship between angler CPUE and fish density in two contrasting situations: (1) an experimental fishery (with standardized angling methods, restricted public access and no heterogeneity in angler experience) and (2) an open-access recreational fishery.

The experimental and open-access fisheries were part of the large multi-stock, spatially structured Rainbow Trout fishery of the south-central region of British Columbia, Canada. All study lakes in the experimental and open-access fisheries were monocultures of Rainbow Trout, except Kentucky Lake, which also contained a population of redside shiner (*Richardsonius balteatus*). The lakes in the experimental fishery were feral hatchery populations (with supplemental stocking) where as the lake in

the open-access fishery were stocked annually with age-0 or age-1 hatchery fish and had no known natural recruitment.

4.2.2 Experimental Fishery

Since it is suspected that heterogeneity in angler skill level can result in densitydependent catchability, we controlled for the effects of angler heterogeneity on angling catch rates by experimentally fishing 6 lakes (in total 10 lake-years of data across 3 years) (Table 4.1). The experimental lakes were located on the Bonaparte Plateau, north of Kamloops, British Columbia at 120°21'54" W, 51°9'1"' N. These lakes were part of a long-term study on fish population dynamics and have restricted public access (and are considered to be in an un-fished state). Experimental angling followed methods in Askey et al. (2006) and angling occurred over a standardized period between August 10 and 17 in 2004, 2005 and 2011. A single angler fished all lake-years using two fly patterns from Askey et al. 2006 (black leech and general green nymph on size 14 hooks). The angler was considered to be an expert angler (fished an average of 20 days per year) and was instructed to behave as would a normal angler by focusing efforts on areas and habitats where catch rates and size of fish would be maximized. Time spent fishing and the number of landed fish were recorded. Fish population densities were estimated in each lake-year using mark-recapture techniques (sampling details are described in Askey et al. 2007). A large number of marked hatchery fish (range 417 - 726) of various sizes (range 50 - 400 mm) were released into each of the lakes approximately one week prior to recapture. Additional fish were marked in each lake using beach seines or fyke nets. Fish were recaptured over five consecutive nights of gillnetting. This sample design is highly

effective, approximately 40% of the population is captured in the gillnets (Askey et al. 2007), and therefore, the population estimates for these experimental lakes are precise (average CV for abundance estimates of fish >150mm = 0.03). Size-dependent vulnerability to angling was estimated in these lakes for the specific fly pattern and hook size as shown in Askey et al. (2006) and fish density estimates for fully recruited fish were adjusted accordingly. Although several of the lakes were experimentally fished in multiple years, the lakes are treated as independent samples as fish densities were altered among years as a result of stocking and depletion removal experiments.

4.2.3 Open-Access Fishery

We conducted creel censuses at open-access recreational fishing lakes (n=18) in the south-central region of British Columbia, Canada (Table 4.1). The lakes ranged from 5.7 to 44.7 ha in surface area and varied in harvest and gear regulations and angler effort (Table 4.1). These particular lakes were selected for creel censuses from a large recreational fishery to maximize contrasts across lakes in fish density and angler effort.

Angler surveys were conducted at each lake from 1000 to 1800 hours from the first ice-free date to September 15 in 2010 or 2011 (sampling details are further described in Ward et al. 2013). Survey days were randomly stratified among lakes between weekends and weekdays, and more intense survey effort occurred in the spring. All study lakes had single access points and no private housing, ensuring that all anglers fishing within the survey day were interviewed. Upon trip completion, all anglers were asked to report on catch, harvest and hours fished, and the fork length of harvested fish was recorded. Since we hypothesize that angler skill level could explain the hyperstability in

the relationship between CPUE and fish density, we also asked anglers to estimate the number of days they spent fishing in the previous calendar year as an approximation of angler skill level. Several studies in human dimensions research have concluded that angler avidity is useful measure for fishing specialization: anglers who fished more frequently corresponded to high levels of skill and greater resource dependency (Graefe 1980; Ditton et al. 1992).

Across a fishing season, it is well known that angler CPUE is affected by seasonality (van Poorten and Post 2005; Askey et al. 2006). Therefore, in order to standardize differential survey effort across lakes (some lakes had more survey effort in the spring when CPUE is typically highest), we expressed CPUE (and similarly, angler experience) as a seasonal average. CPUE is calculated per month, *j*, for lake *i*, as

(4)
$$CPUE_{i,j} = \frac{\sum c_{i,j}}{\sum E_{i,j}}$$

and then averaged across n months of survey data,

(5)
$$\overline{CPUE_i} = \frac{\sum CPUE_{i,j}}{n}.$$

In the open-access recreational fishing lakes, fish density was estimated in 16 of the 18 lakes using mark-recapture techniques and a standard gillnet sampling protocol in the fall following the angler survey (sampling details are described in detail in Ward et al. 2012). Hatchery populations of marked Rainbow Trout (adipose fin-clipped) were released into each lake approximately one week prior to gillnetting. Fish were recaptured using one floating and one sinking gang of multi-mesh gillnets, set overnight in the littoral and pelagic habitat of each lake. Marked fish were assumed to be fully recruited to the sampling gear, but not to anglers. This gillnet design is highly size-selective against
small fish, and essentially non-size-selective for larger fish (Askey et al. 2007). Two of the study lakes (Kidd and Burnell) were considered 'trophy fisheries' and due to the low fish density, fish populations were assessed using mark-recapture techniques rather than gillnets. In these two lakes, fish were captured via angling and adipose fin-clipped. Approximately two weeks later, fish were recaptured (and released alive) using multiple short sets (10 minutes) of multimesh floating gillnets with the same net mesh configuration as in Ward et al. (2012).

Estimates of fish density per 10 mm length-bin (l) from the gillnet sample ($N_{G,l}$) were adjusted for angling vulnerability (except for Kidd and Burnell Lakes as the population estimate includes only the fish vulnerable to anglers as fish were marked via angling). Vulnerability at length to angling (V_l) was calculated assuming logistic selectivity,

(6)
$$v_l = \frac{l^m}{l^m + L_{50} m}$$

where L_{50} is the length at 50% vulnerability, *m* is the steepness of the curve at L_{50} , and *l* is the mid-point of the length-bin. Cox (2000) calculated *m* to equal 7 for similar Rainbow Trout fisheries in British Columbia, so this value is used in the analysis. Estimates of L_{50} varied by lake and were reflective of the size-distribution of the population (Appendix A).

The vulnerable density of fish in the fall following the angler survey (N_T) was calculated as

(7)
$$N_T = \sum_{l}^{L} \left(N_{G,l} v_l \right)$$

and initial fish density (N_o) was back-calculated from the fall density estimate (N_T) using the observed harvest per unit effort (HPUE) per lake across the full season and total angler effort (E),

(8)
$$N_o = N_T + HPUE \cdot E.$$

Angler effort (*E*) was measured using time-lapse cameras in conjunction with groundbased counts (Appendix B). In order to account for in-season changes in fish density as a result of harvest, an average fish density (between the estimated spring and fall density) was calculated and used to explore trends in the average CPUE for the entire fishing season.

4.2.4 Statistical Analysis

Hyperstability in CPUE is commonly assessed by log-transforming Equation (2) (Ricker 1975),

(9)
$$\log(CPUE) = \log(\alpha) + \beta \log(N)$$

and estimating the slope (β) and intercept, log(α), of the relationship between the logtransformed CPUE and fish density. Similarly, catchability (*q*) can be estimated by logtransforming Equation (3), where

(10)
$$\log(q) = \log\left(\frac{\text{CPUE}}{N}\right) = \log(\alpha) + (\beta - 1)\log(N).$$

A linear regression analysis relies on the assumption that the dependent variable (fish density) is measured without error and previous research has shown that erroneous statistical approaches to estimating the slope and intercept of Equation (9) can lead to false detection of hyperstability (Shardlow et al. 1985; Richards and Schnute 1986).

Therefore, a standard linear regression analysis (ordinary least squares) is usually not appropriate to estimate parameters. However, since fish densities in the experimental fishery were measured with a high degree of precision and the error in the estimate of fish density was less than one third of the error in CPUE, a standard linear regression was used to estimate parameters in Equation (9) as recommended by McArdle (1988). For the open-access recreational fishery, fish densities were measured with less precision and therefore, we used a reduced major axis (RMA) regression to estimate parameters in Equation (9). A reduce major axis regression is the recommended method for estimating regression parameters when error is suspected in both the independent and dependent variable (Ricker 1973; McArdle 1988) and this method has been used to detect hyperstability (Erisman et al. 2011). The RMA regression minimizes the product of the dependent (x) and independent deviations (y) from the fitted line and was implemented using the *lmodel2* package in R (version 2.13.2).

4.2.5 Angler Characteristics and Mechanisms of Density-Dependent Catchability

If catchability is not constant (i.e. $\beta \neq 1$) in the open-access fishery, it is hypothesized that catchability might be positively related to the mean angler skill level on an individual lake (Post 2013). Therefore, we examined the relationship between catchability and angler skill level, and fit the data using a RMA regression since error is suspected in both the dependent and independent variable.

It has also been proposed that density-dependent catchability may arise due to the effects of fish learning and angler effort on fish vulnerability resulting from an angler effort response to fish density (Cox and Walters 2002; Askey et al. 2006). Since the

open-access recreational fishing lakes surveyed in this study varied in harvest regulations, fish density and angler effort, we tested for a relationship between angler effort density (angler hours \cdot ha⁻¹), exploitation rate, the proportion of the fish population captured (capture rate) and fish density. Exploitation rate was calculated as the ratio between the total number of harvested fish (*HPUE*·*E*) and fish density and capture rate was calculated as the ratio between the total number of caught fish (*CPUE*·*E*) and fish density. Since the potential for fish learning is affected by the proportion of fish that are released by anglers (which is a function of the daily bag limit and angler effort density), we tested for a relationship between angler catchability and angler effort density, the proportion of released fish and the daily bag limit. If this hypothesis is correct, it is expected that catchability should be negatively related to both angler effort density and the proportion of fish released. We tested for significant relationships by fitting a linear model to the variables and used a t-test to determine if the slope was significantly different than 0.

4.3 Results

4.3.1 Experimental Fishery

Fish density and CPUE varied by approximately 20-fold over the 10 lake-years of data in the experimental fishery (Figure 4.1). Fish density ranged from 7.24 to 135.4 fish \cdot ha⁻¹ and CPUE ranged from 0.20 fish \cdot h⁻¹ to 4.00 fish \cdot h⁻¹. The relationship between CPUE and fish density for an individual angler was linear and therefore showed no evidence of hyperstability. The parameter estimates for β and α were 1.075 (S.E. = 0.1417) and 0.02535 ha \cdot h⁻¹ (S.E. = 0.5754) respectively. The lack of hyperstability in the relationship between CPUE and fish density resulted in little variation in catchability (*q*)

among lakes. Estimates of catchability ranged from 2.372×10^{-2} ha·h⁻¹ to 6.330×10^{-2} ha·h⁻¹. At a fish density of 100 fish·ha⁻¹, CPUE in the previously un-fished experimental angling lakes was approximately 2.5 times higher than the CPUE of expert anglers (defined as anglers who fished more than 20 days per year) in the open-access recreational fishery.

4.3.2 Open-Access Fishery

The lakes in the open-access recreational fishery exhibited large variation in both fish density and angler CPUE: mid-season estimates of fish density varied approximately 40-fold (range 15.2 to 633.7 fish·ha⁻¹), whereas seasonal-averaged CPUE varied 7-fold between 0.32 and 2.22 fish·h⁻¹. A RMA regression detected evidence of hyperstability (p<0.05) in the CPUE data (Figure 4.2). The parameter estimates for β and α were 0.4276 (95% CI: 0.3562< μ <0.5134) and 0.1120 ha·h⁻¹ (95% CI: 0.07425< μ <0.1578) respectively. Catchability (*q*) varied approximately 10-fold across lakes and ranged from 2.982 × 10⁻³ ha·h⁻¹ to 2.276 × 10⁻² ha·h⁻¹. The relationship between CPUE and fish density for fish densities in the same range as the experimental lakes (<135.4 fish·ha⁻¹) was also hyperstable: the estimate of β was 0.5447 (95% CI: 0.3571< μ <0.8310).

4.3.3 Angler Characteristics and Mechanisms of Density-Dependent Catchability in the Open-Access Fishery

A total of 1,765 anglers were interviewed across both survey years (226 anglers interviewed were in 2010, and 1,539 in 2011). Angler experience (measured by the average number of days fished per year) varied across the interviewed anglers and ranged

between 0 to 250 days fished per year (Figure 4.3a). Mean angler experience decreased as fish density increased across lakes and the relationship between mean angler experience and fish density was best described by the power function (Figure 4.3b; $r^2 = 0.77$),

(11) Mean Days Fished Per Year = $(92.62)N^{-0.3007}$.

Similarly, mean angler experience was positively related to the mean size of harvested fish in each lake ($r^2 = 0.51$; $t_{1,16} = 4.31$; p < 0.05) (Figure 4.3c).

We examined several covariates to help identify the mechanistic cause of the observed density-dependent catchability in the open-access fishery. Angler catchability was positively related to angler experience (mean days fished per year *D*) across lakes and the following function best described the relationship ($r^2 = 0.83$) (Figure 4.4a)

$$(12) \quad q = (1.077 \times 10^{-3}) 1.086^{D}$$

An increase in bag limits corresponded to a decrease in catchability across lakes ($r^2 = 0.33$; $t_{1,16} = -3.039$; p<0.05) (Figure 4.4b). There was no evidence that angler catchability was related to angler effort density (Figure 4.4c; $r^2 = -0.06$; $t_{1,16} = -0.135$; p = 0.8944) and the relationship between angler catchability and the proportion of fish released by anglers was slightly positive (Figure 4.4d; $r^2 = 0.28$; $t_{1,16} = 2.743$; p < 0.05). Similarly, there was a lack of support for a relationship between angler effort density and fish density ($r^2 = -0.02$; $t_{1,16} = 0.7950$; p = 0.4382), exploitation rate and fish density ($r^2 = -0.06$; $t_{1,16} = -1.433$; p = 0.1710) (Figure B.1). Our data also suggests no evidence of a relationship between catchability adjusted for variation in angler skill level (the residuals from Equation [12] and angler effort density ($r^2 = -0.06$; $t_{1,16} = -0.0920$; p = 0.9280) or the proportion of fish released ($r^2 = 0.03$; $t_{1,16} = 1.226$; p = 0.2380).

4.4 Discussion

We detected significant hyperstability and density-dependent catchability for the multi-stock, spatially structured, Rainbow Trout fishery of British Columbia and this result compliments several other studies that have estimated the catchability coefficient for open-access recreational fisheries (Shuter et al. 1998; Hansen et al. 2005; Erisman et al. 2011). We observed a linear relationship between CPUE and fish density in the experimental fishery within which we controlled for heterogeneity in angler skill level, and a hyperstable relationship in the open-access fishery. Although fish densities in the experimental lakes had a lower range of densities compared to the open-access lakes (as a result of the productive limits of these higher altitude lakes), observations of CPUE at low fish densities provide the most information on hyperstability. The truncated density range of the experimental lakes does not impact the results as we detected hyperstability in the open-access fishery for the same range of fish densities as the experimental fishery. The observed non-linear relationship between fish density and CPUE needs to be accounted for if measures of CPUE are used to infer stock size or angling quality.

Our results provide no evidence to support the hypothesis that changes in fish behaviour with declines in fish density produced the apparent hyperstability in the openaccess fishery. In the open-access fishery, the observed density-dependent catchability was best described by a segregation of angler experience levels among lakes. Across lakes, declines in fish density corresponded to an increase in the average experience of the anglers. Several studies have noted that experienced anglers prefer "trophy" fisheries characterized by large fish (Chipman and Helfrich 1988; Hutt and Bettoli 2007) and we found that angler experience increased as the size of harvested fish increased across

lakes. Therefore, since low density lakes (that have large fish sizes) attracted experienced anglers, we found a positive relationship between the observed catchability and the average experience of the angler population. This suggests that as fish density declines, the composition of the angler population shifts towards experienced anglers (who have higher individual catchabilities) and produces a net increase in catchability.

Variation in anglers' impacts on stocks has been previously noted (Baccante 1995; Jones et al. 1995) and it is well understood that angler experience varies across the population of anglers (Bannerot and Austin 1983; Fisher 1997; Ward et al. 2013). Across a multi-stock, spatially structured fishery, anglers choose where to fish based on their perceptions of catch and non-catch related angling quality, commonly termed 'utility' in economics and human dimensions literature (Carpenter and Brock 2004; Hunt 2005). Taken together, variation in skill level and factors influencing site choice among anglers are likely to produce density-dependent catchability as more experienced anglers (with higher individual catchabilities) will derive greater utility from fishing low density stocks, in comparison with less skilled anglers (Chipman and Helfrich 1988; Hutt and Bettoli 2007). Therefore, the observed correlation between catchability and the composition of the angler population for the multi-stock spatially structured Rainbow Trout fishery of British Columbia is not surprising.

In the open-access fishery, catchability varied approximately 10-fold and was positively related to angler experience. The large variation in angler skill level across lakes (and the relationship between angler skill and catchability) suggests that the observed hyperstability in the open-access fishery is a result of variation in the composition of anglers among lakes, rather than interactions between fish behaviour and

catchability. Previous work (Cox and Walters 2002; Askey et al. 2006) predicts that lakes with high effort (and/or a high proportion of released fish) would have low catchabilities due to the effects of learned hook avoidance and fish behavior that leads to invulnerability to angling. We observed no relationship between angler catchability and effort or the proportion of fish released, thus it appears that fish behaviour has a smaller impact on catchability than angler behaviour (sorting of experience levels among lakes) once fisheries are established. However, CPUE in the experimental fishery was approximately 2.5 times higher than in the open-access fishery at the same fish density. The seasonal timing of the experimental fishery was mid August, which is a below average catchability period for those lakes (Askey et al. 2006) and Rainbow Trout lakes (Cox 2000, van Poorten and Post 2005) and there are no obvious reasons why catchability should be inherently higher in the experimental lakes. Differential vulnerability of fish to angling has been repeatedly studied and it is well known that intrinsically aggressive (catchable) fish are captured first by anglers (Askey et al. 2006; Biro and Post 2008). Therefore, the high catch rates in the experimental fishery may be a reflection of the un-fished conditions of these lakes, and that even the lowest effort observed in open-access fisheries is sufficient to rapidly condition fish to a lowered (density-independent) catchability.

Catchability represents a fundamental component of the functional response within the predator-prey dynamics of anglers and fish (Hunt et al. 2011a; Post 2013). However, the numerical response of anglers to fish abundance is equally important in understanding whether the interaction between fish abundance and harvest is likely to be sustainable (Schueller et al. 2012; Allen et al. 2013; Askey et al. 2013). Typically there is

a positive relationship between fish abundance and angler effort (e.g. Post et al. 2008; Schueller et al. 2012; Askey and Johnston 2013), yet we observed no significant relationship in this study. It is not clear why there is a lack of correlation in our study, but it could be partially due to differential access/travel costs between lakes (Post et al. 2008). The lack of a relationship between angler effort and fish abundance can be a concern for the sustainability of wild stock fisheries (Walters and Martell 2004; Schueller et al. 2012; Allen et al. 2013), although the lakes in this study are maintained by stocking. If angler effort does not respond to changes in fish abundance, then the possibility for over-fishing exists if angler effort remains high as fish abundance declines.

Exploitation in recreational fisheries results from not only the intensity of angling effort, but also the efficiency of the effort. Since catchability is the key variable that describes the dynamic interaction between angler effort and fish density, several authors have emphasized the importance of understanding the relationship between catchability and fish density (Johnston et al. 2010; Hunt et al. 2011a; Fenichel et al. 2012). However, the more fundamental role of catchability in recreational fisheries is that it dictates an angler's perception of a fishery and influences angler behavior (relating to choice of fishing site). For the Rainbow Trout fishery in British Columbia, variation in site choice among anglers led to more experienced anglers choosing to fish at low density lakes (that have large fish). The large variation in angler skill level among lakes and relationship between angler skill level and catchability suggests that any management action that alters the composition of the population of anglers at a lake (either through catch or non-catch related factors) may have substantial impacts on catch statistics and harvest rates. From a management perspective, our results suggest that restrictive regulations may not

be effective at controlling exploitation rates (except catch and release regulations) as these restrictive bag limits tend to create trophy fisheries (low density, high fish size) that favor experienced anglers. Since experienced anglers have high individual catchabilities, our results suggest that these anglers are attracted to low density fisheries (characterized by large fish size). Low density fisheries are often sustained using restrictive regulations, but if effort and catchability are high in low density fisheries with restrictive bag limits, the possibility for over-fishing exists. In the stocked lake system where we collected our data, sustainability is not a concern, but in a wild fishery, the impact of increasing angler efficiency with decreases in bag limits could have counterintuitive effects on harvest rates, where exploitation rates could increase with more restrictive regulations.

Hyperstability has been documented in a few recreational fisheries (Peterman and Steer 1981; Shuter et al. 1998; Hansen et al. 2005; Erisman et al. 2011). In contrast with our observation that the apparent hyperstability in the multi-stock spatially structure Rainbow Trout fishery of British Columbia was caused by a segregation of angler experience levels among lakes, Erisman et al. (2011) and Shuter et al. (1998) suggested that density-dependent catchability in recreational fisheries can also result from variation in fish behaviour. Specifically, Erisman et al. (2011) demonstrated that fisheries that selectively targeted spawning aggregations of barred sand bass (*Paralabrax nebulifer*) and kelp bass (*P. clathratus*) in southern California, USA, exhibited hyperstable CPUE. Similarly, Shuter et al. (1998) suggested that the observed density-dependent catchability of lake trout (*Salvelinus namaycush*) in several lakes in Ontario is related to anglers selectively targeting spatial aggregations of fish associated with spatial heterogeneity in habitat quality. However, neither of these studies measured angler experience and

therefore, it remains unknown how variation in angler experience with fish density relates to the observed hyperstability in these studies. The potential variation in the processes producing hyperstability across fisheries suggests that the mechanistic cause of hyperstability is likely fishery specific, due to variation in fish behavior across species and angler behavior across multi-stock spatially-structured fisheries.

The increasingly common occurrence of hyperstability in recreational fisheries suggests that fishery-independent surveys are necessary to estimate stock abundance. If fishery-independent surveys are unavailable, fisheries managers should assume that catchability is density-dependent, until data can be collected to suggest otherwise. Assuming density-dependent catchability is precautionary as it results in a lower (and more conservative) population estimate, than would be predicted by the traditional linear relationship. In fact, several theoretical and empirical studies of capture processes in fisheries suggest that density-dependent catchability should be expected (Rose and Kulka 1999; Erisman et al. 2011) and when explicitly tested for, the majority of studies demonstrate the presence of density-dependent catchability.

We have witnessed the collapse of approximately 10% of the worlds' commercially fished stocks (Branch et al. 2011) and increasing evidence suggests that similar outcomes could be seen for recreational fisheries (Coleman et al. 2004; Lewin et al. 2006; Hilborn and Hilborn 2012). In recreational fisheries, population and fishery collapse are often termed 'invisible', in part due to hypothesized hyperstability. Recreational fisheries are often viewed as self-sustaining entities, since fishing effort is expected to decrease with decreases in fish abundance (Carpenter et al. 1994; Askey and Johnston 2013). However, hyperstability results in an 'invisible collapse' in both the

fishery and fish population as CPUE remains high as fish abundance declines, and therefore, fishing effort does not respond to a decline in abundance (Post et. al 2002; Erisman et al. 2011).

We demonstrate that the observed hyperstability in the Rainbow Trout fishery in British Columbia is related to a variation in angler skill level among lakes. Quantifying the strength of hyperstability and understanding the mechanistic cause has important impacts for resource managers. Given this information, resource managers can better use fishery data (CPUE and angler skill level) to estimate stock abundance and develop management strategies for the sustainability of fish populations. The large variation in angler skill level across this fishery suggests that CPUE is not indicative of angling quality for the average angler and that heterogeneity in angler skill level must be quantified in order to optimize management strategies across open-access fisheries. Our results add to the growing body of knowledge that the management of recreational fisheries needs to include both a social and ecological component and developing quantitative models of how social and ecological processes impact fish populations will improve the management of a fishery.

Lake	Years Sampled	Bag	Gear Restrictions
		Limit	
Open-Access Recreational Fishery			
Burnell	2011	0	Artificial fly, bait ban, single barbless hook
Crown	2010	5	None
Doreen	2011	5	Artificial fly only, bait ban
Flyfish	2011	5	None
Gypsum	2010	5	None
Idleback	2011	1	Bait ban, single barbless hook
Jackpine	2011	5	None
Kentucky	2011	5	None
Kidd	2011	0	Artificial fly, bait ban, single barbless hook
Leonard	2011	2	Bait ban, single barbless hook
Loon	2011	5	None
McConnell	2011	5	None
Ripley	2011	5	None
Six Mile	2011	2	Bait ban, single barbless hook
Stake	2011	5	None
Turquoise	2010	5	None
Tyner	2010	5	None
Vinson	2011	1	Bait ban, single barbless hook
Experimental Fishery			
Big Pantano	2004	5	None
Spook	2004, 2005	5	None
Stubby	2004, 2011	5	None
Today	2004, 2005, 2011	5	None
No Fish	2005	5	None
Pantano	2011	5	None

Table 4.1 Sampling details and angling regulations for the study lakes.

Figure 4.1 CPUE as a function of fish density in the experimental fishery. The solid line is the regression fit to the log transformed data. Lakes with multiple years of data are shown with the same plot symbol. Key to point markers: solid circle (Big Pantano); open circle (Spooke); open triangle (Stubby); cross (Today); solid triangle (No Fish) and solid square (Pantano).



Figure 4.2 (a) CPUE and (b) catchability as a function of fish density in the openaccess fishery. Solid line is the Reduced Major Axis regression fit to log transformed CPUE and density data.



Figure 4.3 (a) Frequency distribution of angler experience (days fished per year). The x-axis is on a log scale and the axis labels have been back transformed for interpretation. (b) Mean angler experience (days fished per year) as a function of fish density. (c) Mean angler experience as a function of the mean size of harvested fish. Error bars represent 95% confidence intervals.



Figure 4.4 (a) Catchability as a function of angler experience (mean days fished per year). (b) Catchability as a function of the daily bag limit (points have been jittered for interpretation); (c) catchability as a function of angler effort density and (d) the proportion of fish released by anglers.



Chapter Five: Empirical Evidence of Plasticity in Life History Characteristics as a Function of Climatic Variation and Intraspecific Competition

5.1 Introduction

Variability in density-dependence in somatic growth among fish populations is well documented and suggested to be a function of competition for food resources (Post et al. 1999; Lorenzen and Enberg 2002; de Roos et al. 2003). Identifying and quantifying the strength of the compensatory response of somatic growth rates has important implications for fisheries management (Hilborn and Walters 1992; Askey et al. 2013). It has been suggested that omitting density-dependent growth processes results in an inaccurate prediction of biological references points for exploited stocks; resulting in an over estimation of stock abundance and threatens the sustainability of fish stocks (Beverton and Holt 1957). Therefore, understanding the mechanisms that lead to the compensatory nature of density-dependent somatic growth is a critical aspect of managing for sustainable fisheries.

Identifying the mechanistic cause of density-dependence in somatic growth has been a key facet of fisheries research for decades (Beverton and Holt 1957; Walters and Post 1993; Grant and Imre 2005) and recently, several authors have begun to examine the relationship between life-history characteristics and density-dependent processes (Walters et al. 2000; de Roos and Persson 2002; Lester et al. 2014). Understanding how plasticity in life-history characteristics is related to growth processes is critical to the effective management of fish populations as somatic growth is directly related to demographic processes such as maturation, fecundity, and survival (Rose et al. 2001).

Life-history theory predicts that phenotypic plasticity should be expected so that individuals maximize their fitness by quickly responding to environmental variability (Stearns and Koella 1986; Lester et al. 2014). It is suggested that this plasticity in lifehistory characteristics may counteract evolutionary selective pressures and slow the rate of evolutionary changes (Stearns 1982).

Recent studies in modeling fish growth have suggested that life-time growth patterns in fish are biphasic (made up of two phases): pre-maturation and post-maturation (Lester et al. 2004; Quince et al. 2008; Venturelli et al. 2010). The growth rate in the prematuration phase is constant (i.e. length is linearly related to age) and is related to the net rate of energy acquisition. In contrast, growth rate in the post-maturation phase declines with age as a proportion of surplus energy is invested into reproduction, following the traditional von Bertalanffy growth equation (Ricker 1975; Lester et al. 2004). Since the per capita availability of food resources determines the net rate of energy acquisition (i.e. somatic growth rates), understanding processes that delimit the availability of food resources is critical to understanding variability in somatic growth. Both fish density and/or variation in climatic conditions have been demonstrated to determine per capita food availability (Rieman and Myers 1992; Nicieza and Metcalfe 1997; Post et al. 1999). Therefore, predicting growth rates across environments requires understanding plasticity in the three life-history characteristics that determine life-time growth patterns (immature growth rate, time at maturation, and the proportion of acquired energy invested in reproduction).

Populations with faster somatic growth rates are less vulnerable to overexploitation, as faster rates are hypothesized to reduce the age at maturity, and increase

reproductive investment (Leggett and Carscadden 1978; Conover and Munch 2002; Lester et al. 2014). Growth conditions are maximized when competition for food resources is low, and food availability is high (Walters and Post 1993; Post et al. 1999; Venturelli et al. 2010). However, it is unknown how the trade-off between environmental productivity and density-dependent competition influences somatic growth rates and plasticity in life-history traits. An extensive amount of theoretical work has focused on predicting the response of life-history characteristics to environmental and evolutionary processes, but these theoretical hypotheses have rarely been tested (Kuparienen and Merila 2007; Lester et al. 2014). We used experimental populations of Rainbow Trout (*Onchorynchus mykiss*) to empirically test predictions from life-history theory relating to patterns in immature growth rates, age- and size-at-maturity, and the proportion of surplus energy invested into reproduction across climatic and fish density gradients.

5.2 Methods

5.2.1 Fish population data

To examine plasticity in life-history traits, we used data on growth and maturity schedules from experimental populations (n=23) in the southern interior of British Columbia, Canada (Table 5.1). In order to maximize differences in growth conditions between lakes, Rainbow Trout were stocked annually into the study lakes to examine trends in the three life-history traits of interest related to somatic growth trajectories: immature growth rates, maturity schedules, and the proportion of surplus energy invested into reproduction. The majority of lakes had no known natural recruitment and were primarily monocultures of Rainbow Trout (Table 5.2). Lakes with other species present

were only used to analyze maturity schedules, with the exception of Emerald Lake. Emerald Lake contained a population of lake chub (*Couesius plumbeus*), and the size difference between the stocked fish and lake chub was large enough to assume different food sources (average size of lake chub and size of stocked fish was 110 mm and 125 mm). Fish were stocked as either Age-0 or Age-1 in the fall or spring, and the size at release and stocking density varied from 0.9 to 23.5g and 35.7 to 694.4 yearlings ·ha⁻¹ respectively among lakes (assuming a survival rate of 0.5 for fry to yearlings; Parkinson et al. 2004). Additionally, the study lakes varied in their physical characteristics, harvest regulations and angler effort. Fish populations were sampled between 1993 and 2012, and led to a total of 42 lake-years of data, although not all lake years were used to fit the necessary functions as a result of data limitations (Table 5.2). The group of small lakes were considered to be interchangeable experimental units once productivity is accounted for, and when lakes were used in multiple years, each lake year was considered statistically independent (since stocking densities varied among years).

Fish populations were sampled in each lake using a standard gillnet sampling protocol in the fall (sampling details are described in detail in Ward et al. 2012). Two multi-mesh gangs of gillnets were set overnight in the littoral and pelagic habitat of each lake. This gillnet design is highly size-selective against small fish, and essentially nonsize-selective for larger fish (Askey et al. 2007). The fork length of all captured fish was recorded and Lapilli otoliths were collected from all non-clipped fish. Otoliths were aged using transmitted light (certain year classes in some lakes had unique adipose or ventral clips). The first year class of stocked fish (either Age-0 or Age-1) were fin clipped for at least one year during the study period to assess the presence or absence of natural

recruitment. Lakes with natural recruitment were identified if more than 10% of the first year class were missing fin clips (Table 5.2). Moss, Otipemisewak and Pratt Lakes contained natural populations of Rainbow Trout. Moss Lake and Otipemisewak Lake were used in the maturity analysis and only hatchery fish (identified with unique fin clips) were used in the analysis. All captured fish were examined visually to determine sex and maturity. Since Rainbow Trout spawn in the spring, and fish were captured in the fall, fish were considered immature if they showed no visible sign of gonad development and were assumed to be unable to spawn the following spring. For females, immature fish were identified as having small ribbon-like gonads, that were light pink in color and individual eggs were not visible to the naked eye. Similarly, for males, immature fish had thin transparent testes that lacked milt. Since maturity is not a binary process (immature vs. mature), fish demonstrating visual evidence of gonad development were considered mature in the following analyses.

5.2.2 Model Development

In order to examine plasticity in life-history traits as a function of environmental variation, we conducted a three stage analysis where we analyzed: (1) growth rates of immature fish, (2) maturity schedules and (3) lifetime growth patterns to determine the proportion of surplus energy invested into reproduction.

5.2.3 Immature Growth

Lester et al. (2004) suggests that growth of immature fish is expected to be linear due to a lack of energetic investment in reproduction. Since fish in our experimental lakes were stocked at a known age and size and had similar growth conditions in the hatchery prior to release, we modelled the length of fish (L_T) as a linear function of time in the lake,

$$(1) L_T = hT + L_s.$$

where L_s is the length of fish at T=0 (stocking) and h is the growth rate of immature fish.

While the absolute growth rate in constant in Equation (1), the relative growth rate (% change in size; *G*) will change depending on the initial size. In order to determine the environmental effects on immature growth, it is necessary to standardize growth rates across fish of various initial sizes using a relative growth rate (Hopkins 1992). Under constant environmental conditions, the relative growth rate (% change in length per time, *G*),

$$(2) \qquad G = \frac{L_T - L_S}{L_S T}$$

is expected to decline as a function of initial body size, where L_T is the length of fish at time *T* and L_i is the length of fish at reference time (length at stocking). As fish density increases and food resources decline, it is expected that growth becomes resourcedependent, and declines as a function of both initial body size and resource availability (Mooij et al. 1994; Rosenfeld and Boss 2001; Askey et al. 2013).

In size-structured populations, consumption rates can vary greatly among individuals, and therefore, it has been suggested that an appropriate metric to measure the effects of competition must weight individuals within a population by their consumption rate. Bioenergetics and empirical studies suggest that consumptions rates in fish should scale allometrically with mass (Walters and Post 1993; Post et al. 1999),

(3) Consumption
$$\propto$$
 (Mass)^{2/3}

and since

(4) Mass
$$\propto$$
 (Length)³

then, individual consumption rates can be scaled allometrically to length, where

(5) Consumption
$$\propto [(\text{Length})^3]^{2/3} \propto (\text{Length})^2$$

Walters and Post (1993) used this allometric relationship to suggest that the appropriate metric for expressing the density-dependence of exploitative competition should be

(6) Effective Density
$$\propto \frac{\sum_{i=1}^{n} (\text{Length})^2}{\text{Area}}$$
.

Therefore, we calculated the effective density of fish (*D*) at the time of gillnetting, based on the number of fish caught in the gillnet N_G in 10mm length-bins *l*, the vulnerability of that length bin to gillnets (using parameter estimates from Askey et al. 2007 and Ward et al. 2012), the midpoint of the length bin, L_l and the area, *A*.

(7)
$$D = \frac{\sum_{l}^{L} \left(N_{G,l} v_{l} L_{l} \right)^{2} / A.$$

Walters and Post (1993) and Post et al. (1999) demonstrate theoretically and empirically that growth rates decline as a linear function of effective density. Since fish in the experimental lakes varied in size at T=0 (stocking), it is necessary to model effects of fish density on the relative growth rate as a function of the size at stocking (L_S) and an exponential decline with effective density,

(8)
$$G = G_{max} L_S^{-(\alpha D + \beta)}$$

and therefore, the immature growth increment (*h*) can be expressed as a function of L_s and *D*, by combining equations (1), (2) and (8),

(9)
$$h = G_{max} L_S^{1-\beta} L_S^{-\alpha D}.$$

The second component that may impact immature growth rates involves understanding how immature growth rates are affected by environmental productivity. Growing degree-days (*GDD*, °C·days) are an index of thermal energy and GDD are known to be a better predictor than calendar age of growth patterns in fish (Neuheimer and Taggart 2007; Venturelli et al. 2010). Annual growing degree-days represent the number of Celsius degrees that the mean temperature is above 5°C, implying that growth approaches zero at less than 5°C. Annual growing degree-days (*GDD_A*) for the study lakes were obtained from ClimateBC4.71 based on elevation and latitude and longitude (Wang et al. 2012). *GDD_A* were then used to calculate a thermal age (the cumulative number of growing degree-days fish experienced prior to capture, *GDD_C*),

$$(10) \quad GDD_C = A \cdot GDD_A \cdot 10^{-3}$$

where *A* is the calendar age of the fish. Estimates of GDD_A ranged from 1036 to 1964 °C·days across the study lakes.

To determine if the thermal age concept is useful for analyzing growth patterns in Rainbow Trout, we fit Equation (9) to the observed immature growth rate, based on Equation (1), where

(11)
$$h = \frac{L_T - L_s}{T}$$

for calendar time (*h*; *T*=Years) and thermal time (*h*'; $T' = GDD_C$) in the lake. Equation (9) was log transformed and fit using non-informative priors given in Table (5.3).

5.2.4 Maturity Schedules

A well-documented theory in life-history studies involves the relationship between growth rates of immature fish and the optimal age and size at maturation. It is hypothesized that the optimal time to reach maturity occurs when the fecundity benefits of reaching a large size are maximized, while the costs of delaying the onset of reproduction are minimized (Day and Rowe 2002; Johnston et al. 2007). When growth rates decline, several theoretical studies have suggested that it is advantageous for individuals to delay the onset of reproduction and continue to invest energy into somatic growth, since fecundity is positively correlated with body size (Sterns 1992; Hutchings 1993; Rochet 2000). However, if juvenile mortality rates are high, the benefits of delaying the onset of reproduction may not be beneficial (Hutchings 1996; Cichon and Kozlowski 2000). Variation in growing conditions have been theoretically demonstrated to influence this trade-off of the optimal size and age at maturity, but empirical verification of this relationship across both fish density and environmental gradients is relatively unknown (Stearns and Koella 1986; Roff 1992; Stearns 1992; Day and Rowe 2002).

We used empirical data to determine the variability in age and length at maturity in our experimental lakes. Estimates of length and the thermal age at 50% maturity (L_{50} and T'_{50} respectively) were obtained for each lake year of data using binary data on maturity (1 = mature, 0 = immature). Maturity at thermal age ($M_{T'}$) (or maturity at length M_L ; T' = L) was modeled as a logistic function,

(12)
$$M_{T'} = \frac{e^{aT'+b}}{1+e^{aT'+b}},$$

And the parameters of equation (12) were estimated using a logit transformation where

(13)
$$\ln\left(\frac{M_{T'}}{1-M_{T'}}\right) = aT' + b$$

and T'_{50} is

(14)
$$T'_{50} = -b/a$$
.

5.2.5 Reproductive Investment and Lifetime Growth Patterns

Lester et al. (2004) reparameterized the von Bertalanffy growth model to better explain biphasic lifetime growth patterns in fish populations. Growth patterns of fish prematuration are modeled as a linear process as in Equation (1), and growth patterns of fish post-maturation are a von Bertalanffy process. The depression of fish growth trajectories from the linear growth patterns of immature fish represents the proportion of surplus energy that is invested into reproduction (Figure 5.1). Life-history theory predicts that the proportion of surplus energy invested into reproduction should be positively correlated with growth rates and this is hypothesized to be an adaptive response of populations to changes in density resulting from high mortality (Lester et al. 2014).

Based on the theory of biphasic growth (Lester et al. 2004), length of immature fish (t < T) is described by Equation (1), and when t> T, length at $t(L_t)$ is predicted by the von Bertalanffy growth model,

(15)
$$L_t = L_{\infty} (1 - e^{[-K(t-t_0)]})$$

Lester et al. (2004) reparameterized Equation (15) in terms of the immature growth rate (h), amount of reproductive investment (g) and T, so that

(16)
$$L_{\infty} = \frac{3h}{g}$$
,

(17)
$$K = \ln\left(1 + \frac{g}{3}\right).$$

The t_o parameter must be adjusted from Lester et al. (2004) derivation when modeling fish based on time in the lake, where the length at *T* is

$$(18) \quad L_T = hT + L_S$$

And substituting into equation (14),

(19)
$$hT + L_S = L_{\infty} (1 - e^{[-K(T-t_o)]}),$$

and replacing L_{∞} and K with equation (16) and (17),

(20)
$$t_o = T + \frac{\ln[1 - g(hT + L_S)/_{3h}]}{\ln[1 + g/_3]}$$

To examine the relationship between the proportion of surplus energy invested into reproduction and immature growth rates, we fit the Lester parameterization of the von Bertalanffy growth model to data on length at thermal time in the lake (thermal age, T = T'). Since estimates of T'_{50} reflect an observed thermal age at which 50% of the population is mature based on fish captured in the fall (at the end of the growing season), we assume that the thermal age at which energy begins to be allocated to reproduction (T') occurs at the beginning of the growing season before T^{1}_{50} . It has been suggested that male and female fish populations may exhibit variation in lifetime growth patterns as a result of differential T and g values, and therefore, we fit Equation (15) separately for mature males and females to observed data on length at thermal age by sex. Estimates of g were constrained on the interval $\left[0, \frac{3h}{hT'+Ls}\right]$ as a result of the logarithmic bounds in Equation (20), and assumed to come from a hierarchical distribution with vague priors (Table 5.3). Estimates of h were assigned based on the observed immature growth rates.

5.2.6 Data Analysis

All analyses were conducted using Bayesian techniques as we were interested in exploring the uncertainty of the estimated parameters. The analysis was run using openBUGS (Bayesian Inference Using Gibbs Sampling) software, version 3.2.1 (available at http://www.openbugs.info/w/). Vague priors were used for each model (Table 5.3). For each model, we ran the MCMC for 200,000 iterations, and discarded the first 50,000 to remove any "burn-in" effects. Chains were initialized from two different starting points. Convergence of the chains was visually assessed by monitoring trace plots of the Markov chains as well as examining the Gelman-Rubin convergence diagnostics (provided in the BRugs package for the R programming environment).

We used hierarchical models to estimate parameters for immature growth and the amount of reproductive investment. Hierarchical models allow for information from other sampling units (other lake years) to be incorporated and are known to improve estimates on individual lake years (Askey et al. 2007; Forrest et al. 2010). Vague prior distributions were used for all estimated parameters (Table 5.3). Where stated, we compared candidate models in a Bayesian framework using the DIC statistic (Spiegelhalter et al. 2002). The DIC statistic combines goodness-of-fit measure, $\overline{D(\theta)}$ (the posterior mean of the deviance) with a measure of model complexity (p_D). We calculated a Δ DIC, and models with Δ DIC values between 0 and 5 are considered to have a substantial level of empirical support, and those with Δ DIC values greater than 10 are thought to have essentially no support.

5.3 Results

5.3.1 Immature Growth

Across lakes, immature growth rates varied as a function climatic conditions. The thermal immature growth rate (h') fit the data well whereas there was no observed relationship of growth to calendar time (h; Table 5.4). Therefore we applied the thermal age concept in our analysis to account for differences in growth rates as a function of climatic differences among lakes. The thermal immature growth rate (h') declined as a function of initial stocking size and fish density and including fish density in the model led to a significant decrease in the DIC and therefore, this was considered the optimal model to predict juvenile growth (Table 5.4; Figure 5.2a; R²=0.93). Posterior estimates for the parameters in equation (9) for the relative growth rate per thermal time for immature fish were: $G_{max} = 1.702 \times 10^2 (\sigma=19.2)$, $\alpha = 2.235 \times 10^{-3} (\sigma=1.50 \times 10^{-4})$ and $\beta = 1.10 (\sigma=2.8 \times 10^{-2})$.

Across lakes, estimates of the thermal immature growth increment (h') varied three-fold and ranged from 62.8 to 115.0 mm·°C⁻¹·days⁻¹·10⁻³. Across a range of effective density and growing degree days, these results demonstrate that immature growth rates (h) are negatively related to effective density and positively related to the annual growing degree days (Figure 5.2b).

5.3.2 Maturity Schedules

We detected differences in the size and thermal age at maturity among males and females (Figure 5.3a). Females matured at larger sizes than males (female L_{50} range: 259.0 - 333.7 mm; male L_{50} range: 143.6-277.0 mm) and matured at older thermal ages

than males (female T'_{50} range: 1.17-2.62 °C·days·10⁻³; male T'_{50} range: 0.17-2.2 °C·days·10⁻³). Variation in the thermal age at maturity (T'_{50}) for both males and females was explained by immature growth rates (Figure 5.3b)

(21)
$$T'_{50} = \xi h^{-\lambda}$$

Parameter estimates for females were: $\xi=82.19 \ (\sigma=0.9520) \ \text{and} \ \lambda=0.8833 \ (\sigma=0.2183) \ \text{and}$ for males: $\xi=1.98 \ \text{x} \ 10^4 \ (\sigma=1.4450) \ \text{and} \ \lambda=2.318 \ (\sigma=0.3269)$. This suggests that immature growth rates can be used to predict sex-specific thermal age at maturity (T'_{50}) in the analysis of lifetime growth patterns. The observed relationship between h' and T'_{50} , and h' and density and growing degree days (Equation 9) suggests that the age at maturity (T) varies between 0.5 and 4 years for females across a density and climatic gradient (Figure 5.3c).

5.3.3 Reproductive Investment and Life-Time Growth Patterns

The biphasic growth model fit the observed data on length at thermal time in the lake well (Figure 5.4). Estimates of *g* varied substantially between lakes for both males and females (male range: $0.039 \, ^\circ C^{-1} \cdot days^{-1} \cdot 10^{-3} - 0.659 \, ^\circ C^{-1} \cdot days^{-1} \cdot 10^{-3}$; female range: $0.010 \, ^\circ C^{-1} \cdot days^{-1} \cdot 10^{-3} - 0.557 \, ^\circ C^{-1} \cdot days^{-1} \cdot 10^{-3}$). For lakes where parameter estimates for both males and females were obtained (*n*=12), estimates of *g* were not statistically different between males and females (*t_s*=-1.8672; *df*=11; *p*=0.0887) (Figure 5.5a). Across lakes, estimates of the average *g* (of males and females) increased as a linear function of the immature growth rate (Figure 5.5b), where

(22)
$$g = \rho h + \varphi$$

and parameter estimates for ρ and ϕ are 8.242×10⁻³mm⁻¹ and -0.573 °C⁻¹·days⁻¹·10⁻³.

5.4 Discussion

We analyzed data from experimental populations to determine how climatic productivity and density-dependent competition affect plasticity in life-history characteristics relating to growth processes in fish. Our results provide substantial evidence that the observed plasticity in life-history characteristics is a function of environmental variables and evolutionary processes. In particular, we examined trends in three life-history characteristics that determine somatic growth: immature growth rates, age at maturity and the proportion of surplus energy invested into reproduction. We found that immature growth rates were best explained by climatic and density-dependent competition effects, and that age-at-maturity and the proportion of surplus energy invested into reproduction was a function of immature growth rates.

We applied the thermal age concept in our analysis. Growing degree days are an index of the amount of ambient thermal energy and directly relate to ectothermic organisms cumulative metabolism (Neuheimer and Taggart 2007). Historically, proxies for productivity (such as total dissolved solids, mean depth or shoal area) were used to examine landscape patterns in fish growth (Shuter et al. 1998). Recently, several studies examining trends in fish growth patterns across landscapes have used growing degree days to express temperature effects on fish growth (Venturelli et al. 2010; Lester et al. 2014). For example, Venturelli et al. (2010) demonstrated that GDD accounted for 96% of variation in length among populations of walleye (*Sander vitreus*) and hypothesized that additional variation in length was related to food availability (density-dependent competition). Rainbow Trout populations in our experimental lakes varied substantially in both fish density and growing degree days. We found that both growing degree days

and fish density had large impacts on the growth rates of immature fish. At a constant fish density, immature growth rates varied two-fold across the observed range of growing degree days. Similarly, at a constant growing degree days, immature growth rates varied two-fold across the observed range of fish densities. Therefore, our results suggest that environmental conditions (growing degree days) and fish density are key predictors of relative growth rates of immature fish among our experimental lakes. There is an increasing interest to manage spatially-structured fisheries at the landscape scale (Carpenter and Brock 2004; Post et al. 2008; Hunt et al. 2011). Our results complement other studies that suggest that growing degree days provide a useful method for understanding and interpreting growth patterns at a landscape scale in the absence of more detailed information (Venturelli et al. 2010; Lester et al. 2014).

Fish growth patterns are known to be a function of food availability and temperature (Paloheimo and Dickie 1966; Kitchell et al. 1977; Walters and Post 1993). Therefore, we examined variation in immature growth rates over a large gradient in fish density and growing degree days. In our study lakes, we were able to experimentally alter fish densities in order to both decouple the relationship between climatic influences on productivity and fish density. Highly productive, unfished systems are often correlated with high fish densities. Since fishing alters fish density, it is important to understand how growth patterns vary across a gradient in both fish density and productivity (growing degree days). Our ability to alter fish densities through stocking led to an 8-fold variation in effective density estimates (range: 6.85 to $56.75 \text{ mm}^2 \cdot 10^{-6}$) and we suggest that this represents the broad range of density estimates possible for native lake populations of Rainbow Trout.

We examined sex-specific maturity schedules in our study lakes. As expected, males matured at smaller sizes and earlier ages than females. The optimal time to reach maturity is suggested to occur when the fecundity benefits of reaching a large size are maximized, while the costs to delaying the onset of reproduction are minimized (Stearns and Koella 1986; Day and Rowe 2002). Sexual dimorphism is common in fish populations and is hypothesized to be a function of variation in optimal life history strategies among sexes (Rennie et al. 2008). The presence of precocious males (where certain males in the population mature much earlier than others) in salmonid populations is well-documented and precocious males are often associated with higher mortality rates (Myers 1984). The majority of theoretical and empirical studies on maturation processes in fish involve only females due to more predictable maturation schedules (Lester et al. 2004). However, understanding and quantifying the impacts of variation in life-history strategies among the sexes is critical for managing fish populations.

We found that variation in the thermal time to reach maturity was best explained by variation in immature growth rates among populations. This relationship clearly demonstrates the evolutionary trade-off between the optimal size and age to reach maturity. Our results suggest that neither of these life-history parameters is fixed and that the thermal time to reach maturity declines as immature growth rates increase. In other words, this suggests that if populations have poor growth rates, it is advantageous for individuals to delay the onset of maturation and continue growing until the fecundity benefits of reaching a large size are maximized while the costs to delaying maturation are minimized. This relationship was demonstrated for both males and females, but the

presence of precocious males lead to males maturating at lower thermal ages than females for a given immature growth rate.

Since males and females matured at different thermal ages, we chose to examine life-time growth patterns separately for the sexes. Several bioenergetic studies involving sexual dimorphism suggest that the energetic costs of reproduction are less in males as the energy required to produce sperm is less than the energy required to produce eggs (Rennie et al. 2008). However, it has been argued that in order to fully understand the true energetic costs associated with reproduction in males, one must study the other energetic costs of maturation (such as courtship activities and brood defenses) (Lester et al. 2004). We found no difference in estimates of reproductive investment, *g*, between males and females in the same lake. Since these populations reached maturity (but never actually spawned due to the absence of spawning habitat in the study lakes), this suggests that the energetic costs associated with maturation are higher than previously expected for males. Through an analysis of life-time growth patterns, the observed sexual dimorphism in our study lakes is a function of variation in the thermal age at maturity among males and females, rather than the amount of reproductive investment.

We found strong evidence that the implied proportion of surplus energy invested into reproduction is a function of immature growth rates. Similarly, in an analysis across species, Lester et al. (2004) found that the proportion of surplus energy invested into reproduction was a function of mortality rates, where populations with higher mortality rates exhibited a greater reproductive effort. Our empirical evidence, combined with information from Lester et al. (2004) and Venturelli et al. (2010) suggest that immature growth rates are positively correlated with both growing degree days and mortality. Life-
history and evolutionary theory predict that the evolutionary response of an increase in mortality rates is a decrease in the age at maturity and an increase in reproductive investment (Stearns and Koella 1986; Kuparienen and Merila 2007). Therefore, our observations demonstrate that reproductive effort is positively correlated with immature growth rates and this relationship represents the evolutionary response and optimal life-history strategies.

Lake	Elevation	Average GDD	UTM Zone	Easting	Northing
Amphitheatre	1070	1429	11	299438	5631379
Billy	1450	1111	10	648800	5585572
Buchanan	1020	1062	10	581523	5785339
Butterfly	756	1078	10	488236	5991765
Dennis	1193	1343	11	303180	5634464
Emerald	727	1243	10	525055	6031073
Flyfish	1354	1076	11	346908	5551011
Garcia	1052	1316	10	666542	5547897
Grizzly East	962	1071	10	555849	5951809
Gypsum	1458	1100	10	651687	5579781
Jackpine	1300	1198	11	298681	5533393
McConnell	1258	1250	10	680409	5600241
Moss 1	615	1964	10	596714	5466870
Moss	540	1702	10	595788	5466776
Otipemisewak	803	1089	10	546765	5954442
Pratt	1302	1227	10	710238	5589562
Stake	1320	1212	10	669955	5583457
Ten Mile	707	1388	10	536234	5880377
Tom Campbell	1077	1492	10	699816	5711229
Tory	730	1273	10	592540	5631592
Turquoise	808	1488	10	647437	5572714
Tyner	1332	1219	10	684270	5519611
Yellow	750	1274	11	299024	5468334

 Table 5.1 Physical characteristics of the study lakes

Table 5.2 Fish community data of the study lakes and lakes used to explore relationships among Rainbow Trout life history parameters. Species codes are EB: Eastern Brook Trout (Salvelinus fontinalis); KO: Kokanee (Oncorhynchus nerka); LKC: Lake Chub (Couesius plumbeus); LSU: Longnose Sucker (Catostomus catostomus); NSC: Northern Pikeminnow (Ptychocheilus oregonensis); RSC: Redside Shiner (Richardsonius balteatus); YP: Yellow Perch (Perca flavescens). Model codes are I: immature growth; M: maturity; G: life-time growth.

		Natural	Rainbow Trout	Model
Laka	Year	Recruitment	Monoculture	
Lake		(% of Age-1		
		catch)		
Amphitheatre	2010	Yes – 11	Yes	I, G
	2011			Ι
	2012			Ι
Billy	2009		Yes	I, G
	2010	No – 9		I, G
	2011			Ι
Buchanan	2000	No – 0	No-NSC	М
	2001	No – 0		М
Butterfly	2008	Unknown	No – EB	М
Dennis	2010		Yes	I, G
	2011	No – 1		Ι
	2012			Ι
Emerald	2009	Unknown	No - LKC	I, M, G
Flyfish	2011		Yes	Ι
Garcia	1993	No – 3	No - RSC	М
Grizzly East	2009	No – 9	No – LSU	М
	2010			Μ

		Natural	Rainbow Trout	Model
Lake	Year	Recruitment (%	Monoculture	
		of Age-1 catch)		
Gypsum	2009		Yes	I, G
	2010	No-4		I, G
	2011			Ι
	2012			Ι
Jackpine	2011	No - 0	Yes	G
McConnell	2009	No-3	Yes	Ι
	2010	No – 7	Yes	Ι
Moss	2001	Yes – 48	Yes	М
Moss 1	2003	No - 0	Yes	М
Otipemisewak	2008	Yes – 51	No – LSU, RSC	М
Pratt	2010	Yes – 18	Yes	G
Stake	2009	No – 3	Yes	I, G
	2010	No - 0		I, G
	2011			I, G
	2012			Ι
Ten Mile	2012	Unknown	No - KO	М
Tom Campbell	2003	No – 0	Yes	М
	2004	No - 0		Μ
Tory	2009	No – 3	Yes	I, M
	2010			G
Turquoise	2009	No – 7	Yes	Ι
	2011			Ι
Tyner	2009	No – 1	Yes	G
Yellow	2011	Unknown	No-EB, YP	М

Table 5.2 Continued

Table 5.3 Prior distributions used in the analysis. N indicates a normal distribution (mean, precision); G: gamma distribution (shape 1, shape 2); LN: normal distribution (log mean, precision). I indicates a bounded prior [lower, upper].

Eq	Parameter	Description	Prior and distribution
9	G_{max}	Maximum immature growth rate	N(0.78,0.01)
9	α	Decline in immature growth rate	N(0,0.01)
		with the interaction of density and	
		length stocked	
9	β	Decline in immature growth rate	N(0,0.01)
		with length stocked	
11	h	Immature growth rate	$N(\bar{h}, \tau_h)$
11	τ	Precision of data and hyperpriors	G(0.01,0.01)
11	\overline{h}	Hyperprior for <i>h</i>	N(150,0.001)
12	b	Logistic regression intercept	$N(\bar{b}, \tau_h) I[-\infty, 0]$
12	\overline{b}	Hyperprior for <i>b</i>	N(-7,0.1)
12	τ_{h}	Precision of <i>b</i>	G(0.01, 0.01)
14	T'_{50}	Thermal age at 50% maturity	$N(\overline{T'_{50}}, \tau_{T'_{50}})I[0, \infty]$
14	$\overline{T'_{50}}$	Hyperprior for T'_{50}	N(3,1)
14	$ au_{T'_{50}}$	Precision of T'_{50}	G(0.1,0.1)
15	g	Reproductive investment	$LN(\bar{g}, \tau_g) I\left[0, \frac{3h}{hT + L_s}\right]$
15	ā	Hyperprior for mean g	$N(\ln(0.5), 1)$
15	9 T a	Hyperprior for precision of g	G(0,1,0,1)
21	-y E	Maximum T'_{ro}	N(0.001)
	7	50	
21	λ	Decline in T'_{50} with h'	N(0,0.01)

Table 5.4 Candidate models and DIC statistics to used to predict the immature growth increment as a function of initial size and effective density, where the immature growth rate is based on calendar age (h) or thermal age (h').

	Model	$\overline{D(\theta)}$	$D(\hat{ heta})$	DIC	p_D	ΔDIC
1	$h = G_{max} L_S^{1-\beta}$	372.6	345.2	399.9	27.4	407.7
2	$h = G_{max} L_S^{1-\beta} L_S^{-\alpha D}$	179.8	151.6	208.0	28.2	215.8
3	$h' = G_{max} L_S^{1-\beta}$	147.7	120	175.4	27.67	182.3
4	$h' = G_{max} L_S^{1-\beta} L_S^{-\alpha D}$	-36.15	-64.54	-7.773	28.28	0

Figure 5.1 Graphical representation of the biphasic growth model. Growth prior to the age at maturation (T) is a linear process, whereas growth after T follows a von Bertalanffy trajectory. The depression of fish growth trajectories from the linear growth patterns of immature fish represents the proportion of surplus energy that is invested into reproduction (g).



Figure 5.2 (a) Variation in observed thermal immature growth rate (h') as a function of effective density. Error bars represent 95% confidence intervals. The model predicted relationship from Equation (9) is shown for fish stocked at 50 mm (dashed line), and 150 mm (solid line). (b) Variation in the thermal immature growth increment $(h', \text{mm} \cdot {}^{\circ}\text{C}^{-1} \cdot \text{days}^{-1} \cdot 10^{-3})$ as a function of growing degree days and effective density for fish stocked at 100 mm.



Figure 5.3 (a) Variation in Thermal Age (*T'*) at 50% maturity and length at 50% maturity for females (solid circles) and males (open circles). (b) Variation in thermal age at 50% maturity as a function of immature growth rate and model predicted relationship for females (solid line) and males (dashed line). (c) Age at 50% maturity (T) for females as a function of effective density and growing degree days for fish stocked at 100 mm.



Figure 5.4 Fit of von Bertalanffy growth model to length at thermal age data. Open circles, solid circles and small solid circles refer to males, females and immature fish respectively. Female points have been horizontally offset for interpretation. The short dashed and solid lines are the model fit for males and females respectively.



Figure 5.5 (a) Relationship between the proportion of surplus energy invested into reproduction (g) for males and females. The dashed line represents the 1:1 relationship. (b) Variation in reproductive investment (g) as a function of the immature growth rate and model predicted relationship.



Chapter Six: Understanding and Managing Social-Ecological Feedbacks in Spatially-Structured Recreational Fisheries: The Overlooked Behavioral Dimension

6.1 Introduction

Recreational fisheries constitute a social-ecological system (SES) that is often underappreciated in social and economic importance globally (Arlinghaus and Cooke 2009). Recreational fisheries are characterized by complex interactions between the natural environment and the social and governance systems (Hunt et al. 2013). The natural environment defines the boundaries for biological processes such as fish growth and survival, whereas social systems rely on processes that define the spatial extent of fisheries, management interventions, stakeholder conflicts and well-being of anglers (appropriators). Interactions among anglers and ecosystems can lead to undesirable biological impacts on fish populations, which in turn feed back to anglers and managers across a range of spatial scales, motivating a response by anglers and those who govern recreational fisheries. Such tightly coupled interactions between people and the natural environment are at the core of any SES (Liu et al. 2007). Recreational fisheries are unique for eight main reasons from a SESs perspective with empirically tractable behavioural interactions among anglers, fish populations and fisheries managers:

- Anglers are diverse and are motivated to achieve both food provisioning and cultural services (Hunt et al. 2013)
- Anglers often only observe resource conditions (fish abundance, size, species) through their fishing activity (Ward et al. 2013)

- 3) Fish populations are diverse across spatially-structured fisheries (e.g. species composition, environmental productivity) and dynamics are strongly impacted by anglers as a result of compensatory and depensatory processes, fisheries-induced evolution, food web structure and fish behaviour (Hilborn and Walters 1992; Laugen et al. 2014)
- Anglers and their time spent fishing are largely unmanaged (open-access) and the tools available to those who govern fisheries are often blunt (e.g. catch limits)
 (Cox et al. 2002; Beard et al. 2003)
- 5) In spatially-structured fisheries, the mobility of anglers determines their impact on the resource (Post et al. 2008; Hunt et al. 2011)
- Individuals who govern fisheries often lack adequate information on fish populations or social well-being when developing management actions (Hilborn and Mangel 1997; Fulton et al. 2011)
- 7) The actions of any angler on the system are small, but the actions by all anglers (e.g. harvesting behaviour, illegal introductions and requesting management intervention) are large and can influence resource and social conditions (Hunt et al. 2011; van Poorten et al. 2011)
- 8) While many SESs involve considerable regime shifts at the outset because of development (e.g., agriculture, energy development), fishing activities have a much slower effect on the system that might eventually result in regime changes (Carpenter and Brock 2004)

By examining these interactions within recreational fisheries, it is possible to improve our understanding of how humans and ecosystems interact and develop management strategies for the resilience and sustainability of the natural environment.

The demand for management strategies that consider the broader interactions of the SES is widely recognized because reciprocal feedback loops between the natural environment and people have the potential to create undesirable outcomes such as a loss of social well-being or species conservation concerns (Fulton et al. 2011; Fenichel et al. 2012; Hunt et al. 2013). However, substantial complexity is already inherent in the core SES of recreational fisheries, and thus is the focus of the present paper. The specific management of a fisheries resource and the broader governance systems that define the type and quality of stakeholder or public interactions with the resource provide a rich source of complex interactions that link ecosystem users (e.g., anglers), ecosystem nonusers (e.g., the non-angling public), ecosystem managers (e.g., fisheries agencies) and the natural environment (e.g., fishes, food webs, and the ecosystem) across a variety of spatial scales (Figure 6.1). Change and potential transformations in the SES occur as a result of unforeseen (e.g., Daedlow et al. 2013) or incremental disturbances emerging from local social-ecological interactions and the broader (regional) environment. To understand system responses to social-ecological change, it is important to understand fully behavior-mediated processes and interactions (Arlinghaus et al. 2013).

Several attempts have been made to characterize these behavioural interactions (Fenichel et al. 2012; Hunt et al. 2013), but a limited focus has been given to identify the most important behavior-mediated factors that influence social-ecological outcomes. We

suggest that behavioural interactions between anglers, fish populations and fisheries managers play a key role in determining social-ecological feedbacks, and in turn, system outcomes (Figure 6.2). The objective of this chapter is to review and to identify factors, antecedents to behaviours, and behaviors most important to the outcomes of a coupled SES, with a particular focus the interactions that operate in the spatially structured open access inland fisheries that are typical of North America. Specifically, we provide information on how to reduce uncertainty, identify data gaps and improve management advice when accounting for behavior-mediated interactions in SES.

6.2 Behavioural Interactions Between Fish and Anglers

6.2.1 Understanding Angler behaviour

A substantial amount of research has focused on understanding angler behaviours in response to changes in resource conditions (e.g. Johnston et al. 2010; Allen et al. 2013), and there is an increasing interest in understanding how angler behaviours influence social-ecological outcomes (Fenichel et al. 2012; Hunt et al. 2013). There is also increasing recognition that heterogeneity among anglers can affect social-ecological outcomes such as the spatial or temporal patterns of effort (the amount of fishing over a given time period) and over exploitation (Post et al. 2008; Hunt et al. 2011), angler catchability (the proportion of the stock caught by a unit of fishing effort; Ward et al. 2013) and social well-being (Johnston et al. 2010) (Table 6.1). These studies suggest that simple descriptions of angler behaviour are likely inadequate for comprehending SES outcomes (Johnston et al. 2010). The heterogeneity in system outcomes from angler

behaviours mainly arises from the different fishing tactics that anglers employ. Here, we define these tactics as answers of individual anglers to the where (location), when (timing), how often (frequency), what (target species), and how (gear and/or harvest preferences) questions. At least three factors can influence an angler's choice of fishing tactics including: (1) attribute preferences; (2) personal constraints; and (3) learning and awareness (Table 6.1). For any fishing tactic, some factors are positively while others are negatively related to utility, and these factors will collectively affect system outcomes such as the distribution of effort, harvest rates, catchability, angler well-being and biological sustainability of fish stocks (Figure 6.2).

While several approaches exist for describing human decision-making processes (e.g. Gigerenzer and Gaissmaier 2011), utility maximization has been the dominant approach within interdisciplinary studies of recreational fishing (Fenichel et al. 2013). Utility, or more generally angler well-being, arises from a combination of attributes that describe an alternative such as expected catch-related fishing quality and travel costs for a fishing site and the preferences that people have for these attributes. Individuals are assumed to choose the one alternative from a set of alternatives that maximizes their utility. These utility-based models also account for the uncertainties associated with the ability of a researcher to model individual behaviours (i.e., random utility theory, Manski 1977). For any fishing tactic chosen by an angler, some factors are positively related to utility (e.g., catch-related fishing quality) while others are negatively related to utility (e.g., travel costs). Utility-based models of site choice represent behavioral models of anglers that can be linked to fish population models to study the impact of regulations while accounting

for fish population and angler behavioral responses (Johnston et al. 2010, reviewed in Fenichel et al. 2012).

6.2.2 Key Uncertainties in Understanding Angler Behaviour

The most critical areas of uncertainty about how resource and social conditions affect anglers' behaviours are: (1) improving empirical measures and determinants of angler effort dynamics across a landscape, where regionally mobile anglers link spatially structured ecosystems, and (2) determining the effectiveness of different fishing tactics employed by anglers by impacts on fish stocks.

Quantifying fishing effort has large implications for managing fisheries because high levels of angler effort is hypothesized to be one of the main factors leading to population collapse in many fisheries (Post et al. 2002). Many studies evaluating angler effort dynamics in recreational fisheries use simulation-based approaches that simply assume anglers respond to fish abundance (e.g., Post et al. 2008; Hunt et al. 2011; Allen et al. 2013). There is an urgent need to confront these model results with empirical estimates of angling effort distribution (Fenichel et al. 2012). Angler effort is usually measured using creel or aerial surveys, which are costly and thus, typically only collected on the most important (e.g., largest or economically most relevant) water bodies in a region. Recent developments in technology allow for fishing effort to be measured on large numbers of water bodies using remote measures of effort (e.g. time-lapse cameras in Ward et al. 2013). Because developing landscape level predictions of angler effort are critical for

effectively managing recreational fisheries, we suggest that managers and researchers confront models with data using remote measures of angler effort.

Not all types of angler effort result in the same impacts to social-ecological outcomes (Johnston et al. 2010). It is highly conceivable that anglers' choices of fishing tactics can result in different catch rates and even catchability (Ward et al. 2013). Consequently, it is important to understand total effort, the spatial variability in effort and the effectiveness of the effort in influencing system outcomes. To examine impacts of heterogeneity in fishing tactics among anglers, we suggest that researchers use a controlled design with experiments that evaluate how anglers vary their behaviours based on information exchange processes and learning. We suggest that researchers conduct experiments in systems where it is possible to decouple the relationship between catch and non-catch-related factors. For example, stocked systems provide researchers the ability to change fish density and measure how the heterogeneity in fishing tactics among anglers changes in response to catch-related factors such as fish size and catch per unit effort. Conversely, researchers could manipulate non-catch-related factors such as road access conditions or facility development and examine anglers' responses.

6.2.3 The Impact of Recreational Fishing on Fish Population Dynamics

Although an extensive amount of research has focused on quantifying the impact of fishing on stock structure and vulnerability (e.g. Hilborn and Walters 1992), recent studies suggest behavioural interactions between anglers and fish populations are key to understand system-level outcomes such as total harvest rates (Askey et al. 2006) or

density-dependent catchability (Ward et al. 2013). Several interacting factors and processes directly influence fish population dynamics, the behavioural interaction between anglers and fish, and corresponding social-ecological outcomes (Figure 6.2), including (1) density-dependent vital rates (growth, mortality and recruitment), which determine compensation and depensation; (2) inter- and intra-specific competition, which affect how food webs respond to fishing; (3) fisheries-induced evolution, which alters catchability and life-histories and the (4) behavior of fish to recreational fishing that strongly determines catchability and catch rates (Table 6.1).

6.2.4 Key Uncertainties in the Effects of Recreational Fishing on Fish Population Dynamics

The most critical areas of uncertainty in the interaction between fish populations and anglers include: (1) the interaction between compensation and depensation across diverse fish life-histories; (2) inter- and intra-specific interactions and their effects on vulnerability; (3) evolutionary effects of recreational fishing on stock dynamics and utility and (4) the processes about how fishes behaviorally move among vulnerable and invulnerable states.

To understand how fish populations respond to exploitation, it is important to understand the dynamic relationship between compensatory and depensatory processes (Hilborn and Walters 1992). We suggest that researchers analyze experimental fishing data to understand better the strength of the interaction between compensation and depensation, especially at low fish densities. Conducting experiments in natural systems on low density populations are often impractical because of conservation concerns. Therefore, we suggest that researchers use stocked (feral) monoculture systems in small replicable units such as lakes or ponds coupled with experimental fishing and monitoring of population dynamics. After these systems are understood, simple tri-trophic food chain experiments can be added before moving to complex multi-species communities. Such research can best take place in large ponds that can be regularly drained and enumerated. To reduce uncertainty in these experiments, we suggest that researchers conduct power analyses by simulating the system prior to experimentation to determine the necessary sample size needed to obtain the desired level of precision.

The impact of trophic interactions and demographic truncation on social-ecological outcomes, such as stability of yield, is rarely considered in management practice (Estes et al. 2011). Selective removal of top predators and alterations of the average size and age of the stock can influence community interactions and impact environmental productivity and life-history characteristics. Effects, however, are strongly context specific (de Roos et al. 2003). To improve our understanding of such processes, we suggest that researchers use trophic analyses and size-structured population models coupled with an ecosystem-based survey approach to account specifically for the effects of fishing on demographic truncation and corresponding impacts on growth, mortality and recruitment. Two main modelling approaches exist (Ecopath with Ecosim and physiological structured models) that allow researchers to combine the theory of trophic mass balance and species interactions based on size-structured population dynamics with dynamic modeling to explore the effects of fishing on ecosystem stability (Pauly et al. 2000; Persson and de Roos 2013). These models require that data is collected to parameterize functions that

describe complex size-structured interactions and this data is best obtained through controlled experimental systems as described above that are coupled with fishing.

Population-level effects of fisheries-induced evolution are largely unknown (Heino et al. 2013; Laugen et al. 2014). To detect evolutionary changes from harvesting, we suggest that researchers develop monitoring strategies designed specifically to identify changes in genetic markers for fished populations and/or examine historical data and look for changes in genetic markers over time. Additionally, to detect fisheries-induced evolution, common garden experiments are needed to determine the evolutionary effects of fishing on stock structure, fish behaviour and community interactions. Phenotypic change can best be scaled up to population dynamics by eco-genetic modelling and structured life-history modelling (Laugen et al. 2014).

Fish differ in their behavioural reactivity to recreational fishing gear and many fish have learned to avoid hooks through catch and release angling (Askey et al. 2006). This learned hook avoidance has important implications for understanding catchability and the resulting social-ecological outcomes, such as catch rates, and there is a need to improve our understanding of the severity of avoidance learning behavior and its impacts on survey effectiveness and stock assessment. The impacts on fish behaviour from angling can be assessed by biotelemetry methods (Wilde 2003), some of which now use high resolution techniques (Krause et al. 2013). However, the prevalence and strength of behavioural interactions between fish populations and anglers is still largely unknown at the scale of lakes, and we thus suggest that future research focuses on heterogeneity in vulnerability, learning and behavioral responses to fishing with special attention on how

these processes may have both spatial and temporal components. To address these issues, we suggest that researchers conduct both lab and field-based experiments using high resolution telemetry to evaluate fish behaviour before and after exposure to fishing to separate genetic factors from fish learning.

6.3 Managing Recreational Fisheries

The regulation of recreational fisheries through management intervention has occurred for centuries and it is well-known that fisheries managers attempt to manage people rather than fish populations directly (Fulton et al. 2011). In the open-access fisheries typical of North America, the constitutive institutional design assigns management rights and responsibilities to state, provincial and territorial governments who establish natural resources agencies to manage recreational fisheries. Implementing regulations on individual angler behaviour and enforcement (as well as stocking) are the most common strategies used to manage recreational fisheries in North America (Radomski et al. 2001; Lorenzen 2005). However, fisheries managers also influence anglers through several other actions such as habitat manipulation, outreach and communications, and access manipulation. The social-ecological outcomes of management intervention are influenced by several interacting factors that influence: (1) the behaviours (e.g., decisions) of fisheries managers; (2) the development of monitoring and assessment programs; (3) the response of fish populations to management interventions including stock enhancement; and (4) the response of anglers to management interventions (Table 6.1).

6.3.1 Key Uncertainties in the Management of Social-Ecological Systems

Managing recreational fisheries within a SES framework at the landscape level is in its infancy due to its complexity and outcomes are highly dependent on the behavioral interaction between anglers, fish populations and managers (Lester et al. 2003). The most critical areas of uncertainty in the management of recreational fisheries we identified are: (1) understanding behavioural factors that influence anglers' responses to regulations; (2) understanding the role that social norms, power relations, networks, availability of information and stakeholder preferences play in affecting management and policy decisions; (3) improving monitoring and assessment programs in a cost-effective way; and (4) incorporating uncertainty into management advice to provide robust recommendations in the face of irreducible uncertainty.

Few studies have examined behavioural factors that impact illegal harvest in recreational fisheries (e.g., Sullivan 2002) and research focusing on how compliance rates vary by regulations represents a common plea (Radomski et al. 2001). We suggest that researchers focus on understanding how compliance is realized in anglers, identify the strength of normative pressures on compliance and the relative weight of formal and informal institutions (defined as the rules, norms and strategies that guide interactions among people and the resource) in affecting compliance. The relationship between angler behavior and regulations can be explored by experimentally altering regulations and enforcement. Additionally, non-compliance with regulations might vary with angler awareness (Page and Radomski 2006). To overcome this awareness deficiency, there is a need to study the effects of different communication strategies and how these strategies

affect the spread and acceptance of regulations by anglers. By quantifying angler noncompliance under various management scenarios and reducing non-compliance through outreach programs, managers can develop regulations that maximize angler satisfaction and reduce illegal harvest.

Specific methods for investigating the role stakeholders play in influencing managerial actions and behaviors are scarce. Moreover, there is almost no research on how decisions are actually made and the factors influencing management decision making. Decisions on fisheries management maybe analyzed using revealed (observed) data sets, which may be complemented by network analyses and place-based anthropological techniques (May 2013). To investigate the role external (e.g. the wider social-political and environmental context) and internal (e.g. attitudes and perceived social norms) factors play in influencing managerial decisions, we suggest that researchers survey and measure management responses chosen by decision makers. If such a study was extended over multiple governmental jurisdictions, it is possible to decouple the effects of state laws to determine the influence of social context (at the state level) on management decision making using hierarchical modelling. Other options to improve our understanding of the role that external and internal factors play on influencing managerial actions include studying the decision making processes directly, by using participant observation or discourse analysis. Many factors affect managers' choices and deriving hypotheses from human sciences can help us begin to understand the internal and external factors influencing management decisions.

We argue that statistical tools for incorporating sources of uncertainty into models are well developed and that research should focus on developing rigorous monitoring programs (that are both cost and resource effective) that provide useful information on the status of the stock or other performance criteria considered relevant by the management bodies (Fenichel et al. 2013). To address biases and reduce labor intensive sampling requirements associated with traditional survey methods, we suggest that managers use model-based approaches to survey and inform actual monitoring programs using a virtual ecologist approach, which has been proposed as one method to develop and test optimal monitoring strategies (Zurell et al. 2010). Virtual ecologist techniques utilize simulation to compare engineered ecological systems in parallel to an empirically assessed system.

Managers must also recognize that uncertainty in the data leads to uncertainty in the expected outcome of any management action. We suggest that managers use metaanalysis techniques and adaptive management experiments to reduce uncertainty in stock assessment. The application of meta-analysis techniques in fisheries stock assessment is becoming increasingly widespread. It is widely recognized that many important parameters in fisheries stock assessment models are common amongst species or environments (Myers 2001). Therefore, we suggest that managers take advantage of hierarchal modelling techniques to "borrow" information from other systems to help improve stock assessment models in data-poor situations. In certain data-poor situations, it may be possible to design experiments to help gain information about a system and this is termed 'active adaptive management'. Active adaptive management usually involves a

large-scale experiment to better understand population dynamics to make improved management decisions (Walters and Holling 1990). We suggest that managers consider any management intervention in an adaptive framework and to design and implement appropriate monitoring programs to assess the impact of the management strategy. Such monitoring must address the response of the human agents to reduce the implementation uncertainty of strictly biological management actions (Fulton et al. 2011).

6.4 Discussion

The behavioural responses between fish populations, anglers and managers have the potential to strongly impact social-ecological feedbacks and correspondingly influence a range of social-ecological outcomes (Johnston et al. 2010; van Poorten et al. 2011). Outcomes of a recreational fisheries SES are diverse and often considered the objectives of fisheries management. At a general level, outcomes from recreational fishing include the full range of provisioning, supporting, regulating and cultural ecosystem services. More specifically, system outcomes can also relate to anglers (e.g., effort, catch, economic impacts and angler well-being), fish populations (e.g., changes in stock structure), and managers (e.g., legitimacy and choice of management strategy). Many outcomes are interdependent, and general outcomes such as the biological sustainability of fish populations may involve the more specific outcomes, such as the spatial and temporal distribution of effort, catchability and harvest regulations. All specific outcomes related to fish populations such as stock structure (size and abundance) and fish vulnerability to capture will exert dynamic feedbacks within the SES and impact

other outcomes until a dynamic equilibrium is reached. Understanding the desirability of a specific equilibrium to be expected constitutes an important research question as it relates to the key behavioral processes that are involved. Understanding sources of uncertainty that result from the behaviours of fish, anglers and managers are critical for effectively managing recreational fisheries as these uncertainties can lead to unexpected outcomes within the SES (Fulton et al. 2011).

6.4.1 Examples of How Interactions Between Anglers, Fish and Managers Can Affect Social-Ecological Outcomes:

Preferences for attributes related to fishing tactics are influenced by many components and the choices that anglers make for particular fishing tactics rely on perceived trade-offs. One particularly important trade-off involves catch and non-catchrelated attributes. When an anglers' utility is strongly defined by catch-related factors, declines in fish abundance can correspond to declines in utility. These anglers will likely move or change tactics to maintain high catch rates. Conversely, when non-catch related factors are more important, anglers may be reluctant to relocate their effort as abundance and catch rates decline (Hunt et al. 2011; Allen et al. 2013). This reluctance to leave when fishing quality is poor can increase the probability of overfishing and impact angler well-being (Johnston et al. 2010).

Learning and awareness of resource conditions and fishing opportunities can affect anglers' choices of fishing tactics from both preference formation and search and stop rules that anglers use to evaluate different fishing tactics. It is suspected that the behavioural response of anglers to resource characteristics is highly influenced by information sharing (i.e., anglers learning and diffusion of information through social networks), processes that delimit the diffusion of information (Mueller et al. 2008) and habits. Little and MacDonald (2007) demonstrated through a simulation model that increased social networks (and information sharing) allows anglers to exert higher fishing mortality on fish stocks than if anglers chose fishing tactics in the absence of social networks (Stoop et al. 2012).

Traditionally, anglers affect the decision-making process of managers by requesting specific strategies, such as habitat management or stock enhancement. Increasingly, management paradigms are shifting from traditional command-control forms, where managers make rules to more multi-party platform (e.g., stakeholder) driven and even co-management processes, where stakeholders (e.g., anglers) take an active role (lead) in developing management options and making management decisions. Therefore, internal and external factors can have large impacts on the behaviour of fisheries managers and play a critical role in determining social-ecological outcomes.

Fisheries managers stock hatchery-reared fish to increase fishery yield (either through manipulation of fish abundance and/or trophic interactions), aid in the reconstruction of imperiled and/or over-exploited populations, and provide partial mitigation for the ecosystem effects of fishing (Lorenzen 2005). However, several authors have suggested that the decision of managers to stock fish often occurs with limited knowledge or consideration of the resulting ecosystem impacts (van Poorten et al. 2011) and stocking has resulted in severe consequences and unintended outcomes for the entire aquatic ecosystem (Knapp et al. 2001; Lorenzen et al. 2012).

6.4.2 Optimal Management of Social-Ecological Systems

Traditional management strategies for recreational fisheries have focused on quantifying uncertainty in the biological response of fish populations to harvest (Hilborn and Walters 1992). This approach falls short in addressing the key behavioural feedbacks that drive the system (Arlinghaus et al. 2013). Evidence is mounting that understanding the uncertainty in the human response is critical when planning management regulations (Fulton et al. 2011; Fenichel et al. 2013; Hunt et al. 2013). We argue that successful management of recreational fisheries within the SES requires understanding the strength of the social-ecological feedbacks between fish, anglers and managers, which necessitates a focus on investigations of key behavioural factors in the SES. Such research will generate generic insights, however, SES research emphasizes the place-based context stemming mainly from large variation in the social context of various SESs. Therefore, the final outcome for a given SES results from generic processes that likely operate in many systems (e.g., fish behavioural reaction to reduce exposure to anglers) that interact with the specific contextual conditions of the SES (Figure 6.2).

The specific factors that impact behavioural interactions and the outcome of recreational fisheries we identified can be organized in a general framework that may be of use for analysis of a wide range of recreational fisheries and other similar SESs such as hunting or small-scale artisanal fisheries. Three key behavioral-driven axes are important to understand and address. First, the response of anglers to fish population changes and changes in the social or management environment determines the amount of fishing mortality and in turn angler well-being. Second, the response of fish populations to

anglers or management determines the degree of compensation and hence the ability of populations to withstand harvest pressure. Finally, the response of managers and policy makers to anglers or fish population states determines the choice and effectiveness of a management strategy. Obviously, a range of more fine-scaled behavioral interactions will drive these three key processes, which collectively lead to three key outcomes (i.e., the amount of fishing mortality, degree of compensation and effectiveness of a management strategy).

These outcomes are at the same time key feedbacks inherent in SES. Understanding the scale at which these processes operate and what local and regionallevel outcome is produced, are critical for improving the management of recreational fisheries as SES (Figure 6.1). Managing regional open-access fisheries using a one-sizefits-all management strategy is most likely inappropriate given variations in ecological, social and managerial conditions across fisheries (Cox et al. 2002; Carpenter and Brock 2004). Fisheries researchers and managers must, thus, do better in understanding how all of the seemingly small-scale feedbacks between fish, anglers and managers contribute to uncertainty in fishing-related outcomes and be able to identify feedback mechanisms that are key drivers for a particular system. In the absence of more detailed information, we summarize approaches that managers and researchers can use to address areas of uncertainty in key SES interactions (Table 6.2).

The complex interactions in SES require multi-pronged management strategies to address multiple objectives. We recognize that context matters and factors external to a recreational fisheries SES may impact these processes in systematic and often

uncontrollable ways. Nevertheless, understanding the often-overlooked behavioural interactions inherent in the SES can help foresee how the system might develop in response to external and internal changes. To begin addressing this complexity, successful management of SES requires developing quantitative models to predict the range of plausible responses of the system to both human and non-human-induced changes. There is increasing recognition of the importance of integrated models that link social and ecological processes to understand dynamics in recreational fisheries (Johnston et al. 2010; Hunt et al. 2011; Ward et al. 2013). We argue that a key part of this dynamic interaction includes behavioural feedbacks between fish, anglers and managers and these processes and corresponding uncertainty need to be explicitly specified in integrated social-ecological models.

Recreational fisheries are a unique SES where empirically tractable data exists to understand the role of behaviour-mediated processes and interactions in influencing system outcomes. By studying the behavioural feedbacks that exist within recreational fisheries, it is possible to understand how other systems (e.g. hunting, agriculture, forestry) respond to social-ecological changes across a variety of spatial scales. This integrated approach to natural resource management, where behavioural feedbacks between humans and ecosystems are explicitly considered, will ultimately improve resilience for the natural environment in the face of considerable uncertainty in both human and non-human induced changes.

Table 6.1 Mechanisms influencing the three key feedbacks of recreational fisheries as social-ecological systems, factors that may impact social-ecological outcomes and key supporting references.

	Components	Factors that impact social-ecological outcomes	Key References
	Attribute Preference	• Trade-off between catch and non-catch	• Hunt 2008
		related attributes	• Johnston et al. 2010
		• Attachment to fishing sites	• Hunt et al. 2011
		Catch orientation	
ur		• Changes in resource and social conditions	
avio	Personal Constraints	• Structural (i.e. limited resources, age, health	• Fedler and Ditton
Beh		concerns, lack of leisure time)	2000
gler		• Intrapersonal (i.e. perceived lack of fishing	• Sutton 2007
An		skills)	
		• Interpersonal (i.e. lack of social networks)	
	Learning and	Information sharing	• Mueller et al. 2008
	Awareness	Awareness of resource conditions	
		• Diffusion of information	
	Density-dependent	Growth, mortality and recruitment	• Hilborn and Walters
S	vital rates	• Depensatory response in per-capita growth	1992
amic		rates	
dyn	Inter- and intra-	Ecosystem responses	• Walters and Kitchell
ation	specific interactions	• Truncation of age and size-structure	2001
sh popula	Fisheries-induced	• Genetic change in life-history traits and	• Heino et al. (2013)
	Evolution	vulnerability to fishing	• Laugen et al. (2014)
Ĩ	Behaviour of fish to	• Variability in vulnerability to angling	• Askey et al. 2006
	recreational fishing		

	Components	Factors that impact social-ecological outcomes	Key References
	Behaviour of fisheries	• External factors (social-political and	• van Poorten et al.
	managers	environmental context)	2011
		• Social normative influences	
es	Development of	• Integrated models of fish-angler interactions	• Hilborn and Mangel
sheri	monitoring and	• Model to link observations to fish	1997
ational fis	assessment programs	population dynamics	
	Response of fish	Habitat and/or stock manipulations	• Cowx 1994
ecre	populations to		• Lorenzen 2008
ng r	management		
anagi	intervention		
Ä	Response of anglers to	• Impacted by angler's awareness levels,	• Sullivan 2002
	management	preferences, competencies, perceptions of	• Page and Radomski
	intervention	legitimacy and expected penalties and	2006
		perceptions	

Table 6.1 Continued

 Table 6.2 Recommendations for researchers and managers to improve knowledge
 on the three key feedbacks of recreational fisheries as social-ecological systems

	Advice for Researchers and Managers	Suggested Methodological Approach
behaviour	• Improve empirical measures of angler effort dynamics in landscape systems	• Use remote measures of angler effort to parameterize mechanistic models of the spatial distribution of angling effort
Angler	• Determine the effectiveness of different fishing tactics employed by anglers	• Conduct controlled experiments to validate angler preferences
	 Determine the strength and prevalence of: The interaction between compensation and depensation 	 Analyze experimental fishing data using stocked monoculture systems
Fish population dynamics	- Inter- and intra-specific interactions	• Use trophic analysis and size-structured population models coupled with an ecosystem-based survey
	- Evolutionary effects of recreational fishing on stock structure and vulnerability	• Conduct common-garden experiments and use information to develop eco- genetic modeling
	- The spatial and/or reactive behavioural interactions between fish populations and anglers	• Conduct controlled experiments using high-resolution biotelemetry methods

	Advice for Researchers and Managers	Suggested Methodological Approach
	• Determine behavioural factors that	• Experimentally alter regulations and
	influence anglers' responses to regulations	enforcement
3	• Understand how social norms and	• Survey and measure the management
	stakeholder preferences influence	responses chosen by decision makers
	management	
	• Improve monitoring and assessment	• Use a model-based approach to
2122	programs	surveying such as the virtual-ecological
ll û		technique
Bullag	Better incorporate uncertainty into	• Consider any management intervention
DTAT	management advice	in an adaptive framework and monitor
		impacts of the chosen management
		strategy

Figure 6.1 Recreational fisheries can affect social-ecological outcomes across a wide range of spatial scales. For example, at the global scale, changes in socio-economic conditions can affect angler participation, whereas at the site scale, anglers may locally deplete fish populations. Conversely, changes at the site scale will have effect at the regional scale by shifting angler effort.


Figure 6.2 The interaction of fish populations, anglers and fisheries managers within social-ecological systems and the resulting social-ecological outcomes. Examples of how angler behaviour, the impact of fishing on fish population dynamics and the management of recreational fisheries can influence social-ecological outcomes are described in detail in text.



Chapter Seven: Conclusions and Future Directions

The objective of this thesis was to integrate social and ecological components operating in a multi-stock spatially-structured fishery to examine the dynamic interaction between biological and harvest processes. This thesis was composed of five main research chapters (2-6) and together, these chapters suggest a way improve the management of spatially-structured fisheries by integrating the dynamic interaction between social and ecological processes.

In Chapter 2, I developed a method to estimate fish density using standard sampling techniques in the absence of mark-recapture data. Index netting using standard multimesh gillnets is a common technique used by fisheries managers and researchers, and is considered the provincial standard method in British Columbia. Understanding how gillnet catchability varies among sampling units is useful as it can help to translate an observed CPUE into an estimate of fish density and provide information on how variability in lake characteristics can affect gillnet catches. Using mark-recapture data, I developed a model to predict how gillnet catchability varies as a function of lake-basin characteristics and water temperature. The analysis in this study was conducted using Bayesian statistics, as I was interested in fully understanding the uncertainty associated with the estimated model parameters. Therefore, this study adds to the growing body of literature using Bayesian methods in field ecology studies. In an era of declining resources for fisheries management, this analysis also represents a crucial step forward in

allowing fisheries managers to cost-effectively estimate fish density across a large number of lakes.

In addition to providing an analysis method to estimate fish density, this study also provides insight into how fish ecology and behaviour influence gear efficiency. It is likely that several other covariates not explored in this analysis may impact fish behaviour. For example, it is likely that depth, habitat structure, size-structure of the fish population and water quality may impact the distribution of fish within a lake and thus influence the efficiency of sampling gear. Therefore, I suggest that future research focus on quantifying how these factors impact gear efficiency. Conducting mark-recapture experiments using stocked populations is highly resource effective (as fish can be marked in the hatchery), and I suggest that future researchers use similar techniques to further investigate these factors and improve precision in estimating fish density.

In Chapter 3, I assessed how the population of anglers interacts with the fishery resource. Specifically, I examined how the source (spatial distribution), efficiency (catchability) and behaviour (propensity to harvest fish) of angler effort varies across the landscape of the fishery resource. The results of this study demonstrated that anglers who fished in the spatially structured Rainbow Trout fishery in British Columbia varied substantially in characteristics that determine quantitatively how anglers interact with the fishery. Angler efficiency (catchability) and harvest behavior were strongly correlated with distance travelled to the lake. Anglers who travelled short distances to the lake (local anglers) had lower catchabilities and harvested a higher proportion of their catch in comparison with anglers who travelled long distances to fish (non-local anglers). This

suggests that the angler population does not interact homogeneously within this spatially structured fishery, and therefore it is useful to understand and quantify how different angler types affect the fishery. Using a hierarchical cluster analysis, four distinct angler groups were identified based on three variables that directly describe how anglers interacted with the fishery (spatial distribution, catchability and harvest behaviour). Additionally, angler characteristics varied between groups, and the relative proportions of the four discrete groups varied among management regions.

The work conducted in this chapter is the first attempt to simultaneously quantify variation in angler characteristics among groups, characteristics that directly link to interactions with fish populations (such as catchability and propensity to harvest) and spatial behavior over a spatially distributed fishery. The substantial variation in angler characteristics across groups and variation in the relative distribution of the groups across regions implies that a "one size fits all" management approach is not optimal for this fishery. Instead, management strategies that are attuned to angler characteristics would constitute a better approach for managing this large, spatially structured fishery. Given these quantitative relationships that describe how social and ecological processes interact across space, it is possible to develop process models that examine optimal management strategies for this fishery. Therefore, I suggest that future research involving characteristics of anglers focus on understanding predicting the response of anglers to changes in management strategies.

In Chapter 4, I examined mechanisms resulting in hyperstability (where catchper-unit-effort, CPUE, remains high as fish density declines) by collecting data on angler

CPUE and fish density. I contrasted the relationship between CPUE and fish density in an open-access recreational fishery with an experimental fishery (a set of lakes that had restricted access, standardized fishing methods and no heterogeneity in angler experience) to assess the mechanistic cause of hyperstability. There was no evidence of hyperstability in the experimental fishery, but significant hyperstability in the open-access fishery. In the open-access fishery, the composition of the angler population varied among lakes: anglers who fished at low density lakes were more experienced than anglers at high density lakes. This segregation of angler experience across lakes appeared to explain the observed hyperstability in this fishery. These results provide a mechanistic understanding of hyperstability in an open-access recreational fishery and suggest that CPUE data be used in conjunction with data on angler experience if assessing the status of a fishery.

The results of this study did not support the hypothesis that changes in fish behaviour with declines in fish density produced the apparent hyperstability in the openaccess fishery, as previously suggested by Walters and Cox (2000). Instead, in the openaccess fishery, the observed density-dependent catchability was best described by a segregation of angler experience levels among lakes. Future research involving densitydependent catchability and heterogeneity in angler characteristics should focus better describing how fish behaviour varies as a function of fish density and harvest pressure. It has been suggested that fish learning may have strong impacts on angler CPUE (Askey et al. 2006) and therefore, examining how these processes interact with angler characteristics across fish density gradients would improve our understanding of

mechanisms resulting in hyperstability. There is a strong need for empirical studies that examine how social and ecological components of recreational fisheries interact, especially at low density, in order to improve the management of a fishery.

In Chapter 5, I examined how the trade-off between environmental productivity and competition influences somatic growth rates and plasticity in life-history traits. I used experimental populations of Rainbow Trout to empirically test predictions from lifehistory theory specifically related to patterns in immature growth rates, age and size at maturity, and the proportion of surplus energy invested into reproduction across climatic and fish density gradients. The results of this study support theoretical predictions that plasticity in life-history characteristics is a function of environmental variables and evolutionary processes. In particular, I demonstrate that immature growth rates are best explained by climatic and density-dependent competition effects, and that age at maturity and the proportion of surplus energy invested into reproduction depends on juvenile growth conditions.

Empirical evidence of these relationships helps to improve our understanding of evolutionary responses and optimal life-history strategies of fish populations. Using this information, it is possible to understand how the impact of fishing impacts somatic growth rates and optimal management strategies for a fishery. This study benefited from the ability to create contrasts in fish density across the full range of environmental conditions found in the Rainbow Trout fishery in British Columbia. Further research on factors influencing growth among fish populations should focus on describing how other environmental variables affect growth (such as total dissolved solids and lake-basin

characteristics). The fish populations in this study were stocked populations from a single strain. However, it is likely that local adaptations may also play a large role in influencing growth rates. Therefore, controlled experiments should be developed to test hypothesis relating to plasticity in life-history characteristics and local adaptation and other evolutionary effects (including the effects of fish).

In Chapter 6, I examine how the interaction between anglers, fish populations and fisheries managers influence social-ecological outcomes (such as the spatial and/or temporal distribution of effort, catchability, angler well-being, and stock abundance and size-structure). Traditionally, research in social-ecological systems is often focused on either angler behaviour or the impact of recreational fishing on fish population dynamics. By reviewing the current state of knowledge on the interaction of anglers with fish populations, I identify factors, behaviors and antecedents to behaviours most important to the outcomes of a coupled social-ecological system. Based on these findings, I provided information on how to reduce uncertainty, identify data gaps and improve management advice for recreational fisheries.

The results of this conceptual analysis suggest that the seemingly small-scale feedbacks between anglers, fish populations and managers are key behaviour-mediated processes of recreational fisheries within a social-ecological system. Understanding the scale at which these processes operate is critical for managing for the sustainability of recreational fisheries. In this chapter, I identify large areas of uncertainty in the behavioural interaction between anglers, fish and managers. In the future, researchers and managers must evaluate the level of knowledge available for a particular system and

collect the necessary data needed to describe these social-ecological interactions and most importantly, understand the uncertainty associated with managing for particular social-ecological outcomes.

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APPENDIX A: LITTORAL AREA MODEL COMPLEXITY

Table A.1 Candidate models to predict littoral area. AT, C and D refer to total lake area (ha), lake complexity $(m \cdot ha^{-1})$ and maximum depth (m) respectively. DIC model selection criteria are presented for each model. Models 6 through 8 were logtransformed before fitting. Parameter estimates for the best-fit model are given in text.

	Model	$\overline{D(\theta)}$	$D(\hat{ heta})$	DIC	p_D	ΔDIC
(1)	$A_{Lit} = \alpha A_T$	8224	8221	8226	2.005	1012
(2)	$A_{Lit} = \alpha A_T + \beta C$	8218	8215	8221	3.01	1007
(3)	$A_{Lit} = \alpha A_T + \beta D$	7929	7926	7932	3.01	718
(4)	$A_{Lit} = \alpha A_T + \beta C + \gamma D$	7744	7740	7748	4.027	534
(5)	$A_{Lit} = \alpha A_T{}^\beta$	8216	8213	8218	2.824	1004
(6)	$A_{Lit} = \alpha A_T{}^\beta e^{\gamma D}$	7221	7217	7225	3.95	11
(7)	$A_{Lit} = \alpha A_T{}^\beta e^{\delta C}$	8213	8212	8215	1.602	1001
(8)	$A_{Lit} = \alpha A_T{}^\beta e^{(\gamma D + \delta C)}$	7210	7206	7214	4.338	0

APPENDIX B: CATCHABILITY ANALYSIS

B.1. Angling vulnerability

It is hypothesized that anglers change their methods of fishing to relate to the expected size composition of the population in order to increase their catch rates (Cox 2000). As a result, length at vulnerability to angling should vary with the length composition of the population. Cox (2000) assessed angling vulnerability for Rainbow Trout in lakes in British Columbia and demonstrated that the ratio between length at 50% vulnerability (L_{50}) and the maximum asymptotic size (L_{∞}) is constant across populations and this ratio was measured to be 0.433 (σ =0.052). Vulnerability at length (v_l) was calculated using this ratio and an estimated L_{∞} from fall gillnet samples.

Lapilli otoliths were collected from all non-clipped fish in the fall gillnet sample and aged (certain year classes in some lakes had unique adipose or ventral clips). A von Bertlanffy growth model was fit to the length-at-age data, L_a ,

(1)
$$L_a = L_{\infty} (1 - e^{-K[A - t_o]})$$

where *K* is a metabolic growth coefficient, *A* is the age in years and t_o is the predicted length at *t*=0. Equation (1) was fit the observed length at age data assuming normally distributed residuals using *optim* in R and the lake-specific parameter estimate for L_{∞} was used to calculated L_{50} for each lake.

B.2. Methods for Measuring Angler Effort

Angler effort was assessed using time-lapse cameras in combination with ground based counts. Several other authors have used time-lapse cameras to assess water-based recreational activities (Smallwood et al. 2011; Sunger et al. 2012). Cuddeback (Expert Model) cameras were installed at each lake on a tree at the shoreline. The cameras were programmed to take a picture of the lake every hour. The number of anglers in each picture was counted manually, using the program Time-Lapse (Greenberg and Godin 2012).

In order to account for anglers not seen by the camera, ground-based creel counts occurred at the same time. The total number of anglers seen by the camera at time t ($A_{Cam,t}$) can be described by the binomial distribution,

(1)
$$A_{Cam,t} \sim dbin(p, A_{Creel,t})$$

where *p* is the proportion of anglers seen, and $A_{Creel,t}$ is the number of anglers recorded in the ground-based count at time *t*. The number of anglers missed by the camera (A_{Missed}) is described by the negative binomial distribution,

(2)
$$A_{Missed} = dnegbin(p, A_T)$$

where A_T is the total number of anglers for all camera counts. Therefore, the total annual effort from all anglers

$$(3) \qquad N = A_{Missed} + A_T$$

N and *p* were estimated in OpenBUGS. A beta distribution was used to describe the prior for *p* with shape parameters (1,1).


Figure B.7.1 (a) Angler effort density; (b) exploitation rate and (c) capture rate as a function of fish density. Exploitation rate is the ratio between the total number of harvested fish and fish density and capture rate is the ratio between the total number of caught (both harvested and released) fish and fish density. The y-axis in figure (c) is on a log scale and the axis labels have been back transformed for interpretation.

APPENDIX C: PREVIOUSLY PUBLISHED WORK

Three chapters within this thesis have been published before completion of my thesis. Although these published papers were collaborate efforts with committee members and other co-authors, I was responsible for designing the studies, conducting the research, analyzing the data and writing the manuscripts. The full citations are:

Chapter Two:

Ward, H., Askey, P.J., Post, J.R, Varkey, D. and M. McAllister. 2012. Basin characteristics and temperature improve abundance estimates from standard index netting of small lakes. Fisheries Research 131-133: 52-59.

Chapter Three:

Ward, H., Quinn, M.S. and J.R. Post. 2013. Angler characteristics and management implications in a large multi-stock spatially structured recreational fishery. North American Journal of Fisheries Management 33(3): 576–584.

Chapter Four:

Ward, H., Askey, P. J. and J.R. Post. 2013. A mechanistic understanding of hyperstability in catch-per-unit-effort and density-dependent catchability in a multi-stock recreational fishery. Canadian Journal of Fisheries and Aquatic Sciences 70: 1542-1550.