ANGLING QUALITY, EFFORT RESPONSE, AND EXPLOITATION IN

RECREATIONAL FISHERIES: FIELD AND MODELING STUDIES ON BRITISH

COLUMBIA RAINBOW TROUT (*ONCORHYNCHUS MYKISS*) LAKES

by

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Abstract

Creel surveys and mark-recapture experiments were used to assess the dynamics of catch per unit effort (CPE), fishing effort, and exploitation on eight rainbow trout lakes in British Columbia's southern interior. CPE was high 3.8 fish per angler day (ad), and fishing effort and gross exploitation (15 ad ha^{-1} and 0.15, respectively) were both low on two limited-access lakes. CPE was generally low (1.7 fish ad^{-1}) on lakes that were easily accessible (open-access) to anglers and fishing effort and gross exploitation were both high (50 – 100 ad ha^{-1} and 0.50 – 0.60, respectively). Seasonal patterns of CPE and effort were similar among-lakes with peak values being observed during the late-spring/early summer, followed by more or less rapid declines as the season progressed. Maximum exploitation rates in the range 0.50 to 0.60 were observed over a wide range of total seasonal fishing effort density (50 ad ha^{-1} to 100 ad ha^{-1}), which suggested that fish vulnerability may have been limited.

Fish population characteristics of growth, age- and size-at-maturity, vulnerability to harvest, and natural mortality were assessed using fall gillnet survey and mark-recapture data. Estimates of the von Bertalanffy growth parameter K were between 0.19 yr^{-1} to 0.36 yr^{-1}, but most single-species (rainbow trout only) lake estimates were between 0.25 yr^{-1} and 0.36 yr^{-1}. Asymptotic body length (L_∞) estimates varied among-lakes from 416 mm to 887 mm. Size-at-50% maturity for female rainbow trout varied among-lakes from 290 mm to 387 mm, but age-at-50% maturity fell within the narrow range 2.95 yr to 3.08 yr. Size-at-50% maturity of female trout was approximately equal to 50% of L_∞. Male

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rainbow trout typically matured during their second year at body lengths between 150 mm and 250 mm. Patterns of size-selective exploitation showed rapid increases with body length, and occasional decreases at body lengths greater than 450 mm. Increasing natural mortality, or behaviours associated with spawning, may explain these apparent decreases in exploitation at large size. Exploitation rates on fully vulnerable (large body size) rainbow trout ranged from 0.21 to 0.36 in low effort lakes and from 0.60 to 0.80 in high effort lakes. Relative vulnerability of smaller fish followed a smooth power function with lengths-at-50% vulnerability between 204 mm and 345 mm. Age-at-50% vulnerability ranged from 1.70 yr to 2.79 yr suggesting that most fish become vulnerable to harvest during their second year in the lakes. Estimates of natural mortality for adult fish in two lakes were 0.41 yr^{-1} and 0.46 yr^{-1} (annual survival rates of 0.64 and 0.63, respectively. Egg to age 2+ survival was 0.0014 for one lake where virtual population estimates of total eggs laid and age 2+ recruitment could be obtained. Maximum egg to age-2+ survival estimated from a life history model was 0.0028 age 2+ fish egg^{-1}.

A model of angling quality, effort response, and exploitation was developed for recreational fisheries (limited vulnerability/effort response model), where anglers remove fish from behaviourally reactive pools. Angling quality (CPE) is predicted to decline with increasing angler effort for given fish abundance, and the rate of decline depends on hypotheses about reactive/unreactive exchange dynamics of fish. Effort responses to fish abundance were modeled under the assumption that anglers attempt to equalize CPE among-fisheries within a region. Solutions to the model equations taken over the fishing season predict: (*i.*) total seasonal effort that is linearly proportional to initial fish

abundance with slope inversely proportional to the expected catch rate c_o; (*ii.*) a lower

limit to fish abundance (N_∞) below which angler effort is no longer attracted (*y*-axis

intercept <0); (*iii.*) asymptotic exploitation rates ≤ 1. Numerical analysis results show that

analytical solutions based on equilibrium assumptions are generally robust to moderate

deviations from the equilibrium conditions. Fitting the exploitation component of the

model to observed fully vulnerable exploitation rates on B.C. rainbow trout lakes gave an

asymptotic exploitation rate estimate of 0.79.

The limited vulnerability/effort response model was fitted to observed effort and stocking

rate data for rainbow trout lakes in three management regions (Regions 3, 5, and 8) in

British Columbia's southern interior. The observed effort response appeared linear in all

regions, and all regional estimates of effort response slope were significantly greater than

zero. Statistically significant differences could not be detected between the regional effort

response slopes. Intercept values for Regions 5 and 8 were less than zero, while Region 3

showed a positive intercept. Multiple comparisons among intercept values revealed that

only Regions 3 and 5 were significantly different from one another. Effort response

parameters implied by the linear model coefficients were 1.35 fish ad^{-1} for the pooled

catch rate (c_o) and –99, 180, and 43 fish ha^{-1} for the lower abundance limit (N_∞) in

Regions 3,5, and 8, respectively.

I developed an approach for combining equilibrium calculations implied by the limited

vulnerability/effort response model with an age structured population model based on life

history and fishery characteristics. Results from this method show that classic recruitment

over-fishing is possible on B.C. rainbow trout lakes. In particular, where access to lakes is open, and c_o values are low (0.10 – 0.85 fish ad^{-1}), effort would be much higher and recruitment much lower than levels necessary to give MSY.

The limited vulnerability/effort model was also fitted to 105 lake-specific time series of fishing effort. Annual lake-specific stocking rates were used to drive the model after accounting for density-dependent fish survival and harvest. This analysis provided (*i.*) a test of among-year stationarity in c_o values, (*ii.*) a broad test of the assumption that anglers equalize catch rates among-lakes within-regions, and (*iii.*) a method by which c_o values may be predicted as a function of access. Model results showed that catch rates tend to be stationary among-years within-lakes, c_o values are predictable from access factors, and catch rates do tend to be equalized after accounting for access differences. Therefore, the effects of access control on angling quality and sustainability of fisheries on wild-stocks can be directly assessed.

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Chapter 1: General introduction: recreational fishery management challenges in the 21st century

Between 1955 and 1996, demand for angling opportunities in the United States increased at approximately twice the rate of human population--an increase of 138% (USFWS 1996) that is unlikely to abate due to increasing pressure for economic development on public waters (Swanson and McCollum 1991). Similar increases have occurred in Canada as well (Stone 1988), although recent trends show that interest in recreational fisheries is either stable or declining. Concurrent with these trends, exploitation and angling quality have become important concerns to managers in North America (Mather et al. 1995). This leaves research scientists with the challenge of designing new management strategies that effectively deal with high demand while acknowledging the full scope of processes that influence management success.

Changing management paradigms in recreational fisheries

Since the 1950's, the management paradigm for recreational fisheries has changed from one that is based on maximum sustainable yield (MSY) to a basis in optimal yield (OY; Roedel 1975; Larkin 1977). In contrast to MSY goals, which attempt to simply maximize fish yield, OY attempts to balance sociocultural, economic, human health, and ecosystem values affected by fishery (Malvestuto and Hudgins 1996). OY management is considerably more complex than its MSY predecessor, and the design of policies that address OY goals will likely be a difficult challenge that researchers will face in the future.

Current views on angling quality generally fit into the OY model. Although the specific definition of angling quality varies among individuals, quality fisheries defined here imply either (*i.*) put-and-take, or put-grow-and-take fisheries that consistently produce high catch rates of small to medium sized fish or slightly lower catches of larger, perhaps trophy sized fish, or (*ii.*) high catch rates of wild fish where the population and ecosystem viability (in both a natural and recreational sense) are not impaired by the fishery. Quality in the OY sense also implies generating a sustainable economic benefit, but not at the aesthetically unappealing cost of crowding a limited number of fishing sites or wilderness areas. This definition agrees with the results of angler surveys and sociological studies in Canada (Stone 1988) and the United States (Holland and Ditton 1992), as well as definitions put forth for quality fishing experiences in wilderness (Fraley 1996) and non-wilderness areas (Moeller and Engelken 1972; Manning 1979). Designing management policies that address angling quality will require a delicate balance between the two, sometimes conflicting approaches that currently dominate recreational fisheries management programs.

Current themes in recreational fisheries management

Management of recreational fisheries involves two main strategies. First, there are biological, or production-side strategies that attempt to (*i.*) increase the scope for growth and survival of fish populations by methods such as habitat restoration, fertilization, and predator/prey control, and (*ii.*) enhance, via hatchery production, depressed populations or areas where fish did not historically exist (Kohler and Hubert 1993). Production side

management is fundamental to most biologists' training, so it has been heavily emphasized in the past. In addition, where the effects of land use practices, over-fishing, and exotic species introductions or invasions have occurred, manipulation of production frequently appears to be the obvious short-term response (Heidinger 1993). However, success of production-side approaches in both the short- and long-term remains far from certain. In many cases, enhancement programs have led to increased exploitation on wild stocks (Argue et al. 1983; Moring 1993; Winton and Hilborn 1994) or adversely affected prey species (McMahon and Bennet 1996). Thus, production-side management cannot in principle be used in isolation to achieve fishery objectives.

The second type of management involves sociological, or consumption-side strategies where catch and size-limit regulation, and access controls are used in an attempt to limit fish harvest by individual anglers (Kohler and Hubert 1993). Despite a large amount of modeling research and implementation, the usual methods of catch and size limit regulation have not been effective at achieving even the simplest management goals (e.g., MSY ; at least theoretically speaking) in both commercial (Beverton 1998) (Ludwig et al. 1993) and recreational fisheries (Wilde 1997; ASMFC 1998). Policies based on regulation of individual angler harvests are typically doomed from the start for two reasons. First, bag or size limits tend to be unrealistically high and most anglers seldom catch a full bag. The actual limits on both catch and size needed to protect fish populations are usually so drastic that their implementation is discouraged due to fear of public outcry or perceived losses in total catch (Goodyear 1984). The second cause of regulation failure is an angler effort response to fish abundance. When anglers increase

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the amount of effort exerted in response to the abundance of fish present, a generally pathology occurs in which "success breeds failure" (Walters and Cox 1999): short-term increases in abundance due to successful production- or consumption-side programs result in higher effort and potentially higher exploitation until catch rate and angling quality (per angler) declines to the point where no further effort is attracted. Management strategies that do not address the open-access nature of recreational fisheries directly may ultimately fail, at least in terms of angling quality.

Key scale and process issues for optimal yield management

Obviously, it is difficult for a single fishery (spatial sub-area, lake, or stream) to meet the entire suite of OY management goals even where production- and consumption-side strategies are successfully implemented. Individual fisheries tend to have somewhat unique characteristics that set them apart from the surrounding opportunities, and attempting to homogenise fisheries does not appear to be the appropriate solution. Diversity of opportunity in the form of different types of angling experiences (harvest, family, or wilderness oriented) is important in the OY model. Also, few individual fisheries actually have the necessary information base for intensive management. Increasing angler demand on almost all freshwater fisheries, combined with requirements for a paradigm shift (from MSY to OY), point to the need for a new approach to recreational fisheries assessment and management. A shift in focus from managing individual high-profile fisheries to managing on larger, regional scales may provide better information and understanding of key components that are important for successful OY management.

One of the major stumbling blocks to developing regional management policies in recreational fisheries is a general lack of sound information for assessment and research. While intensively managed commercial fisheries number a few thousand worldwide, recreational fisheries in freshwater alone occur on tens or even hundreds of thousands of individual stocks. This makes research difficult due to the high cost of monitoring so many small, isolated fisheries (individual lakes or streams). At the regional level, the size and economic importance of the resource may be large, but low socio-economic and information value associated with studying individual systems makes intensive research impractical except in the most high profile cases (Shuter et al. 1998). Therefore, many of the world's freshwater fisheries are managed on limited experience where results from a few studies are extrapolated to hundreds of independent stocks. As a consequence, management failures such as stock declines and poor angling quality are increasingly common but proceed virtually unnoticed (Post et al in prep; Griffith 1993).

Regional-scale management of recreational fisheries

Many freshwater recreational fisheries (lakes or streams) can be grouped at the regional level into classes that share similar physical, biological, and sociological characteristics (Walters 1986; Quinn et al. 1994; Shuter et al. 1998). For example, in British Columbia's southern interior plateau there are hundreds of lakes that support wild- or hatchery-stocked rainbow trout (*Oncorhynchus mykiss*) fisheries. Most of these lakes are less than 500 hectares in size and they have moderate to high total dissolved solid contents (100-1000 ppm; Northcote 1964). High standing crops of benthic organisms

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such as freshwater shrimp (*Gammarus* spp.), larval and pupal forms of aquatic insects (*Diptera, Tricoptera, Odonata, Notonecta*) and forage fishes such as lake chub (*Couesius plumbeus*) and redside shiner (*Richardsonius balteatus*) contribute to relatively high growth rates of rainbow trout.

As a whole, the southern interior rainbow trout lakes are recognized as British Columbia's largest source of recreational fishing effort (Stone 1988). Anglers from British Columbia, Alberta, and the northwestern U.S. states spend more than 3 million angler days fishing rainbow trout lakes each year, and their economic activity is important to southern interior communities. In addition, license fees from small lake anglers contribute significant amounts toward the conservation of important game and non-game fish species, as well as the Provincial tax base. A few other examples of *regional-scale fisheries* include: Alberta walleye lakes (*Stizostedion vitreum),* Ontario lake trout (*Salvelinus namaycush*) lakes, Minnesota northern pike (*Esox lucius*) lakes, Wisconsin walleye (*Stizostedion vitreum*) lakes, Montana rainbow, cutthroat (*Oncorhynchus clarkii*), and brown trout (*Salmo trutta*) streams, and brown and brook trout (*Salvelinus fontinalis*) streams in Pennsylvania and New York. Individual fisheries (one lake, stream, or stream reach) within these groups are seldom recognized as socio-economically significant; but when aggregated at the regional level, they constitute a large proportion of total angler use and socio-economic impact in their respective province or state. Some detailed assessment and simulation studies have been done at the scale of individual fisheries, but few attempts have been made to develop a general

framework for incorporating regional level variables, processes, and values into fishery management plans.

Developing regional-scale models

Shuter et al. (1998) used information from a sub-sample of Ontario lakes to develop a general life history model for regional assessment of lake trout (*Salvelinus namaycush*) fisheries. Lake-specific growth, maturity, natural mortality, and vulnerability to harvest were correlated to lake area and total dissolved solids. They used life history theory to argue that once such correlations between physical variables and life history parameters have been identified, those relations can be used to forecast behaviour of other populations within that region. Thus, general life history models represent a fundamental step towards effective regional management because they can be used to predict sustainable levels of angler effort and yield for populations that are not well studied (Shuter et al. 1998), and they recognize unique contributions that individual fisheries make toward overall management objectives. This provides managers with a tool for generating expected values of several important quantities associated with the fish populations and can be readily combined with socio-economic models to design regional management policies in relation to fishery management goals.

Shuter et al's approach to regional modeling can be extended in two important ways that result in a more comprehensive modeling framework. First, models for angler catch and exploitation should be developed specifically for recreational fisheries. Traditional fisheries theory assumes that catchability is constant over a wide range of fish abundance

and fishing effort, and that all fish are available to the gear (Hilborn and Walters 1992). However, recent evidence suggests that this may not be the case, because catchability appears to be is inversely proportional to fish abundance (Shuter et al. 1998) and possibly angler effort (Engstrom-Heg 1986). If this pattern is common to recreational fisheries in general, then perhaps new fishery models, that exhibit this behaviour as an underlying property, should be developed.

The second important extension is to incorporate the open-access nature of recreational fisheries. Numerical response of anglers to fish abundance is a key component that should be included in regional models, to allow for more explicit evaluation of how management policies affect dynamics and socio-economic value of the entire fishery. Strong numerical responses by the angling community can easily reduce or eliminate the effectiveness of any management actions aimed at meeting stock conservation, angling quality, or more complicated OY management goals (Kitchell and Carpenter 1993). It is clear that an inability to quantify and control effort dynamics has led to the poor state of many important commercial fisheries (Ludwig et al. 1993). Where effort dynamics have actually been considered in sport fisheries, results have been inconclusive due to lack of replication, poorly determined response cues (catch rate, time of year, marketing, etc.), and improper temporal and spatial scales (Carpenter et al. 1994; Johnson and Carpenter 1994). Lack of replication is a common problem in recreational fisheries assessment because most studies are done on individual high profile systems. The problems of seasonality and long established angler habits become particularly distressing when relationships between angler effort and fish abundance are examined on such small

space/time scales (Collie and Walters 1991; Carpenter et al. 1994). In situations where anglers choose among several alternative opportunities, a broader, regional perspective could provide better effort dynamics models (Carpenter et al. 1994).

Failure to recognize, or admit, the open-access nature of recreational fisheries is probably the most critical oversight that has occurred in fisheries management (Walters and Cox 1999). Limitations on our current knowledge about open-access effects on exploitation and angling quality is mostly due to a continuing disregard for the importance of effort dynamics when developing fisheries models (Hilborn 1985; Johnson and Carpenter 1994). If management policies are to provide high quality angling opportunities then it is time for scientists to invest more research energy into studying these effects and into developing fair and efficient means of managing angler effort.

Angling quality and the problem of open-access fisheries

Effort responses in recreational fisheries may be so pervasive as to completely eliminate the possibility of sustaining angling quality. They are analogous to numerical responses frequently studied in predator/prey systems where predator abundance increases in response to increases in available prey. Numerical responses as they apply to fisheries have been extensively reviewed and applied elsewhere (Lapointe 1989). In the section below, I provide a high profile case example to show how ignoring angler numerical responses may lead to the "success breeds failure" pathology. The Atlantic striped bass is chosen because it is prominent in the fisheries literature. Other examples include Kitchell and Carpenter (1993), Moring (1993) and Post et al. (in prep).

Atlantic striped bass

The Atlantic striped bass (*Morone saxitalis*) is one of the most important commercial and recreational fish species on the U.S. east coast (Field 1997). They are pursued intensively in almost all river, estuary, and coastal habitat in which they occur from North Carolina to Maine. A strong decline in the Chesapeake Bay population, which contributes over 75% to the total coastal migratory stock, occurred between the mid-1970's and early 1980's, and in 1979 the Emergency Striped Bass Study concluded that the population had collapsed due to uncontrolled and excessive fishing mortality (Richards and Rago 1999). In response to these findings, the Atlantic States Marine Fisheries Commission (ASMFC) prepared a management plan that recommended severe size-limits and spawning period closures in all states. However, the stocks continued to decline during the early 1980's under these severe harvest restrictions. With further restrictions and complete closures, the Chesapeake Bay population eventually recovered and by the mid-1990's it and several other stocks were declared healthy (ASMFC 1998). The successful recovery of this stock can be attributed to two direct causes. (1.) During the recovery period, complete closures and minimum size-limits up to 36 inches protected spawning fish from harvest. Very few fish in the population during the 1980's were of harvestable size, so essentially all fish were protected and fishing mortality was extremely low. (2.) Harvest restrictions along with the presence of a complete crisis discouraged a large proportion of recreational anglers and fishing effort during this time was low (Richards and Rago 1999).

Following the recovery, commercial and recreational fisheries were re-opened under new minimum length limits (from 18 in to 36 in.), slot size limits, bag limits (1-2 per day and catch-and-release), seasonal closures, and commercial quotas. Several Atlantic states did not re-open commercial fisheries (ME, NH, CT, NJ, PA, DC). Increases in striped bass abundance in the 1990's spurred renewed interest in the fishery and current recreational trip estimates indicate that angler effort continues to increase (ASMFC 1998).

Can the current regulatory structure used to manage this stock be considered successful in an OY sense? Obviously, the measures taken during the early 1980's to protect the stock were successful from a conservation perspective. Current spawning stock biomass levels appear extremely healthy and continue to increase albeit slowly in recent years. But the severe harvest regulation strategies that were used to facilitate the recovery had strong negative impacts on the economic structure of the fishery (Kahn and Buerger 1994). Under the new regulatory structure, the economic outlook is very good, but these measures are already beginning to reveal their weakness in the face of increasing angler demand. Current tagging programs and stock assessments show that target fishing mortality rates ($F = 0.31$) are again routinely exceeded by as much as 25%, and this trend is expected to continue under present harvest restrictions (ASMFC 1998). Should these trends continue unabated, destabilization of the economic structure and quality of the fishery are likely to occur again via a return to more stringent harvest regulation, excessive effort and crowding, and declines in stock size with increasing fishing mortality. So the long-term success of management remains unknown, especially if

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myopic economic objectives supersede the long-term goals of preserving the stock (Richards and Rago 1999).

Some suggest that the list of regulatory options available to fishery management will include access control if interest in the striped bass fishery (and other fisheries) continues to increase (Griffith 1987; Richards and Rago 1999). The problem will then be to determine the best rates of access in relation to optimal yield management goals (Walters and Cox 1999).

The primary motivation for this thesis was to develop angling quality and effort response models for use in regional policy analysis of British Columbia's rainbow trout lakes. In order to accomplish this, it was necessary to (*i.*) study in detail the dynamics on specific rainbow trout fisheries, (*ii.*) develop models of angling quality, effort response, and exploitation, and (*iii.*) test these models against empirical data from a larger set of fisheries distributed over several management regions. Thus, the thesis is organized around this basic structure. In Chapter 2, I describe the set of British Columbia rainbow trout lakes and results upon which much of this thesis is based. Two general observations arose from those results. First, long-term patterns in fishing effort on the study lakes appeared to change in response to variation in stocking policies and in some cases, in-season changes in effort appeared related to the severity of depletion early in the season. Second, total annual exploitation rates on the study lakes appeared limited in comparison to the intensity of angling pressure suggesting that behavioural characteristics of the fish may limit exploitation rates in situations where effort is very high. In Chapter 3, I

examine in more detail the life history characteristics and size-selective harvest of rainbow trout resulting from different levels of angling effort. Results and observations from these two chapters suggested that modeling the dynamics of angling fisheries requires a unique approach compared to traditional models used for commercial fishery research. Chapter 4 identifies some of the unique characteristics of angling fisheries that warrant a new approach, and I develop a model that can be used to explore the many possible alternatives available for managing recreational fisheries. The basic model is flexible enough to examine such effects as catch-and-release, size limits, and access controls and how these polices may affect effort dynamics and angling quality. In Chapter 5, I show the first test of the model against empirical data on effort and stocking rates in British Columbia rainbow trout lakes. Results from that analysis are then applied to an age-structured model of wild trout, and the impacts of development and enhancement are assessed. Chapter 6 provides a broader application of the model to over 500 lake-years of effort and stocking data. There I show that access is the main controlling factor of angling quality in British Columbia's rainbow trout lakes. Finally, concluding remarks are presented in Chapter 7 where I discuss effort dynamics in the context of optimal yield. Specifically, I describe how the current field and modeling approaches may be used to assess the efficacy of potential access control solutions to particular optimal yield management problems.

Chapter 2: Creel census and mark-recapture studies on British Columbia's southern interior rainbow trout (*Oncorhynchus mykiss*) lakes

Introduction

Despite their status as one of Canada's premier recreational and economic opportunities, management of British Columbia's southern interior lakes have received relatively little research attention. Pearse (1970) recognized that high angler use on rainbow trout lakes had the potential to erode the angling experience by crowding an increasing number of anglers into a fixed set of accessible sites. He argued that continued increases in angler demand would probably require new and perhaps dramatic changes in the way B.C.'s small lakes are managed. Despite this warning, there has been little pro-active management of the fishery during the past thirty years. Closed seasons and bag and size limits have been implemented on some high profile lakes, but on average there has been little improvement in average quality of angling, or on insurance for conservation of wild stocks. While it is clear that many anglers have embraced the "catch-and-release" ethic as a means of conservation (National Survey of Sport Fishing, 1995), declines in angling quality and even complete stock collapses still occur (B. Chan, B.C. Ministry of Environment, Land, and Parks, Kamloops, B.C., pers. comm.).

Interest has grown recently in expanding the fishery through increases in access and resort development. If these initiatives are to be successful, there needs to be a systematic

assessment of angler impacts on fish populations and the potential effects of alternative

regulatory measures. In this chapter, I provide some basic data on current angling quality

and exploitation in British Columbia rainbow trout lakes. I describe the set of study lakes

and procedures used for collecting the data upon which the remainder of this thesis is

based. Much of the data and methods presented here are unique in the sense that such

studies have rarely been attempted on B.C.'s rainbow trout lakes. In particular, it will

become apparent that anglers can be a potent force of population change by generating

relatively high exploitation rates from modest amounts of fishing effort. More

importantly, I show that anglers themselves are highly adaptive, changing their behaviour

in response to both natural and management-induced changes in fish populations. Thus,

several important results reinforce Pearse's (1970) forewarning that traditional

management tactics may not be capable of improving angling quality in British

Columbia.

Methods

Study Sites

British Columbia's southern interior lakes are divided into three management regions

(Fig. 2.1). Regions 3 (Thompson-Nicola) and 8 (Okanagan) are easily accessible (2.5 to 5

hours by vehicle) from Vancouver which is the source of most small lake fishing effort.

Region 5 (Cariboo-Chilcotin) is 5-7 hours by vehicle from Vancouver, and is the most

remote. Access to lakes within regions varies mainly by mode of transportation (four-

wheel drive, two-wheel drive, walk, boat, and air) and level of shoreline development.
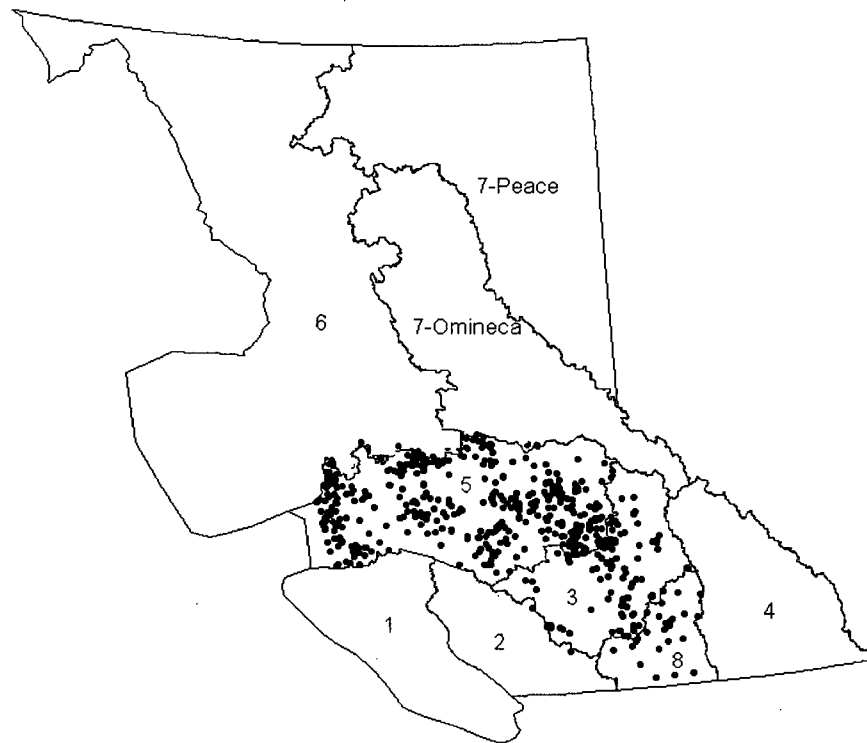
Figure 2.1. Map of British Columbia fisheries management regions. Dots indicate location of lakes between 30 ha and 500 ha in size for Regions 3 (Thompson-Nicola), 5 (Cariboo-Chilcotin), and 8 (Okanagan).

Lakes included in this study were selected to provide contrasts in angler effort (high/medium/low), stock type (wild/hatchery), and species mix (mono/mixed). B.C. Ministry of Fisheries biologists from management Regions 3, 5, and 8 provided lists of candidate lakes that met these criteria. Candidate lakes were sub-classified by number of access points and the presence/absence of lodges, in order to provide a convenient system for data collection. Thirteen lakes with relatively few access points or few access points combined with the presence of a resort were selected because of expected ease in obtaining angler information. From this original set of thirteen lakes, only eight were studied in enough detail to warrant inclusion in this study. Five lakes were not included because of inadequate data collection (Corbett and Wavey; volunteer CPE data only), extremely low sample size (Beckwith and Malarky), and long periods without sampling (Alleyne).

Of the remaining 8 lakes, 7 are located within Region 3 and 1 (Fawn) is located within Region 5. Region 3 lakes are distributed from its northern boundary with Region 5 (Crystal, Rock Island, and Hardcastle) to its eastern boundary with Region 8 (Pillar). Lakes range in surface area from 2 to 140 hectares with mean depths of 3 to 12 m and the percentage of lake area shallower than 7 m (shoal area) varied substantially among lakes (Table 2.1). Most lakes have some form of shoreline development such as B.C. Forest Service campgrounds, B.C. Provincial Parks, resorts, private cabins or some combination. One lake (Hardcastle) has no shoreline development or road access, but is within walking distance from a resort. Both Rock Island and Hardcastle lakes require travelling over a difficult four-wheel drive road within a privately held land lease, so their access tends to

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be limited. For this reason, I refer to these lakes as *limited-access* in several places in this thesis, and to all other lakes as *open-access*.

Three lakes (Rock Island, Pillar and Roche) have closed seasons from November 1 to April 30. All other lakes are subject to both summer and winter fisheries. Daily bag limits are 2 fish per day on Roche and 6 per day on all other lakes within Regions 3 and 8. All Region 5 lakes including Fawn have daily bag limits of 5. There are no minimum length limits on any of the study lakes, however a province-wide limit of one fish over 500 mm is in effect on all lakes. Gear restrictions are used only on Rock Island (single-hook only, bait ban) and Roche (single barbless hook).

Fish Populations

Six lakes in this study require annual stocking of juvenile rainbow trout from B.C.'s Ministry of Fisheries in order to maintain recreational fisheries where no natural spawning streams are available to trout, and two lakes are sustained through natural reproduction. Wild-stock lakes (Rock Island and Hardcastle) acquired their rainbow trout populations via introductions to the Nehalliston Creek watershed during the 1940's. Pillar Lake once held a reproducing population of rainbow trout, but that stock was eliminated due to lake poisoning in the 1950's and it is now stocked annually (Table 2.1). Lake poisoning was used in the past as a management device aimed at eradicating the redside shiner (*Richardsonius balteatus*) from popular angling lakes. Only two study lakes presently contain coarse species. Crystal has populations of both lake chub (*Couesius*

plumbeus) and long nose sucker (*Catostomus catostomus*), and Fawn contains a large

population of lake chub.

Table 2.1. Physical, and biological characteristics of study lakes. Shoal area is the percent of total lake area that is less than 7 m deep. Numbers of fish stocked annually was obtained from B.C. Fisheries archives for 1995.

Region / Lake	Elevation (m)	Lake area (ha)	Shoal area (%)	Mean depth (m)	No. Stocked (yr^{-1})	No. fish species
Cariboo-Chilcotin						
Fawn	1100	32	80	4	15 000	2
Thompson-Nicola						
Pillar	853	41	39	10	15 000	1
Hardcastle	1250	18	90	2	-	1
Rock Island	1250	56	90	2	-	1
Crystal	1158	55	40	8	20 000	3
Roche	1134	140	46	8	35 000	1
Dairy	1463	26	60	6	6 000	1
Duffy	1158	21	48	7	3 000	1

Data collection and analysis

For each lake, effort, catch rate, harvest, and fish size in the catch data were collected on

a weekly time scale for one or two years. This information was combined with mark-

recapture experiments to determine exploitation rates, fish abundance, and fishery size-

selectivity patterns.

Angler Effort

Angler effort data were obtained by daily counts on most days of boats, float tubes, and

shore anglers taken at 3 predetermined time intervals (8-10am, 12-2pm, 6-8pm). The

daily average of the instantaneous counts was multiplied by the total number of angler

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hours in the fishing day (15) to arrive at total hours for each boat type. Total angler hours were then computed by multiplying the total hours for a given boat type times the average number of anglers per boat (2 per boat, 1 per float tube,1 per shore count) and then summing over boat types. Angler days (ad), which is the primary effort measure used in this study, was calculated by dividing total angler hours by the number of hours per angler day (4). I used the factors 4 hours per angler day and 2 anglers per boat so that results would be generally comparable to B.C. Ministry of Environment effort estimates (Tredger 1992). Actual values for hours per angler trip and number of anglers per boat were similar to these general factors. Angler effort estimates were calculated for biweekly (15 days) and monthly periods, as well as total effort for the season. Actual season length varies in B.C. lakes primarily with differences in lake elevation, but the typical season lasts from May through September. Because effort counts were completed each day, I simply summed these daily estimates over days to get biweekly, monthly, and annual effort estimates. In cases where a count was missed, I used the average fishing effort for the two adjacent days. In only two lakes was it necessary to use a stratified sampling scheme due to incomplete daily boat counts. On Dairy and Duffy lakes (1998), the creel technician alternated weekday sampling from Monday-Tuesday in one week to Thursday-Friday in the following week. All weekends were sampled completely. I therefore used the average of the two weekday effort estimates as the average daily effort for the week.

For Rock Island and Hardcastle lakes, all data were collected by resort personnel for a fee of $300.00 per month. Because the resort fished these lakes almost exclusively, the creel

survey was considered complete and I used total hours reported on interview forms. This created non-independence in the effort and CPE data, but it was a necessary sacrifice due to time constraints on lodge owners. Independent boat counts on Hardcastle lake would be nearly impossible because it is located approximately 2 km by trail from the lodge. The lake is also split in half by a small, shallow channel so it is not easily viewed from the trails' end.

Angler day estimates were converted to effort density after dividing by total lake area and lake shoal area separately. I added the shoal effort density measure because most of the interaction between fish and anglers is concentrated on the shoals, and the models I develop in later chapters include this spatial dependence.

Creel Surveys

Catch rate, harvest, tag returns, and length-at-capture data were collected via completed-trip creel surveys on all lakes. For lakes with significant public access, creel clerks were stationed at access points and they made frequent rounds through campsites during slow periods. Similar procedures were followed on lakes with mixed resort/public access, except that clerks made additional rounds through resort campsites, cabins, and lodges. Access at Crystal lake was not convenient for any of these approaches, so creel clerks visited the public campsite for one hour either daily or every other day. In situations where only resort access existed (Rock Island and Hardcastle), resort personnel interviewed all anglers upon completion of their trips or during mealtime hours. These lakes provided the advantage of full reporting of catch, effort, and tag returns. For lakes

where survey coverage was less than complete, I used the ratio of total angler days accounted for by creel surveys to total angler days estimated from boat counts as an estimate of the sampling fraction. This rate is important because it is used in the mark-recapture analysis where observed tag returns need to be expanded to account for partial observation of the catch.

Catch per unit of effort (CPE) and harvest per unit of effort (HPE) were calculated biweekly and monthly. For the CPE calculation I used the total number of fish harvested and released by each angler as a catch observation and for HPE I used only fish harvested in the calculation of c_i in the following formulae.

$$CPE = \frac{\sum_{i=1}^{n} c_i}{\sum_{i=1}^{n} e_i} \qquad (2.1)$$

where c_i and e_i are the catch and effort of ith angler. The sampling variance of equation 2.1 is (Cochran 1975)

$$V(CPE) = \frac{(1-f)}{n \cdot CPE^2} \cdot \left(\frac{\sum c_i^2 + 2CPE \sum c_i e_i + CPE^2 \sum e_i^2}{n-1} \right) \qquad (2.2).$$

I chose to include the finite population correction factor (f) in equation 2.2 because in many cases sampling fractions were large (> 0.20). The retention rate (proportion of catch that is harvested) was computed as the ratio of HPE to CPE.

Total catch (or harvest) estimates were obtained by multiplying the CPE (or HPE) for a given month by the independent boat count estimate of effort for that month

$$Catch = CPE \cdot E \qquad\qquad (2.3).$$

The sampling variance of the estimated catch is

$$V(Catch) = CPE^2 \cdot V(E) + E^2 \cdot V(CPE) \qquad\qquad (2.4).$$

Because anglers may misreport the numbers of fish caught and released, I conducted a small-scale test of the assumption that anglers reports of total fish caught were reasonably accurate. This study was conducted on Fawn Lake where the on-lake fishing activity of 30 anglers were observed from shore. Subsequent angler reports of total catch did not disagree at all with visual observations of catches made by the creel clerk. Thus, potential errors in estimating total catch (fish harvest plus released) were ignored.

Mark-recapture experiments

For all lakes included in this study, I used mark-recapture methods to determine exploitation and fish abundance. Fish tagging experiments were conducted in two consecutive years at Fawn (1996-97), Rock Island (1997-98), Roche (1997-98), and Crystal (1997-98) and in one year only for Pillar (1996), Hardcastle (1997), Dairy (1998), and Duffy (1998). The latter two lakes were added just prior to the final year of the project in place of Fawn lake because they were expected to be in the mid-range of effort densities that I observed in the 1996 and 1997 studies. Having more lakes in this range could help in detecting any non-linearity in effort-exploitation relationships.

Rainbow trout were captured by a combination of gillnet and angling methods shortly after ice-off each spring. This period presented the best physical conditions in the lake for collecting large numbers of fish in a short period of time. For gillnet sampling, short sets

of approximately 10-12 minutes duration were used in order to minimize fish injury, mortality, and recovery time. The use of relatively short (50-70m), multi-mesh gillnets and rapid deployment and retrieval generally resulted in a minimum of injury and mortality to the fish. Occasional large catches or adverse weather conditions sometimes extended the set duration to over 30 minutes, but under typical conditions set duration varied from 10-18 minutes. Fish captured in these collections were held temporarily in 75 L holding tanks before being transferred to open-water pens, usually for a recovery period of 24 hours.

Because of the urgency involved in capturing and handling fish, the number of sets and catch-per-set were not recorded. Nevertheless, some qualitative observations were made. Most capture success occurred from one hour prior to sunset until one hour after sunset. During this time catch rates for one boat simultaneously working two nets varied from 5-30 fish per hour. Catch rates declined sharply beyond two hours after sunset. The largest catches generally occurred within the littoral zone from 1-3 m depth. Significant catches in deeper water (>5 m) were rare except on one occasion in Fawn where approximately 130 fish were captured from 5-7 m depth over a two day period.

Fish were also captured by angling during the midday hours. Although gillnets are sometimes as effective in shallow water during the day as they are in the evenings, I chose to collect as many fish as possible by angling during this time. Fish collected by angling tend to suffer less physical damage such as scale loss, scarring, and hypoxia

compared to gillnetted fish where the effects of these factors can be difficult, if not impossible, to detect and distinguish from other mortality components.

All fish were held overnight in floating net pens that were 1.8 m long x 1.2 m wide x 1 m deep. Pens were constructed of rigid ¾" black, Vexar ™ polyethylene mesh with a ½" PVC pipe frame and lock down lid. This design provided a portable, lightweight holding pen that was easily transported to different locations on the lakes. Also, the rigid nature of the pen provided maximum volume for fish to swim about during recovery, and a large bottom surface area for fish that were temporarily unable to maintain an upright position.

After an overnight holding period, fish that were judged to be incapable of maintaining an upright position were removed and sacrificed for scale, sex, and maturity samples. Healthy fish were placed in an anesthetic solution prior to the tagging procedure. In 1996, Alka Seltzer™ was used for anesthetic , while in 1997 and 1998 I used a 40mg/L solution of clove oil and water. The active ingredient (eugenol) in clove oil affects the central nervous system of the fish and has been shown to be a safe and effective anesthetic (Anderson et al. 1997). Clove oil anesthetic produced relatively rapid induction (approx. 4 min) and recovery (5-8 min) with negligible after-tag mortality (< 1 % in 1997 and 1998). In contrast, the use of Alka Seltzer™ required longer induction and recovery times and subsequently more fish (2-4 %) died after the tagging procedure presumably due to hypoxia. Higher after-tag mortalities in 1996 may have also resulted from the harsher netting conditions (longer sets, generally poor weather, and conical, soft mesh pens) during that field season.

All fish greater than 150 mm fork length were tagged at the base of the dorsal fin with alpha-numerically coded Floy T-bar™ anchor tags. Fork lengths of all tagged fish were measured and sex and maturity were judged by visual inspection. Mature males were typically identified by morphological traits (hooked snout, dark colouration) and the presence of milt and mature females were identified by the degree of anal vent swelling. Fish that did not exhibit any of these characteristics were considered immature. After the tagging procedure, fish were held in a second, smaller pen (1.2 m long x 1 m wide x 1 m deep) for an additional 2-3 hours before being released.

Handling mortality and tag loss experiments

Handling mortality and tag loss can be significant sources of unobservable mortality in tagging studies. Because tagging programs that employ gillnets are somewhat rare, I attempted two experiments aimed at defining potential bounds on handling mortality associated with this method of capture. In May 1996, I held a sample of 25 randomly chosen individuals in a floating, conical, soft-mesh net pen in Fawn lake. The pen was anchored in a shaded area of the lake that was approximately 4 m deep. It extended just over 1.5 m down the water column so that fish in the pen were largely restricted to the surface water. Fish were held in this enclosure for two weeks without deliberate feeding and they were checked every few days for signs of distress or mortality.

In May 1997, I attempted a more rigorous experiment in pothole lakes adjacent to Bluey Lake in the Merritt area. My objective was to replicate the conditions under which fish

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were captured, tagged, and released in the main study lakes. Approximately 200 fish were captured in gillnets and subjected to the identical tagging procedures previously described. After recovery from tagging, fish were transported via plastic bags and barrels to Bluey pothole lakes (BPH2 and BPH3) nearby (10-15 min lake-lake travel time). BPH2 and BPH3 are small, winterkill lakes that have high standing crops of invertebrates due to their lack of fish. In the fall, both lakes were depleted by gillnetting by Ministry of Fisheries personnel along with a research team from the University of Calgary. Unfortunately, BPH3 experienced a complete summer-kill due to high temperatures so no recoveries were made. The total number of fish recovered from BPH2 was used to estimate survival directly without accounting for the possibility that some fish likely remained at large in the lake. All recaptures were also inspected for tag loss.

Analysis of tag return data

In this section, I use estimators from mark-recapture theory to estimate exploitation rates and initial population sizes in the study lakes. For all studies, I used an exploitation-based design where tag recoveries were obtained by sampling angler catches. Because the sampling rates are known relatively well, I chose to adjust all observed tag recoveries according to the sampling rate in the month of recovery before any further analysis. The number of recaptures are then treated as being known exactly. This will hopefully avoid confusion associated with going back and forth between adjusted and unadjusted values in deriving specific estimators.

The mark-recapture analysis proceeds by first computing the rate of exploitation, u (Ricker 1975)

$$u = \frac{R}{M} \qquad (2.4)$$

where R is the adjusted (by sampling rate) total number of recaptured fish during the year and M is the adjusted (by survival and tag retention) number released. For the sake of clarity, I will ignore the fact that R and M are adjusted values and henceforth refer to them as recaptures (R) and marks (M). The sampling variance of the exploitation rate in (2.4) is (Ricker 1975)

$$V(u) = \frac{R(C - R)}{M^2 C} \qquad (2.5)$$

where C is the total catch for the season estimated from creel surveys. The estimate of total population at the time of marking, N, is then estimated using the ratio

$$N = \frac{C}{u} \qquad (2.6).$$

Ricker (1975), assuming that the catch is know without error, gives the following variance formula for N

$$V(N) = \frac{M^2 C(C - R)}{R^3}.$$

In this study however, catch estimates are subject to error so I derived the following variance formula that includes this additional source of uncertainty

$$V(N) = \frac{M^2}{R^2}\left(V(C) + \frac{C(C - R)}{R}\right). \qquad (2.7)$$

where $V(C)$ is the variance of the total catch estimate. I computed 2.4-2.7 only for fish that were recovered within the year of marking. In the lakes where I conducted a mark-

recapture experiment in the following year, I used the independent mark-recapture results from both years to estimate natural mortality. This analysis is done in Chapter 3 along with other life history parameter estimates. Because of their large size, statistical results tables (effort, CPE, and catch) are located in appendices at the end of this thesis.

Results

Creel surveys

Angler Effort

Total angler effort in the study lakes ranged from approximately 300 ad yr^{-1} on Hardcastle to over 16 000 ad yr^{-1} on Roche (Appendix 1; Table A1). This range appears to adequately represent the range of effort on B.C. small lakes that was observed during the late 1980's (Fig. 2.2). In terms of effort density, Roche (114.7 ad ha^{-1} yr^{-1}), Pillar (114.2 ad ha^{-1} yr^{-1}), and Fawn (157.6 ad ha^{-1} yr^{-1}) represent some of the highest effort densities observed in B.C., while Rock Island (13.4 ad ha^{-1} yr^{-1}) and Hardcastle (18 ad ha^{-1} yr^{-1}) are among the lowest. Since the 1986-1992 SLIM effort surveys (B.C. Ministry of Fisheries, unpublished data), effort density on several lakes has changed considerably and in several cases these changes coincide with changes in stocking policies. For example, effort declines on Roche (41%) and Duffy (76%) coincide with stocking rate reductions of 36% and 65%, respectively between the SLIM period and the present, and an increase of 51% on Fawn coincides with a stocking rate increase of 66% (Fig. 2.3). Effort changes on other lakes are more difficult to interpret because they are not clearly related to numbers of trout stocked although they do appear related to other
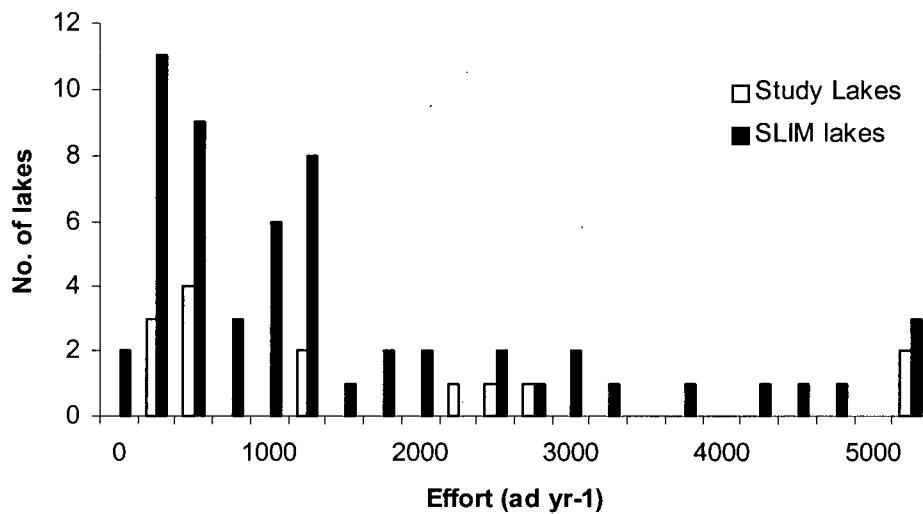
Figure 2.2. Distribution of fishing effort on 54 British Columbia small lakes in 1992 compared to fishing effort for all years combined on the study lakes. The final bin class contains observed effort greater than 5000 ad yr-[1].

fish stocking policies. Number of trout stocked annually into Crystal lake has not changed since the 1980's and stocking rates have actually declined in Dairy lake, yet fishing effort on these two lakes has increased by 176% and 280%, respectively. In each case, however, the stock- and size-composition of trout released into the lakes has changed. During the 1980's, 20 000 Pennask-strain rainbow trout at an average size of 6.8 grams were stocked annually into Crystal lake. In 1995, the stock changed to 20 000 Blackwater-strain fish at 20 grams each. The Blackwater-strain of rainbow trout appears to perform well under intense competition from non-salmonid fish species (E. Parkinson, pers. comm.) so this stock may have experienced greater survival than previous strains. These Blackwater fish would have recruited to the fishery in 1997 and 1998, which were the years of highest effort densities ever observed on Crystal lake. In Dairy lake, similar changes in average size-at-stocking (5 g prior to 1992 to 16 g after 1993) occurred

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between the periods and stocking of Eastern Brook trout (*Salvelinus fontinalis*) ended in 1989; both of these conditions probably benefited rainbow trout survival.

Between-year differences in annual fishing effort were minor on the study lakes from 1996-1998 except for Roche lake where effort declined from 16 079 ad in 1997 to 12 555 ad in 1998. Such a significant (z-test, $z = -1.65$, df $= 1$, $P < 0.05$) change may reflect a continuing trend toward lower stocking rates as well as a bag limit change from 6 to 2 fish per day.
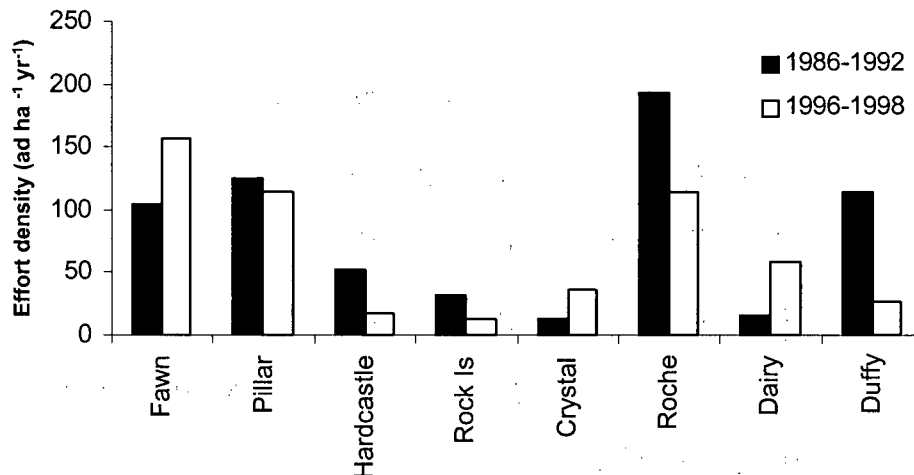
Figure 2.3. Observed average fishing effort compared to average effort during the 1986-1992 SLIM effort surveys. Fawn, Roche, and Pillar lake values are among-year averages and Rock Island, Hardcastle, and Crystal are based on only one year.

Within-year patterns in fishing effort showed consistent seasonality. Effort peaks occurred early in the season usually by mid-June on open-access lakes and by early July on limited-access lakes (Fig. 2.4). For open-access lakes, effort in the latter half of May was typically high, but harsh conditions early in the month resulted in only average effort levels. By June, probably the most popular month for fishing B.C. lakes, fishing effort

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peaked in most open-access lakes due to abundant, active fish and decent weather. After the main peak, fishing effort typically declined rapidly in both limited- and open-access lakes and only a few showed effort increases in September.

Very few open-access lakes showed high proportions of total effort during the mid-season (July) in 1997 and 1998. While this observation is typically explained by higher water temperature effects on fish catchability, in-season effort and subsequent exploitation may have an effect as well. Effort declines during the season appear to be proportional to the magnitude of the initial early-season peak. For example, in 1996 most lakes remained ice covered into May due to cold temperatures and unstable weather. In that year, strong effort peaks in May and early-June did not generally occur on most lakes and the total effort was spread rather evenly over the season. The 1997 spring season was slightly warmer, although most lakes still remained ice covered during the first week of May. Effort during this period was subsequently higher and as the season progressed it declined more sharply than in 1996. The spring period in 1998 was exceptionally warm and all lakes showed strong effort peaks at the earliest point in the season and subsequent effort declines were the strongest.
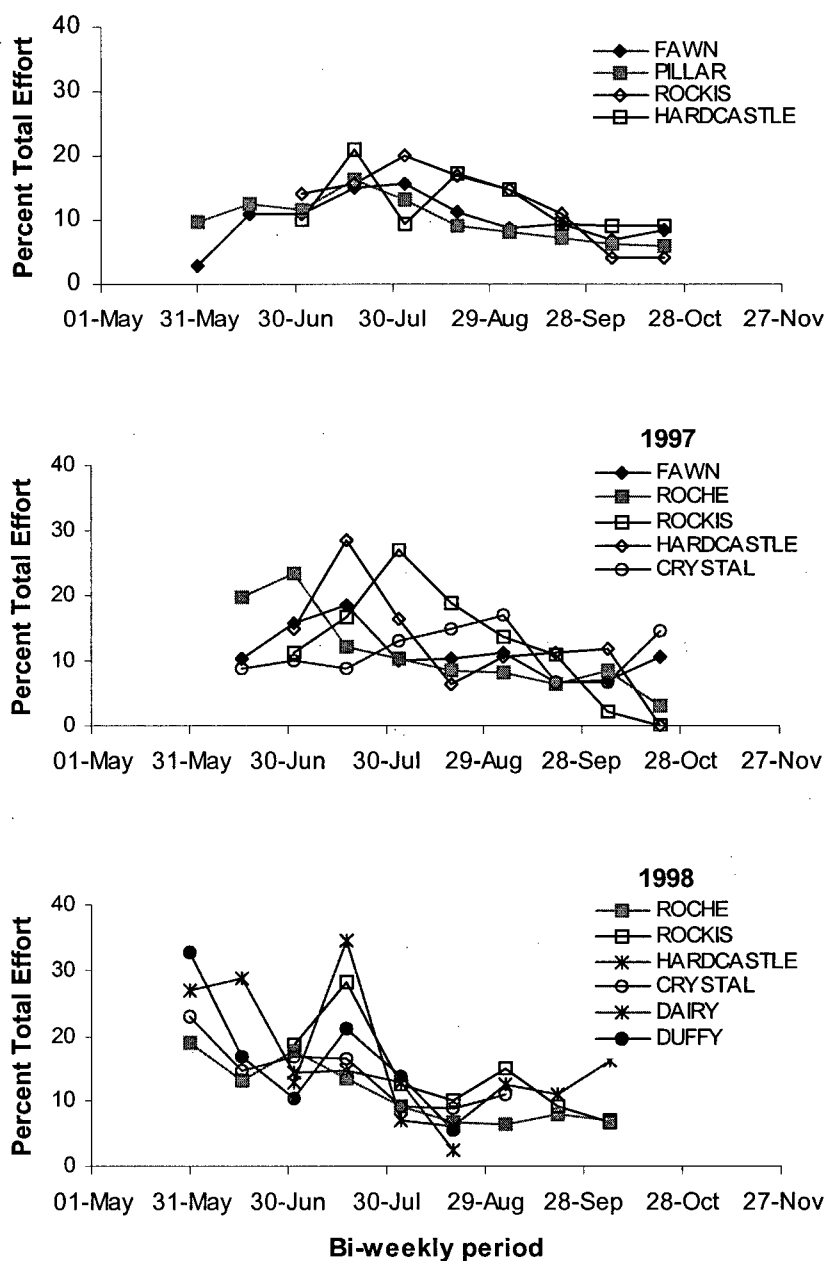
Figure 2.4. Percent of total fishing effort for each biweekly period (15 d) during the open-water fishing seasons in 1996 (top), 1997 (middle), and 1998 (bottom). Data points correspond to the 15-d period ending on the date shown.

Catch rate

Average number of anglers interviewed per month ranged from 40 on Hardcastle lake in 1997 to 442 on Roche lake in 1998. Extremely low numbers of interviews were rare and only occurred during September. When these numbers were unacceptably low (< 20), I defined the sampling time frame so as not to include those months. Sampling rates on open-access lakes were between 4 and 40% (Appendix 1; Table A2) and for limited-access lakes, sampling rate was assumed *a priori* to be 90%. Low sampling fractions occurred in June and July (1996) on Fawn lake, so the CPE and HPE estimates may not be particularly accurate and their interpretation should be treated with caution. Very low sampling fractions during that time indicate that perhaps only anglers who caught fish were interviewed. The problem is likely isolated to that year because sampling was conducted by an inexperienced volunteer.

Anglers fishing on limited access lakes caught an average 3.8 (± 3.2) fish per day and harvested 2.0 (± 0.54) fish per day. On open access lakes, anglers caught an average 1.7 (± 2.3) fish per day and harvested 0.64 (± 0.20) fish per day. Variation in CPE among open-access lakes was 42% which did not indicate a large diversity in fishing success.

In-season variation in catch rates was similar among years for both Hardcastle and Rock Island lakes. On Hardcastle lake, high CPE in the first few weeks of the season was followed by sharp declines as the season progressed (Fig. 2.5). In contrast, catch rates on Rock Island were relatively stable over the season, and in all three years, did not decline until August. Several factors may contribute to these temporal patterns.
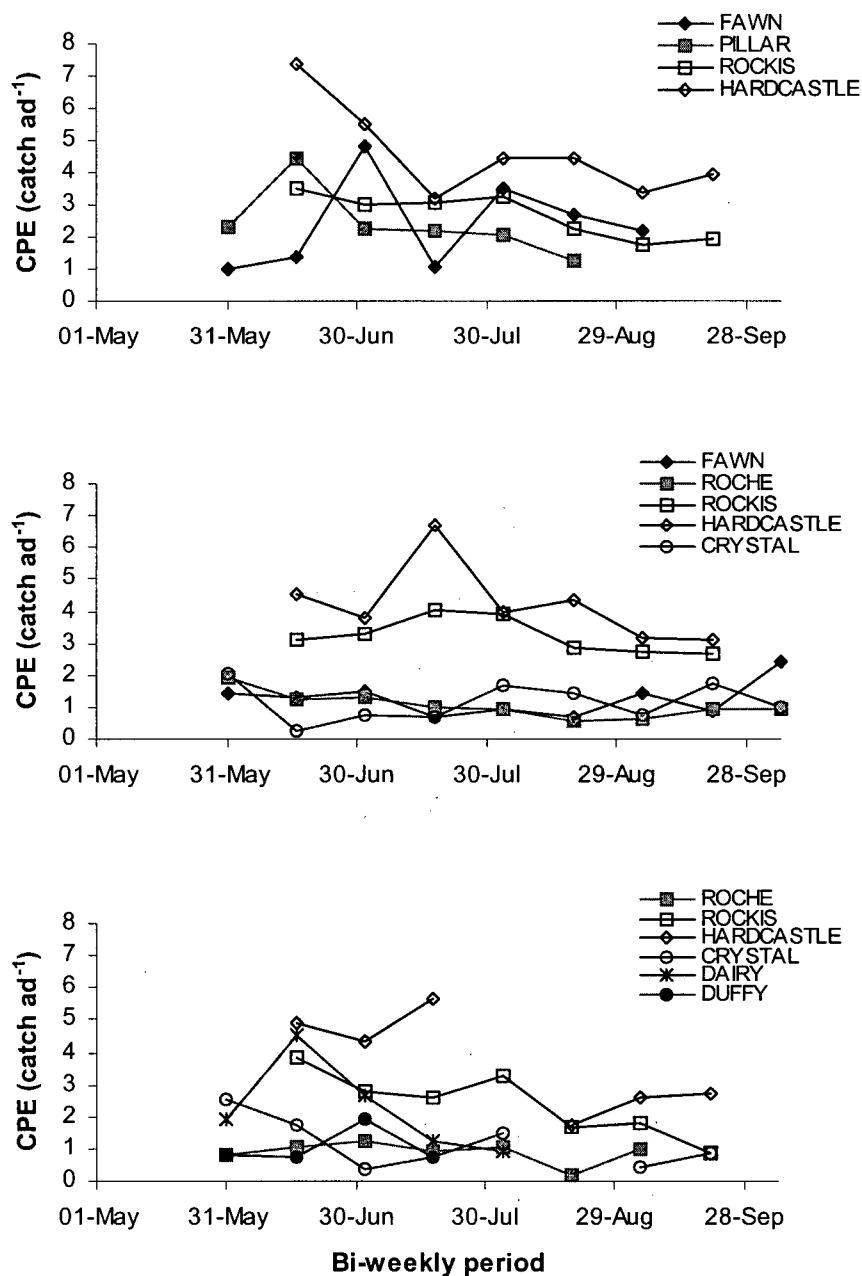
Figure 2.5. Catch per effort for each biweekly period (15 d) during the open-water fishing seasons in 1996 (top), 1997 (middle), and 1998 (bottom). Data points correspond to the 15-d period ending on the date shown.

In Hardcastle, large early season catches may deplete the standing crop of vulnerable fish leaving fewer for the anglers that followed, but a total harvest of only 263 fish in the

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month of June (Appendix 1; Table A3) seems unlikely to cause the observed catch rate decline of over 50%. Total numbers of fish caught and released were 740, which represents a much larger proportion of the total population (see Population estimate; Table 2.4). If these fish remained invulnerable to anglers for some time following release then anglers arriving later in the season would most likely experience substantially lower catch rates. An alternative explanation is that fish are less prone to enter shallow feeding areas as water temperature increases during the summer. However, in 1996, catch rates declined and subsequently increased during the warmest months of the year while catch rates on Rock Island lake, which experiences similar environmental conditions, remained stable. Biweekly total catch and harvests on Rock Island represented a smaller proportion of the population in comparison to Hardcastle and this likely contributed to the stability of CPE over most of the season.

In contrast to the limited-access lakes just described, CPE patterns on open-access lakes tended to be quite stable. Although Pillar experienced a brief peak in June, CPE on high effort lakes remained virtually unchanged throughout much of the fishing season on Roche (both years), Crystal (1997), and Fawn (1997). Stocking policy changes may have resulted in higher fish densities in Crystal in 1998 and this likely contributed to the observed improvement in early season CPE and higher effort between years. However, by mid-June CPE for both years was essentially the same.

Mark-recapture experiments

Handling mortality and tag loss

At the end of two weeks 18 fish were recovered alive from the floating pen in Fawn lake. Most of the mortalities probably occurred within the last 4-5 days because prior to that, very few fish appeared in distress. In BPH2, 66 fish were recovered from an initial stocking of 77 individuals and of these, 63 fish retained their tags. This gave a survival rate of 0.86 (std. error = 0.04) and a tag retention rate of 0.95 (std. error = 0.02). The two survival estimates s_{FAWN} (0.79) and s_{BPH2} (0.86) probably represent extremes of the possible range of survival from capture in gillnets and handling. s_{BPH2} is most likely high due to the above average growth conditions in BPH2 compared to Fawn where the conditions were unusually difficult (no feeding, little space, and no access to deeper, cooler water). To combine the two estimates, I used a normal approximation for both survival rates, s_{BPH2}, s_{Fawn}, and calculated the precision-weighted average of the two values which is

$$s' = \frac{\dfrac{1}{\sigma^2_{BPH2}} s_{BPH2} + \dfrac{1}{\sigma^2_{FAWN}} s_{FAWN}}{\dfrac{1}{\sigma^2_{BPH2}} + \dfrac{1}{\sigma^2_{FAWN}}}$$

where σ^2 is the variance of the estimated survival rate. I combined the survival rate estimate with the tag retention rate from BPH2 to compute an adjustment factor for the effective number of tagged fish released into each lake (Table 2.2). I applied the survival/tag retention factor to all tagged cohorts of rainbow trout released into the study lakes. No differentiation was made between gillnet- and angling-caught fish, because for most situations all fish that were released were in relatively good physical condition.

Table 2.2. Summary of handling mortality and tag loss estimates. Combined survival estimate is precision weighted average of BPH2 and Fawn estimates. Adjustment factor is the survival and tag loss adjustment applied to total releases of tagged fish in all study lakes.

Lake	Released	Recovered	Survival	Tag retention	Adjustment factor
BPH2	77	66	.85 (.04)	.95 (.02)	-
Fawn	25	18	.72 (.09)	1.0	-
Combined	-	-	.83 (.04)	.95 (.02)	**.79 (.04)**

Total adjusted numbers of tagged fish released into the study lakes ranged from 77 fish in Duffy lake in 1998 to 446 fish in Roche lake 1998 (Table 2.3). Roche lake received the most fish in both years because of an expected large fish population size as well as an expected low sampling rate. Low numbers of releases (< 100) typically occurred because of difficulty in capturing fish particularly in Duffy (1998), Crystal (1997) and Rock Island (1998).

Table 2.3. Data summary for captures by gillnet and angling and tagged releases of rainbow trout on study lakes by year and lake. Differences between. Adjusted number released is the total number released multiplied by the survival/tag loss factor to account for mortality and tag loss after release.

Lake	Gillnet	Angling	Total	Adjusted no. released
		1996		
Fawn	334	75	409	**323**
Pillar	298	-	298	**235**
		1997		
Fawn	276	12	288	**238**
Hardcastle	66	127	193	**152**
Rock Island	122	149	271	**214**
Crystal	62	54	116	**90**
Roche	316	165	481	**380**
		1998		
Rock Island	83	30	113	**90**
Crystal	78	172	250	**197**
Roche	293	271	564	**446**
Dairy	201	25	226	**178**
Duffy	91	7	98	**77**

Exploitation

In general, the size distribution of fish in gillnet collections was shifted toward smaller sizes compared to size distributions in fishery catch. This introduces bias in the estimates of exploitation because the tagged population that is vulnerable to angling is actually smaller than it appears. In most case, however, fish collected in gillnets were of large enough size so as to become vulnerable to angler harvest at some point in the season of tagging. Therefore, the biases are probably not overly large. Recognizing this, I present the results below as general or "gross" exploitation estimates for the purpose of comparing rates and population sizes among lakes. I deal with the issues of size-selectivity and fully vulnerable exploitation rates later in Chapter 3.

Observed recaptures of tagged rainbow trout ranged from 8 fish in Crystal lake in 1997 to 50 fish in Fawn lake in 1997 (Table 2.4). These represent raw numbers of recaptures that depend on exploitation and also on the sampling rates within the month of recapture. Actual numbers of recaptures were estimated by adjusting each observed recapture by the sampling rate of the month in which the tagged fish was observed. These adjusted values ranged from 31 recaptures in Duffy lake (1998) to 166 fish recaptured in Roche lake (1998).

Adjusted recapture numbers indicated relatively high exploitation (0.40 – 0.60) on several study lakes. Effort density on Pillar and Fawn lakes are among the highest in B.C.'s southern interior and their exploitation rates (0.60 and 0.50, respectively) were the highest of all study lakes. Interestingly, much lower effort density on Crystal lake

produced similar high exploitation rates (0.40 and 0.50 in 1997 and 1998, respectively). Other lakes (Dairy, Duffy, and Roche) fell in the mid-range of exploitation (0.30 – 0.40) and Hardcastle and Rock Island (0.14 – 0.30, respectively) were lowest. Low exploitation occurred, as expected, on limited access lakes even though retention rates in these lakes were higher (Appendix 1; Table A3). Hardcastle and Rock Island could easily be defined as "meat fisherman" lakes because anglers typically retained a high proportion of their catch (0.40-0.50). In contrast, very high effort on Roche lake did not produce an exploitation rate as high as expected. This may have been due to the consistently low retention rates (0.15 – 0.30) of fish captured by anglers. Whether or not low retention is due to a 2-fish bag limit is unclear because the mean CPE of 1.05-1.13 fish per angler day at Roche indicates that few anglers actually catch two or more fish during a typical trip. It is more likely that such a low bag limit discourages "meat fisherman" or those anglers who are intent on keeping as many fish as possible. A similar retention rate effect, in combination with increasing effort, occurred at Fawn lake where effort and retention rate increased by 20 and 104 %, respectively. These increases coincided with an exploitation rate increase of 40%.

Rock Island lake is interesting because it appears to be managed on a "constant harvest" basis. Despite a decrease in fish abundance and CPE between 1997 and 1998, total harvest changed relatively little (1452 in 1997 and 1252 in 1998). The adjusting factor in this case was the retention rate which increased by 47 % to make up for the shortage in CPE. Such a simple change in angler behaviour is disturbing because it effectively increased exploitation on the fish population from 0.21 in 1997 to 0.30 in 1998. It also

shows how the current bait ban combined with single-hook-only regulation strategy is completely ineffective at protecting this wild population.

Total catch ranged among lakes from 527 in Duffy lake to approximately 20 000 fish in Roche (1997) (Appendix 1; Table A3). Ratios of total catch to population size estimates from mark-recapture were between 0.39 (Rock Island) and 1.80 (Fawn), which indicated that that fish in most lakes must have been captured on more than one occasion.

Table 2.4. Fishery statistics obtained from tagging experiments in British Columbia rainbow trout lakes. The Period column indicates the time frame over which the estimates were obtained. Numbers released are the adjusted total from Table 2.3. Standard errors of estimates appear in parentheses.

Lake	Period	No. released	Observed recaptures	Adjusted Recaptures	Gross exploitation	Initial population
				1996		
Fawn	May – Aug.	323	32	115	0.36 (0.04)	5 302 (1 016)
Pillar	May – Sept.	235	32	140	0.60 (0.05)	7 958 (1 089)
				1997		
Fawn	May – Sept.	238	50	118	0.50 (0.04)	5 815 (745)
Hardcastle	June – Sept.	152	21	21	0.14 (0.03)	4 943 (1 077)
Rock Island	June – Sept.	214	44	44	0.21 (0.03)	7 227 (1 081)
Crystal	May – Aug.	92	8	37	0.40 (0.06)	2 628 (708)
Roche	May – Aug.	380	35	153	0.40 (0.03)	13 218 (1 545)
				1998		
Rock Island	June – Sept.	90	27	27	0.30 (0.06)	4 173 (802)
Crystal	May – Aug.	197	18	98	0.50 (0.05)	5 013 (1 521)
Roche	May – Aug.	446	18	166	0.36 (0.03)	10 330 (2 833)
Dairy	May – July	178	17	62	0.35 (0.04)	4 246 (1 923)
Duffy	May – July	77	13	31	0.40 (0.07)	621 (337)

Fish abundance

Estimates of fish abundance varied strongly among lakes from 612 in Duffy (1998) to 13 218 in Roche (1997). Relative standard errors in abundance estimates were lowest for Roche (0.12; 1997) and highest for Duffy (0.54; 1998).

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Fish density based on total lake area varied over a five-fold range from 29 fish ha^{-1} in Duffy to 274 fish ha^{-1} in Hardcastle. Suspicion of low fish density in Crystal lake in 1997 (due to low gillnet and angling catches) was supported by the very low density estimate (47 fish ha^{-1}) in that year. However, the following year fish density approximately doubled to over 90 fish ha^{-1}. The increase was reflected in both angling and gillnet success rates during the tagging project, May-June angler CPE, and a small increase in total fishing effort. Increased fish abundance was mostly likely due to a high survival rate of Blackwater strain rainbow trout that were stocked in the lake in 1995. Despite such an apparent abundance increase, mid-season angling quality remained largely unchanged most likely due to the increase in exploitation from 40% in 1997 to 50% in 1998. Population estimates for Rock Island lake also indicated changes in abundance between years from 7 227 in 1997 to 4 173 in 1998. Again, such a decline was suspected during the fish collection period as it was difficult to capture adequate numbers of fish for tagging. An angler CPE decline of approximately 20% between the two years also tends to indicate a decrease in fish abundance. Population estimates for Roche lake indicated a possible decline in abundance from approximately 13 000 fish in 1997 to just over 10 000 fish in 1998. Though not statistically significant (z-test, $z = 1.10$, df $= 1$, $P > 0.05$), this change likely reflects effects of stocking rate reductions from over 45 000 yr^{-1} (age 1+) before 1996 to 35 000 yr^{-1} from 1996 to the present.

The relationship between CPE and effort density suggests that for similar levels of fish density, CPE declines with increasing effort (Fig. 2.6).
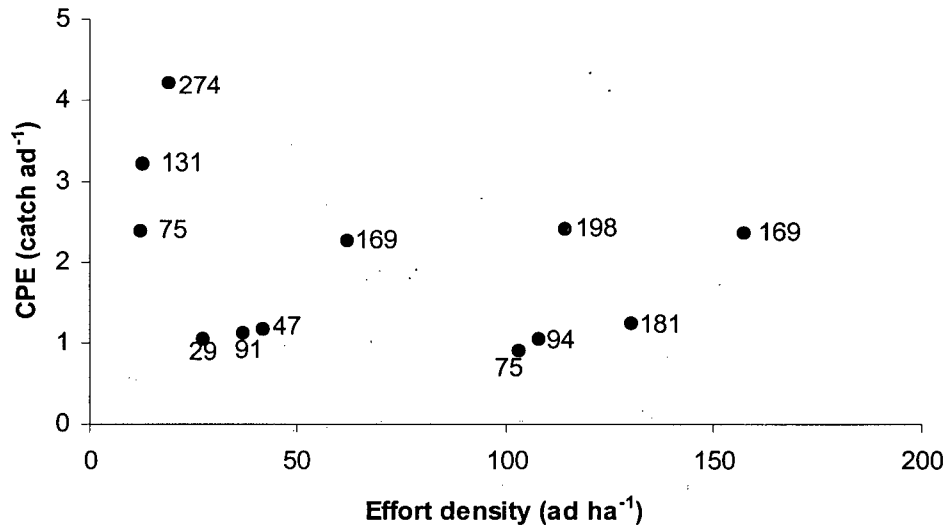
Figure 2.6. Relationship between fishing effort density and catch per effort on the study lakes. Data point labels are estimated fish densities at the start of the season.

Multiple linear regression revealed a significant positive effect of fish density (slope = 0.012 fish ha ad^{-2}, $t = 5.56$, df = 6, $P < 0.05$) and a negative effect of fishing effort (slope = -0.011 ha ad^{-1}, $t = 3.31$, df = 6, $P < 0.05$) that explained a significant proportion of the variation in CPE ($r^2 = 0.79$). Such a relationship suggests that the concentrated fishing effort during the early season, as was observed for most open-access lakes, may have offset the effects of higher abundance by depleting fish and suppressing CPE as the season progressed.

Discussion

Three key results arise from creel surveys and field studies on B.C. rainbow trout lakes. (1.) Angler effort appears to have changed in response to changes in fish stocking policies on some lakes. Also, there is some indication that fishing effort within a season declines in response to early-season stock depletion. (2.) Total catches taken over the season were typically greater than the total population size in most high effort lakes. However, total catch to fish population size ratios were not large in relation to the fishing intensity on high effort lakes. (3.) Retention rates of fish caught varied both among lakes and between years within lakes, presumably in response to lower fish abundance and angling success. The first two of these are key components that will be dealt with in the remainder of this thesis because both are typically ignored by recreational fisheries model developers. The third, I partition into retention changes with body size, which I determine in Chapter 3, and an issue to be dealt with here - retention changes that may depend on angling success.

Angler effort responses

Despite increasing evidence to the contrary, the numerical response of anglers to fish abundance has not generally been included in recreational fishery models (Carpenter et al. 1994). Yet, even on a limited set of study lakes, I showed that in the few cases where fish abundance (or stocking policies) changed between adjacent years or longer terms, angler effort changed as well; increases (decreases) in fish abundance were typically followed by increases (decreases) in angler effort. In addition, declining angler effort within a fishing season also appeared to be proportional to declines in fish abundance,

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although some of the effort decline is likely due to traditional patterns in the effort distribution over a season (Tredger 1992). Empirically, effort responses have been an important component of fishery dynamics in both commercial (Gillis et al. 1993; Lapointe 1989; Wilen 1976) and recreational fisheries (Argue et al. 1983; Kitchell and Carpenter 1993; Carpenter et al. 1994; Shaner et al. 1996). Such responses are beginning to be included for policy analysis on commercial fisheries, but they continue to be largely ignored by recreational fisheries professionals.

Limits on total catch in angling fisheries

High (> 1) total catch to population size ratios for many lakes in this study may provide two key insights into fishery dynamics on B.C. lakes. First, it indicates that not all fish captured are vulnerable to harvest and fish that are released become vulnerable to capture later during the season, i.e., at least some fish must be captured more than once to explain the observed ratios. Vulnerability to harvest is typically related to body size, and this topic is treated in more detail in Chapter 3. Total catch ratios also provide information about potential fish behaviours that determine vulnerability to capture in general. Where fishing intensity is high and retention rates are low, total catch to population size ratios should be much higher than the maximum of 1.84 that was observed on the study lakes. This suggests that perhaps only a small proportion of fish in a lake are available (at appropriate depths) and behaviourally reactive to angling gear at any moment.

Walters and Bonfil (1999) showed that for groundfish fleets in British Columbia, area swept calculations indicated that some intensively trawled areas were likely covered

several times per year. Yet, observed fishing mortality rates appeared to be small in relation to the expected mortalities computed from these swept area methods. Such a situation may occur on B.C.'s small lakes as well. Considering only intensively fished lakes, effort on those lakes (50-150 ad ha^{-1} yr^{-1}) is probably sufficient to intensively "sweep" the area over which vulnerable fish are distributed many times per year. For example, if anglers fish a minimum of 1 ha ad^{-1} then, for high effort lakes, each hectare of lake surface is effectively swept 50-150 times per fishing season. If every fish caught is subsequently kept, then the ratio of total catch to population size, i.e., maximum rate of exploitation on the population must be equal to 1 if angling effort and fish are distributed over the same areas or < 1 if angling effort is distributed over a smaller area than that which is inhabited by the fish population. On the other hand, if all fish caught are released, then the total catch to population size ratio should be directly proportional to the total area swept by anglers during the year. Of course, this likely never occurs because, despite being within the area swept, all fish are not equally reactive to a given fishing method, i.e., flies, lures, or bait. Thus, catch ratios may indicate maximum levels of depletion for high retention rates, and maximum turnover rates between reactive and unreactive behavioural states as retention rates approach zero. Between these two extremes lies an area that is partially influenced by depletion, behavioural exchange (between reactive and unreactive states), and differences between the fishable lake area swept and the area occupied by the stock. Figure 2.7 shows the actual catch ratios versus the proportion retained for high effort study lakes, along with a fitted exponential decay model [$TC/N_0 = 2.13\exp(-1.27*Retention)$]. Only high effort lakes were chosen because it is reasonable to assume that such effort levels are effectively sweeping the entire lake

many times per year. Although the data are limited in number and contrast, they do

suggest that turnover rates between reactive and unreactive behavioural states of fish may

be quite small. For a retention rate of 0, the y-axis intercept value suggests a maximum

"turnover rate" of 2.13 yr^{-1} and for a retention rate equal to 1, the total catch ratio

becomes a maximum exploitation rate which is predicted to be approximately 0.60. The

maximum turnover rate is likely an under-estimate because the effects of harvest cannot

be separated from the data. However, it does suggest that fish in catch-and-release lakes

(or fish released due to small size) will react to angling methods and get caught

approximately 2 to 3 times per year and where all fish are kept (or fully vulnerable to

harvest given their body size) the same effects acting on the turnover dynamics will tend

to limit the total exploitation rate to less than or equal to 1.
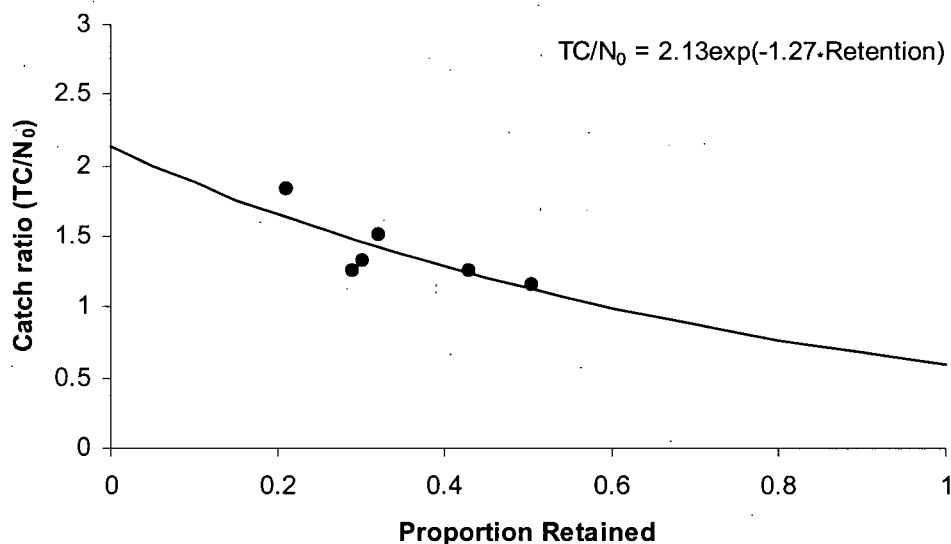
Figure 2.7. Ratio of total catch (TC) to population size (N_0) as a function of retention rate of fish caught for high effort study lakes. Inset equation is an exponential model fit through the data. Predicted values of total catch ratio are 2.13 and 0.59 at retention rates equal to 0 and 1, respectively.

Catch-and-release fisheries provide further insights into potential turnover dynamics. Champeau and Denson (1987) showed that upon opening a Florida largemouth bass (*Micropterus salmoides*) lake to catch-and-release angling, CPE of angling test fisheries declined to approximately half the value observed prior to the opening. For catch-and-release trout fisheries, Griffith (1987) reviewed several studies that appeared to show limits on capture frequency in high intensity fisheries. Rainbow trout in Idaho's Silver Creek were caught approximately 3 times per year, and some fish (1 in 5) were likely never caught at an angling pressure of 500 hours per acre. Brown trout (*Salmo trutta*) in Hot Creek, CA exhibited a similar capture frequency of 3 yr^{-1} despite much higher angler effort (3800 hours per acre; Deinstadt 1977). Hunt (1987) also showed that total catch to population size ratios for brown trout in three high use Wisconsin streams averaged 2.4. The highest capture frequencies have been observed for Yellowstone River cutthroat (*Oncorhynchus bouvieri*; $10 yr^{-1}$; Griffith 1987). In all of these studies, authors presumed that each time a fish was captured, its subsequent "re-catchability" was reduced. While this has been shown experimentally for cutthroat (Lewynsky and Bjornn 1987), few have explained why some fish are apparently never captured. Lewinsky and Bjornn (1988) showed that refractory periods for caught-and-released cutthroat averaged 3-4 weeks, but 20% of fish in their experiments were not captured at all.

Both effects just described - behavioural effects of catch-and-release and low probability of capture for a proportion of the population, probably limit the total number of fish available to anglers in recreational fisheries. In terms of harvest fisheries, these effects will likely also limit the total rate of exploitation on the population. The data in Table 2.4

show that maximum exploitation rates on high effort B.C. lakes were limited to approximately 0.50-0.60 which suggests that limitations to vulnerability may exist in B.C. rainbow trout lakes as well.

In Chapter 4, I discuss several possible reasons for turnover dynamics and limitation of exploitation rates, as well as their implications for recreational fisheries models and exploitation. Before doing so, I remove some of the effects of retention rates by dealing with issues of size-selective harvest in Chapter 3 where I determine fully vulnerable exploitation rates. These values should show more clearly the limits to total exploitation caused by the above mentioned exchange dynamics because retention rates of fully vulnerable fish are quite high.

Retention changes with fishing success

Changes in retention rates by individual anglers can have drastic impacts on fish populations regulated by daily bag limits. This was particularly evidenced by changes of 104 % and 47 % retention by anglers on Fawn and Rock Island lakes, respectively. CPE on Rock Island lake is typically high ($3 - 4$ fish ad^{-1}), but when it did decline due to decreased fish abundance, anglers harvested a larger proportion of the total catch and in doing so, increased exploitation. Although over-exploitation is not an important issue on hatchery stocked lakes such as Fawn, a similar shift in retention rate occurred for unexplained reasons. Such changes depend on aggregated decisions of individual anglers to keep fish, and although their cumulative impacts may be large, changes in retention rates are difficult to model explicitly. While it may be simple to model individual

decisions based on statistical methods (Naito 1992), we cannot be certain that such methods are appropriate for modeling aggregate behaviour. From a stock conservation perspective, the only way to deal with these types of unpredictable decisions is to limit total angler effort thereby minimizing cumulative effects.

Chapter 3: Life history and size-selective exploitation of rainbow trout in British Columbia's southern interior lakes

Introduction

One of the most important challenges facing fishery science today is to identify sets of life history and exploitation characteristics that can be generalized for management of exploited fish populations (Shuter et al. 1998). Recent work on both freshwater and marine species has revealed that certain demographic characteristics of fish populations tend to be either similar among populations and species (Myers et al. 1999), or else predictable from environmental covariates (Shuter et al. 1998). While the power of such studies to improve overall management has yet to be tested, it is clear that such studies provide valuable information that may increase our understanding fish population dynamics and the effects of exploitation. They also provide a reasonable starting point for exploration of management policy options on less intensively studied systems.

Rainbow trout are the single most important game fish in British Columbia (Pearse 1970). They occur in a variety of habitats from oligotrophic streams and lakes to large rivers and eutrophic lakes. In British Columbia's southern interior, rainbow trout are the primary target species of recreational anglers during both summer and winter fisheries in over 1800 small, eutrophic lakes where they occur naturally or via hatchery stocking of age 0+ and age 1+ juveniles (Ashley et al. 1992). Despite its importance as a recreational

species, little is know about the demographics of rainbow trout in B.C.'s southern interior. Most studies on these lakes have focussed on comparing relative growth and survival of various strains of hatchery-reared trout in relation to physical characteristics of lakes (Hume and Tsumura 1992; Ashley et al. 1992). Patterns of lifetime growth, survival, and vulnerability to harvest of established or enhanced populations have received considerably less attention.

In a study of 11 unexploited or lightly exploited coastal, montane, and subalpine lakes in western Canada, (Donald and Alger 1986) found that life history characteristics of rainbow trout varied considerably among biogeoclimatic regions. For example, in coastal and montane lakes, trout populations were characterised by relatively stable age structure, annual survival rates of approximately 50%, and a maximum longevity of 7 years. In subalpine lakes, age-structure was less stable, growth patterns were different, and maximum longevity was up to 13 years. Their longevity results from several lakes tended to agree with Pauly's (1980) regression estimates of natural mortality in that survival, implied by longevity, was correlated to annual mean water temperature. Such results suggest that demographic parameters of rainbow trout may be similar within regions, but may vary considerably among regions that differ in typical lake characteristics.

In this chapter, I use gillnet survey and tag return data from the study lakes to estimate several life history parameters of wild and hatchery stocked rainbow trout in British Columbia lakes. These include the familiar von Bertalanffy growth parameters, L_∞ and K,

age- and size-at-maturity, natural mortality rate, and vulnerability to harvest parameters that describe the relationships between length or age and exploitation.

Methods

Data

Growth and maturity data from fall gillnet samples

Towards the end of each fishing season, I conducted population surveys in most lake-years to obtain age composition, length-at-age, sex, tag, and maturity information. Fish were captured using a series of overnight gillnet sets (14-18 hours soak time) in a variety of habitats (shoreline cover, shoals, weedbeds, drop-offs, open surface-water, open deep-water) on each lake until 100-300 fish were captured. In a few cases, much smaller sample sizes were obtained and data from these were used sparingly. All fish were sacrificed and measured for fork length and stage of gonadal development, and a sub-sample of scales were obtained for age determination. All scale samples and their corresponding length measurements were interpreted by B.C. Ministry of Fisheries, Abbottsford Hatchery personnel. Presence/absence of white testes for males and enlarged, pink, egg-bearing ovaries for females were used as an indication that fish would be fully mature by the following spring (Hume and Tsumura 1992).

Growth rate data from tagging experiments

In most lakes, rainbow trout achieve the majority of their annual growth increment during the open water period (May-October). Therefore, I used the growth increment observed for fish that were released in May and subsequently recaptured in September/October of the same year as an approximation for the annual growth increase that would have

occurred if fish were at liberty for an entire year (May-May). Five lakes had creel surveys during these months and recaptures numbered between 5 and 9 fish.

Mark-recapture data for estimating exploitation and survival

Exploitation-at-length was estimated using the mark-recapture data after adjusting for sampling fractions. Adjustments were made by dividing each observed recapture by the sampling fraction for the month in which the recaptured fish was observed. Total adjusted recaptures were then tallied according to length interval at release, and exploitation-at-length was calculated by dividing these values by the total number initially released from the length interval. Length intervals (50 mm) were chosen by trial and error until at least one (unadjusted) recapture was observed within each length category.

Data for estimating natural mortality was limited to lakes with two years of mark-recapture data and in those cases, only those where significant numbers of recaptures were observed in both study years. Only Fawn and Rock Island lakes met these criteria. Although Roche had two lake-years of mark-recapture data, no fish from 1997 releases were observed in 1998.

Analysis

Growth parameters, L_∞ and K

The von Bertalanffy growth function (VBGF) describes the relationship between age and length of fishes according to

$$L_a = L_\infty \left(1 - e^{(-Ka)}\right)$$

3.1

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where L_a is a fishes length at age a, L_∞ (mm) is the asymptotic length, and K (yr^{-1}) is a metabolic constant. This model predicts that (*i.*) growth increments between adjacent ages are linear, and (*ii.*) growth increments approach zero fish length approaches some maximum value, L_∞. Walford (Ricker 1975) used this result to derive a linear model for predicting length-at-age based on length at the previous age

$$L_{a+1} = \alpha + \rho \cdot L_a \qquad\qquad 3.2$$

where

$$\alpha = L_\infty \left(1 - e^{-K}\right) \text{ and } \quad \rho = e^{-K} \qquad\qquad 3.3$$

Thus, fitting a Walford line to observed mean length-at-age data gives the VBGF estimates

$$L_\infty = \frac{\alpha}{1 - \rho} \quad \text{ and } \quad K = -\ln(\rho) \qquad\qquad 3.4$$

The procedure I used to apply this method to length-at-age data from the study lakes involved first fitting the linear model (3.2) to mean length-at-age and then calculating L_∞ and K from (3.4). For hatchery-stocked lakes, I assumed all age 1 fish were released at 100 mm fork length (E. Parkinson, B.C. Ministry of Fisheries, Vancouver, B.C., pers. comm.). Variance estimates of α and ρ were transformed into respective variances of L_∞ and K by applying the Delta method to 3.4 (ignoring covariance terms) giving

$$\text{var}(L_\infty) = (1 - \rho)^2 \, \text{var}(\alpha) + \left(\frac{\alpha}{(1 - \rho)^2}\right) \text{var}(\rho)$$

$$\text{var}(K) = \left(-\frac{1}{\rho}\right)^2 \text{var}(\rho).$$

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Maturity

Fish obtained in fall gillnet samples were grouped into 50 mm length classes, and the proportions mature in each length category were calculated separately for males and females. The resulting proportions were analysed using linear regression between logit transformed proportions and fork length. The logistic maturity-at-length model, fitting procedures, and calculation of age-at-50% maturity, AM_{50}, are identical to those performed for the vulnerability analysis described in the next section.

Vulnerability

Exploitation of fishes is typically related to body size; small fish are relatively less prone to capture (or harvest) than fish in larger size classes. Reasons for this include the direct use of size-selective fishing gear (body size dependent), fishing in areas where small fish are less likely to be captured (spatially dependent), or intentional release of small fish by anglers (angler behaviour dependent). Because any of these capture modes can produce changes in vulnerability with size, it is not necessary to explicitly model each one separately and often a single function that describes relative vulnerability increase as fish grow is enough for practical purposes.

A common functional relationship used to represent size-selectivity is a power model of the form (Hilborn and Walters 1992)

$$v_l = \frac{l^m}{l^m + L_{50}^m} \tag{3.5}$$

where v_l is the relative vulnerability of fish at length l, L_{50} is the length at 50% relative vulnerability, and m is the steepness of the curve at $l = L_{50}$. This function produces a

gradual increase in vulnerability at small sizes but then increases steeply as fish size approaches L_{50}. For $l > L_{50}$, rate of increase slows as vulnerability approaches a maximum value of 1 indicating that fish in all larger size classes are equally vulnerable to harvest. In some cases, vulnerability may decline as fish approach very larger sizes due to either selection for behavioural avoidance of the gear, deliberate release of trophy fish, or natural factors such as spawning or migration that place them in unfished areas. As I will show, vulnerability may decrease at large size for fish in some lakes; however low marking and recapture rates for fish in very large size classes for most lakes precludes explicitly modeling this behaviour.

To assess size dependent vulnerability, I computed a maximum exploitation rate for each lake using the average of the two highest exploitation-at-length observations. Then I expressed vulnerability-at-length, u_l, as being relative to the maximum exploitation rate in the population.

The parameter of interest for the vulnerability analysis is L_{50}, the length at which 50% of the maximum exploitation occurs. Initial trials using a simple sum of squares minimization between predicted vulnerability and observed values showed that the steepness parameter, m, was well defined by the data on most lakes (mean among-lake estimates of m were 7.09 with CV = 0.09) so I eliminated it from the estimation by setting it to a constant. The difference between $m = 6$ and $m = 7$ was minimal and the former accommodated one lake that had a relatively low m value, so I used $m = 6$ for all

subsequent analyses. To obtain estimates of L_{50}, relative vulnerability-at-length data were

logit transformed [logit(u_l)=log($u_l/(1-u_l)$)] in order to fit a linear model of the form

$$y_l = \alpha + \beta \cdot l \qquad\qquad 3.6$$

where y_l is the transformed vulnerability-at-length l and (α, β) are parameters to be

estimated (not to be confused with Walford α). These estimates were obtained using

simple linear regression and an estimate of L_{50} was calculated by solving 3.6 for l after

setting $y_l = 0$, i.e., $u_l = 0.50$

$$L_{50} = -\frac{\alpha}{\beta} .$$

The variance formula for L_{50} is

$$\text{var}(L_{50}) = \left(-\frac{1}{\beta}\right)^2 \text{var}(\alpha) + \left(\frac{\alpha}{\beta}\right)^2 \text{var}(\beta) .$$

I also calculated the age-at-L_{50}, A_{50}, for each lake and compared these values to determine

whether a simpler vulnerability assumption can be made in the absence of length-based

data. I used the VBGF parameters for each lake to calculate A_{50} from L_{50} according to

$$A_{50} = -\frac{\ln\left(1 - \frac{L_{50}}{L_\infty}\right)}{K} - a_o$$

where a_o is the hypothetical age at zero length which I assumed to be zero for all lakes.

Survival

Only two lakes met the data criteria for estimating natural mortality. Both of these lakes,

Fawn and Rock Island, had enough recaptures in both years to obtain reasonable length-

specific exploitation estimates in the year of release and the subsequent year. Survival

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rates of adult rainbow trout (> 200 mm) were calculated using these year- and length-specific exploitation estimates along with the Walford growth parameters α and ρ. I first calculated exploitation-at-length for only those fish that were marked and recaptured in the *same* year using the methods described above. These estimates were then used to generate expected numbers of rainbow trout tagged in year 1 that survived harvest using the relationship

$$N_{l,t+1} = N_{l,t} * (1 - u_{l,t}).$$

Exploitation at length l, based on the following years tagging experiment, was then used to estimate the actual number of survivors, $\hat{N}_{l,t+1}$, according to

$$\hat{N}_{l,t+1} = \frac{R_{l,t+1}}{u_{l',t+1}}$$

where, using the growth parameters, l', is the expected length in year $t+1$ of fish originally released at length l in year t, $u_{l',t+1}$ is the exploitation-at-length l' in year $t+1$, and $R_{l,t+1}$ is the number of fish originally released at length l in year t that were subsequently recaptured in year $t+1$. Rate of survival was then calculated simply as

$$s_a = \frac{\sum_l \hat{N}_{l,t+1}}{\sum_l N_{l,t+1}} \tag{3.7}$$

where a indicates that the estimate is for adult fish and the summation is over all length classes in the original marked sample. Taking the sum over all lengths serves to average out the effects of correction factors used to generate R and also absorbs some of the errors due to inaccurate predictions of l'.

In addition to these estimates, I also performed an analysis of maturity-specific survival based on data from Fawn lake. Post-spawning mortality is suspected to be an important problem in B.C.'s small lakes because fish tend to disappear soon after maturity (Naito 1992; Hume and Tsumura 1992). If mature fish do, in fact, survive at a lower rate than immature fish, then recapture rates in the year *following* tagging should be disproportionately lower for mature fish. To show this, I set up a simple population model for tagged mature and immature fish that were marked in year t and subsequently recaptured in year $t+1$. Suppose that a sample of fish marked at length l in year t has both immature and mature proportions, $p_{l,\text{imm}}$ and $p_{l,\text{mat}}$ respectively. Then the total number of fish surviving to year $t+1$ can be calculated using a weighted combination of immature and mature mortality rates

$$N_{l,t+1} = (N_{l,t} - R_{l,t})e^{-(p_{l,imm}M_{imm} + p_{l,mat}M_{mat})} \tag{3.8}$$

where $R_{l,t}$ is the observed recapture numbers at length l in year t and M_{imm}, M_{mat} are the instantaneous rates of natural mortality for immature and mature fish, respectively. The expected number of fish recaptured in year $t+1$ can then be computed as $R_{l,t+1} = u_{l',t}N_{l,t+1}$. I applied this model to the length-specific data from Fawn lake with l' and $u_{l',t+1}$ computed as above. $p_{l,\text{imm}}$ and $p_{l,\text{mat}}$ values were calculated for each length class in the original marked sample using the visual maturity determinations described above. Parameter estimates, M_{imm}, and M_{mat}, were obtained by minimizing the sums of squares (Microsoft Excel 8.0, Solver function) between observed and predicted $R_{l,t+1}$ values.

Recruitment rate

One of the most important parameters used in stock assessments is the maximum survival rate of juveniles at low spawner abundance. These values are used to determine optimum fishing mortality as well as to detect potential recruitment over-fishing (Hilborn and Walters 1992). Actually observing such values is difficult without actually over-exploiting a stock, but recent meta-analysis work shows that maximum reproductive rates tend to be similar among several fish taxa (Myers et al 1999).

In an attempt to place potential bounds on maximum reproductive rates (α_{max} for a Beverton-Holt recruitment model) for B.C. rainbow trout, I estimated recruits per spawner (R/S) and recruits per egg abundance (R/E) for current population levels on Rock Island lake. This lake was used because it is a wild stock, current fishing mortality rates are likely to be low, and I was able to reconstruct population abundance for the years 1996-1998. Numbers-at-age for a given year were simply back-calculated using the familiar virtual population analysis (VPA) equation

$$N_{a,t} = \frac{N_{a+1,t+1} - C_{a+1,t+1}}{s_a}$$

where $N_{a,t}$ is the numbers-at-age in year t, $C_{a,t}$ is the catch-at-age in year t, and s_a is the annual adult survival rate computed in the previous section. Catch-at-length data were converted to catch-at-age using an inverse age-length key method described in (Bartoo and Parker 1983).

The analysis was initialized from mark-recapture abundance estimates in 1998 and $N_{2,1998}$ was used as the recruitment index. Spawner (S_{96}) abundance for 1996 was calculated

from the reconstructed population after adjusting for proportions of mature females. Egg (E_{96}) abundance was calculated using spawner abundance-at-age along with length-at-age and a linear fecundity-body length relationship ($f(l) = 17$ eggs $+ 0.6$ eggs cm^{-1}*l cm) obtained from the user's manual for the small lakes integrated management model (SLIM; Korman et al. 1994). R/S and R/E values were then calculated by dividing S_{96} and E_{96} into $N_{2,1998}$. These estimates approximate reproductive rates at spawner abundance much larger than those needed to estimate α_{max}, but may be useful given empirical evidence about the relationship between α' values calculated here and α_{max}.

Results

Growth

Total numbers of rainbow trout captured in fall surveys, and subsequently aged, ranged from 25 fish in Fawn lake (1997) to 174 in Roche (1997-98 combined). Large numbers of captures were obtained in Roche lake for both study years and no significant differences in size-at-age data were detected, so the two samples were combined. Figure 3.1 shows the catch-at-age and mean length-at-age for the fall gillnet data. Numbers captured indicated that very few fish probably survive beyond age 5 in the study lakes, and for hatchery lakes in particular, few fish survived to age 4 and older. Rock Island and Hardcastle were the only lakes where fish of ages 5 and 6 were observed.

For most lakes, growth in length followed the general pattern implied by the VBGF; length increments between adjacent ages were approximately linear and asymptotic lengths between 400 and 900mm were detectable by eye. Walford plots of the size-at-age

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data along with estimates of the growth parameters α and ρ appear in Figure 3.2. VBGF

parameter estimates for these data ranged from 444 to 887 mm and 0.19 to .36 mm yr^{-1}

for L_∞ and K respectively (Table 3.1). Low representation of older age classes and

increasing aging errors beyond age 3 (E. Parkinson, B.C. Ministry of Fisheries,

Vancouver, B.C., pers. comm.) probably induced a positive bias in L_∞ on some lakes.

Size-selective exploitation, in particular has been shown to induce biases on the order of

+10% and –15-20% for L_∞ and K, respectively (Martinez-Garmendia 1997). However,

greater size at age 1 than predicted on the basis of the growth function was common on

hatchery stocked lakes and this effect likely reduces some of the bias in L_∞ at the expense

of producing positive bias in K. The K estimate for Dairy lake was much lower than for

other mono-culture lakes which may indicate that L_∞ is strongly biased upward. For the

wild stock lakes (Rock Island and Hardcastle) where fish enter the lake as fry during the

summer, apparent growth from age 0 to age 1 generally followed the assumed growth

function and exploitation was relatively low. Thus, bias in VBGF estimates for these

lakes may be small.
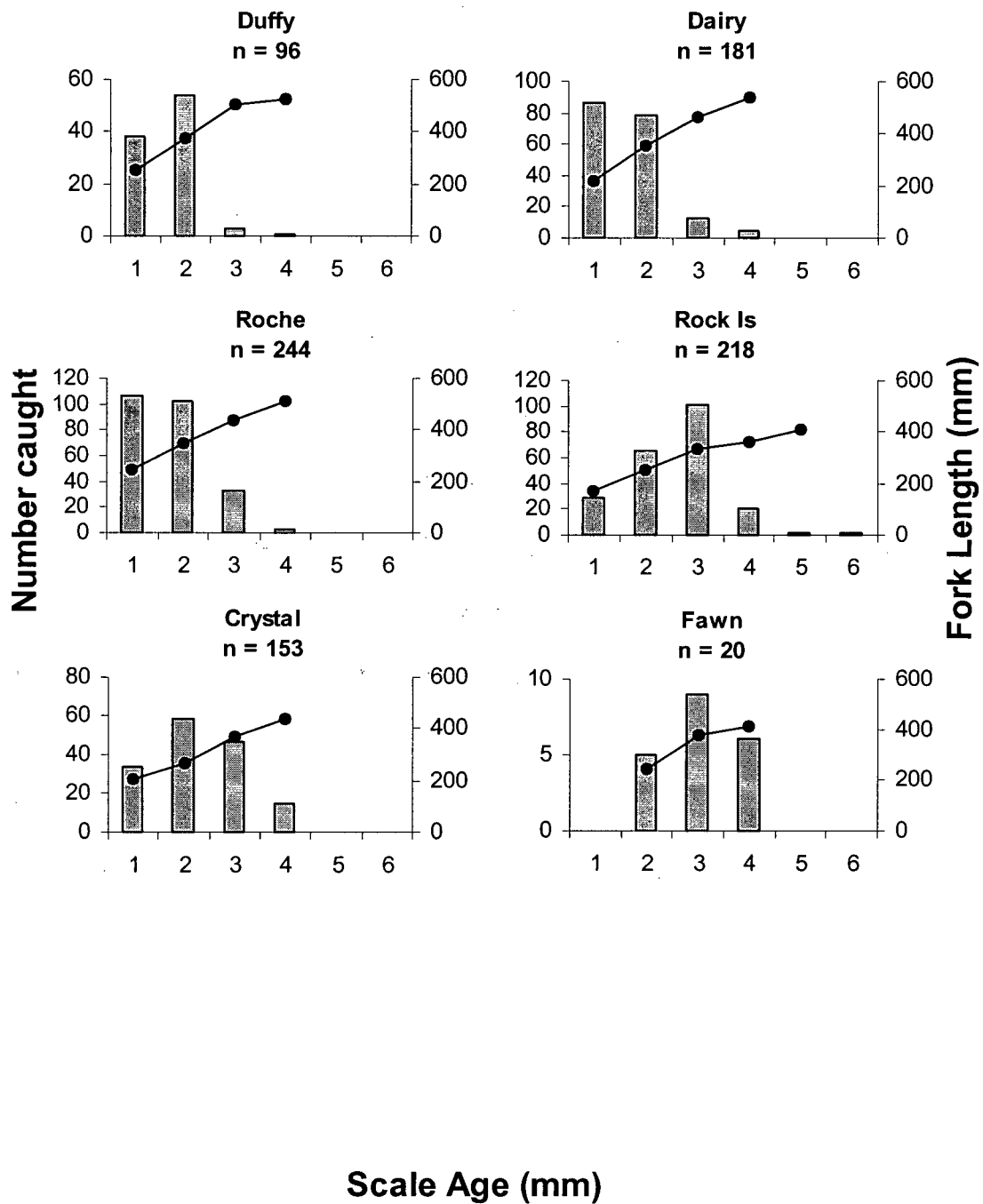
Figure 3.1. Numbers caught and mean length-at-age for fish captured in fall gillnet surveys.
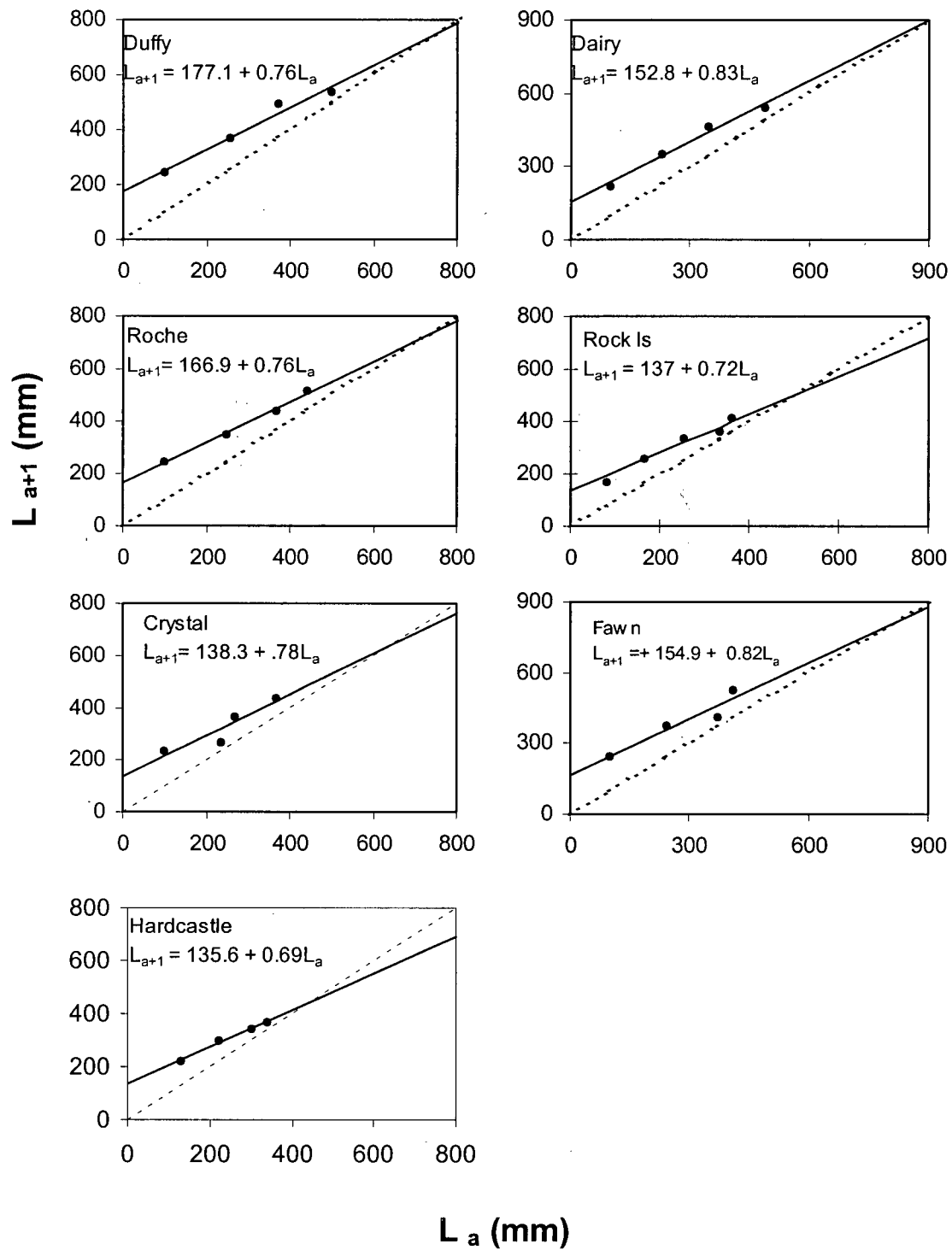
Figure 3.2. Walford plots of length-at-age a versus length-at-age a+1 for the fall gillnet data. Lengths represent mean length-at-age using the data in figure 3.1. The dashed lines represent 1:1 correspondence and the final Walford equations are shown on each plot.

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Estimates of L_∞ and K from tag returns were substantially different compared to those

obtained from size-at-age data. In particular, K values tended to be higher and L_∞ values

were lower. Bias in either one of the values will produced an opposite bias in the other

due to negative correlation between them. Higher apparent K values may arise due to

size-selective harvest of faster growing fish (Martinez-Garmendia 1997), post-mortem

shrinkage of large fish whose growth increments may be small (Ricker 1975), or from

the fact that growth from May-September did not represent annual growth particularly

well. Water temperature during this period is typically higher than the annual mean and

this could result in higher apparent metabolic costs. For subsequent analysis that required

growth parameters, I used only those obtained from the gillnet surveys.

Table 3.1. Asymptotic length (L_∞) and growth rate constant (K) estimates for rainbow trout captured in fall gillnet surveys and mark-recapture experiments. Estimates were obtained by applying Walford's method to fall gillnet samples and tag returns (approximately one growing season at liberty) separately. Standard errors of the estimates appear in parentheses.

		Fall Gillnet Survey			Tag Returns		
Lake	Year	L_∞(mm)	K	n	L_∞(mm)	K	n
Duffy	98	740 (282)	0.27 (0.12)	86	-	-	-
Dairy	98	887 (444)	0.19 (0.10)	124	-	-	-
Roche	97-98	706 (113)	0.27 (0.05)	174	-	-	-
Hardcastle	97	444 (88)	0.36 (0.09)	36	331 (44)	0.41 (0.07)	6 [A]
Pillar	96	416 [B]	0.30 [C]	-	404 (167)	0.40 (0.20)	9 [A]
Rock Is	98	503 (197)	0.32 (0.15)	167	415 (640)	0.40 (0.77)	5 [A]
Crystal	97	626 (655)	0.25 (0.30)	83	556 (181)	0.38 (0.15)	8 [A]
Fawn	97	803 (699)	0.23 (0.22)	25	713 (782)	0.31 (0.35)	9 [A]

A- recaptured fish that were at liberty May-September in the year of release.

B- estimated from relationship between gillnet and tag return estimates.

C- average K value from mono-culture lakes (Duffy, Roche, Hardcastle, and Rock Island).

Maturity

As expected, high proportions of male rainbow trout were mature at 200-250 mm. This

has been observed in the past for B.C. rainbow trout (Hume and Tsumura 1992) and it

likely reflects the lower cost of reproduction for males. Maturity of female trout was

spread smoothly over several length classes for all lakes (Figure 3.3).
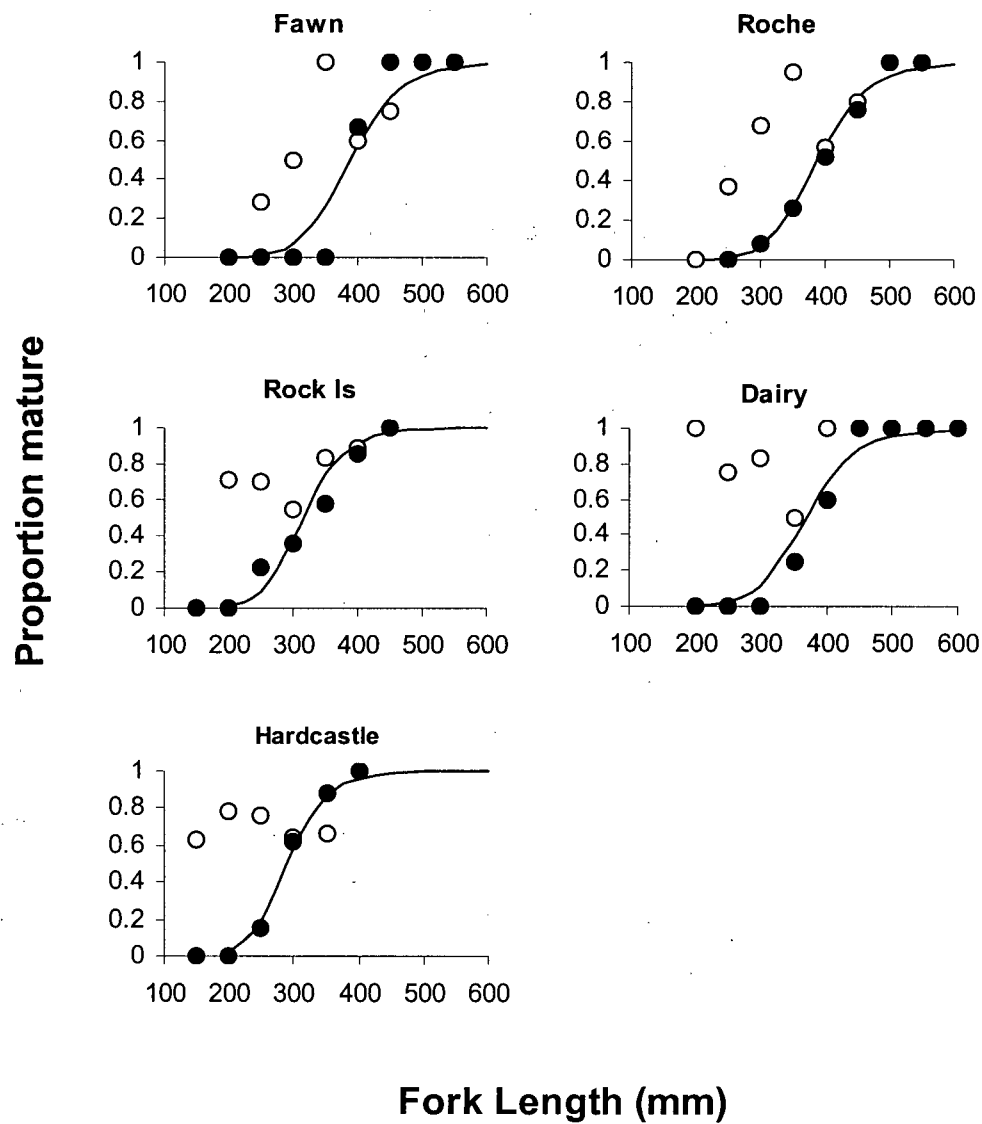
Figure 3.3. Maturation schedules for female (solid circles) and male (open circles) rainbow trout in B.C.'s southern interior lakes. Solid line is the logistic model fit for females.

Minimum size-at-maturity for females was approximately 250-300 mm, but the proportions mature at this size were small. Estimates of LM_{50} for female trout ranged between 290 and 387 mm with larger size-at-maturity occurring on lakes with larger asymptotic lengths (Table 3.2).

Life history theory predicts that age and size-at-maturity should be closely associated with lifetime growth and mortality patterns (Shuter et al 1998). Roff (1992) showed that when iteroparous fishes attempt to maximize lifetime fecundity, optimal size-at-maturity has the simple solution

$$L_{opt} = L_\infty \left(\frac{3K}{3K + M} \right)$$

where L_∞ and K are the VBGF parameters and M is the instantaneous rate of natural mortality. Assuming that size-at-maturity is optimized at LM_{50}, at least for wild stock lakes in B.C., the above formula can be rearranged to provide the following estimate of M

$$M = 3K \left(\frac{L_\infty}{LM_{50}} - 1 \right).$$

This model predicts that M should be linear in K, and the effect of L_∞ will be mediated by the optimum length-at-maturity which may change over time due to varying environmental conditions and population density. Walters and Post (1993) used bioenergetic and behavioural arguments to show that in fact L_∞ is more likely to change under varying conditions than K. If the ratio L_∞/LM_{50} remains relatively constant over a typical range of growth conditions, then M should be primarily influenced by K. Pauly (1980) developed the statistical model

$$\log M = 0.654 \log K - 0.28 \log L_\infty + 0.463 \log T$$

for predicting M from VBGF parameters and mean annual water temperature (T) for 175 fish populations. Applying both equations to the rainbow trout growth and maturity data gave the natural mortality rate estimates $M = 0.56$ yr^{-1} and $M = 0.37$ yr^{-1} (annual survival $s = 0.56$ and 0.69, respectively) for the Roff and Pauly ($T = 8°$ C) methods, respectively. Because of potential positive biases in L_∞ values and lower sensitivity of Pauly's model to L_∞, the Roff mortality rate is probably biased low compared Pauly's. Lowering L_∞ values by 10% resulted in a Roff natural mortality estimate of $M = 0.49$ yr^{-1} ($s = 0.64$) while not affecting Pauly's estimate appreciably.

Table 3.2. Logistic regression results for length at maturity of female rainbow trout in 5 study lakes. n is the total number of females used to estimate mature proportions, (α, β) are logistic regressions parameters, LM_{50} and AM_{50} are estimates of length and age at 50% maturity, respectively. Standard errors of the estimates appear in parentheses.

Lake	n	α	β	LM_{50}	LM_{50}/L_∞	AM_{50}
Fawn	27	-8.5 (1.18)	0.022 (0.003)	387.7 (74.8)	0.482	2.86
Roche	144	-5.1 (0.66)	0.013 (0.001)	386.7 (67.5)	0.548	2.93
Rock Island	131	-3.84 (0.78)	0.012 (0.002)	315.3 (84.0)	0.627	3.08
Dairy	158	-6.15 (1.18)	0.017 (0.003)	367.5 (95.4)	0.414	2.81
Hardcastle	149	-4.22 (0.71)	0.014 (0.002)	290.5 (62.8)	0.654	2.95

Exploitation-at-length

Exploitation rates increased with body length for all tagging experiments (Figure 3.4). Apparent selectivity patterns were characterized by rapidly increasing exploitation between 200 and 300 mm and slower increases at lengths larger than 300 mm. For the three cases where exploitation-at-length data were available for two years, exploitation-at-length patterns were similar for fork lengths less than 450 mm.

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Figure 3.4. Estimates of exploitation-at-length for tagged rainbow trout in the study lakes. Numbers released (shaded bars) are adjusted for handling mortality and exploitation rates (solid circles) are corrected for reporting rates in the month of recapture. All results are based on pre-season fork length grouped into 50 mm length classes.

Fawn 1996 · Fawn 1997 · Roche 1997 · Roche 1998 · Rock Is 1997 · Rock Is 1998 · Dairy · Pillar · Crystal 1998 · Hardcastle · Duffy

Number Released

Exploitation
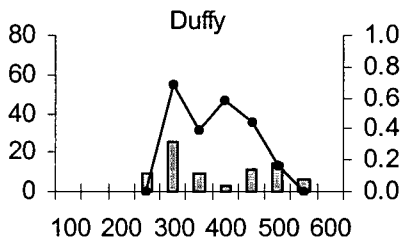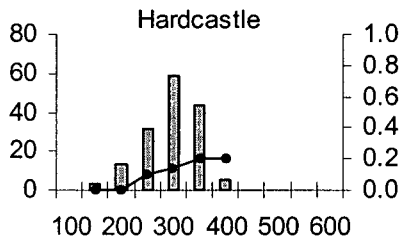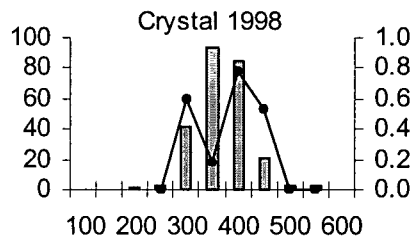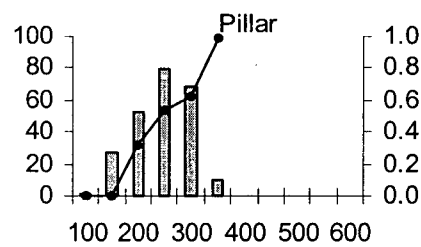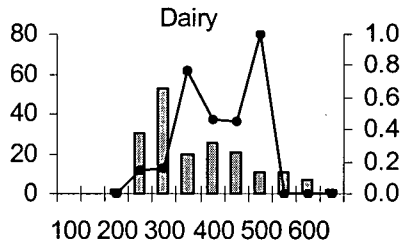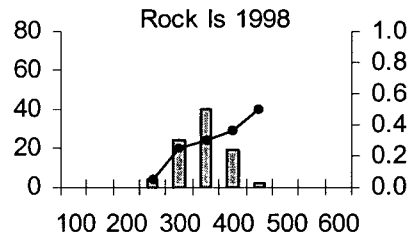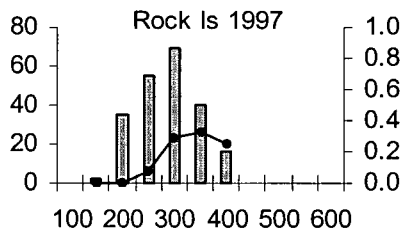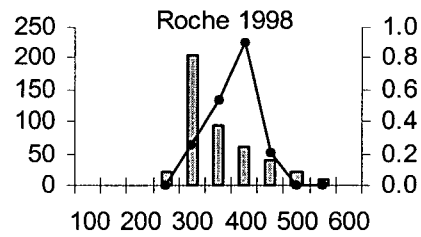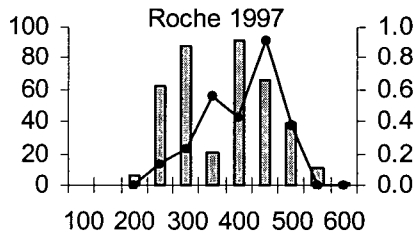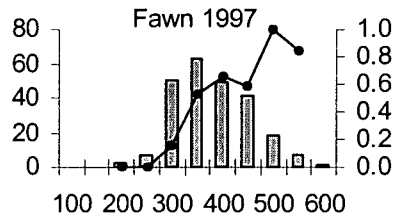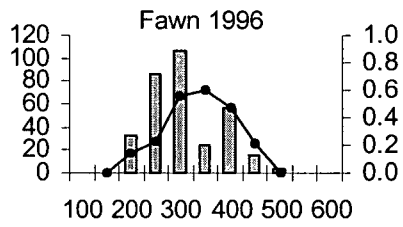
Length at release (mm)

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Several tagging experiments showed evidence of a decrease in exploitation or higher natural mortality rate at fork lengths greater than approximately 450 mm. This effect occurred at Roche lake in both study years and at Fawn (1996 only), Crystal, Duffy, and Dairy lakes. In all cases except Roche, it is difficult to make a definitive statement about the apparent decreases in vulnerability at large size because low tag return rates for large fish make the exploitation estimates particularly sensitive to the correction factors I used to expand tag returns. For Roche lake, tag return corrections were relatively small, and the fact that nearly identical patterns were observed in both study years warranted further analysis.

Reduced exploitation at large body size may have several possible causes; (1.) anglers may release exceptionally large trout in the hope of returning to catch them again, (2.) the fact that a high proportion of large trout are sexually mature provides two possibilities: (2a.) during the spring peak in angler effort, mature fish are typically concentrated in shallow areas or else are actively migrating up lake tributaries to spawn and (2b.) mortality associated with maturity and spawning is high, (3.) anglers may intentionally avoid reporting these fish to creel personnel because of maximum size limit regulations that are in effect on all study lakes (only 1 fish > 500 mm per day), and (4.) large trout may have developed gear or boat avoidance behaviour that makes them less vulnerable to capture. Of these possibilities, (1.) is unlikely given the rare occurrence of actually catching a trophy fish. Most anglers travel great distances to fish B.C.'s small lakes and from my observations they are more than willing to keep the few large fish they catch. Item (3.) is certainly possible and has been shown to occur in some Alberta walleye lakes

(M. Sullivan, Alberta Environmental Protection, Natural Resources Service, Edmonton, AB, pers. comm.), but there is little information upon which to base such an assessment for B.C. rainbow trout lakes. Large fish may also develop gear avoidance behaviour (4.); however catch rates of large (>450 mm) fish during the marking occasions in this study suggest that gear avoidance behaviour is also unlikely. In fact, the opposite may occur for large, mature fish because they appeared to be extremely aggressive during the spring and were easily captured by typical angling methods used on B.C. lakes. Large, mature fish tended to concentrate in shallow areas and creek mouths which suggests that perhaps item (2.) is an important factor in determining exploitation of mature fish.

If anglers were not able to locate spawning aggregations or if mature fish leave the lake or if post-spawning mortality is high, then the proportion of mature tagged fish in the recapture samples should be lower compared to the proportion of mature fish in the original marked sample. To test this hypothesis, I used 2 X 2 contingency table analyses (Zar 1984) between total mature and immature numbers of trout in the marked sample compared to total numbers in the recaptured samples. Marked and recaptured fish in all tagging studies were grouped by maturity status and I tested the null hypothesis $p_M = p_R$, that is, mature proportions in marked (M; not to be confused with instantaneous natural mortality rate) and recapture (R) samples were equal. Results of this analysis showed that mature proportions were different ($p_M > p_R$) in both years at Roche lake, but were not significantly different between samples in any other studies (Table 3.3). The Roche result is potentially misleading because it is also possible that the original marked sample was biased toward mature fish and the recapture sample just reflects the true mature

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proportion in the population. If the marked samples in spring of 1998 were indeed biased, then mature proportions in that sample should be greater than in the fall gillnet survey (presumed unbiased) conducted in 1997. Contingency table analysis between these two samples actually showed the opposite; the mature proportion in the spring 1998 marked sample (p_S) was less than the mature proportion in the 1997 fall gillnet survey (p_F) ($p_F >$ p_S, $\chi^2 = 9.90$, $\chi^2_{(1,0.05)} = 3.88$). The discrepancy between these two proportions is not surprising because maturity of fish sampled in the fall was determined by direct inspection of the gonads, while maturity in spring samples was assessed by external traits. Spring maturity assessments performed on gillnet mortalities showed that mature fish quite often do not necessarily exhibit strong morphological differences compared to immature ones. Thus, mature proportions in the spring were probably higher than originally estimated.

Table 3.3. Contingency table results for comparing proportions of mature (*Mat*) and immature (*Imm*) rainbow trout in marked (M) and recapture (R) samples. Bold-face type indicates that differences are significant for $\chi^2_{1,0.05}$ (**) and $\chi^2_{1,0.10}$ (*).

		Marks			*Recaptures*			
Lake	Year	Mat	Imm	p_M	Mat	Imm	p_R	χ^2
Fawn	1996	115	294	0.28	9	26	0.26	0.01
Fawn	1997	94	200	0.32	18	31	0.37	.24
Roche	1997	169	312	0.35	5	35	0.13	**7.51****
Roche	1998	191	368	0.40	2	18	0.10	**4.05****
Rock Is	1997	51	220	0.19	6	35	0.15	0.18
Rock Is	1998	22	92	0.19	8	18	0.31	1.04
Dairy	1998	87	139	0.38	6	11	0.35	<.01
Pillar	1996	83	215	0.27	3	24	0.11	**2.75***
Crystal	1998	31	219	0.12	0	18	0.00	0.02
Hardcastle	1997	29	164	0.15	1	8	0.11	0.02
Duffy	1998	41	57	0.41	3	10	0.23	1.00

While it appears that maturation may explain some of the decrease in vulnerability of older, larger fish in Roche lake, it is difficult to determine whether maturation effects are important for other lakes.

Relative vulnerability

Despite the difficulties in assessing vulnerability of large fish, most of the exploitation-at-length data showed consistent patterns of increasing vulnerability with increasing body size. The exceptions to this pattern were Crystal and Duffy lakes which did not show a smooth increase in exploitation with length as would be expected on the basis of a length-vulnerability model. Instead, both lakes showed low exploitation on 200-250mm fish and high exploitation on all larger size classes except for one low exploitation value at 350 mm for Crystal. This pattern implies a strong, "knife-edge" selection for fish larger than 250-300 mm so I omitted these lakes from the vulnerability analysis. For lakes that exhibited a decline in exploitation at large size, I used only the ascending portion of the exploitation-at-length relationship to fit the vulnerability model.

Final estimates of L_{50} ranged from 213.9 to 345.4mm with coefficients of variation between 20 and 30% (Table 3.4).
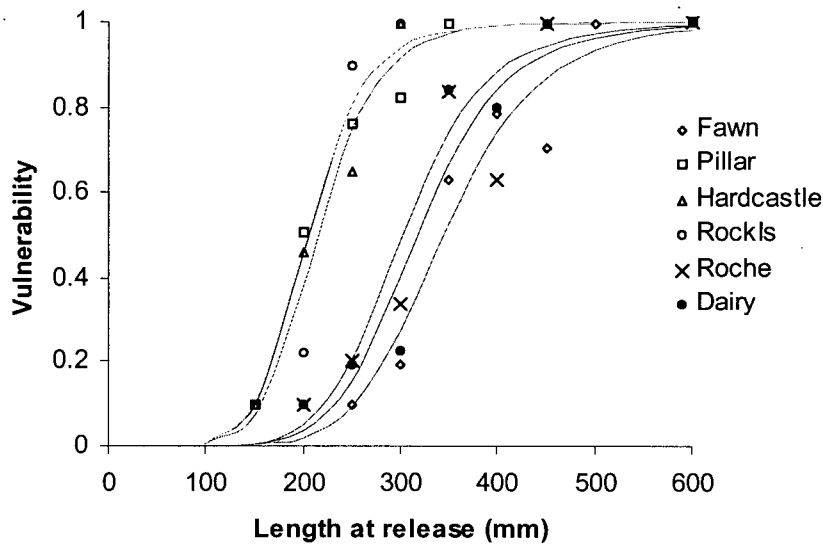
Figure 3.5. Relative vulnerability-at-length for rainbow trout in six British Columbia lakes. Solid line represent the logistic model fits for each lake.

L_{50}/L_∞ ratios were quite similar among lakes with a mean value of 0.433 (S.D. = 0.052; Table 3.4) suggesting that L_{50} depends strongly on maximum fish size in a given lake. For example, L_{50} values in Hardcastle (204.5 mm) and Pillar (213.9 mm) were much lower than in Fawn (345.4 mm) or Dairy (317.8 mm) lakes where average fish size tended to be much larger. Because growth rates determine size-at-age, it is reasonable to expect that vulnerability could be more accurately predicted by age. For example, a 213.9 mm fish in Pillar lake would have the same relative vulnerability (0.50) as a 317.8 mm fish in Dairy, but these fish are essentially the same age (2.24 and 2.56 yr in Pillar and Dairy, respectively). Resulting calculations of A_{50} showed that most fish in the study lakes recruit to the fishery between 1.70 and 2.79 yr with a mean value among lakes of 2.24 yr (S.D. = 0.44 yr).

Table 3.4. Logistic regression estimates of L_{50}, the ratio L_{50}/L_∞, and A_{50} for six study lakes. Regression sample size, slope, intercept, and coefficient of determination are given for each lake and standard errors appear in parentheses.

Lake	n	α	β	L_{50}	L_{50}/L_{∞}	A_{50}
Fawn	6	-9.4 (2.4)	0.03 (0.006)	345.4 (119.1)	0.429	2.79
Pillar	5	-7.5 (1.8)	0.04 (0.007)	213.9 (66.2)	0.512	2.24
Hardcastle	4	-10.1 (3.0)	0.05 (0.013)	204.5 (79.9)	0.461	1.70
Rock Island	4	-11.2 (2.1)	0.05 (0.009)	204.5 (51.5)	0.407	1.75
Roche	6	-8.3 (2.3)	0.03 (0.007)	302.6 (115.1)	0.429	2.42
Dairy	5	-6.5 (1.6)	0.02 (0.005)	317.8 (110.0)	0.358	2.56

The vulnerability results have two important implications for the model I develop in later chapters, in addition to value for fishery assessment. First, using A_{50} in place of L_{50} removes the need to model length effects on vulnerability to harvest making population model computations and parameter estimation much simpler to perform. Second, the fact that most fish become vulnerable to anglers in their second year (as shown strongly in Crystal and Duffy) greatly simplifies age-structured models because it is relatively safe to assume a knife-edge increase in vulnerability at age 2. The similarity among lakes in A_{50} also improves age-structured assessments of sustainable fishing mortality (or effort) by reducing uncertainty associated with size-dependent vulnerability (Peters 1996).

Survival

Natural mortality rate estimates from mark-recapture data on Fawn and Rock Island lakes were $M = 0.41$ yr^{-1} ($s = 0.64$) and $M = 0.46$ yr^{-1} ($s = 0.63$), respectively.
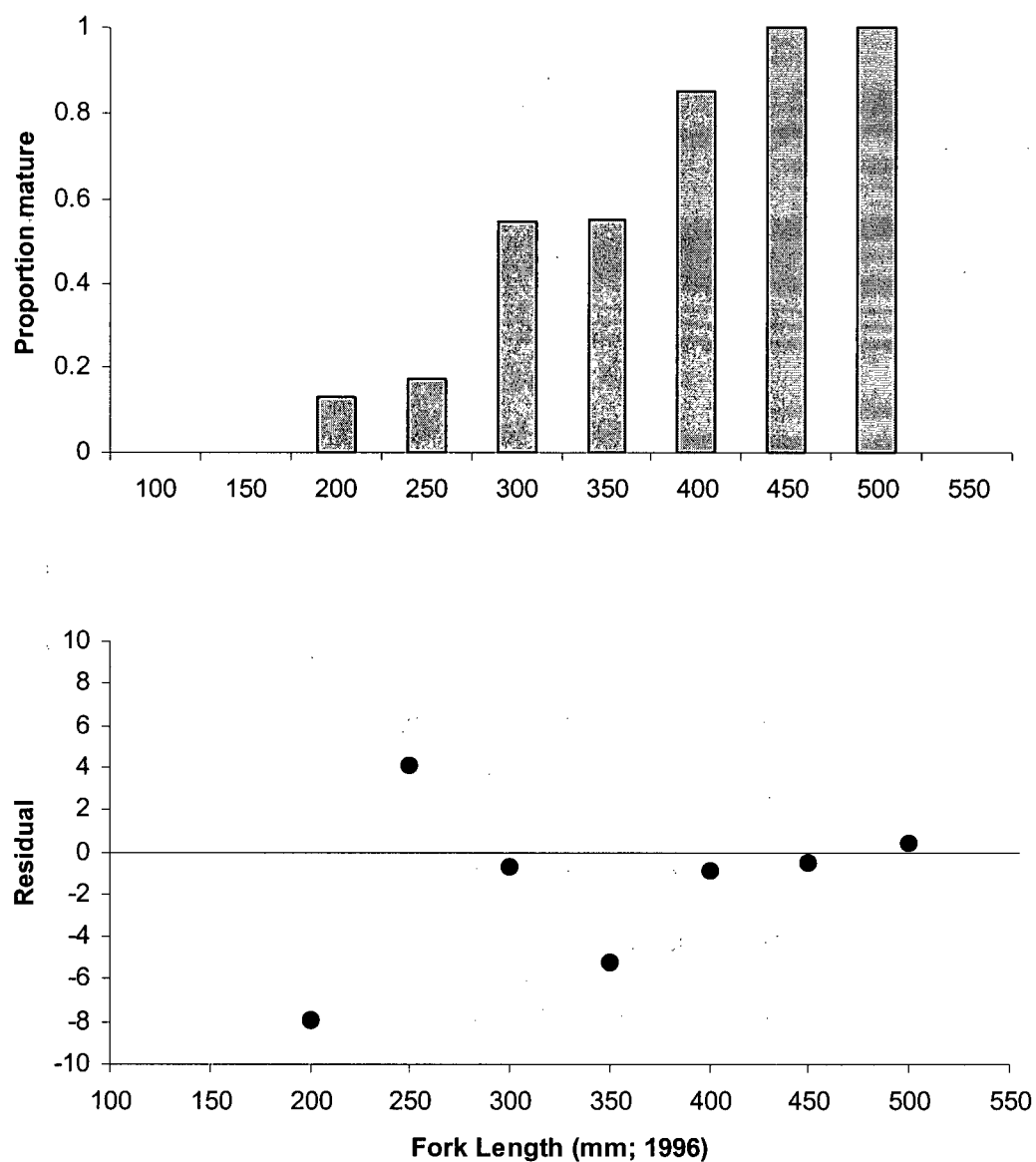
Figure 3.6. Proportion mature-at-length for rainbow trout tagged in Fawn lake (1996) (top panel) and the residual values of predicted recaptures in 1997.

The agreement between these two values might be surprising to some biologists given the

extreme physical and biological differences between the two lakes (c.f. Chapter 2; Table

2.1).

Estimates of survival for immature and mature fish in Fawn lake (1996-97) were 0.72 (M

= 0.28 yr^{-1}) and 0.12 (M = 2.12 yr^{-1}), respectively. Although residual values from the

observed recaptures (Figure 3.6) indicated large prediction errors for small fish, those

errors are also influenced by correction factors that generate the observed recaptures. The

range +/- 8 fish seems reasonable given that observed recaptures depend not only on

these corrections, but also on survival rates of tagged fish. A relatively large proportion

of small trout tagged in Fawn lake (1996) were captured by angling (by "himself" Dr.

Carl Walters) and these fish may have (surely) suffered lower handling mortality

compared to larger fish captured by gillnet (and mishandled by graduate students).

Recruitment rate

Table 3.5 shows the reconstructed numbers-at-age (1996-1998), maturity, and fecundity

schedules for Rock Island lake. Total spawner (S_{96}) and egg (E_{96}) abundance were 1 847

and 3.2 x 10^6, respectively in 1996 and numbers-at-age 2 in 1998 were 4 546. Recruits

per spawner and recruits per egg estimates were 2.46 and 0.0014, respectively.

Table 3.5. Reconstructed population, spawner abundance and egg abundance for Rock Island lake VPA, 1996-1998. Totals in final column are for age 2+ fish in first three rows and total spawners and eggs in final two rows. $P_{mat,f}$ is the proportion of mature females.

	Age						
	1	2	3	4	5	6	Total
1996	9 204	2 455	2 923	867	568	65	6 880
1997	8 284	5 051	1 171	1 324	304	232	8 083
1998	-	4 546	1 550	561	95	95	6 849
Length (mm)	80	167	254	333	362	370	
$P_{mat,f}$	0	0	0.37	0.50	0.50	0.50	
Fecundity (eggs)	-	-	1 541	2 015	2 189	2 237	
S_{96}	-	-	1 096	433	284	32	1 847
E_{96}	-	-	1.7x10^6	8.7x10^5	6.2x10^5	7.2x10^4	3.2x10^6

Discussion

My objective in this chapter was to describe the life history and size-selective exploitation of rainbow trout in the study lakes. From these results, several generalizations emerge that can be used to improve management of these stocks, as well as providing a basic guide for modeling other rainbow trout populations where little information currently exists.

Demographics parameters such as age- or size-at-maturity, and age-at-50% vulnerability were similar among B.C. rainbow trout populations and their values were typically related to VBGF parameters, L_∞ and K. The consistency in LM_{50}/L_∞ and L_{50}/L_∞ ratios suggest that estimates of asymptotic length, obtained from routine survey or angler catches, can provide important baseline information on maturity schedules and vulnerability to angler harvest. Shuter et al. (1998) used a similar approach to describe the life history and sustainable exploitation of lake trout (*Salvelinus namaycush*) in Ontario lakes. They showed that most important life history parameters were related to growth conditions which, in turn, were correlated with physical habitat characteristics such as lake size and total dissolved solids. For the lakes in this study, I showed that one can either (*i.*) make simple assumptions about age-at-50% maturity (3 yr) and age-at-50% vulnerability (2 yr), (*ii.*) or use observed L_∞ values along with mean observed LM_{50}/L_∞ and L_{50}/L_∞ ratios from this study to estimate LM_{50} and L_{50} directly. Although it was not done here, it is also possible to use Shuter et al's approach to first develop a statistical relationship between L_∞ and lake physical characteristics and then use it to get LM_{50} and

L_{50} from observed values. Of these choices, Shuter et al.s's approach is obviously the most costly in terms of data acquisition, (*ii.*) requires a relatively inexpensive fish survey, and (*i.*) should only be used in the complete absence of growth data.

Although my results for adult survival were limited in number, they generally agreed with existing empirical evidence. For example, the survival rates for Fawn and Rock Island lakes calculated from life history, empirical, and mark-recapture methods agreed closely with one another suggesting that a range of annual survival of 0.60-0.70 may be a reasonable approximation for most B.C. small lakes. These values agree with those obtained for other studies on rainbow trout lakes (0.40 – 0.60; Naito 1992), as well as from mark-recapture studies (0.60; Kwain 1981).

The set of life history parameters provides a basis for fishery assessments. An additional parameter required for such studies is the juvenile survival rate at low stock size, referred to as α_{max} by Shuter et al. (1998). Estimates for their lake trout populations from several sources ranged from 0.0035 to 0.0055. Unfortunately, estimates of α_{max} for rainbow trout are rare. Walters and Speas (unpublished data) estimated α_{max} for rainbow trout in the Lee's Ferry reach of the Colorado River to be approximately 0.003. Recent meta-analysis work on α_{max} for several fish taxa show remarkable similarities, at least within scientific families (Myers et al 1999); maximum annual reproductive rates at low stock size are typically three to five times the reproductive rate at equilibrium unfished levels. Recruits per spawner estimated from the Rock Island lake VPA were 2.5 and egg to age 2 survival was 0.0014. If it is assumed that spawner or egg abundance in Rock Island is somewhere

between unfished, equilibrium levels and extremely low levels then this estimate is consistent with Myers et al's prediction. That is, maximum reproductive rate should be slightly less than 3 times the current R/S estimate and maximum egg to age 2 survival (α_{max}) should lie between 0.002 and 0.004.

Another estimate of maximum egg to age 2 survival can be made on the basis of life history theory, which predicts that the intrinsic rate of population increase, r, should be directly related to survivorship and fecundity schedules (Roff 1992). First, note that survivorship to age a can be written as

$$l(a) = pe^{-Ma}$$

where $l(a)$ is survivorship to age a, M is the rate of natural mortality following an initial high mortality period where fish survive at p. Here, p is taken to be the initial egg to age 2 survival or α_{max}. Roff (1992) shows that if the r is taken to be the measure of fitness, then the optimal age at first reproduction (a_{opt}) can be written as a function of growth and fecundity parameters

$$a_{opt}\left(\frac{3Ke^{-Ka_{opt}}}{1-e^{-Ka_{opt}}}\right) - \log_e\left(\alpha_{max} fec(a_{opt})\right) = 0$$

where K is the VBGF growth constant and $fec(a_{opt})$ is the fecundity-body length function evaluated at a_{opt}. Note that this does not depend on M in any way. This equation can be rearranged to solve for α_{max} which is

$$\alpha_{max} = \frac{\exp\left(a_{opt}\left(\frac{3Ke^{-Ka_{opt}}}{1-e^{-Ka_{opt}}}\right)\right)}{fec(a_{opt})}$$

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Assuming that a_{opt} is well approximated by the empirical $AM_{50} = 3.08$ value computed earlier for Rock Island lake, α_{max} should be 0.0028 which is remarkably consistent with the value found by Walters and Speas (unpublished data) as well as the value expected from Myers et al. (1999).

Chapter 4: Theory, prediction, and sensitivity of a new model for angling quality, effort response, and exploitation in recreational fisheries

Introduction

There are two fundamental components to sport fisheries that warrant more attention when developing fisheries models. The first relates to the "passive" nature of sport fishing as a capture method. Traditional models developed for commercial fisheries assume that catch per unit effort is linearly proportional to total fish abundance or density and that catchability is constant over all levels of abundance and fishing effort (Hilborn and Walters 1992). In commercial fisheries, capture methods such as trawling or seining are of the active type meaning that fishers physically sweep the fish habitat in a way that removes a large proportion of the fish independent of fish behaviour. Should this assumption be blindly applied in recreational fisheries where angling success is dependent upon purely passive capture methods? Passive capture methods such as trolling or casting baits require that fish in a given area "swept" react to the gear used. In recreational fisheries, where a single vessel or individual angler typically uses one or two baits at a time, success requires locating these behaviourally reactive fish. Though abundance in a given area may be high, fish behaviours and local intensity of effort may limit the available fish density due to short-term exchange and removal of fish from sub-populations or pools of fish that are behaviourally reactive to gear at any moment.

The second, and likely more important component is the *open-access* nature of sport fisheries. Effort dynamics in open-access systems can cause systematic and powerful effects on CPE, population abundance, and fishery stability (Botsford et al. 1983; Caddy 1975; Hilborn 1985; Kitchell and Carpenter 1993). Yet, most recreational fishery assessments continue to disregard the importance of effort responses (Carpenter et al. 1994). Studies of commercial and some larger sport fisheries reveal that effort response patterns are usually clear and even agree with the predictions of relatively simple models (Argue et al. 1983; Gillis et al. 1993; Hilborn and Ledbetter 1979; Lapointe 1989).

In this chapter, I develop a framework for incorporating both of these components into models of angling quality and exploitation in recreational fisheries. I show that for certain assumptions about how anglers distribute their fishing effort over a set of opportunities, angling quality is expected to be insensitive to production-side management measures aimed at enhancing or protecting fish populations from over-exploitation. Comparisons between model predictions and empirical data as well as the implications of effort dynamics on sustainable fisheries then appear in later chapters, in order to simplify the presentation. However, I use fully vulnerable exploitation estimates from earlier chapters and fishery data from Ontario lake trout to compare some of the model predictions to current theories of exploitation and catchability in sport fisheries.

Model Specification

Angling success

Rod and reel sport fishing is a passive capture method where success is determined by (a) locating fish aggregations, (b) presentation of baits or lures and (c) reactivity of fish to baits or lures. Parts (a) and (b) are fundamental components of angling that are under direct control of sport fishers. Part (c), on the other hand, depends strongly on fish behaviour and can be regarded as a continuous exchange process in two parts; *i.*) exchanges in space and time as fish move and migrate into (and out of) areas that are accessible to angling gear and *ii.*) exchange between reactive and unreactive (to fishing gear) behavioural states while in those areas and times. Exchanges between these reactive states may be due to such natural processes as feeding rhythms, spawning aggregation, or predator avoidance. The exchange process can be represented by the following set of differential equations, shown schematically in Figure 4.1

$$dV / dt = v_1(N - V - R) - v_2 V - qeV - MV$$
$$dR / dt = (1 - r)qeV - v_3 R - MR$$
$$d(N - V - R) / dt = -v_1(N - V - R) + v_3 R + v_2 V - M(N - V - R)$$

where V (fish ha^{-1}) is the density of reactive fish, N (fish ha^{-1}) is the total density, so N-V-R is the density of unavailable fish, v_1 and v_2 (yr^{-1}) are exchange rates between reactive and reactive states, q is the catchability coefficient (ha ad^{-1}), e is the instantaneous fishing effort density (ad ha^{-1}) and M (yr^{-1}) is the instantaneous rate of natural mortality. R (fish ha^{-1}) represents the density of fish that have been caught and released, v_3 is the recovery rate of these fish back to the fishable stock, and r is the proportion of fish caught that are retained by anglers. Inclusion of R in the system acknowledges that fish may exhibit refractory behaviour after being caught and released. Evidence does exist for such

phenomena, however including an *R*-pool in the model results in a complex analytical solution that is not easily interpreted. Appendix 5 presents this solution in order clarify the distinction between effects of partial retention and limited vulnerability on asymptotic exploitation predictions. It is suggested that the reader view Appendix 5 after the current presentation is absorbed. My purpose in the present analysis is to derive a simple model for the prediction of catch success, effort, and exploitation, so I assume that such refractory effects are minimal and that fish behave the same regardless of capture history.

Recreational Fishery Model
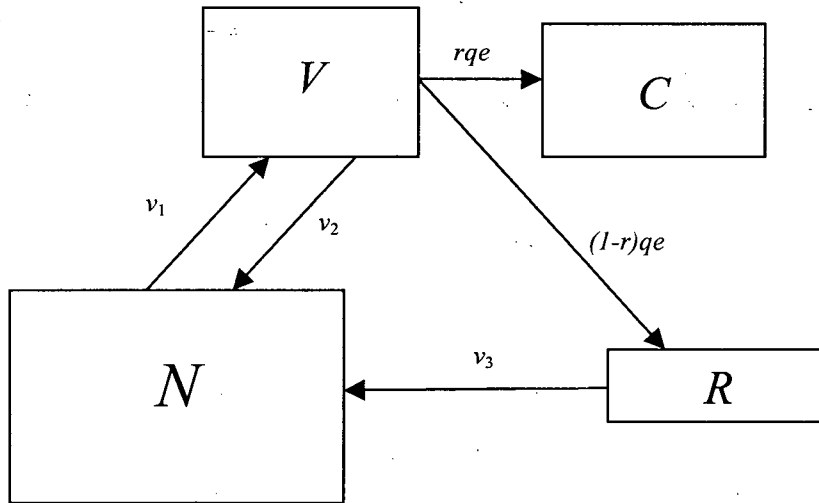
Figure 4.1. Schemmatic representation of a sport fishery. N: density of unavailable, unreactive fish; V: density of available, reactive fish; R: density of fish that are in a refractory state (unreactive) following catch-and-release; C: harvest; qe: fishing rate; r: retention rate of captured fish. Natural exchange rates between states are represented by subscripted constants.

A further simplification ignores natural mortality effects on abundance within the fishing season, because including *M* requires solving a transcendental relationship of the form

$$N_t = N_0 e^{\left(-v_1\left(1-\frac{N_\infty}{N_t}\right)-M\right)t}$$.

That is, N_t depends on the ratio N_∞/N_t and only in the special case of $N_\infty = 0$ does a closed

form solution exist. The form of this model and the specification of N_∞ will become

apparent in the derivations to follow. If the fishing season is short enough (3-4 months)

natural mortality can probably be ignored for in-season assessments and included in inter-

annual assessments as an over-winter mortality that is applied between years (c.f.,

Chapter 6).

Eliminating release/recovery and natural mortality effects results in the simplified system

of differential equations

$$dV / dt = v_1(N - V) - v_2 V - qeV \qquad (4.1)$$
$$dN / dt = -qeV \qquad (4.2).$$

If the exchange rates, v_1 and v_2 are larger than the decline rate of N (due to depletion) so

that V rapidly reaches equilibrium with respect to N, it is reasonable to set $dV / dt = 0$

and solve (1) for the short-term equilibrium density of available fish

$$V = \frac{v_1 N}{v_1 + v_2 + qe} \qquad (4.3).$$

This result follows from variable-speed splitting arguments (Walters et al. 1997; Walters

and Korman 1999) that assume changes in V are much faster than changes in N. If we

assume further that angling success is directly proportional to available fish density then

catch per unit effort, c (catch ad^{-1}), can be expressed as

$$c = qV = q\left(\frac{v_1 N}{v_1 + v_2 + qe}\right) \qquad (4.4).$$

Notice that for fixed N, catchability, and exchange parameters, this model predicts that

angling success should be a non-linear, decreasing function of instantaneous fishing

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effort density, e (Figure 4.2). The degree of non-linearity in the relationship depends on the exchange rate parameters, v_1, v_2, and q. When v_1 is relatively large compared to v_2, then a large proportion of the total stock, N, is vulnerable to fishing. This will cause initial catch success to be high and less sensitive to increasing effort until a significant amount of stock depletion occurs. When v_1 is low, the vulnerable stock at any moment is small, initial catch success will be relatively low, and will decline rapidly with small increases in effort. Low v_1 values tend to protect the stock from severe depletion unless effort is extremely high (the maximum rate of stock depletion for very high effort is $v_1 N$).

Such a non-linear relationship between CPE and effort was also found empirically for brown trout (*Salmo trutta*) in New York streams (Engstrom-Heg 1986). However, his model did not provide an explanation as to why effort may affect CPE. The above formulation indicates that high angling intensity suppresses vulnerable fish density on very short time scales, thus leading to lower CPE for a given total abundance of fish. From the results shown in Chapter 2, population turnover rates (v_1) between unavailable and available states appear to be in the range 2 –5, which suggests that the lower curve in Figure 4.2 may be appropriate for many trout fishery situations. That curve shows a halving of CPE as effort increases from 0 to 50 ad ha^{-1}, and CPE much lower than the theoretical potential for higher effort levels. Thus, reducing effort on intensively fished systems may not produce measurable gains in quality unless effort is severely restricted to levels much lower than those currently observed on many fisheries. I develop an estimation method below for obtaining v_1 and q values from the implied relationship between effort and exploitation.
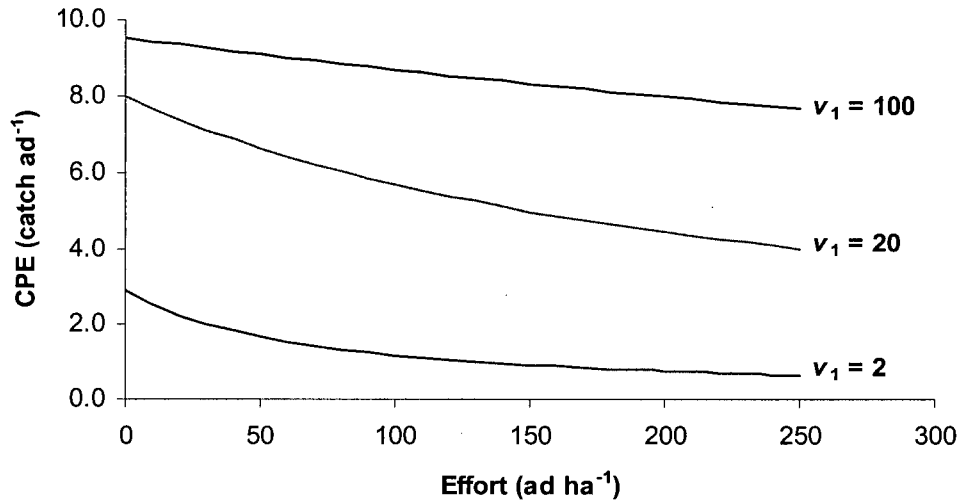
Figure 4.2. Predicted relationship between CPE and effort for different levels of the delivery rate parameter, v_1. All predictions are generated from the same total abundance, catchability, and v_2 values.

Effort response

Equation 4.4 can be used as a basis for predicting the numerical response of fishing effort to changes in fish abundance within a specific region. To do so requires two key assumptions. First, I assume that the rates, v_1, v_2, and q are similar enough among fisheries so that we can use "regional estimates" of their values. Similarity in these values may be expected where species assemblages, physical characteristics, and angler populations are similar among lakes (Shuter et al. 1998). Also, maximum turnover rates (v_1) were shown to be similar over a wide range of species and fisheries (c.f. Chapter 2; Discussion).

A second, more critical assumption for predicting effort responses to abundance is that anglers attempt to equalize attractiveness, c_j (catch per effort), among fisheries within a

region so that $c_j = c_o$ for all j, where c_o is a regional average success rate. That is, anglers actively target those fisheries that "stand out" ($c_j > c_o$) as attractive opportunities, until they are no longer more attractive than equally accessible opportunities. Equalization of attractiveness follows from ideal free distribution theory (IFD; Gillis et al 1993) which supposes that fishers have perfect knowledge of the scope of opportunities available at any moment and they are free to move among fisheries without cost. Under the "no lake stands out" or IFD prediction, fishery-specific effort should reflect the abundance of available fish better than the actual attractiveness or CPE (Gillis et al. 1993). IFD theory also considers information exchange among fishers to be an instantaneous process where there is generally no time lag from discovery of opportunities to effort response and exploitation. In some cases, time lags may be sufficiently short for us to be confident in this assumption. In others, however, significant delays may occur due to very short, pulse opportunities such as fish migration, spawning periods, or feeding rhythms that are difficult to access before the opportunities pass. Delayed responses can be particularly insidious because effort responses may be out of phase with actual abundance resulting in risk of over-exploitation (Botsford et al. 1983; Eswaran and Wilen 1976). For regional-scale fisheries, where a large number of opportunities exist at any moment, Hilborn (1985) suggested that an equalization of CPE assumption, i.e., IFD, is usually the best starting point.

Substituting the regional average or "no lake stands out" catch rate c_o for c_j in equation 4.4, the predicted equilibrium effort density as a function of the regional average catch rate, c_o, abundance, exchange rates, and catchability is

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$$e_j = \frac{v_1 N_j}{c_o} - \frac{v_1 + v_2}{q} \qquad (4.5).$$

That is, instantaneous fishing effort density should be a *linear* function of total fish density, and the slope of the relationship should be inversely proportional to the regional average catch rate.

To avoid the complications associated with simultaneously predicting total annual effort and age- or size-structured population dynamics, it is necessary to define the total stock at the start of the season N_j, as the fully recruited fish population

$$N_j = \sum_a v_a n_{a,j}$$

where v_a and $n_{a,j}$ are the age- or size-specific selectivity (defined in Chapter 3) and abundances, respectively and the summation is over all age/size classes in the population. Then, the decline in fish density at time t can be written as a simple function of the catch

$$\frac{dN_{j,t}}{dt} = -c_o e_{j,t} \qquad (4.6)$$

where $c_o e_{j,t}$ is the catch at time t.

Total season effort for fishery j, $E_{j,T}$, is predicted by integrating equation (4.6) over the fishing season (Appendix 2)

$$E_{j,T} = \frac{N_{j,0} - N_\infty}{c_o}(1 - e^{-v_1 T}) \qquad (4.7)$$

where $N_{j,0}$ is the initial fish density in lake j, T (yr) is the total length of the fishing season and

$$N_\infty = \frac{c_o\left(1 + \dfrac{v_2}{v_1}\right)}{q} \qquad (4.8)$$

is the *regional* minimum population density below which fishing effort will no longer be attracted. Thus, N_∞ represents a hypothetical population size at which "recreational extinction" of a fishery occurs.

Equation 4.7 provides three key predictions that can be compared directly to empirical data. (1) Effort within a season should be highest when the fishery first opens and it should decline rapidly as the season progresses. The rate at which decline occurs should be directly proportional to the initial effort response due to both depletion of the stock and the instantaneous suppression of available fish density. (2) Total annual fishing effort for the season should be a linear function of initial fish density. (3.) There should exist a lower limit to initial fish density below which fishing effort will equal zero, i.e. presence of an x-axis intercept ≥ 0 in plots of abundance versus effort. Quantitative evaluation of prediction (1.) is difficult on an individual lake-by-lake basis due to local variation in access conditions within a season. For example, recall the delays in effort responses in the study lakes that were presumed to be related to annual access conditions associated with weather. But, from a qualitative standpoint, the observed effort declines described in Chapter 2 were proportional to the magnitude of early season peaks. Predictions (2.) and (3.) are easier to assess and I do this in Chapter 5 where effort model predictions are tested against observed effort and stocking rate data. In the sections to follow, I elaborate on some other interesting predictions of the model and test their key underlying assumptions.

Effort-exploitation relationship

The limited-vulnerability model structure that I proposed for predicting angling success and effort has an interesting implication for the relationship between fishing effort and exploitation. As I will show, the model predicts an effort-exploitation relationship that has not received much attention in fisheries theory, yet it appears in actual fishery data. The basic form of the exploitation equation is

$$u = \frac{N_0 - N_T}{N_0} = 1 - \frac{N_T}{N_0}$$
(4.9)

where u is the exploitation rate, N_0 is the fish density at the start of the season and N_T is the fish density left at the season's end. The effort response model predicts that the fish numbers in the lake will decline as

$$\frac{dN_t}{dt} = -qV_t e_t = -\frac{qv_1 e_t}{v_1 + v_2 + qe_t} N_t$$
(4.10)

where the quotient represents the instantaneous fishing mortality rate, $f(t)$ at time t. Integrating (4.10) over the fishing season gives the numbers surviving the fishery as

$$N_T = N_0 e^{-F}$$

where the total fishing mortality rate, F is

$$F = \int_0^T f(t)dt = \int_0^T \frac{qv_1 e_t}{v_1 + v_2 + qe_t} dt$$
(4.11).

Evaluating the F integral is difficult analytically due to the proposed dependence of e_t on N_t. However, in many cases, it is necessary to at least show the expected relationship between total effort and exploitation regardless of how the effort was generated. Thus,

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evaluating F becomes a simple numerical exercise if the distribution of e_t over time within a season is known.

Standard fishing mortality models assume that all fish are available to the gear so that as effort increases toward infinity, F increases without limit and the exploitation rate $(u = 1\text{-}e^{-qE})$ approaches 1. Exploitation resulting from equation 4.10, on the other hand, differs from this in two aspects. First, as fishing effort increases toward infinity, the maximum exploitation rate achieved approaches the asymptotic value $(v_1 T)$ that may be much less than 1 depending on the behavioural characteristics of the fish species as well as their encounter rates with anglers (Figure 4.3), which may be more complex than the simpler mass action behaviour assumed in traditional models. Consider the case of an infinite amount of fishing effort distributed over the fishing season. If the exploitation rate is generated by removal of fish from the vulnerable pool only, then the maximum fishing mortality rate cannot be greater than the delivery rate of fish into the pool. Thus, setting the instantaneous fishing effort to large values in (4.11) gives the maximum exploitation rate as

$$u_{max} = 1 - e^{-v_1 T}$$

where T is the total length of the fishing season. This represents an important departure from traditional models, because it recognizes how exploitation can be limited by fish behaviour as represented by the rate v_1 at which fish enter the behaviourally vulnerable pool.

Second, the distribution of effort in time over the fishing season will have impacts on short-term exploitation rates, since high efforts can suppress vulnerable numbers of fish available to be captured. It is possible that higher levels of effort, if distributed in concentrated pulses over time, can actually inflict lower rates of fishing mortality than the same, or slightly lower levels of effort distributed more evenly over the season.
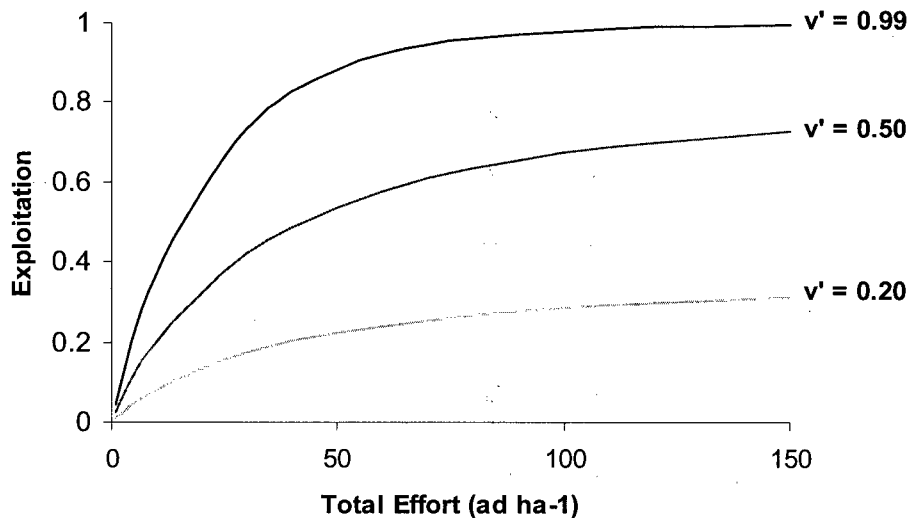
Figure 4.3. Relationship between fishing effort and exploitation for the limited vulnerability model. Catchability values were fixed at 0.07 ha ad^{-1} and the ratio $v'=v_1/(v_1+v_2)$ represent different hypotheses about the rate of movement v_1 into the vulnerable stock. High v' values indicate high vulnerability and as v' approaches 1, traditional mass-action behaviour is implied. Note how the asymptotic exploitation decreases as lower proportions of the total stock are available.

Model Analysis

Equilibrium and transient behaviour of model components

When the IFD assumptions are met, equilibrium predictions of the model will be exact; depletion of the fish stock will be accompanied by exit of anglers from the fishery, and CPE will be maintained at the regional average. The resulting equilibrium behaviour is

one of high effort during the early season followed by a smooth decline as anglers exit

the fishery in order to keep the catch rate exactly equal to c_0 (Figure 4.4).
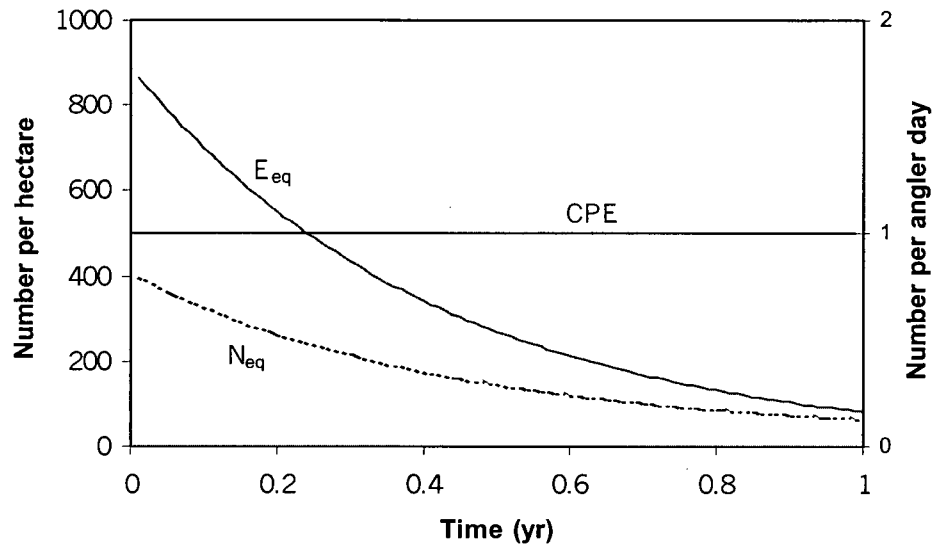
Figure 4.4. Fish abundance, fishing effort and CPE predictions for the equilibrium solution to the model equations. The time axis represents the fishing season.

In actual fishery settings, however, IFD assumptions will rarely be met, so it is necessary

to at least determine the direction and magnitude of errors that may occur if one uses the

equilibrium predictions for total annual fishing effort and exploitation where in fact there

are time lags in effort response. In the sections below, I show that the model is relatively

robust to violations of assumptions about perfect knowledge and instantaneous response.

Although the equilibrium solutions are qualitatively similar to those observed in the study

lakes, actual effort will rarely be at exact equilibrium with fish abundance. Imperfect

information, access, and motivation are just a few factors that act as limiting forces on the

rate at which anglers enter and exit a fishery when CPE is more or less attractive. In that

case, CPE may vary substantially from the regional average within a season and the actual patterns observed will depend on the time scale of effort response, which could range from days in very intense fisheries to years in some lesser known or inaccessible ones. For intensely fished systems such as B.C. small lakes, effort response time scales could be on the order of days to weeks for at least two reasons. As I described in Chapter 2 most fishing effort occurs on a small proportion of lakes, so anglers are typically intimate with conditions at those sites. Also, a large pool of potential anglers for any lake is kept informed of current conditions via weekly newspaper, radio, and internet media fishing reports and local tackle stores typically provide high quality information to active anglers. Ultimately, the combination of a large, well-informed effort pool and intimate local knowledge probably results in short time scale responses in B.C. rainbow trout lakes.

To assess effects of lags on effort response predictions, I examined the transient patterns in effort response, catch rate, and stock size that would arise under several hypotheses for the effort response time scale, which I defined as the number of days required to drive the lake-specific catch rate down from its early season maximum, to a regional average of 1.0 fish ad^{-1}. Imperfect information, represented by time lags in effort response, were included by adding the following differential equation to the system:

$$\frac{dE_t}{dt} = k(qV_t - c_o) \tag{4.12}$$

where

$$k = \begin{cases} k_g, & qV_t - c_o \geq 0 \\ k_d, & qV_t - c_o < 0 \end{cases}.$$

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Thus, k_g and k_d represent effort growth and decline rates, respectively if predicted catch rates are greater or less than c_o. Their values (e.g., $k_g = 1000$ and $k_d = 2000$) indicate the total annual increase (decrease) in effort that would occur per 1 unit change in CPE. The resulting range of effort response time-scale used was $0.05 - 0.1$ yr (9 to 22 days) to drive CPE down from the early season maximum to c_o (effort growth) and $0.32 - 1.0$ yr for effort to decline enough to bring CPE back up to c_o (effort decline) following the early CPE decline. Beyond this range, the change in errors tended become minimal and proceeding further would imply that the IFD does not apply at all. The system of differential equations (4.1, 4.2, and 4.12) were solved using a fourth-order Runge-Kutta integration scheme (Press et al. 1992) with a time step Δt of 1 day taken over a 100 day season, i.e., $\Delta t = 0.01$ yr. Note that solving 4.1 directly also implies relaxing the assumption of instantaneous equilibrium between V and $N-V$. This should lead to early-season variation in CPE if v_1 is large relative to v_2; high v_1 values imply a large vulnerable stock at the season opening and this will be translated into a higher early season CPE. Lower v_1 values imply a lower early-season vulnerable stock size causing less potential for variation in the CPE transient.

Figure 4.5 shows the transient patterns for both strong and weak effort response fisheries. The strong response case, represented by a time lag of approximately one week, exhibits a rapid build-up of fishing effort early in the season when a large pool of available fish is present. CPE drops rapidly during this phase toward the regional average and a short-term equilibrium is reached within approximately 1.5 weeks. At this point, the rate of effort build-up drops to zero and a net exit of anglers follows. The period of effort growth

however causes an over-shoot of the IFD equilibrium so CPE proceeds slowly back up toward the regional average even though effort is declining. Finally, the system approaches equilibrium near the mid-point of the season. A weaker effort response, that requires three to four weeks to drive the catch rate down to the regional target, shows very different transient patterns in both effort and CPE compared to the strong response. In this case, a similar positive effort response occurs early in the season due the large stock of available fish. However, depletion of this built-up stock is rapid due to the non-linear relationship between effort and catch rate. The slow time scale of the exit response creates a persistent over-shoot of the equilibrium effort, so the CPE decline fails to abate and exploitation remains relatively high despite low CPE. The primary difference between the weak and strong effort response dynamics is the lack of exit from the fishery as CPE declines below the regional target; "lingering" anglers cause excessive fishing effort that drives CPE further and further below the regional target and never allows a recovery. The ultimate effect is that a higher exploitation rate is generated from the slow response system compared to the fast one. This seems counter-intuitive, but it actually makes sense. If the regional average catch rate is high, then abundance must remain high
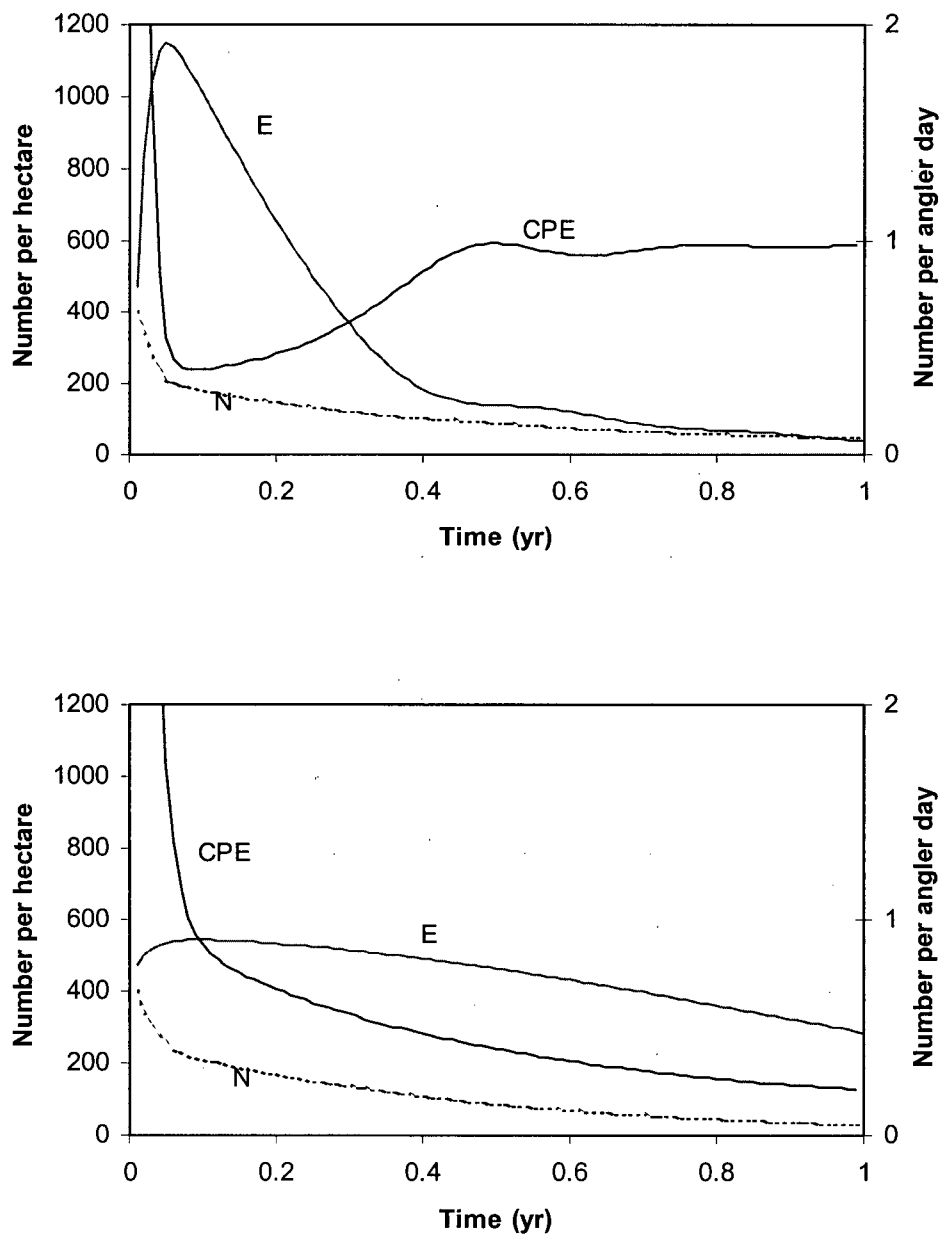
Figure 4.5. Transient patterns in abundance, fishing effort, and CPE for strong (top panel) and weak (bottom panel) effort responses. In both cases, the target CPE is equal to 1.

and anglers quit early. A fishery that responds rapidly to both increases and decreases in

abundance will drive the stock to the level that produces the regional average and will

remain near the (declining) equilibrium effort for a high proportion of the time. On the

other hand, a slow response fishery has higher initial catch rate, due to low effort, but does not respond to abundance declines and continues to exploit the stock to levels well below that required to achieve the regional average CPE. A similar result was found by Eswaran and Wilen (1976) in a study of effort dynamics in a seal fishery. They found that fisheries with rapid effort responses were safer from an exploitation perspective because dangerous overshoots of the equilibrium between effort and stock size were avoided.

Effects of transient responses on model error

To determine the magnitude of errors that result from IFD departures, I computed the relative error between equilibrium predictions and numerical solutions for total annual effort, mean CPE, and exploitation for several effort response hypotheses. I repeated the previous analysis and compared the results to IFD effort predictions based on equation 4.4. The effort calculation at each step was just the annual total from (4.4) times Δt with N_0 set to $N_t = N_{t-1} - c_o E_{t-1}$, i.e., N_{t-1} minus harvest.

Model errors that arise due to violation of IFD assumptions ranged from 2-25%, 3-28%, and 5-9% for CPE, effort, and exploitation, respectively (Table 4.1). As expected, faster effort response dynamics gave lower errors than slow responses, and a time scale of 12-14 days resulted in the most accurate effort model predictions with errors of 2-5% in CPE, effort, and exploitation. At fast time scales, CPE was overestimated and effort was underestimated by the equilibrium predictions, but errors tended to be small. Errors for fast response dynamics (positively biased exploitation) imply a short-term "mining" effect on the vulnerable stock early in the season. Modeling equation 4.1 explicitly

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assumes a disequilibrium between V and $N - V$, and vulnerable fish in excess of the equilibrium prediction $v_1 N /(v_1 + v_2)$ contribute to the overestimation of CPE and exploitation. Fast effort responses quickly drive the vulnerable stock toward the equilibrium level necessary to meet the regional average CPE, but this takes very little time. Once the vulnerable stock is reduced to the equilibrium level, the catch rate is completely controlled by the delivery rate v_1 to the vulnerable pool, and exploitation is maintained at the maximum rate implied by the equilibrium prediction $u_{max} = 1 - e^{-v_1 T}$.

At slow time scales, CPE was overestimated, and effort and exploitation were both underestimated. Larger errors in equilibrium predictions of exploitation occur due to longer-term mining of the "excess" vulnerable stock. When effort responds slowly to early season excesses caused by the disequilibrium between V and $N - V$ it causes less suppression of vulnerable fish density, and CPE remains higher for a longer period than for fast responses (Fig. 4.5). These gains in CPE are then translated directly into exploitation and the equilibrium predictions are less accurate. This result clearly shows how cumulative fishing mortality is affected by the in-season distribution of effort as described earlier (Eq. 4.11); intensive pulse fishing suppresses vulnerable fish density and cumulative fishing mortality, while more evenly distributed effort responses inflict higher exploitation rates.

Figure 4.6 shows the effects of effort growth rate, k_g (Table 4.1 data) for constant decline rate, k_d and also the ratio of decline to growth rates, k_d/k_g, on model error. It appears that relatively low effort decline rates are the main error source for CPE and effort

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predictions. The minimum errors appear due to a particular combination of growth and decline rates (decline rate double the effort growth rate) that track the disequilibrium between V and $N - V$ in a way that closely resembles the equilibrium prediction.

Table 4.1. Comparison of CPE, effort, and exploitation for equilibrium (*Equil*) and fully integrated (*Integ*) solutions to the model equations for different levels of the effort growth parameter k_g. Values under D_{co} represent the approximate number of days required to drive CPE down to the regional target $c_o=1.0$ for the effort response strength k_g. Best error performance is indicated by bold type.

k_g	D_{co}	CPE			Effort			Exploitation		
		Equil.	Integ	Error	Equil.	Integ	Error	Equil.	Integ	Error
4000	9-10	1.0	1.13	-0.12	333	310	0.08	0.84	0.88	-0.05
2000	10	1.0	1.11	-0.09	333	318	0.05	0.84	0.88	-0.05
1000	**12-14**	**1.0**	**1.03**	**-0.02**	**333**	**345**	**-0.03**	**0.84**	**0.88**	**-0.05**
500	16	1.0	0.90	0.11	333	404	-0.175	0.84	0.914	-0.08
250	18-20	1.0	0.83	0.21	333	444	-0.25	0.84	0.92	-0.09
125	22	1.0	0.80	0.25	333	460	-0.28	0.84	0.92	-0.09
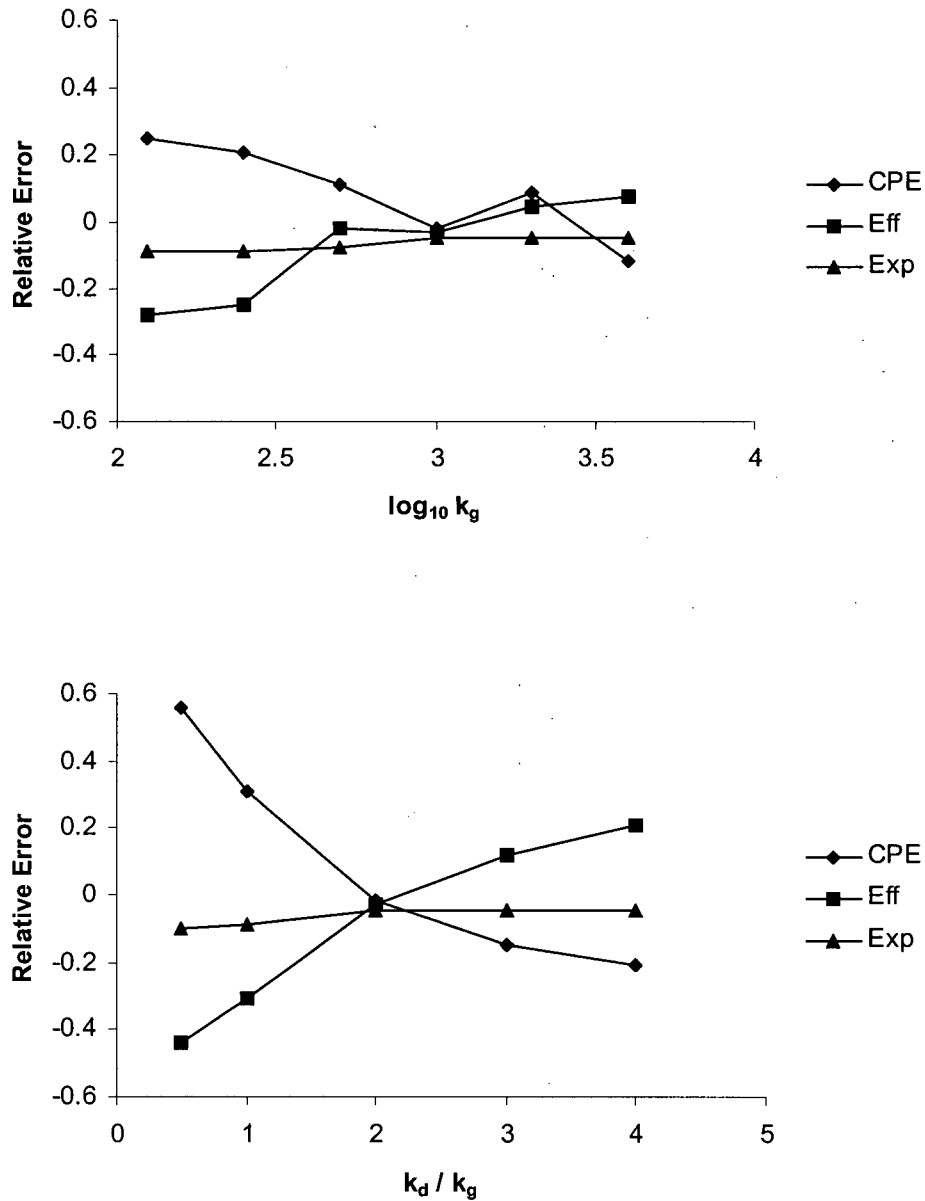
Figure 4.6 Effects of effort response parameters on accuracy of the equilibrium model predictions. Top panel shows error in relation to effort response growth rate k_g. Bottom panel shows the error for different levels of effort decline to effort growth rate ratios when effort growth is set to 1000.

Effort, CPE, and fish density in the study lakes

Comparing the model predictions to specific observations of in-season dynamics is difficult for at least two reasons. First, observed CPE is likely affected by seasonal variation in access conditions, fish activity, and vulnerability. Short-term activity changes typically occur due to changes in feeding rates, spawning, or water temperature, and these effects are functionally related to vulnerability through the exchange process (represented by v_1 in the model). As long as there is no consistent trend toward lower (or higher) vulnerability during the season, the exchange rate in the model v_1 should effectively represent the average rate at which fish become vulnerable. However, when strong seasonal patterns in activity do in fact occur, v_1 values may be fundamentally different from one season to another. For example, in some BC lakes water temperature can become so high that fish will remain at or near the thermocline (usually 5-6 m) for most daylight hours. If such physical habitat effects persist for long periods, fish may be much less vulnerable than at other times of year when they are actively feeding in shallow water during daylight hours. Comparisons between seasonal CPE patterns on high and low effort lakes should provide some insights into potential seasonal changes in exchange dynamics.

The second difficulty with comparing model predictions to data is that in-season fishing effort may have underlying traditional patterns (Lapointe 1989). For example, it is generally assumed in BC that effort will be high in May/June, but low in August (Tredger 1992). Whether or not such observed patterns are due to the effort response dynamics described here, or are simply due to traditional patterns is not clear, because most of the

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observed data in Tredger's analyses were obtained from high effort fisheries where the two effects cannot be separated.

Acknowledging these potential difficulties, I made some qualitative comparisons between the model predictions described above and those observed on BC rainbow trout lakes. Figure 4.7 shows the effort, CPE, and fish density dynamics on the study lakes for all lake-years in which mark-recapture estimates of fish density were available. While the effort responses on limited-access lakes are not expected to be comparable to open-access lakes, the patterns in CPE and fish density are interesting, because they show either very limited numbers of vulnerable fish, or the type of seasonal changes in exchange rates described above. In both lakes, total stock depletion is not particularly strong, yet CPE declined sharply during mid-season. Both lakes are very shallow and have limited amounts of deep water habitat and fishable water between 2 - 5 m depth; most of the lake area is very shallow (<1.5 m) and fish are usually not observed in these areas even when water temperature is considered high quality (8 – 12° C). Thus, anglers must access a very limited stock of vulnerable fish as they move into and out of deeper water. In the spring, these areas would be subject to short-term depletion of vulnerable fish, but in the summer, lower movement rates between deep and shallow water may also serve as an additional limit to the total vulnerable stock. This process likely occurs on other lakes as well, but it is particularly evident on limited-access lakes where depletion is not severe.

As mentioned in Chapter 2, effort on open-access lakes was typically low in the early May followed by a peak in June and then a slow decline over the July-August period. A

slow build-up of effort during the early season suggests an effort response much like the slow time scale response described above. CPE in some cases remained high during the initial phase, and did not decline until after the effort peak when total stock depletion was most rapid. Crystal lake showed a very slow effort response and little effect of depletion on CPE during 1997 compared to 1998 when abundance and early season angler effort were higher. This suggests that the effort response may have flipped from slow to fast. Roche lake appears to have the strongest effort response, which was repeated in both years. CPE in Roche remained between 1 and 2 fish ad^{-1} in both years despite strong variation in effort, suggesting the type of IFD behaviour used in the model. In almost all lakes, there appears to be an excess of vulnerable fish leading up to the initial effort peak, after which declines in effort are proportional to declines in total fish density. Again, this implies that intensive fishing effort drives the vulnerable stock to an equilibrium level.

Figure 4.7. Monthly effort (E), total catch rate (CPE), and fish density (N) in the study lakes for all years in which mark-recapture estimates of total fish abundance were available.
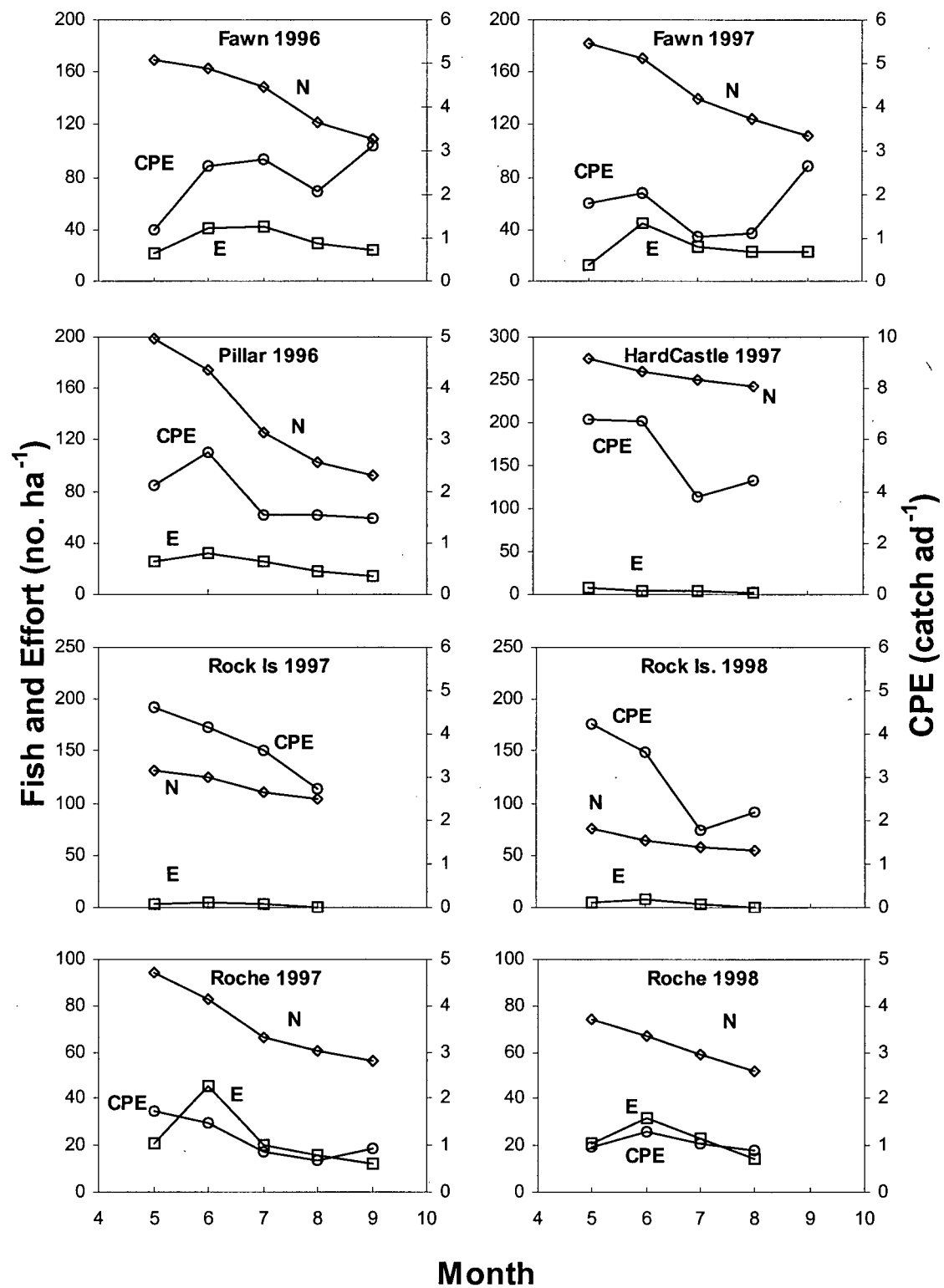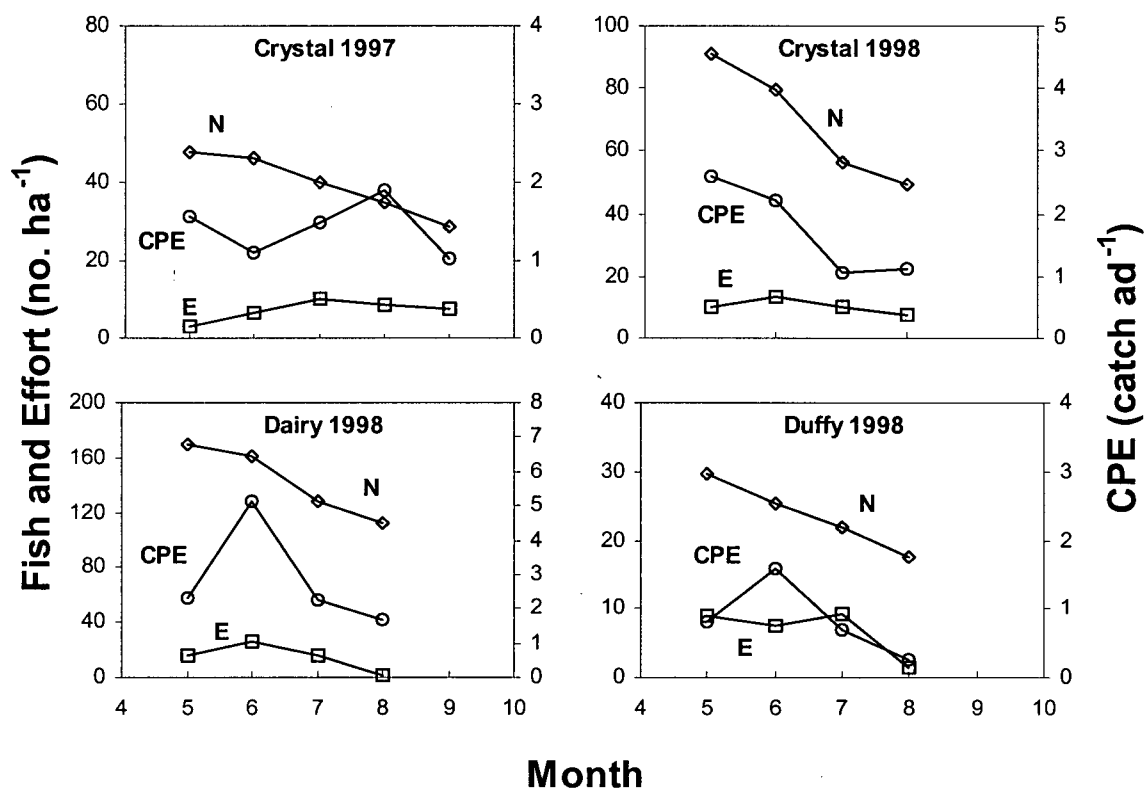
Figure 4.7 continued.

Discussion

My goal in this chapter was to develop a framework for recreational fishery models that
includes fish behaviour and angler effort responses as key components. Using a minimum
number of assumptions, I derived several models for the relationships between fish
abundance, effort, exploitation, and angling quality. These relationships can advance our
understanding of recreational fishery dynamics and when applied to management
problems, they should provide more realistic assessments of the range of potential
outcomes that could result from management actions. The simplicity of the models retain

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the essential link between prediction and understanding that is critical to any scientific advance.

Three basic predictions are implied by the angling success, effort, and exploitation models: (*i.*) effort responds linearly to initial fish abundance, (*ii.*) angling success is strongly suppressed by fishing effort, and (*iii.*) exploitation rate increases with increasing effort to an asymptotic value ≤ 1.0. All of these models are based on simple equilibrium calculations that are relatively robust to moderate deviations from equilibrium assumptions. Tests of the IFD assumptions are done in more detail in Chapter 6 where I fit a complete model to observed distributions of fishing effort on B.C. lakes. In the following section, I discuss the implications of predictions (*ii.*) and (*iii.*) above for expected relationships between effort, exploitation, and catchability. Exploitation and catchability are chosen because they provide important contrasts between the predictions outlined above and current fisheries theory.

Density-dependent catchability in recreational fisheries: are we looking in the right place?

Catchability is probably the most ubiquitous model parameter in recreational and commercial fisheries assessments. It provides the link between a CPE index, or angling quality and underlying fish abundance and, when its value is assumed to be constant, it is the only parameter used to describe the relationship between fishing effort and exploitation. As important as it may seem that we know its value with certainty, catchability is one of the least understood properties of fish populations for two reasons.

First, catchability is a product of interactions between fish and fishers which may be influenced by fish behaviour, distribution, and vulnerability. Each of these component factors may itself be a function of others, i.e., prey/predator regimes, climate cycles, or population abundance. The second difficulty in studying catchability is that values are often estimated from noisy data. While statistical errors may not be critical, the fact that they may be large enough to disguise important shifts or trends is disturbing. The ability to predict changes in catchability, or at least define it within a reasonable range, is an important task in any fisheries research program.

Population abundance is usually an important factor that influences catchability in both commercial (Csirke 1989) and recreational fisheries (Shuter et al. 1998). Existing theories suggest a non-linear, decreasing function of fish abundance of the form (c.f. Shuter et al 1998 for discussions as to why this is so)

$$q = \frac{q_0}{1 + q_1 N} \qquad\qquad (4.13).$$

Recent studies of Ontario lake trout fisheries (Shuter et al. 1998) show that this model fits catchability and abundance data very well; however, here I argue that in open-access fisheries, such as Ontario lakes, such a result may imply a very different phenomenon.

In deriving the catch success model, I proposed that CPE is a function of angler effort, as well as fish abundance. This functional relationship arises at the base, "instantaneous", level as each fisher limits the number of fish that are available to surrounding and subsequent fishers. As angler effort gets very large, the standing stock of available fish is reduced to nearly zero and catch success becomes strongly controlled by fish behaviours

that expose them to capture. The model then predicts that *apparent* catchability measured as a function of the total stock, i.e., $q = C/EN$ (where abundance is measured as the total stock N in the schematic diagram shown earlier; Fig. 4.1), will decrease as fish abundance increases. When effort is linearly related to fish abundance according to the IFD effort model with constant CPE, i.e., CPE = c_0, the standard catchability formula becomes

$$q = \frac{C}{EN_0} = \frac{c_o}{N_0}.$$

Thus, catchability plotted as a function of total abundance will appear to decrease in a $1/x$ type fashion. Density-dependent catchability in recreational fisheries was suspected in Ontario lakes where (Shuter et al. 1998) argued that it probably arises due to interference among fishers when competing for patchily distributed fish schools. Other explanations for the inverse relationship between catchability and abundance include gear saturation, handling time increases at high abundance, reduction in range area occupied by a fish stock (Hutchings 1996), or reformation of fish schools following depletion (Csirke 1989). However, it is not clear that recreational fisheries should exhibit gear saturation and handling effects that typically cause catchability to decrease with increasing abundance especially where catch rates of 1 fish ad^{-1}, or less, are common. Instead, negative relationships between catchability and abundance suggest the type of model structure described in this paper: a linear response of angler effort to fish abundance, a non-linear decrease in numbers of available fish as effort increases, and an asymptotic fishing mortality as effort and abundance get large.

To compare the two theories, I fit the limited-vulnerability model described above to effort and exploitation rate data for B.C. rainbow trout lakes to obtain estimates of the exchange rates v_1, v_2, and the catchability coefficient, q. I then used these estimates along with abundance data published in Shuter et al. (1998) to predict effort, exploitation, and catchability on their Ontario lakes.

For the B.C. lakes, I used the exploitation model

$$\hat{u} = \int_0^T \frac{v_1 q e_t}{v_1 + v_2 + q e_t}$$

which I integrated numerically over the effort observations, e_t in time to account for the instantaneous suppression of catch rates by high effort peaks during the season. Note in this equation that estimates of the catchability coefficient will be correlated with v_1 and v_2 values. Information about q should be best at low effort density where the effects of effort suppression of catch rates are minimal, i.e., proportion of the stock vulnerable roughly equal to $v_1/(v_1+v_2)$. For low effort, similar exploitation rates may be generated by either high v_1 (large proportional vulnerable) and low q, or low v_1 and high q. However, recall that the maximum rate of exploitation, $u_{max} = 1-e^{-v_1 T}$, is independent of q. I estimated u_{max} by eye from the effort-exploitation relationship on the study lakes and set $v_1 = -\ln(1-u_{max})$. This removes some of the uncertainty associated with the correlation, but the effect of v_2 remains. The parameters v_2 and q were then estimated by minimizing the sum of squares between observed and predicted u values (Microsoft Excel 8.0, Solver Function).

The resulting fit shown in Figure 4.8. Note that the solid curve is computed for an average effort distribution over time and the predictions based on lake-specific effort

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patterns are more accurate. Exploitation rates increased rather abruptly with small increases in effort in the range $0 - 50$ ad ha^{-1}. Beyond that range, exploitation clearly appears to approach an asymptote. Estimates of v_1, v_2, and q were 1.6 yr^{-1}, 1.5 yr^{-1}, and 0.0743 ha ad^{-1}, respectively and the implied value of u_{max} was 0.79.

Deviations from the predicted exploitation rates were relatively homogeneous over all levels of exploitation, and they probably arise from minor differences among lakes in catchability and exchange process parameters as well as a rough (15 d) numerical integration interval of F. Variation in catchabilities could occur due to differences in regulation among lakes; however these differences were probably minor because most lakes had liberal bag limits (5 or 6 fish per angler day) which were rarely achieved. Only one lake was regulated with a restricted bag limit (2-fish per angler day) and the observed exploitation did not appear as an outlier, although it was less than expected on the basis of the model. At high effort levels, catch success is typically so low that few anglers actually catch a limit of trout even in the restricted bag limit lake. Therefore, small bag limit changes are not expected to cause strong departures from the exploitation predictions.
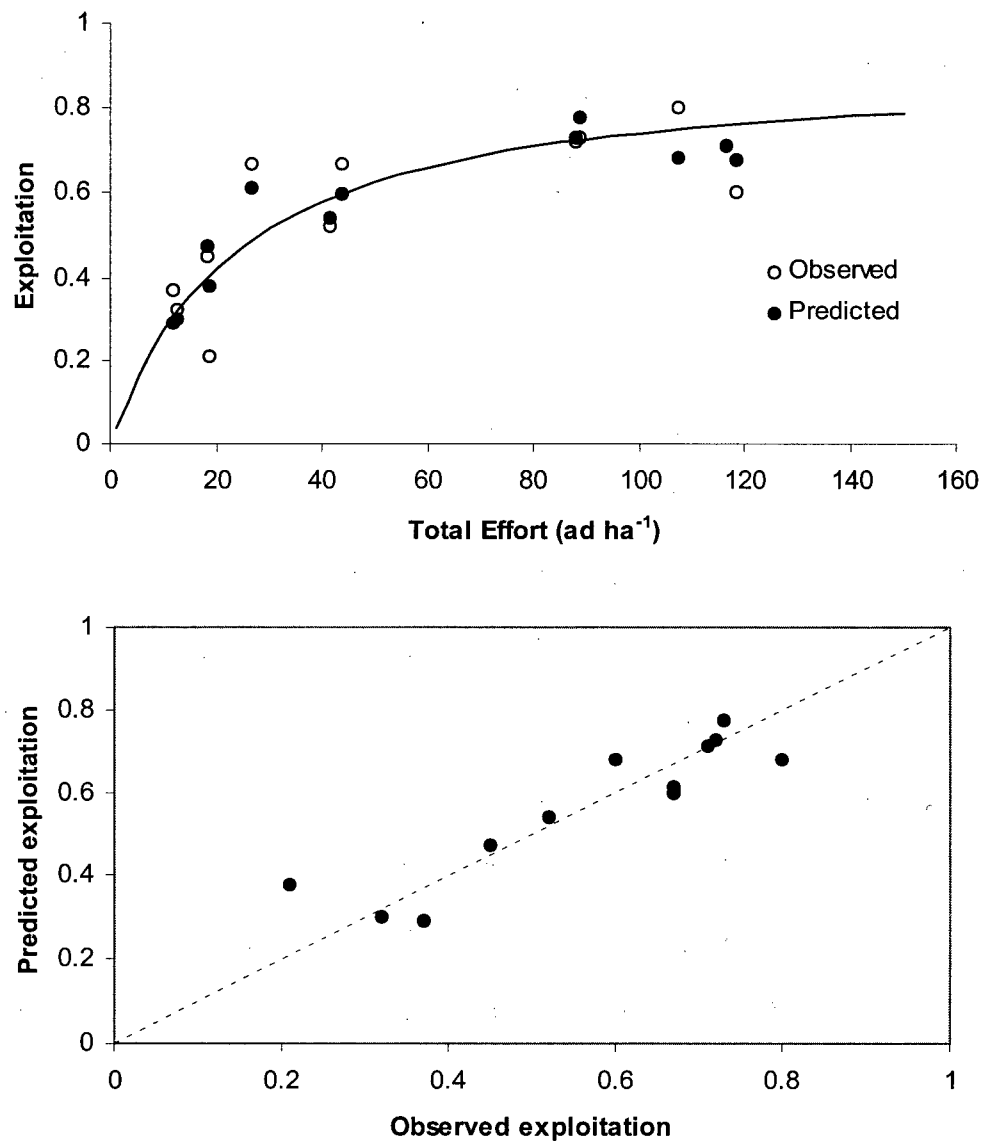
Figure 4.8. Relationship between fishing effort and exploitation for the study lakes. The top panel shows observations (open circles), predicted values (closed circles) using lake-specific time distributions of effort, and an average relationship using the mean effort distribution over time. The bottom panel compares the actual lake-specific predictions and observations.

Figure 4.9 shows the emergent relationship when apparent catchability is plotted against

total fish abundance estimated from mark-recapture. When fish are assumed to be fully

vulnerable at all times, i.e., $q = C/EN$, the pattern appears to be density-dependent.

However, for lakes where effort is limited due to access constraints, effort is largely

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independent of abundance and catchability does not appear to change at all (open circles in fig. 4.8). This difference between limited- and open-access lakes is exactly as predicted by the limited vulnerability model, but not by models based on assuming that q decreases with increasing N because of distribution changes or handling time effects.
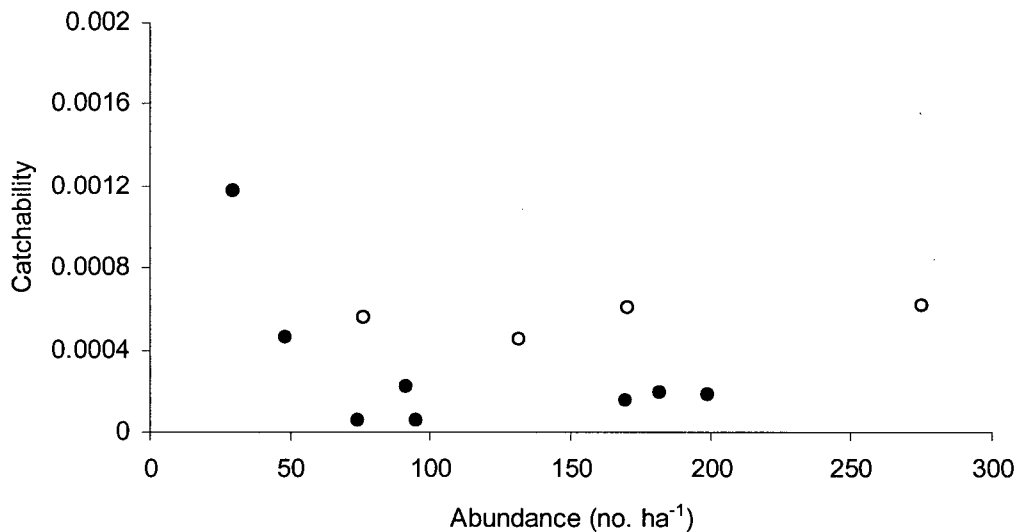
Figure 4.9. Apparent density-dependent catchability for B.C. rainbow trout lakes. Closed circle values are for open-access lakes and open circles are values from limited-access lakes. The high data point at approximately 165 fish ha^{-1} is for Dairy lake where effort is particularly low due to a difficult access road.

The observed asymptotic relationship between exploitation rate and fishing effort can also be explained by a model that assumes no effort response or vulnerable fish pool, but accumulation of released fish in an invulnerable recovery pool for at least the season of capture. This alternative model can be represented by the seasonal decay/accumulation equations

$$\frac{dN}{dt} = -rqE(N - R)$$

$$\frac{dR}{dt} = (1 - r)qE(N - R)$$

where N is total fish alive, R is the number of fish that have been captured and released, assuming these fish remain invulnerable for the remainder of the season, r is the retention rate, and E is mean seasonal effort density. The solution to these differential equations over season length T, starting with $R = 0$ and $N = N_0$ is just

$$N(T) = (1 - r)N_0 + rN_0 e^{(-qET)}$$

$$R(T) = (1 - r)N_0 (1 - e^{(-qET)})$$

For this model, the predicted asymptotic exploitation rate ($U = 1 - N(T)/N_0$) as effort E increases is just the retention rate r. Retention rate for fully vulnerable fish in the study lakes is on order 0.7 which is close to the estimated asymptotic U predicted by the limited vulnerability/effort response model. However, we know that this model is incorrect on at least two counts: (*i.*) fish do not remain in a recovery pool for the whole season, as evidenced by good tag recoveries of fish tagged by angling at the beginning of the season; (*ii.*) this model does not predict the observed apparent density dependence in q (decrease in C/EN_0 with increasing N_0) since exploitation rate C/N_0 is predicted to be just $r[1 - \exp(-qET)]$ which is independent of N_0.

For the Ontario lake trout data, I fit the effort model to abundance and catchability values published in Shuter et al (1998) by (*i.*) predicting effort from the abundance estimates assuming $v_1 = 1.6$, $v_2 = 1.5$, $N_\infty = 0.06$ ha^{-1} (which is well below the minimum lake trout densities in their data) and while allowing c_0 to vary freely, (*ii.*) calculating numbers of fish remaining at the end of the year using $N_{end} = N_\infty + (N_0 - N_\infty)e^{-v_1}$, and (*iii.*)

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calculating apparent q as $(N_0-N_{end})/EN$ as in Shuter et al. Note that calculating N_{end} this way ignores some of the in-season variation in exploitation due to the distribution of effort over time. As mentioned earlier, the effects of strong seasonality will reduce exploitation slightly for fixed effort and will ultimately make the apparent density-dependence in q stronger. The only parameter used to fit the data was c_o, and I minimized the sum of squares between observed and predicted q's (Microsoft Excel 8.0, Solver function).

The general form of the two catchability models predicted a strong decline with increasing fish abundance. However, the log-likelihood ratio (2.16) revealed that the limited vulnerability/effort model fit the data more than twice as well as the original hyperbolic model of Shuter et al. (Fig. 4.10). The final estimate of c_o was 0.17 fish ad^{-1} which was within the range of catch rate values published for Lake Opeongo lake trout (Shuter et al 1987). Catchability predictions from the limited vulnerability/effort model fit tended to i.) be higher at very low abundance, ii.) drop more quickly as abundance increased, and iii.) approach a lower limit for high lake trout abundance.

The key difference between the limited vulnerability/effort response model structure and traditional density-dependent theory lies in predictions about exploitation at low stock size. The density-dependent catchability model predicts that exploitation at low abundance will be depensatory, i.e., exploitation rate actually increases as abundance decreases, and the risk of total stock collapse at low abundance is high. Depensatory exploitation has likely been involved in collapses of both Atlantic cod (*Gadus morhua*;

Hutchings and Myers 1994) and Peruvian anchovetta (*Engraulis ringens*; Csirke 1989) due to range contraction and reformation of fish schools following depletion. The limited vulnerability model, which is probably more applicable to non-schooling fish, predicts that exploitation at low abundance is just proportional to effort without a depensatory response. In addition, fishing effort is expected to decline at low stock size, so the risk of stock collapse should be lower.

Although a complete test of the model would require the Ontario effort data, it appears that the model I describe presents an alternative view of density-dependent catchability. Further, it suggests a completely different approach for detecting density-dependent effects in regional fisheries data.
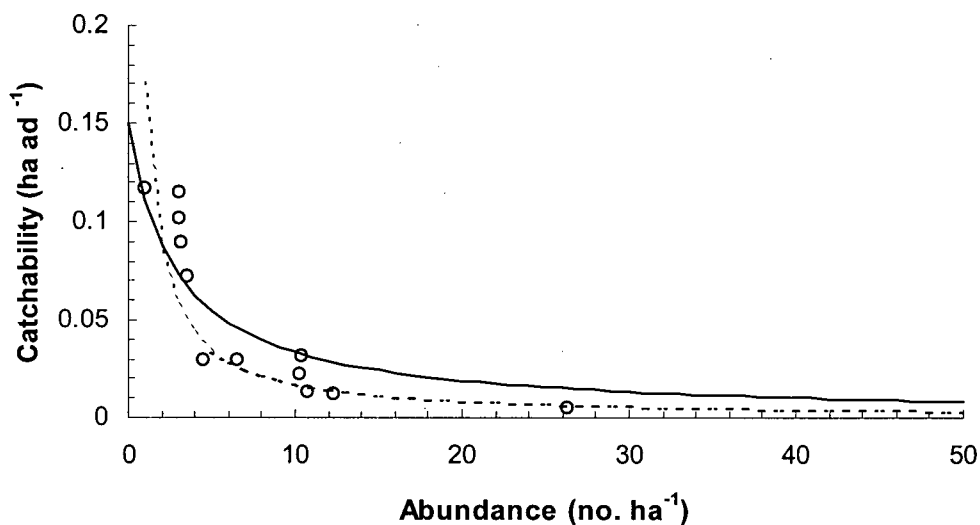
Figure 4.10. Relationship between catchability and fish abundance for the Shuter et al (1998) lake trout data. Solid line is the published hyperbolic model fit and the dashed line is the fit using the limited vulnerability/effort model.

Chapter 5: Combining angler effort responses with age-structured models for recreational fisheries assessment

Introduction

Although there is a substantial literature on recreational fisheries modeling and assessment, very few studies attempt to include angler effort responses and behavioural/spatial vulnerability as key components. In this chapter, I show how empirical data may be used to parameterize effort models which may then be applied in the context of traditional equilibrium age-structured analyses. Effort model predictions described earlier are first compared to observed effort responses on hatchery stocked rainbow trout lakes in British Columbia's southern interior. Results from the effort analysis are then used in an equilibrium age-structured model of rainbow trout population dynamics in order to assess the impacts of potential angler effort responses and supplemental hatchery stocking on unproductive wild-stock lakes.

Methods

BC rainbow trout fisheries data

British Columbia's southern interior lakes are divided into three management regions. Regions 3 (Thompson-Nicola) and 8 (Okanagan) are easily accessible (2.5 to 5 hours by vehicle) from Vancouver which is the source of most small lake fishing effort. Region 5 (Cariboo-Chilcotin) is 5-7 hours by vehicle from Vancouver, and is the most remote.

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Access to lakes within regions varies mainly by mode of transportation (four-wheel drive, two-wheel drive, walk, boat, and air) and level of shoreline development.

Within these three regions, over 1800 lakes (Ashley et al. 1992) are stocked annually with juvenile (age-0 to age 1+) rainbow trout by the B.C. Ministry of Fisheries (B.C. Fisheries). The effort response analysis was restricted to these stocked lakes because they provided reasonably reliable estimates of initial fish density and most small lake fishing effort is concentrated on them. I used the average number stocked per hectare between 1986 and 1990 as a fish density index. The analysis was further restricted to "small" lakes with surface area less than 500 ha and for which there were total shoal area measurements (surface area where depth < 7 m). Fish stocking densities were calculated on the basis of total shoal area for two reasons: (1.) most angler effort is exerted along the edges or within the shoals, and (2.) the use of shoal area adds a realistic spatial component to the limited vulnerability model structure. The total numbers of lakes meeting these criteria were 36, 21, and 17 in regions 3, 5, and 8, respectively.

During the 1980's, B.C. Fisheries estimated annual fishing effort on lakes in each region using aerial boat count surveys (Tredger 1992). In all regions, fishing effort was usually concentrated on the most easily accessible lakes. For example, in region 3 (1.5 million ad total effort) and region 8 (.8 million ad total effort) 50-60% of total fishing effort was concentrated on only 35% of the lakes (B. Chan, B.C. Ministry of Environment, Lands, and Parks, Kamloops, B.C., pers. comm.). Fishing effort in region 5 (0.5 million ad total effort) was even more concentrated with over 90% of effort occurring on 35% of lakes

Berezay and Lirette (1997). Average effort densities (based on shoal area) from 1986 to 1990 were used as an effort index for the above hatchery stocked lakes.

Regional effort response model analysis

The model described in Chapter 4 for relating fish abundance to angler effort predicts that (*i.*) seasonal total angler effort is linearly proportional to total initial fish density and (*ii.*) at some low abundance value greater than zero, effort declines to zero. Thus, effort-abundance relationships were assessed by fitting the following linear model to angler effort data from each management region

$$\hat{E}_j = b_o + b_1 N_j \tag{5.1}$$

where N_j is the stocking density in lake j, and the parameters b_0 and b_1 are defined in terms of the limited-vulnerability/effort response model parameters as

$$
\begin{aligned}
b_o &= -b_1 N_\infty = \frac{u_{max}}{q}(1 + v_2/v_1) \\
b_1 &= \frac{u_{max}}{c_o}
\end{aligned}
\tag{5.2.}
$$

This model assumes that IFD catch rates (c_0) are constant within regions, but may vary among regions due to regional differences in average access conditions. Note that b_0 is predicted to be independent of regional c_0, while the slope b_1 should vary with c_0. After performing regressions independently on the data from each region, differences among regions in the effort response slopes and intercepts were assessed using analysis of covariance (Zar 1984). Where regions were found to have similar slopes or intercepts, I used the average within-region regression coefficients as the pooled estimate. Final estimates of the regression coefficients were transformed into effort response model

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parameters N_∞ and c_0 along with their standard errors by rearrangement of (5.2) using the estimates of u_{max}, v_1, v_2, and q from Chapter 4.

Application of the limited vulnerability/effort model to age-structured assessments

Age-structured population models are widely accepted and used in fisheries stock assessment (Hilborn and Walters 1992). Typical applications in recreational fisheries involve treating fishing mortality (Shuter et al 1998; Goodyear 1984), size-limits (Goodyear 1984; Richards and Rago 1999), and effort (Engstrom-Heg 1986) as leading (i.e., forcing or known) variables and assessing the effects of these on equilibrium stock size, yield and recruitment. No applications to date treat fishing mortality or effort as a function of equilibrium stock size. Including the dynamic response of anglers is not an easy task and this is likely the reason why research has not progressed on this topic. Equilibrium analyses still require leading variables, and in the section below I show how angler expectations (IFD catch rate, c_o) may be treated as such to assess how they affect effort and sustainability of recreational fisheries. Formulated in this way, the model should provide more realistic assessments of changes in response variables given observed catch rates and access conditions. In Chapter 6, I show that values of c_0 in B.C.'s rainbow trout lakes are associated with access or travel time from major human population centres. Thus, the age-structured model can then have applications in situations where access control policies are seen as the only way to facilitate stock rebuilding or maintenance of angling quality.

Botsford (1981) gives the equilibrium age-structured model predictions for survivorship (l_a), eggs-per-recruit (ϕ_e), adults-per-recruit (ϕ_a), recruitment (R), total egg production (E), and numbers (N) in a fishery where recruitment follows a Beverton-Holt relationship between egg production and age 2+ recruits as

$$l_a = \prod_{i=k}^{a} s^{i-1}(1-v_iU)^{i-1} \qquad \text{(survivorship to age } a \geq k)$$

$$\phi_e = \sum_a l_a f_a \qquad \text{(egg production per recruit)}$$

$$\phi_a = \sum_a l_a v_a \qquad \text{(survival per recruit)}$$

$$R = \frac{\alpha_{max}\phi_e - 1}{\beta\phi_e} \qquad \text{(mean age } k \text{ recruitment)}$$

$$E = R\phi_e \qquad \text{(mean annual egg production)}$$

$$N = R\phi_a \qquad \text{(mean } vulnerable \text{ population)}$$

where k is the age at recruitment, s is the adult survival ($s = e^{-M}$), v_i is vulnerability at age i, U is the fully vulnerable exploitation rate, f_a is fecundity at age a, and α_{max} (maximum survival at low stock size) and β (scale) are Beverton-Holt stock-recruit parameters. For a fixed value of α_{max} this leaves β as the only unknown parameter which can be found by solving the recruitment equation if an additional assumption is made about unfished recruitment R_0. Given an equilibrium harvest rate and unfished recruitment, (U, R_0), the above set of equations predict total vulnerable population size (N), minimum stock sizes (N_∞), c_0, effort, catch, and recruitment. This prediction normally proceeds as follows. First, the harvest rate is used to compute ϕ_e and ϕ_a which

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are then used to give R and N. Once N is known, N_∞ may be calculated by rearrangement of the exploitation formula (ignoring in-season effects)

$$U = (1 - N_\infty / N)u_{max} \tag{5.4}$$

giving

$$N_\infty = N(1 - U / u_{max}) \tag{5.5}$$

where u_{max} is the maximum exploitation rate ($1-e^{-v1}$; 0.80) from Chapter 4 assuming limited vulnerability applies. Also recall from Chapter 4 that N_∞ is

$$N_\infty = \frac{c_o(1 + v_2 / v_1)}{q} \tag{5.6}.$$

With N_∞ now predicted from 5.5, Eq. 5.6 can be rearranged to give apparent c_o which is just

$$c_o = \frac{N_\infty q}{1 + v_2 / v_1} \tag{5.7}.$$

Effort and catch are then calculated using

$$E = \frac{(N - N_\infty)u_{max}}{c_o} \tag{5.8}$$
$$C = UN$$

The model is now completely specified and it will show the equilibrium relationship between effort, catch, and recruitment as a function of potential changes in c_o if c_o is now treated as the leading parameter rather than U. This is not a circular argument; rather, it simply involves using U as a convenient lead for calculating the equilibrium relationships between c_o, N, and R. c_o cannot be used as a leading parameter because it depends on N_∞, which cannot be calculated until U is specified.

The method is applied here using life history parameters from Rock Island lake (55 ha) and a four-fold range of α_{max} values. For each α_{max}, unfished age 2 recruitment R_o was varied until the catch rate, total harvest, and effort at an exploitation rate of 0.31 (current estimate) approximately matched the average values observed at Rock Island from 1996-1998.

Results

Effort response

The observed effort response appeared linear in all three regions (Fig. 5.1) and all regional estimates of the effort response slopes were significantly greater than zero (Table 5.1). Variation around the mean effort response was largest for Region 3, which also showed a high number of positive residuals at the lower range of abundance values. There are two possible explanations for this. First, much of the variation in effort response is probably due to lake-specific differences in access that I did not include in the analysis. Accounting for these effects within regions could be included in the model by weighting each fishery's attractiveness by additional criteria such as access cost or travel time from major population centres. This problem is addressed further in Chapter 6. A second possibility is that expected catch rates, c_o, on low density lakes are systematically lower than for high density lakes. Lakes stocked at low density are typically managed to produce trophy-sized rainbow trout and these larger fish could attract a disproportionate amount of effort. These situations likely require a more comprehensive "total angling quality" index that reflects access cost, CPUE, and average fish size.

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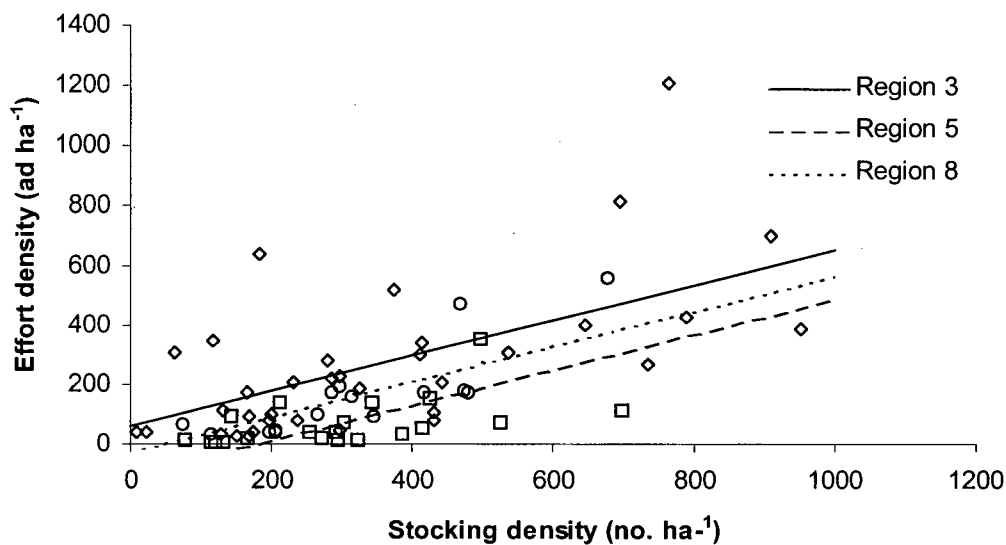
Figure 5.1. Relationships between stocking density and fishing effort for Region 3 (diamonds, solid line), Region 5 (squares, heavy dashed line), and Region 8 (circles, light dashed line). Regression lines are computed using a pooled slope and regional intercepts. Both density measures are based on lake shoal area.

Differences in effort response slopes were expected to be greatest between Regions 3, 8 versus Region 5 because of the relative inaccessibility of region 5. Recall that an access gradient exists in B.C. rainbow trout lakes such that Regions 3 and 8 are more easily accessible than Region 5, so effort should be more responsive to changes in stocking rates in these regions. Analysis of covariance, however, revealed that slope values did not differ significantly among the three regions (F-test, $F_{0.05} = 1.56$, df $= 1, 64$, $P > 0.05$). This is likely due to a marginally significant slope for region 5 combined with very similar values for regions 3 and 8, thus the ANCOVA could not detect any differences among regions.

Intercept values were significantly different among regions (ANCOVA, F-test, $F_{0.05} = 4.19$, df $= 1, 64$, $P < 0.05$), whereas the model predicts similar intercepts (but different

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slopes). That is, N_∞ appears to vary among regions as expected due to variations in c_o, despite the lack of evidence of the c_o effect on b_1. Multiple comparisons among intercepts showed that only Regions 3 and 5 were significantly different from one another (Tukey q-test, $q = 5.28$, df = 64, 3, $P < 0.05$).

Table 5.1. Results of effort response model fits to fishing effort and rainbow trout density data from three management regions in British Columbia. Independent estimates of intercepts (b_0) , slopes (b_1), coefficients of determination, r^2, and number of lakes used, n, are based on region-specific linear regressions of fishing effort on fish density. Standard errors appear below each estimate. Statistically significant regression F-statistics calculated for $F_{(0.05, 1, n-2)}$ appear in bold type. Pooled value is the average within-region regression slope following analysis of covariance. Model estimates are the regression estimates transformed into effort response model parameters c_0 and N_∞.

| Region | Independent regression statistics | | | | | Model | |
	n	b_0	b_1	F	r^2	c_0	N_∞
3	36	39.9	0.64	**21.6**	0.39	1.24	-62.0
		(55.9)	(0.13)			(0.25)	(87.6)
5	21	-7.2	0.25	**5.7**	0.24	3.09	27.7
		(31.1)	(0.94)			(1.17)	(120.3)
8	17	-71.3	0.73	**22.6**	0.54	1.10	97.6
		(44.2)	(0.13)			(0.19)	(62.9)
Pooled	74	-	0.59			1.35	-

	Pooled regression statistics			Model	
3	59.0	0.59		1.35	-99.8
5	-106.5	0.59		1.35	180.2
8	-25.7	0.59		1.35	43.5

The lower abundance limits for an effort response, N_∞ , inferred from the adjusted intercept values were greater than zero in Regions 5 and 8 (Table 5.1), but less than zero in Region 3. Again, large positive residuals at low stocking density probably contributed to this. In general, intercept values tended to increase (N_∞ decrease) as average fish abundance increased from 293, 299, to 327 ha^{-1} in Regions 3, 5, and 8 respectively;

however the estimates were highly uncertain and encompassed a narrow range, so

potential effects of density-dependent catchability could not be assessed.

Effects of c_0 on equilibrium stock size, yield, and recruitment

Table 5.2 gives the biological parameters used in the age-structured assessment for Rock

Island lake rainbow trout. The values for survivorship, numbers, and spawner numbers

were calculated with no fishing, and egg production is based on the linear fecundity-body

length relationship presented in Chapter 3. Although a small proportion of age 2 females

were shown to be mature in Chapter 3, I assumed that these fish contribute very little to

total egg production.

Table 5.2. Biological parameters for the rainbow trout population in Rock Island lake under no fishing. Annual survival is assumed constant for all age 2 and older fish, maturity is the proportion of mature females, and egg production is based on a linear fecundity-body length relationship. Total egg production is the expected lifetime fecundity per recruit. Numbers-at-age and spawner numbers-at-age are calculated based on an unfished age 2 recruitment of 69 ha^{-1} ($N_2 = 3795$; see Table 5.3).

	Age						
	2	3	4	5	6	7	Total
Survival	0.63	0.63	0.63	0.63	0.63	.63	
Length (mm)	137.7	237.8	310.4	363.1	401.4	429.3	
Vulnerability	0.5	1	1	1	1	1	
Survivorship	1	0.63	0.39	0.25	0.16	.08	
Maturity	0	0.37	0.50	0.50	0.50	.5	
Eggs	0	325	349	249	168	109	1202
Numbers(ha^{-1})	69.0	42.1	25.7	15.7	9.6	5.8	167.8
Spawners(ha^{-1})	0	15.6	12.8	7.8	4.8	2.9	43.9

Figure 5.2 presents equilibrium abundance-effort relationships for the Rock Island lake

data, for α_{max} values over the range 0.002 – 0.005. These values represent the range of

compensatory improvement in survival at low stock size from 2 to 5 times the unfished

state (assumed 0.001) suggested by Myers et al. (1999).
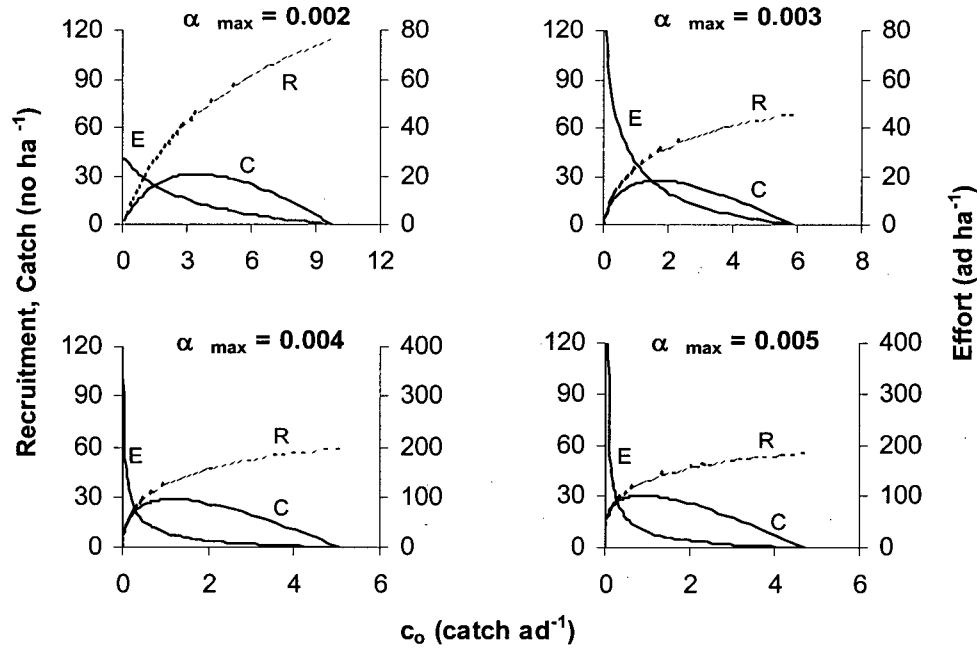
Figure 5.2. Equilibrium relationships among IFD catch rate (c_o), recruitment, catch, and angler effort. Note changes in both effort and catch rate scales for different α_{max} values.

Note that c_o in Figure 5.2 represents the catch rate expressed in terms of harvest per effort

(HPE), not total catch per effort (CPE). For each curve, the x-axis shows the equilibrium

catch rate which, in combination with abundance, drives the effort. The resulting pattern

shows lower catches to the left of MSY (maximum level of catch) that occur due to

recruitment over-fishing when c_o is low (high effect even when N is low), while lower

catches to the right of MSY are due to low effort when c_o is high (effect low even at high

N).

These results suggest that serious recruitment over-fishing is possible for α_{max} values of 0.002 and 0.003, given base catch rates co typical of B.C. small lakes with good access. At IFD catch rates in the range (0, 1.07 fish ad^{-1}) and (0, 0.85 fish ad^{-1}), respectively, recruitment is reduced to 0-50% of virgin levels for fishing effort in the range (25.4 - 18.9 ad ha^{-1}) and (94.5 - 28.4 ad ha^{-1}). For low productivity stocks, such a narrow range over which the stock is driven low enough to cause a recruitment effect is disturbing. The effort level at MSY for α_{max} = 0.002 and α_{max} = 0.003 are 9.12 ad ha^{-1} and 15.94 ad ha^{-1}, respectively (Table 5.2), which represent extremely low effort compared to the observed efforts on accessible B.C. lakes (Chapter 2, Fig. 2.1). Thus, the potential to seriously over-fish rainbow trout stocks exists in B.C. and it is likely that difficulty of access (high c_o) is the only reason that any unproductive natural populations are not recruitment over-fished.

For more productive populations, represented by α_{max} values of 0.004 and 0.005, recruitment over-fishing is more difficult, primarily due to the constraint on exploitation generated by the imposed limited vulnerability model structure. At these α_{max} values, exploitation rates required to reduced the total stock to zero were 0.79 and 0.88, respectively. Recall that in Chapter 4, I showed that maximum exploitation was approximately 0.79 and in Chapter 3, I showed that age 2 fish were only partially vulnerable to harvest. Both of these factors tend to protect the stock from complete collapse, but recruitment may still be reduced to 20 - 30% of virgin levels for accessible lakes with low c_o values (Table 5.3).

Current estimates of exploitation, α (current egg-age 2 survival), HPE, angler effort, catch, and recruitment on Rock Island are shown in the last row of Table 5.2. These values agreed quite closely to the values predicted by the model with $\alpha_{max} = 0.003$, implying a virgin recruitment of 69 age 2 fish ha^{-1} (lake total $N_2 = 3795$). This α_{max} value is also in agreement with the estimate for Lee's Ferry rainbow trout found by Walters and Speas (unpublished data) as well as the estimate I obtained in Chapter 3 based on life history arguments. Optimum effort in this case is 15.94 ad ha^{-1} which indicates that the current fishery at Rock Island may be exploiting the rainbow trout stock at approximately the MSY fishing rate and c_o.

If Rock Island lake were more accessible, say the average for management region 3, then c_o for the lake would to be approximately equal to the estimate in Table 5.1 (1.35 fish ad^{-1}). In this case, recruitment would be expected to decline from 65% of the virgin state (at current c_o and effort levels) to 56%. However, the effort analysis was done using stocking rates which may not accurately reflect the actual abundance. In reality, abundance must be less than or equal to the stocking rate (probably much less). Thus, lower c_o values (0.50 – 0.80) would not be unreasonable as the results in Chapter 6 based on more realistic abundance calculations will show. For this range of c_o, recruitment would be reduced to 36 and 46 % of virgin levels respectively.

Table 5.3. Results of equilibrium model predictions for four levels of maximum egg-age2+ survival, α_{max}. U_{crit} is the exploitation rate required to drive the stock to zero, R_0 is the unfished recruitment, $c_{0,MSY}$, E_{MSY}, C_{MSY} are the catch rate, effort, and harvest for MSY, respectively, and $c_{0,20\%}$, $E_{20\%}$ are the catch rate and effort that reduce recruitment to 20% of virgin levels. The last row shows the current values of α, fully vulnerable exploitation (U), catch rate (HPE), effort, and catch for Rock Island lake. All values of recruitment, effort, and catch are on a per hectare basis.

α_{max}	U_{crit}	R_0	$c_{0,MSY}$	E_{MSY}	C_{MSY}	R_{MSY}	$c_{0,20\%}$	$E_{20\%}$
0.002	0.43	114.91	3.41	9.12	30.85	68.29	0.69	21.31
0.003	0.65	69.00	1.71	15.94	27.05	44.79	0.20	58.73
0.004	0.79	59.41	1.14	25.20	28.52	39.34	0.07	182.48
0.005	0.88[A]	55.41	0.89	34.20	30.30	37.98	0.04[B]	433.40[B]
0.0013	0.31	-	1.83	12.70	25.91	45.45	-	-

A- u_{max} used in calculations because U_{crit} exceeds maximum exploitation rate.

B- 20% was not reached. Values represent 31% of virgin recruitment.

Potential effects of enhancement on unproductive populations

Where management agencies use enhancement of unproductive stocks to improve angling quality, a pathological increase in exploitation is expected to occur. When a stock held at any equilibrium abundance due to exploitation is supplemented with additional fish, total abundance increases and this leads to a more or less rapid increase in exploitation depending upon c_0 for the lake (Fig. 5.3). Assuming that both hatchery and wild stocks are exploited at the same rate regardless of origin (Argue et al. 1983) (Hilborn 1976), c_0 values in the range 0.50 to 2.50 cause rapid increases in exploitation for relatively small (< 50 ha^{-1}) increases in total abundance. Current stocking rates on hatchery lakes in B.C. are typically between 100 and 300 age 1+ fish ha^{-1}, and when combined with survival rates of 50% or less, could easily generate age 2+ abundance increases of 50 fish ha^{-1}.
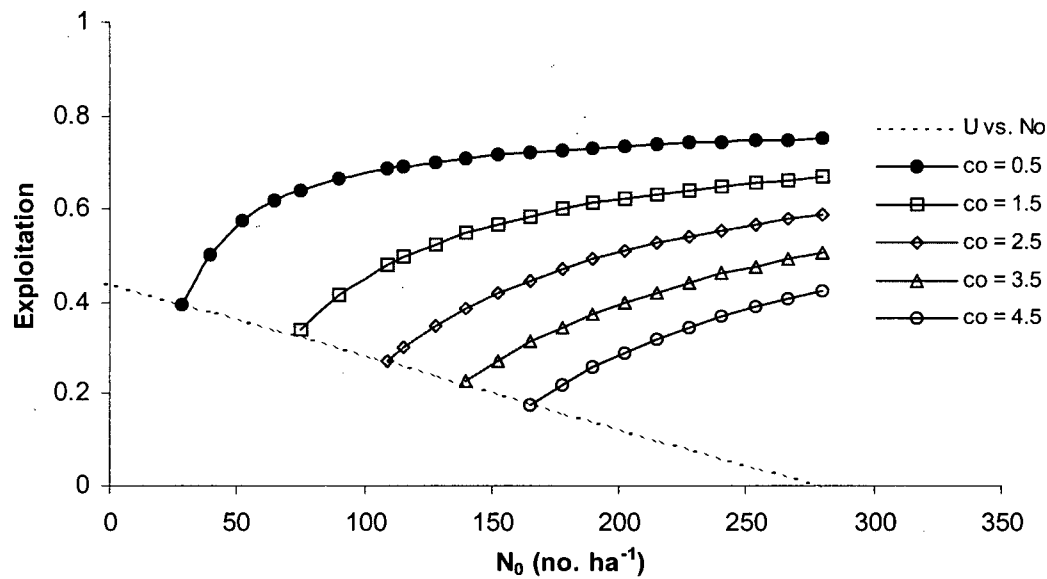
Figure 5.3. Expected pattern of increasing exploitation with increasing abundance. Curved lines show how increasing total abundance affects exploitation for a range of c_0 values. The dashed line shows the equilibrium abundance-exploitation relationship for a low productivity wild stock (α_{max} = 0.002). All exploitation curves begin at the equilibrium point between exploitation and abundance in the absence of stocking.

Discussion

The results found in this chapter show that (*i.*) anglers respond to fish abundance to varying degrees among regions that vary in cost of access, (*ii.*) such numerical responses can have strong impacts on sustainability of wild stock fisheries, and (*iii.*) enhancement programs aimed at improving catches of recreational anglers can seriously reduce the ability of unproductive wild stocks to recover from over-fishing. The observation that anglers respond to fish abundance has been known in both commercial and recreational fisheries for some time. Yet few studies have attempted to quantify and incorporate effort responses into recreational fisheries models (Carpenter et al. 1994). Replacing current simple rules of thumb, e.g., effort *may* increase with abundance (Andrews and Wilen 1989), that simply acknowledge potential effort responses, with quantitative ones that

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explicitly account for effects on fish populations may provide two distinct advantages in recreational fisheries management: (1.) where empirical data are available, such an approach allows a more realistic representation of the alternative outcomes of management policies such as whether or not to enhance fish production or improve access, and (2.) quantitative modeling provides consistency checks compared to simpler intuitive models that may overlook hidden assumptions (Andrews and Wilen 1989; Walters et al. 2000). In the following section, I discuss some of the implications of effort dynamics in B.C. rainbow trout lakes, particularly where violation of IFD assumptions at low abundance may have important consequences for stock dynamics.

Effort responses and the shifting baseline in recreational fisheries

The effort response analysis showed several lakes where relatively high angler effort occurred at low stocking density, suggesting that some anglers are not particularly responsive to fish abundance especially for relatively accessible lakes. Such a response may be strongly dependent upon historical abundances that do not necessarily reflect current attractiveness measures. This represents a fundamental violation of the IFD assumption that anglers attempt to equalize current, i.e., instantaneous, attractiveness among fisheries. In the model, I used the regional average catch rate to represent attractiveness and I assumed that anglers are omniscient. Some would argue that such an assumption is unrealistic and may lead to over-estimates in the effort predictions. This is a valid concern and, indeed, anglers have been shown to be rather oblivious to large differences in fish abundance. For example, in British Columbia, anglers were not able to detect a 40% difference in abundance between two (side-by-side) hatchery stocked lakes

(Parkinson 1990). This suggests that expectations of those anglers were not strongly influenced by current conditions and were most likely dominated by past performance, ease of access, or other non-abundance related factors. As I showed in Chapter 4, under these conditions the fishery will tend to over-exploit a fish stock because anglers do not exit a fishery in the case of population declines. A similar modeling result was shown for northern seal hunters in the north Pacific by Eswaran and Wilen (1976). In put-and-take fisheries, where over-exploitation is not an issue, relatively unresponsive anglers only serve to erode fishing quality for all.

Evidence also exists for highly responsive, seemingly omniscient anglers whose expectations are strongly dependent on the present level of fish abundance. This group of is typically composed of avid anglers who tend to be informed of current fishing opportunities via direct experience or by well developed communication networks, i.e., print, radio, television media and word of mouth (Kitchell and Carpenter 1993; Carpenter et al. 1994).

Another possibility for effort responses at low abundance is that attractiveness depends on more than CPE. Accessible, low stocking density lakes are typically managed to produce relatively low numbers of trophy sized rainbow trout. This represents an added complication to the simple attractiveness measure that I used in the model because anglers may be quite responsive to fish size. For most hatchery stocked lakes in B.C., this should present little cause for concern. However, for wild populations that exhibit periodic recruitment failure, effort responses to fish size can be particularly dangerous.

The magnitude of the risk on a given lake depends on growth responses of fish at low abundance as well as the adaptiveness of angler expectations.

Most salmonid populations exhibit body growth that tends to be inversely related to population density (Bigler et al. 1996; Post et al 1999, Walters and Post 1993), so when anglers respond to fish size, N_∞ decreases (via decreasing c_0) and anglers continue to fish (perhaps even more) during population declines. Such a chain of events is suspected to occur in several large British Columbia lakes (Eric Parkinson and Brian Chan, B.C. Ministry of Fisheries, pers. comm.) where kokanee growth rates increased in response to severe population declines, but angler effort remained high due to the attractiveness of large kokanee.

The real danger lies not only in the short-term response to fish size, but also in the long-term adaptiveness of angler expectations. Where expectations change over time (Eswaran and Wilen 1976), a "shifting baseline" (Pauly 1995) may occur where a fishery eventually becomes reputed for low catch rates of large fish, thus maintaining stock depletion. In a recreational fisheries context, a shifting baseline may occur when effort responses fail to adapt to current abundance, and instead, are based on measures of past performance such as the weighted mean of historical CPE or fish size (Eswaran and Wilen 1976). Botsford et al. (1983) showed that such a case existed in a crab fishery where responses to current price, moderated by past catches, influenced effort dynamics and actually affected the period of crab population cycles. In reality, expectation formulation in angling communities is probably adaptive, lying somewhere between

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oblivious and omniscient; any given fishery will have a group "regulars" who are relatively unresponsive to stock size changes, and a more transient group of opportunists who arrive on-scene to take advantage of short-term improvements in fish abundance (or size). Explicit modeling of these dichotomies in fisher behaviour was done by Allen and McGlade (1986) and Eswaran and Wilen (1976), but it is not clear whether such complicated models provide a better understanding of effort response patterns compared to a simpler "omniscient" assumption. Only via direct management experimentation can the effects of abundance and fish size be separated in determining the most appropriate measures of attractiveness in recreational fisheries.

Implications for enhancement of unproductive or over-exploited populations

The implications of effort responses are most severe for unproductive, or over-exploited stocks. Yet, these are the most likely candidates for traditional management measures such as supplemental hatchery stocking aimed at improving angling quality (Engstrom-Heg 1986; Johnson et al. 1995). In New York brown trout streams, wild yearling population densities are typically used as an index of the need for supplemental stocking (Engstrom-Heg 1986). Stocking of catchable sized trout is also used in Oregon streams to supplement wild production (Moring 1993). Such management tactics ignore increasing evidence that stocking hatchery fish tends to increasing angler effort and subsequent catches of wild fish (Argue et al. 1983; Moring 1993; Walters 1994). Where stocking rates have been reduced or eliminated, angler effort usually decreases and exploitation of wild stocks decreases as well (Moring 1993). When accompanied by no-kill regulations, elimination of stocking programs actually increased angler effort and catch rates of wild

fish on a Pennsylvania spring creek (Carline et al. 1991). All of this empirical experience is consistent with the model results shown above in that the best management policy for protecting wild stocks is direct exploitation control without resorting attempts at enhancement.

Chapter 6: Access control of angling quality in recreational fisheries

Introduction

There are two main questions to be addressed in this chapter. The first is whether or not fishing effort varies among years (within lakes) so as to maintain stationary, lake-specific expectations of catch rate (c_o). As I showed in Chapter 5, fishing effort on B.C.'s rainbow trout lakes follows the general pattern that is implied by the effort model, i.e., effort is directly proportional to trout abundance as measured by stocking density. However, using stocking density as a predictor for effort suffers from two potential problems: (*i.*) stocking density may not be an accurate index of true fish abundance and (*ii.*) in some lakes, stocking rates may be determined by historical effort levels, i.e., biologists using prior knowledge of effort to set stocking rates. These problems can be partially overcome by predicting abundance from stocking data after adjusting for survival and harvest in years prior to the observed effort. This removes some of the uncertainty in actual fish abundance and all of the uncertainty about whether stocking rates are calculated on expected effort. To do this, I obtained annual stocking rate and fishing effort density estimates on 105 lakes spread over the three management regions previously described. I then estimated $c_{o,j}$, the lake-specific IFD catch rate, on each lake to determine how fishing effort responds to changes in fish abundance on interannual time scales.

The second problem to be addressed here involves the patterned departures from IFD model predictions that I showed in Chapter 5. Some lakes appeared have catch rate expectations that systematically differ from the regional averages. In deriving the original

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effort model, I proposed that no lake should stand out from these regional averages if fishing effort is free to move about according to IFD theory except where lakes differ with respect to cost of access. Therefore, I derive an access index for each lake and I determine whether systematic differences in catch rate estimates can be explained by these indices. I then determine what level of diversity, as measured by variation in catch rate among lakes, remains in B.C.'s southern interior lakes.

Methods

B.C. lakes data

Rainbow trout stocking

Stocking rate data used in this analysis were obtained from B.C. Fisheries archives (Dave Stanton, B.C. Fisheries, Victoria B.C., pers. comm.). In order to use a representative sample of small lakes, I included only those lakes smaller than 500 ha and where rainbow trout were the primary species stocked. In several cases, Eastern brook trout (Salvelinus fontinalis) were stocked in conjunction with rainbow, but I ignored this species due to lack of data on their biology as well as potential differences in catchability. I placed a further restriction on the lakes used to those where stocking occurred in at least three of the years between 1982 and 1985, which encompasses the three years before the first effort observations. Stocking density was calculated on the basis of total lake area, which differs somewhat from the analysis in Chapter 5 where I used shoal area for the density calculation. Using total area allowed me to apply the model to a much larger set of lakes.

Angler effort

From 1986 to 1993, the MELP conducted aerial flight count surveys to estimate total annual fishing effort on B.C.'s rainbow trout lakes. The methodology and calculation of survey estimates of effort are described in (Tredger 1992). Because many lakes had only a small number of years sampled, I further restricted the analysis to lakes with greater than four years of effort data and lakes without continuous gaps between observations greater than two years. This condition avoided obvious small sample size problems (though not excluding it entirely), but more importantly avoided the need to project fish abundance for several years over which fishing effort was not measured. The final dataset included 105 lakes with effort observations for 4 to 8 years. Total lake numbers were 24, 26, and 55 in Regions 3, 5, and 8, respectively. For all lakes combined there were 588 individual lake-year data points upon which to fit the effort prediction model.

B.C. lakes access data

B.C. small lakes vary in accessibility according to factors such as distance from major urban centres, road conditions, presence/absence of lodge facilities, private/public access rights, and boat launch facilities. One of the key hypotheses or assumptions of the IFD effort model is that lake-specific estimates of catch rate (c_o) that I obtain from the effort model analysis should be closely related to these access conditions. I test this hypothesis by comparing lake-specific catch rate estimates to a lake-specific access index measured as total travel time from Vancouver, B.C. which is the main source of fishing effort on B.C.'s rainbow trout lakes. This index uses (*i.*) travel distances from Vancouver to the city nearest the lake (British Columbia Recreational Atlas, MELP, 4th edition) and (*ii.*)

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travel distances by road type (i.e., paved, gravel, dirt, 4-wheel drive, trail) from that city

to the lake (BC Freshwater Fishing Directory, BC Outdoors 1997). Each distance

measurement is then weighted by the inverse of average speed over the road type. I used

the following values for average speed: highway-80 km hr^{-1}, paved-60 km hr^{-1}, gravel-30

km hr^{-1}, dirt/4wd-10 km hr^{-1}, and trail-2 km hr^{-1}.

Effort model specification

Table 6.1. Notation for the effort dynamics model.

	Value	*Units*	*Description*
E_t	predicted	ad ha^{-1}	Fishing effort density in year t
N_t	predicted	fish ha^{-1}	Fish density at the start of year t
U_t	predicted	yr^{-1}	Total exploitation in year t
S_t	data	fish ha^{-1}	Stocking rate in year t
c_o	estimated	catch ad^{-1}	Lake-specific IFD catch rate
N_1	estimated	fish ha^{-1}	Fish density in the first year
s_a	.7	yr^{-1}	Over-winter adult survival
s_{max}	.5	yr^{-1}	Maximum age 1-2 survival at low fish density[A]
s_1	0.02	ha^{-1}	Density-dependent juvenile survival coefficient[A]
u_{max}	.7	yr^{-1}	Maximum exploitation rate
q	0.16	ha ad^{-1} yr^{-1}	catchability coefficient

A-Estimated from instantaneous mortality rates published in (Post et al. 1999).

The model used to predict angler effort, E_t, on each lake in year t is

$$E_t = \frac{(N_t - c_o / q)u_{max}}{c_o}$$
6.1.

Note that this formula is identical to the original model described in Chapter 4 (equation 4.7) except for the biological process constant $1 + v_2/v_1$ which I omit here in order to simplify the model structure. Leaving this term out induces a slight (-7%) bias in the c_o estimates, but since it is a biological (fish behaviour) constant it should not affect among lake inferences. Also note that N_0 in the original model is now written as N_t where t indexes years and c_o represents a lake specific catch rate; it still applies that N_t is the fish density present in the lake at the start of a year. No explicit modeling of in-season dynamics is done. The population dynamics model used to predict N_t in each year is (see Table 6.1 for notation)

$$N_t = s_a N_{t-1}\left(1 - U_{t-1}\right) + s_{j,t-1} S_{t-1} \qquad\qquad 6.2$$

where $U_{t-1} = c_o E_{t-1}/N_{t-1}$ and the density-dependent survival term, $s_{j,t-1}$ is the familiar Beverton-Holt form

$$s_{j,t-1} = \frac{s_{max}}{1 + s_1 N_{t-1}}.$$

The density-dependent parameters, s_{max} and s_1, were estimated from survival rate data published for B.C. lakes (Post et al. 1999) and other parameter estimates (s_a-adult survival, u_{max}, vulnerability, and q-catchability) were obtained directly from the results given in preceding chapters.

Equation 6.2 assumes that rainbow trout recruit to the catchable stock after one full year in the lake, i.e., knife-edge increase in vulnerability at age 2. This assumption is made in order to simplify the dynamic model and should be reasonably accurate given the results in Chapter 3. There, I showed that rainbow trout in B.C. lakes typically recruit to the

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catchable stock at between two and three years of age with a mean age at 50% vulnerability of 2.3 yr. This implies that most fish are available to anglers during their second year in the lake. For many lakes, in particular mixed species lakes, fish probably recruit at older ages due to below-average growing conditions. Unfortunately, fish growth data for the above dataset are scarce and where they exist, growth parameters are difficult to estimate due to low representation of a wide range of age classes. Therefore, including such effects would not necessarily reduce the uncertainty in parameter estimates. If better quality growth and recruitment data were available they could easily be included in the model by defining a recruitment function that calculates the proportions of fish stocked in year i that become fully vulnerable in years $i + 1$, $i + 2$, etc. The vulnerable stock at the start of the year could then be calculated by substituting

$$R_t = \sum_{i=t-k}^{t} s_{j,i} S_i p_{i,t}$$

in equation 6.1 in place of $s_j S_{t-1}$, where $p_{i,t}$ is the proportion of stocked fish in year i that recruit in year t and k is the total number of years required for a single cohort to enter the fishery (Hilborn and Walters 1992).

Parameter estimation

Because of the limited amount of effort data, I added the nuisance parameter, N_1, which represents fish density in the first year for which effort data were gathered. This tactic was preferred over using the first year or two of effort data in order to get a reasonable starting point for N_t (Walters 1986). In most cases, effort observations numbered 4 to 8, so using even one or two would seriously restrict the total number of useable datasets.

Equations 6.1 and 6.2 are non-linear in the parameters c_o and N_1 so I used a Levenburg-Marquardt minimization algorithm (Press et al. 1992) programmed in Microsoft Visual Basic 5.0 to minimize the weighted sum of squares between predicted and observed fishing efforts. The weights, σ_t, are standard deviations of the observed effort estimates based on the total number of aerial flight counts during a season that were used to estimate total effort on a given lake. Numbers of flight counts were first converted to coefficients of variation (CV) by the formula $CV_t = 0.3 + \exp(-.\pi*counts_t)$, where the constant π was chosen *a priori* to lie between 0.1 and 0.3. Tredger (1992) showed that a CV in the effort estimates of 30% is about the best that can be expected from aerial flight count observations that number 12-20 per season. The above formula simply serves to exponentially un-weight effort estimates that were obtained from fewer than 10 counts. Application of the weighting scheme affected the results markedly compared to an unweighted one, however in the range of $\pi = 0.10$ (approximately linear decrease in CV with number of counts) to $\pi = 0.30$ (highly non-linear decrease) the results were similar so I set $\pi = 0.2$ for the analysis. Final σ_t estimates were obtained for each year of effort data on each lake by multiplying CV_t times E_t^{obs}.

The minimization algorithm uses information from the approximate Hessian matrix, $J'J$, along with the asymptotic covariance matrix, $\Sigma = SS\,(J'J)^{-1}$ to move along the two-dimensional sums of squares surface toward the minimum. Appendix 6.1 gives the derivation of the required Jacobian matrix elements J_{ij} . Analytical derivatives of the model equations found in J were checked for errors against their approximate values obtained by Ridder's method for numerical derivatives (Press et al. 1992). Exact

(analytical) values agreed with numerical estimates to approximately 10^{-4} for both parameters; however, sensitivity of the effort model to N_1 tended to dampen more rapidly over time for the exact solution. Standard errors of the parameter estimates were calculated by taking the square root of each Σ_{ii} element in the covariance matrix and parameter correlations were calculated by the formula (Zar 1984, p. 307)

$$\rho = \frac{\Sigma_{ij}}{\sqrt{\Sigma_{ii}}\sqrt{\Sigma_{jj}}}.$$

Access model for predicting IFD catch rate

I used the effort model results to further test the IFD assumption that no lake should stand out from the regional average except where differences in access cost exist among lakes. Specifically, I used a logistic model of the form

$$\hat{c}_{o,j} = \frac{c_{o\,max}}{1 + e^{(-\lambda(TT_j - TT_{50}))}}$$

to predict lake-specific c_o values based on travel time data. In this model, $c_{o,max}$ is the maximum expected catch rate (chosen *a priori* to be 16 fish ad^{-1}), TT_j is the travel time (from Vancouver, B.C.) required to reach lake j, TT_{50} is the travel time required to produce $\hat{c}_{o,j} = c_{o\,max}/2$, and λ is a rate parameter. In preliminary analyses, logistic fits with constant rate parameter, λ, showed consistent lack of fit due to an apparent "threshold" travel time of approximately 7hr. At greater travel times $c_{o,j}$ estimates increased more sharply than the constant λ model could produce. I accounted for this by modeling λ as a linearly increasing function of travel time. The resulting logistic function used was

$$\hat{c}_{o,j} = \frac{c_{o\,\text{max}}}{1 + e^{(-(\lambda_1 - \lambda_2 TT_j)(TT_j - TT_{50}))}} \ .$$

The model was fitted by minimizing the sum of squares between predicted $\hat{c}_{o,j}$ based on the logistic function with travel time and $c_{o,j}$ estimated from the effort model. Minimization was performed using the Solver function in Microsoft Excel 8.0. Standard errors of the estimates were obtained by first evaluating the asymptotic covariance matrix

$$\Sigma = \frac{SS}{n - m}(J'J)^{-1}$$

where SS is the sums of squares evaluated at the maximum likelihood estimates, n and m are the number of lakes and parameters, respectively, and J is the Jacobian matrix with elements

$$\frac{\partial \hat{c}_{o,j}}{\partial TT_{50}} = \frac{c_{o\,\text{max}}(\lambda_1 - \lambda_2 TT_j)e^{(-(\lambda_1 - \lambda_2 TT_j)(TT_j - TT_{50}))}}{(1 + e^{(-(\lambda_1 - \lambda_2 TT_j)(TT_j - TT_{50}))})^2}$$

$$\frac{\partial \hat{c}_{o,j}}{\partial \lambda_1} = \frac{c_{o\,\text{max}}(-TT_j + TT_{50})e^{(-(\lambda_1 - \lambda_2 TT_j)(TT_j - TT_{50}))}}{(1 + e^{(-(\lambda_1 - \lambda_2 TT_j)(TT_j - TT_{50}))})^2}$$

$$\frac{\partial \hat{c}_{o,j}}{\partial \lambda_2} = -\frac{c_{o\,\text{max}}TT_j(TT_j - TT_{50})e^{(-(\lambda_1 - \lambda_2 TT_j)(TT_j - TT_{50}))}}{(1 + e^{(-(\lambda_1 - \lambda_2 TT_j)(TT_j - TT_{50}))})^2} \ .$$

Standard errors were then calculated by taking the square root of the resulting Σ_{ii} elements.

Bayesian hierarchical analysis of access-adjusted IFD catch rates

The logistic model analysis in the previous section essentially attempts to remove variation in catch rate estimates among lakes that can be accounted for by access differences. After taking the residuals from this relationship, the remaining variability can

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be quantified in order to examine whether any angling quality diversity exists naturally in B.C.'s southern interior lakes. In other words, do catch rates on a significant proportion of lakes actually stand out from the others after access affects are removed? The hypothesis, according to IFD theory, is that they should not. In this section, I show how this hypothesis can be tested using Bayesian hierarchical modeling (Gelman et al. 1995) of residual values $y_j = \hat{c}_{o,j} - c_{o,j}$ from the logistic model fit. Standard errors of each y_j are assumed known and equal to standard error values σ_j of $c_{o,j}$ from the limited vulnerability/effort model fit. Note that this assumption ignores additional uncertainty added from the logistic fitting procedure.

Before describing the procedure, I alter the notation a bit to reflect the change in focus from lake-specific results to inference about angling quality or catch rates in general, i.e., B.C.-wide. In particular, I will refer to residual values from the logistic fit as data, , which represent estimates of their true values, θ_j, and have known standard. In addition to these lake-specific parameters, I refer to the B.C.-wide average value as μ with random effects standard deviation τ. The value of μ should be centered at approximately 0 because it is a mean of residuals.

Hierarchical model structure

Bayesian hierarchical modeling is a particularly useful method for performing meta analysis, or the combining of results from several independent studies of the same phenomenon. When parameter estimates, θ_j, from J studies are potentially linked to each other by the underlying structure of the problem, i.e., no lake stands out in quality

because effort is proportional to abundance for all, θ_j estimates are considered a random sample from some population distribution of all possible θ's. This is known as the random effects model which is typically used in analysis of variance. Each of these θ's thus represents a sample value of the population or B.C.-wide mean, μ, with variance τ^2. These values give rise to a set of unobservable θ's each with variance V_j, that depends on both τ and the measurement error σ_j. The final data that we observe, y_j ($j = 1,...J$), are then determined by the hyperparameters (μ,τ) and the observation standard error, σ_j. The goal of hierarchical modeling is to use information supplied by the data, (y, σ) to estimate μ and τ, which are then used to estimate the θ_j's which, in this case, are the true parameters of interest. Derivation of the joint posterior distribution $p(\theta,\mu,\tau \,|y,\sigma)$ follows from the presentation of (Gelman et al. 1995), and a full specification is given in Appendix 4.

Posterior computation

The main focus in this analysis is to characterise the distribution of access-adjusted catch rate estimates, θ_j. To accomplish this, I computed values of the θ_j's from their joint posterior distribution

$$p(\theta,\mu,\tau \mid y) \propto p(\tau \mid y)p(\mu \mid \tau,y)p(\theta \mid \mu,\tau,y)$$

according to the following scheme:

1. compute $p(\tau \mid y)$ from equation A4.6 over a uniformly spaced grid of τ and set $\hat{\tau}$ equal to the modal value.

2. compute $\hat{\mu} \mid \hat{\tau}, y$ using equation A4.5

3. compute V_j, and θ_j in that order from equation A4.1

4. repeat 3 for all j.

Note that this scheme of conditioning on modes ignores some of the posterior uncertainty about μ and τ. Preliminary analyses suggested that μ and τ were both highly concentrated about the modal values, so I use their point estimates in order to keep the results relatively simple. The resulting distribution of θ was plotted and assessed using a cumulative distribution function.

Results

Effort responses to abundance

Before describing the effort model results, it should be noted that catch rate estimates from the effort model are not necessarily comparable to precise catch rate estimates that would be obtained from creel surveys. The estimates that I describe depend upon such things as constant (over time and among lakes) natural mortality rates, retention rates, and an assumed density-dependent survival relationship that probably vary widely among lakes. The ultimate result of deviations from these assumed values will be to shift the scale of catch rates up or down depending on the actual physical and biological conditions in individual lakes. Because much of the data used to estimate constant parameters was obtained from a range of lake categories, these scaling effects should not substantially affect among lake inferences.

Figure 6.1 shows the effort model fits to observed effort data for all lakes. Out of 105 lakes originally attempted, only 8 failed to converge upon reasonable values of $c_{o,j}$ and N_1. In six of these cases, stocking ceased just prior to the first effort observation and in

one, rainbow trout were stocked in only two of the years between 1986 and 1990, inclusive. These lakes may have been stocked with other species, or perhaps were left alone after establishment of a self-reproducing population. Trio lake, the remaining failure, was stocked in all years, however the first effort observation was over ten times greater than values in the remaining years which suggested an error in the effort data.

Several lakes showed strong increases or decreases in stocking rate, and in most of these cases, observed effort data clearly show a response. Model predictions agreed fairly well with most of these cases; however a few lakes showed systematic departure from the model predictions. In particular, observed effort at Fawn lake increased monotonically despite a stable stocking rate and it is likely that these differences were not simply due to measurement error alone. During the 1980's a rather large resort was developed on Fawn lake and this may have caused a shift in the underlying expectations of anglers. Singular positive outliers for Alleyne and Kentucky lakes are from the years of stocking experiments where anglers did not appear to detect differences in abundance (Parkinson 1990).
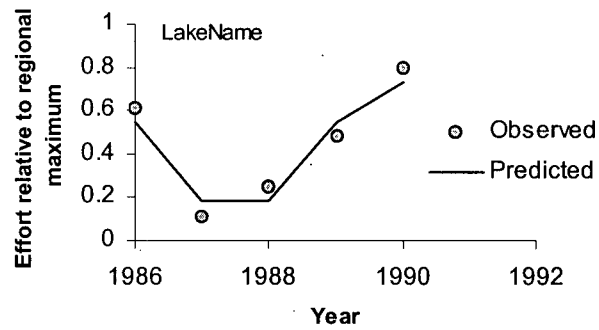
Figure 6.1. Example plot of observed and predicted effort for the figure on the following page showing completely labeled axes. x-axis is over years 1986 – 1991 and y-axes are scaled to the region-specific maximum effort prediction. Effort model fit (solid line) to observed data (circles) on 105 B.C. rainbow trout lakes from Region 3 (BLUE – WOODS), Region 5 (108 MILE – TYEE), and Region 8 (AILEEN – YELLOW). Estimation procedure failed for lakes where no prediction line is shown.

HEFFLEY	SHEA	DUGAN	HOWARD	TYEE	CHAIN	HIGH	LAIRD	PEACHLAND	SUNDAY	
HARMON	ROCHE	DORSEY	HORN	TRIO	BURNELL	HIDDEN	LADY KING	DYAMA	STREAK	
GLIMPSE	PLATEAU	CUISSON	HATHAWAY	TIMOTHY	BRUNETTE	HAYNES	KUMP	OSPREY	SQUARE	
ERNEST	PAUL	CHIMNEY	GREENY	STARLIKE	BROWNE	FRIDAY	KIDNEY	MUNRO	SILVER	
DUFFY		BENNY	GREENLEE	RUTH	BOSS	EASTMERE	KENTUCKY	MISSEZULA	RUTH	
DOMINIC	MCCONNELPASS	108 MILE	FRESHETTE	ROSE	BORGESON	DRY	JACKPINE	MINNOW	RIPLEY	YELLOW
COURTNEY	MARQUART	WOODS	FOREST	RAIL	BLUEY	DOREEN	SINTOK	MADDEN	RAMPART	WILMA
FORREST	LUNDBOM	WALLOPER	FELKER	LORN	ALLISON	DAVIS	IDLEBACK	LOST	POSTILL	WHITEHEAD
BULLION	LEIGHTON	TUNKWA	FAWN	KLINNE	COLLEYNE	DARKE	IDABEL	LINK	PINAUS	WESTMERE
BLUE	JACKO	STAKE	ELK	JACKSON	AILEEN	CRESCENT	HYDRAULIC	LAMBLY	PEAR	SWALWELL

Figure 6.2. Mean residual values by region and year for the effort model fits. Error bars represent +/- 1 standard deviation from the mean residual value.

Residual patterns showed no strong lack of fit, except that large prediction errors

occurred for several lakes in 1987 and 1991 in Region 3. For all regions, low mean

residuals occurred in 1986 which is primarily due to the nuisance parameter N_1, i.e., extra parameter is able to explain first data point very well. Thus, poor performance in 1987 in Region 3 may be due to over/under estimation caused by N_1. Negatively biased effort predictions in Region 8 in 1988 may be due to increases in effort caused by development of the Coquihalla Highway in 1987 which made access to this region easier.

Catch rate estimates for all lakes ranged from 0.16 to 9.70 fish ad^{-1} with coefficients of variation in the estimates of 6 to 56% (Table 6.2). Low estimates (strong effort response) tended to be most precise. As catch rate estimates increased, precision degraded accordingly. This should be expected because increasing c_o implies a less pronounced effort response to abundance so that a wider range of values are able to fit the observed data.
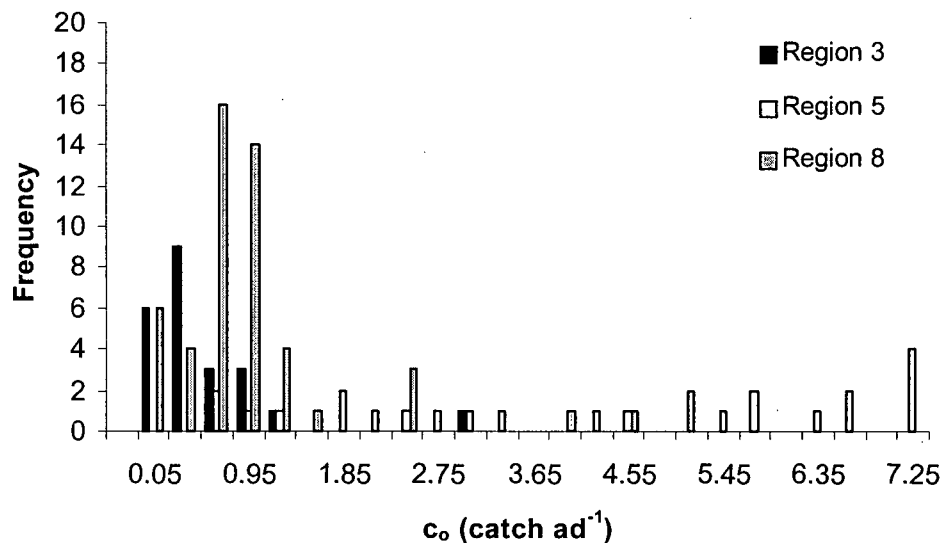
Figure 6.3. Distribution of c_o estimates by management region for B.C.'s southern interior lakes.

Figure 6.3 shows the distribution of $c_{o,j}$ estimates for all three regions. Estimates for Regions 3 and 8 tended to be highly concentrated at low values while region 5 estimates were dispersed over most of the estimated range.

Correlation between the parameters c_o and N_1 was strong in some cases with values ranging between -0.28 and 0.90, however most were in the range 0.20-0.60. These moderate correlations probably resulted from lack of contrast in the stocking rate data. In fact, for many lakes, fitting the model becomes almost trivial due to flat patterns in stocking rate. On the other hand, flat effort patterns in response to flat stocking rates is just what the effort model predicts; no change in stocking rate implies no change in effort.

Table 6.2. Effort model parameter estimates for B.C.'s southern interior lakes. Number of years of data is given as n and ρ is the correlation coefficient between c_0 and N_1. Standard errors appear to the right of each estimate.

Lakename	Region	n	c_o	s.e.	N_1	s.e.	ρ
BLUE	3	5	0.55	0.11	16.44	10.17	0.35
BULMAN	3	6	0.83	0.15	75.60	29.55	0.47
CORBETT	3	6	0.16	0.03	55.74	19.87	0.39
COURTNEY	3	5	0.44	0.09	45.85	15.41	0.47
DOMINIC	3	6	1.10	0.22	36.46	10.52	0.46
DUFFY	3	6	0.60	0.11	120.71	45.58	0.45
ERNEST	3	6	0.57	0.10	37.42	14.28	0.44
GLIMPSE	3	5	0.52	0.10	59.50	39.42	0.29
HARMON	3	6	0.23	0.04	41.56	14.06	0.40
HEFFLEY	3	7	0.34	0.05	32.61	11.93	0.42
JACKO	3	6	0.69	0.12	147.68	51.55	0.47
LEIGHTON	3	6	3.34	0.70	483.09	470.57	0.14
LUNDBOM	3	5	0.50	0.09	54.95	33.01	0.30
MARQUART	3	5	0.47	0.09	196.72	353.16	0.07
MCCONNELL	3	6	0.71	0.13	72.62	90.24	-0.05
PASS	3	7	0.53	0.10	78.64	29.24	0.52
PAUL	3	7	1.10	0.21	40.77	14.07	0.50
PLATEAU	3	6	0.45	0.19	57.64	29.91	0.76
ROCHE	3	6	0.26	0.10	67.92	34.19	0.72
STAKE	3	6	1.31	0.24	111.84	148.30	0.12
TUNKWA	3	6	1.02	0.24	80.38	33.88	0.56
WALLOPER	3	6	0.20	0.04	35.54	12.32	0.45
WOODS	3	6	0.26	0.06	68.16	27.65	0.47
108 MILE	5	6	8.76	0.91	94.16	45.33	0.22
BENNY	5	6	2.81	1.17	26.42	12.21	0.90
CHIMNEY	5	8	5.90	0.61	92.44	33.43	0.32
CUISSON	5	8	5.96	0.48	62.56	37.26	0.12
DORSEY	5	7	4.52	0.68	192.12	208.07	0.14
DUGAN	5	8	2.10	0.44	151.17	82.04	0.33
ELK	5	7	9.71	0.89	454.86	171.50	0.27
FAWN	5	7	0.73	0.12	113.61	57.06	0.38
FELKER	5	8	5.28	0.32	71.32	18.44	0.24
FOREST	5	7	5.29	1.07	217.87	68.28	0.64
FRESHETTE	5	5	5.73	0.92	64.62	20.07	0.83
GREENLEE	5	6	2.20	0.35	116.78	97.12	0.25
GREENY	5	8	2.74	0.41	162.99	264.22	0.19
HATHAWAY	5	6	3.51	0.34	54.51	22.13	0.33
HORN	5	6	1.92	0.33	65.12	31.72	0.35
HOWARD	5	6	0.80	0.13	74.12	43.21	0.28
JACKSON	5	7	6.79	0.88	173.36	166.36	0.14
KLINNE	5	7	9.54	3.89	251.45	272.37	0.52
LORIN	5	6	1.18	0.67	55.49	62.49	0.53
RAIL	5	7	7.38	0.56	92.41	26.62	0.32
ROSE	5	7	6.89	0.42	84.06	61.82	0.13
RUTH	5	6	3.11	0.35	69.70	30.78	0.27
STARLIKE	5	6	6.57	0.77	73.74	22.44	0.35
TIMOTHY	5	6	1.32	0.23	34.01	30.45	0.20

Lakename	Region	n	c_o	s.e.	N_l	s.e.	ρ
TYEE	5	7	4.60	0.43	55.40	16.72	0.32
AILEEN	8	4	0.66	0.14	114.95	59.88	0.30
ALLEYNE	8	5	0.68	0.13	114.43	48.40	0.28
BLUEY	8	5	1.08	0.20	167.27	95.54	0.27
BORGESON	8	5	1.57	0.30	193.08	260.04	0.20
BOSS	8	5	0.35	0.06	45.20	26.11	0.26
BROWNE	8	5	0.64	0.13	143.11	120.24	0.33
BRUNETTE	8	5	2.60	0.48	63.76	24.18	0.45
BURNELL	8	5	0.94	0.22	51.10	16.03	0.74
CHAIN	8	5	0.32	0.06	93.59	42.06	0.31
DARKE	8	5	1.15	0.31	42.34	83.90	0.26
DAVIS	8	5	0.21	0.05	68.09	46.04	0.25
DOREEN	8	5	0.68	0.12	89.22	62.79	0.19
DRY	8	5	0.82	0.15	64.96	42.50	0.21
EASTMERE	8	5	1.54	0.28	73.18	22.34	0.32
FRIDAY	8	5	2.49	0.55	353.87	138.97	0.57
HAYNES	8	5	1.30	0.24	39.14	14.07	0.51
HIDDEN	8	5	0.34	0.07	7.53	2.68	0.49
HIGH	8	5	1.43	0.25	41.57	23.73	0.20
HYDRAULIC	8	5	1.24	0.21	26.69	10.46	0.45
IDLEBACK	8	5	0.56	0.12	24.35	9.95	0.43
JACKPINE	8	5	0.93	0.18	95.59	45.81	0.41
KENTUCKY	8	5	1.09	0.20	113.74	79.22	-0.05
KIDNEY	8	4	0.73	0.15	158.01	70.02	0.34
KUMP	8	5	0.71	0.14	115.16	96.85	0.26
LADY KING	8	5	0.97	0.20	301.60	245.05	0.25
LAIRD	8	5	0.84	0.17	55.29	22.97	0.45
LAMBLY	8	5	0.97	0.18	61.09	27.01	0.41
LINK	8	5	0.33	0.07	156.40	206.26	0.15
LOST	8	5	0.69	0.26	128.38	119.17	0.81
MADDEN	8	5	2.72	0.58	1056.38	732.81	0.26
MINNOW	8	5	0.89	0.19	167.37	76.15	0.53
MISSEZULA	8	5	4.09	0.80	83.81	78.08	0.12
MUNRO	8	5	1.24	0.23	49.94	19.13	0.45
OSPREY	8	5	0.30	0.06	74.70	29.73	0.40
OYAMA	8	5	1.11	0.20	54.45	20.07	0.47
PEACHLAND	8	5	1.19	0.21	54.59	42.17	0.23
PEAR	8	5	0.91	0.21	148.07	217.57	0.20
PINAUS	8	5	1.03	0.21	91.09	35.42	0.50
RAMPART	8	4	0.82	0.18	57.31	22.63	0.54
RIPLEY	8	5	0.53	0.11	414.58	139.83	0.45
RUTH	8	5	1.39	0.37	268.50	90.11	0.77
SILVER	8	5	0.61	0.13	226.77	95.82	0.38
SQUARE	8	5	0.93	0.20	138.45	104.20	0.26
STREAK	8	5	0.95	0.21	6.73	37.74	-0.28
SUNDAY	8	5	1.10	0.25	63.47	80.23	0.16
SWALWELL	8	5	0.83	0.16	69.40	27.81	0.42
WESTMERE	8	5	1.19	0.24	177.02	56.90	0.47
WHITEHEAD	8	5	1.19	0.24	71.65	30.06	0.47
YELLOW	8	5	1.18	0.22	149.17	109.27	0.16

Access model results

The distribution of estimates shown in figure 6.3 indicates that predicted catch rate c_o varies substantially among lakes. Whether this variation is natural, i.e., violates IFD assumptions, or not depends primarily on the affects of access which I assessed by fitting the logistic model to travel time data.

Travel time indices from Vancouver, B.C. to lakes in all three regions ranged from approximately 3.5 to10 hr. Between 3.5 and 6 hr travel time, catch rate estimates increased very little which suggests that CPE does in fact tend to be leveled among these lakes (Figure 6.4). For travel times greater than 6.5 hr, the c_o estimates increased sharply. This general this pattern was fit relatively well by the logistic model; however, judging by the residual plot in Figure 6.4, it appears that catch rates increase more abruptly in the neighborhood of 6.5 hr than the smooth logistic can reproduce. This apparent threshold at 6.5 hr is likely due to constraints on how far anglers are willing to travel for short 2-3 day excursions into the interior. Region-specific patterns in the relationship were not apparent over the observed range because where lakes from different regions overlapped in travel time, $c_{o,j}$ estimates tended to be similar; however, region 5 data did show larger deviations from the predictions.
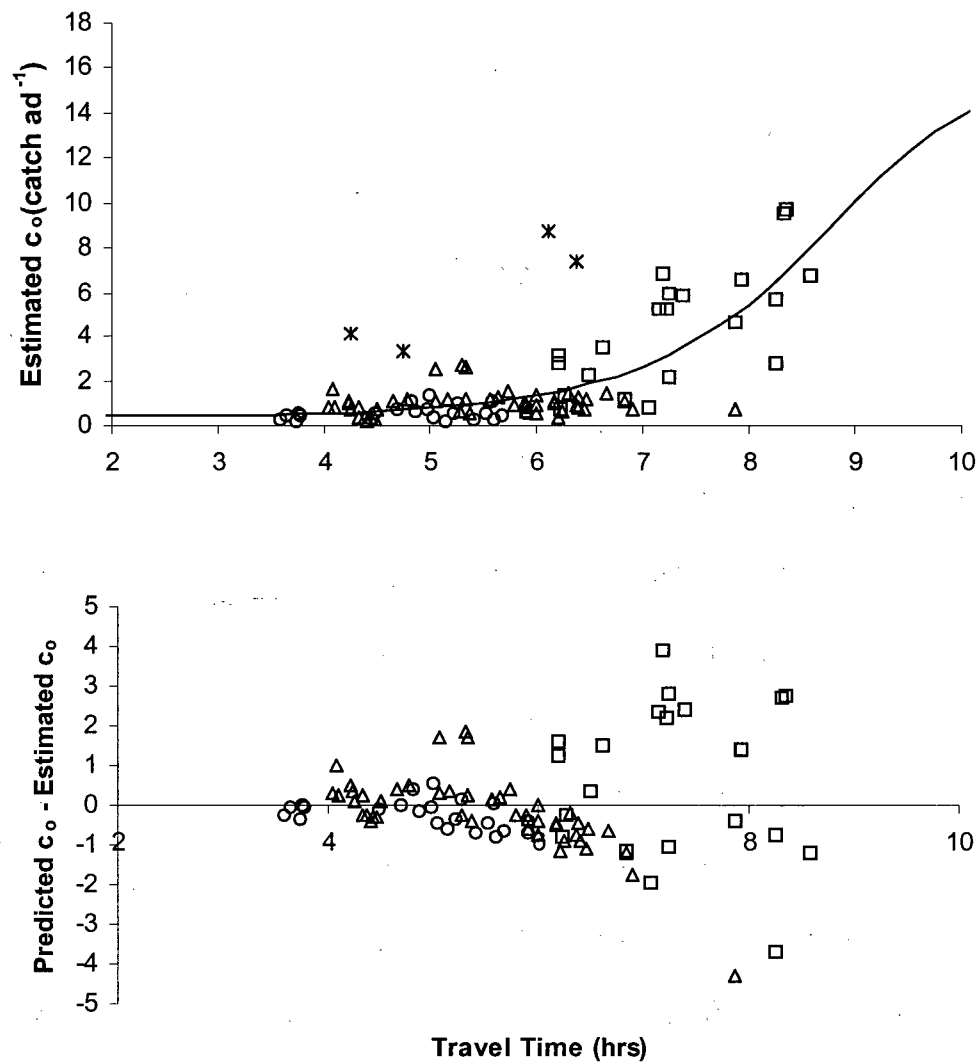
Figure 6.4. Relationship between travel time to B.C.'s southern interior lakes and the estimated IFD catch rate, c_0 (top panel). Points represent Region 3 (circles), Region 5 (squares) and Region 8 (triangles). Bottom panel shows residual values for the logistic fit between travel time from Vancouver and estimated co. The four stars appeared to be outliers with respect to the within-region relationships and they are not included in the logistic fit.

The estimate of TT_{50} was 8.75 hr with standard error 1.29 hr, indicating that the estimate

was well defined by the data. However, TT_{50} itself holds little meaning: it merely serves

as a statistical convenience that was used to approximate the functional form of the travel

time-catch rate relationship. The important point from this analysis is that 6.5 hr appears

to be a threshold travel time, beyond which anglers are not willing to go for higher catch rates.

Bayesian hierarchical analysis of access-adjusted catch rates

Figure 6.5 shows the approximate posterior distributions for the hyperparameters μ and τ. As noted earlier, both values were well determined by the data with $\hat{\mu} = -0.065$ and $\hat{\tau} = 1.019$. The small negative value for $\hat{\mu}$ indicates a slight negative bias from the logistic fit, but it is quite small so I chose to ignore its deviation from 0.

Figure 6.6 shows the influence of the hierarchical model structure on conditional estimates of θ (conditioned on $\hat{\mu}, \hat{\tau}, y$). Values of y_j in the range +/- 1.0 were not affected substantially which indicates that these values were relatively precise to begin with, i.e., hyperparameters had little affect. Outside this range, imprecise estimates tended to be adjusted toward $\hat{\mu}$ and in some cases rather strongly depending upon the original effort model estimation performance. The lower panel in Figure 6.6 shows how the conditional standard errors are adjusted toward $\hat{\tau}$ as the estimation error component, σ_j, increases.
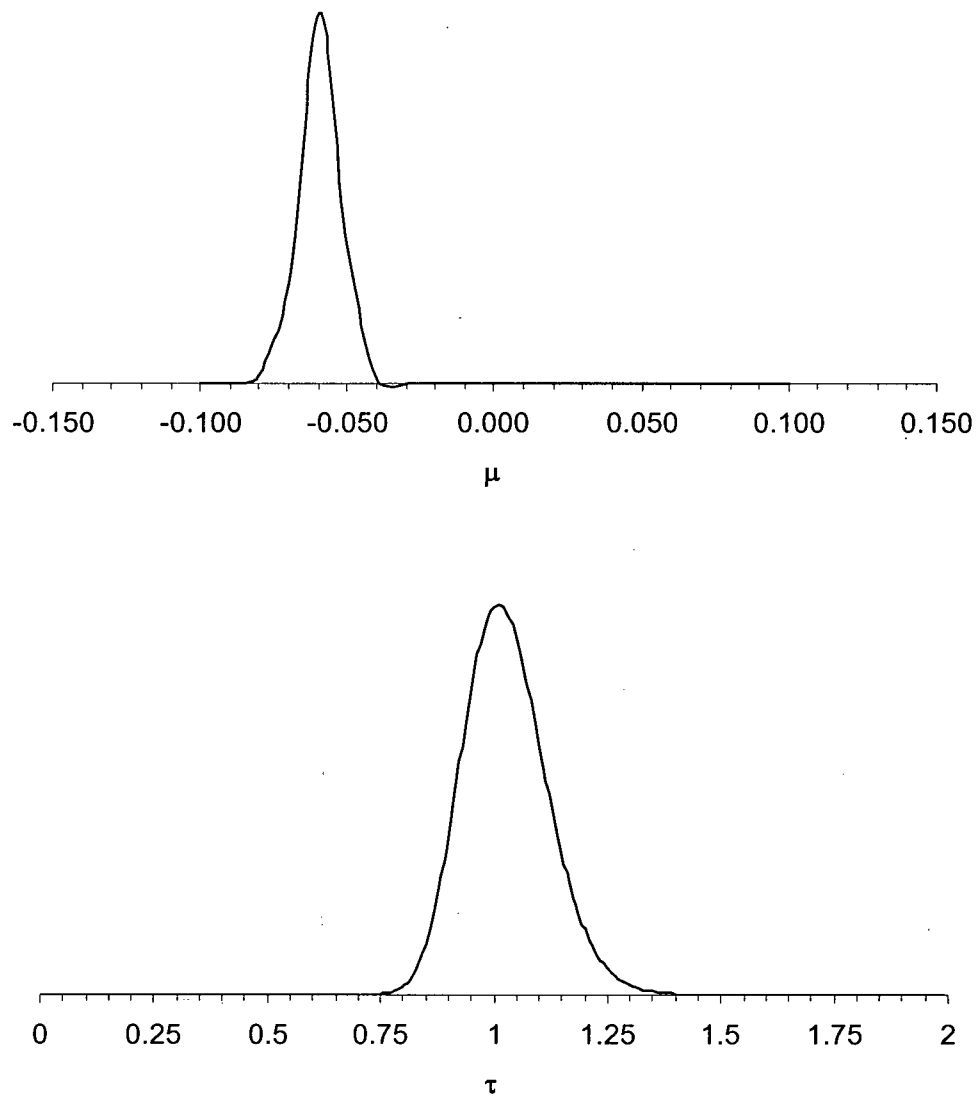
Figure 6.5. Marginal posterior distributions for the hyperparameters μ and τ of the hierarchical model. Note that the distribution of μ does not include 0 which indicates some problems with the logistic fit (see text). Posterior modes of μ and τ are –0.065 and 1.019, respectively.
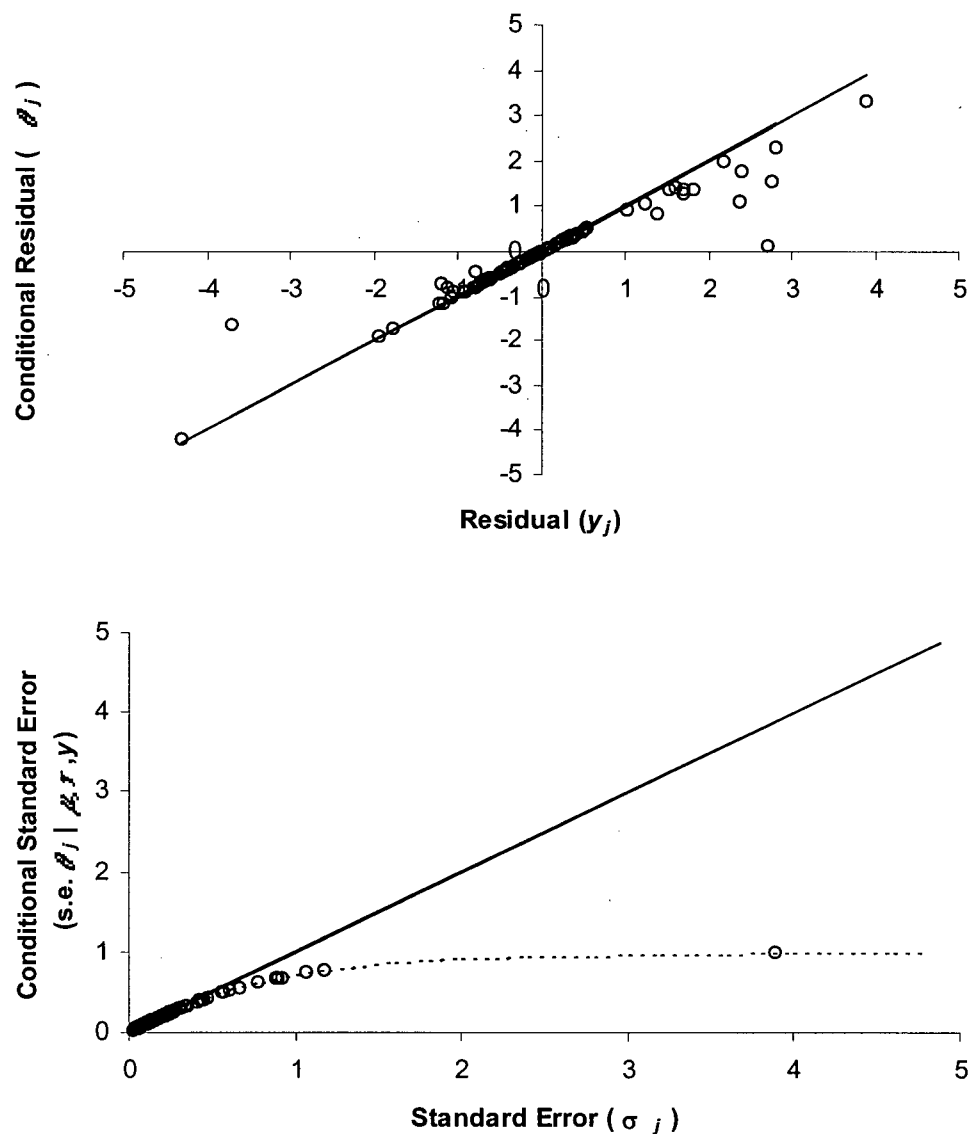
Figure 6.6. Relationships between original residual values from travel time fit and their conditional estimates after including information about the hyperparameters, μ and τ, from the hierarchical analysis. Solid lines in both panels are for 1:1 reference. Notice in the top panel how some estimates are adjusted rather strongly toward the regional value while others did not change substantially. The lower panel shows how the conditional standard errors (given μ, τ, and the data) are adjusted in proportion to imprecision of the original estimates, i.e., poor estimates adjusted more than precise ones.

The histogram of final (conditional on μ,τ,y) θ estimates shows much less variation in c_o among lakes than the raw frequencies before access-adjustment (Fig. 6.7). Conditional values are highly concentrated about $\hat{\mu}$ (S.D.= 0.75 fish ad^{-1}) which suggests that catch rates do not tend to vary substantially among lakes after access affects are removed. In fact, 95% of the estimates were within +/- 1.5 fish ad^{-1} of the mean.
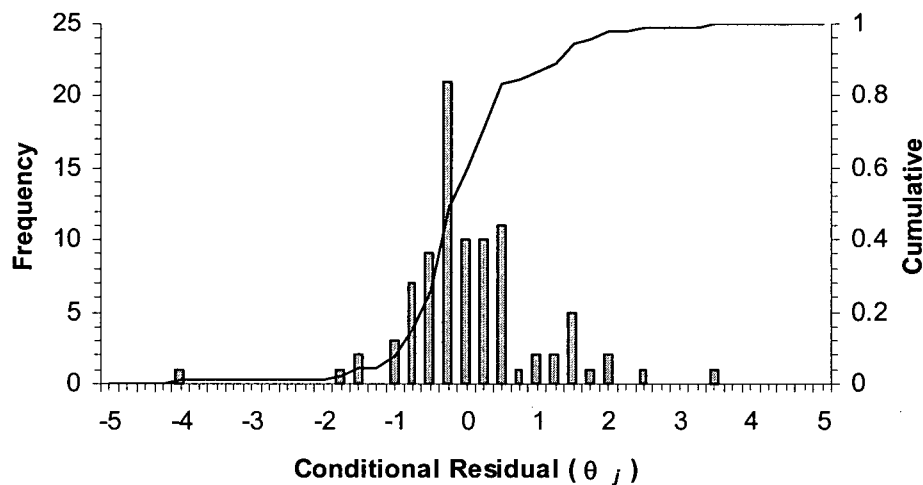
Figure 6.7. Histogram and cumulative proportion of θ for all lakes. Note how the distribution is concentrated between –0.75 and +0.75 which indicates strong similarity among lakes in catch rate after accounting for access differences.

Discussion

The purpose of this chapter was to test two of the key IFD assumptions used to derive the effort dynamics model. Effort and access model fits to observed data indicated that the first assumption -- variation in catch rates among B.C.'s southern interior lakes is primarily due to differences in access -- is not clearly violated and the data actually fit well with the general IFD predictions. After accounting for these access affects, I showed

that the second assumption -- catch rates tend to be equalized among lakes toward a B.C.-wide average -- also cannot be rejected in a strong sense because the access-adjusted estimates were highly concentrated between +/- 0.75 fish ad^{-1} of the B.C.-wide mean.

Before discussing the potential implications of the observed effort dynamics, a few caveats with the above analyses should be presented. First, the effort data for B.C.'s southern interior lakes are known to be error prone, and in some cases, estimates obtained via Tredger's (1992) method do not agree with more accurate estimates. For example, Berezay and Lirette (1997) presented results of effort surveys in Region 5 that were sometimes in disagreement (up to 100%) with SLIM effort estimates that I used. In general, the temporal pattern and scales of increases/decreases in effort were similar for the Region 5 lakes used in this study, so the differences may not have strong effects on the results. More precise effort estimates were not available for other regions, but I expect that similar discrepancies would exist. Fortunately, large errors in the Region 5 data were uncommon so the results presented here should remain valid for the most part.

A second, more obvious difficulty in a modeling attempt such as this is the use of regional constants for many important population dynamics parameters. Clearly, values for particular lakes could be much different from ant regional average. For example, a knife-edged vulnerability at age 2 ignores some of the recruitment dynamics that occurred in the study lakes (c.f. Chapter 3). This problem could be particularly acute in areas such as region 5 where a larger proportion of mixed species lakes exist compared to regions 3 and 8. The result of such errors, as well as errors in survival rates, would be to

over-estimate N_t which would introduce errors in catch rate estimates that are proportional to errors in N_t. This can be seen by rearranging the effort model prediction so that "apparent catch rate" is calculated based on predicted abundance and the observed effort

$$\tilde{c}_{o,j} = \frac{N_t u_{max}}{E_t \left(1 - \frac{u_{max}/q}{E_t} \right)} .$$

Notice that this relationship is linear in N_t so errors in catch rate estimates will be biased downward (stronger effort response) for negative biases in N_t and positively biased (weaker effort response) for overestimates of N_t. Although it is difficult to assess exactly which lakes may show these effects, E. Parkinson (pers. comm.) identified Missezula lake (region 8) as one possible candidate. This lake is large, contains coarse species of fish as well as other salmonids, and is noted for low survival of stocked rainbow trout. The catch rate estimate for that lake was well above the value predicted by its access and was subsequently removed from the analysis because it was an obvious outlier (c.f. Figure 6.4). What is surprising is how few lakes actually showed this type of behaviour; only four catch rate values out of 97 estimates appeared as outliers in the access-catch rate data. If these type of biases do exist in the remaining lakes, they are probably not large or else they tend to cancel each other out.

Finally, there is the general problem of violating perhaps many statistical assumptions in moving from lake-specific catch rate estimates to regional scale inference using the normal model. Parameter estimation results on individual lakes showed that catch rate estimates were often correlated with N_1 estimates. This would likely affect the underlying

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probability model of the catch rate estimates, so that the errors are not normally

distributed as I assumed. I originally attempted to avert this problem by using a Markov

Chain Monte Carlo (MCMC) estimation procedure that essentially maps out the posterior

distribution of each parameter in the model without making assumptions about its

functional form (Gelman et al. 1995). This would have produced an accurate

approximation of the true probability distribution of the parameter, but the procedure was

computationally intensive and required an unacceptable amount of computer time.

Preliminary results using MCMC showed that posterior distributions of N_1 were quite

broad and skewed toward lower values for some lakes, while posterior distributions of c_0

were consistently normal. The fact that c_0 estimates appeared normal is what originally

led me toward using the asymptotic results from the Levenburg-Marquardt algorithm. In

addition to these arguments, the hierarchical model structure is much simpler to work

with and understand for the normal model compared to using an approximation such as t-

distribution that I would have needed for the MCMC estimates.

Effort modeling

Probably the most interesting result that I found in this work is how a simple effort model

can capture fishery dynamics in many situations. Effort dynamics studies in commercial

fisheries settings have shown convincingly that these patterns do exist, but surprisingly,

substantial studies of recreational fisheries effort dynamics have been few. Instead,

recreational fishery modelers have tended to focus quite intensively on production-side

dynamics such as habitat improvement, stocking policies, survival, and growth, without

recognizing how these factors ultimately affect angling quality or the possibility of

sustainable fisheries. In many cases, it remains questionable whether traditional production-side management tactics ultimately affect angling quality, or simply lead to higher exploitation rates (Wilde 1997).

Access as a controlling factor for recreational fisheries

It appears from the results presented here that access from major population centers can have strong affects on the outcome of recreational fishery management policies. Yet, these affects have rarely been quantified. The broad regional analysis of access effects on angling quality shown in this chapter have some important management implications. For example, it was clear in Chapters 2 and 3 that limited-access study lakes such Rock Island and Hardcastle were able to produce higher angling quality as well as lower exploitation rates compared to open-access lakes. Making a management decision to increase road development and access to these types of lakes would likely involve a huge risk of rapid over-exploitation which would, in turn, affect the potential viability of remote resorts that rely completely on wild stocks. If such developments were allowed to occur, the chance of recovery by means of traditional production-side management prescriptions (habitat enhancement, stocking, regulation), would be minimal.

Concluding remarks and perspectives for future research

One of the major problems in recreational fisheries management is the lack of physical, biological, and sociological data needed for intensive management of individual fisheries. However, the results in Chapter 3 confirm what has become more widely known: basic biological and angler behaviour characteristics do tend to be similar among fisheries within geographical regions. The among-population data for B.C. rainbow trout are remarkably consistent, which suggests that calculating sustainable fishing effort for wild stocks should not be a difficult problem.

My results strongly suggest that direct effort control is needed where high angling quality or conservation of wild fish populations are the main objectives. But, there are at least three practical reasons why effort control policies will be difficult to implement for these objectives. First, there are few alternatives to highly intensive monitoring and enforcement necessary for direct effort control, especially in areas such as B.C.'s southern interior where hundreds of lakes are distributed over a wide geographical range. However, it is possible that anglers will effectively monitor themselves once the benefits of limited-effort become widely known. Where anglers wait a long time for high quality fishing opportunities, they will surely stand up and defend their rights in the same way as they now defend their rights to open access.

Second, as I showed in Chapter's 4 and 5, access restrictions necessary to improve the general quality of angling or protect wild-stocks may be severe. If effort control policies

are to be considered, we need to determine how displaced anglers will direct their activity following effort limitation. Will they move to other fisheries in order to maintain constant total time spent fishing? Perhaps the act of limiting fishing effort will produce higher angling quality for some anglers, so their desire to fish more (at lower quality) will be reduced, but anglers who are not fortunate to participate in limited-effort fisheries will likely shift their effort to other open-access lakes. The limited vulnerability model predicts large negative impacts of such an "effort redistribution", because increasing effort suppresses angling quality. However, the effort model I proposed uses no assumption about total (regional) angler effort. Fishing effort is predicted to be linearly proportional to initial stock size in a given lake with no explicit dependence on activity outside that lake. That is, total regional effort should act simply as the sum of effort over a set of independent lakes, and effort redistribution should not create negative impacts on open-access fisheries. This "effort redistribution" hypothesis is likely to be very important when researchers are asked to design limited-entry policies, because total fishery value depends on both regional angling quality *and* total angler activity. Managers will be in the most difficult position when faced with conflicting predictions of costs and benefits from alternative effort redistribution hypotheses, especially when distinguishing among the alternatives can only be achieved through direct experience.

The final problem with implementing effort management involves the deep sociological and political conflicts that will ultimately arise when effort controls are proposed for specific lakes. My experience with biologists and managers in B.C. clearly indicates that such conflicts are real, and are likely weighted far more heavily than any uncertainty

about effort redistribution, fish population/angling quality dynamics, or logistics of enforcement. Again, these problems can only be overcome by actually showing that effort control is indeed a better way of managing fisheries.

As effort modeling gains more acceptance within recreational fisheries management, we may see a shift away from production-side domination toward creative development of consumption-side approaches such as effort management. Such approaches are already being mentioned within management agencies, although they are generally referred to as access controls, which attempt to limit development of access factors such as boat ramps, lodging, or road building in sensitive areas. Defined in this way, access control measures are more easily sold to the public than direct attempts to limit effort as occurred in the management of hunters. It is likely that direct effort control in fisheries is a long way away, but it may be inevitable as anglers are forced to incur larger costs associated with getting better angling quality.

The full model I presented in Chapter 4 (including catch-and-release effects) can address a wide range of factors affecting angling quality and exploitation from partial retention to complete catch-and-release and from open-access to total (or seasonal) effort controls. The effects of catch-and-release, exchange processes, and effort redistribution hypotheses will probably become important as recreational fishery managers attempt to prescribe specific effort control policies for angling quality and harvest management objectives.

Catch-and-release programs are becoming more widely accepted among management and anglers in North America (c.f. contributions in Barnhart and Roelofs 1987), because it is an effective way to limit exploitation and produce higher catches from limited stocks of fish. Up to this point, there has been little progress at developing the quantitative tools to assess "optimal" effort or access in catch-and-release fisheries (Griffith 1986). The limited vulnerability/effort model can be used as a policy analysis tool in these situations as well as a guide for identifying specific areas for research. In catch-and-release fisheries, such areas will likely include assessment of multiple capture frequency on fish recovery (already underway on the Lee's Ferry reach of the Colorado River), seasonal changes in base vulnerable/invulnerable exchange rates, and effects of effort redistribution.

Development of spatially explicit models for highly valued migratory species such as steelhead (*Oncorhychus mykiss*) or striped bass (*Morone saxitalis*) may also be an important area for future research. Where these fish actively migrate up rivers or along coastlines, they are typically subject to intense fisheries along the entire route. Closing or limiting access to a few specific areas along the way may provide a means of exploitation control (by limiting vulnerability directly) as well as time to recover from previous hooking (in catch-and-release cases).

Increasing attention is being paid to the economic and social value of recreational fisheries, yet most studies have not combined fishery value with fish abundance or effort in realistic ways. Where we are able to assign a specific relationship between CPE (or

other quality measure) and value, the model described here provides explicit predictions of total fishery value associated with specific effort control policies. For example, preliminary analyses using a linear relationship between CPE and value, predicts an optimum effort that is typically much less than we observe for B.C. rainbow trout lakes. Such an approach should provide a direct way to evaluate optimal access rates where information on the value of quality can be expressed in terms of catch per effort.

Some model results may not need further research. For example, the prediction of increased exploitation on wild stocks following augmentation with hatchery fish has already been shown to occur both empirically and in models. My results, based on a model that is consistent with empirical data, provide strong evidence that such programs are likely to be harmful and should be abandoned if wild-stock recovery is a management objective.

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Appendix 1: Monthly fishery statistics for British Columbia rainbow trout lakes

Table A1. Monthly fishing effort estimates on the study lakes for 1996-1998. Total effort density is based on total lake area and shoal effort density is based on the amount of lake area that is less than 7 m deep. (-) indicates that an estimate was not possible due to lack of fishing or sampling effort.

Lake	Angler Days	Total Density (ad ha^{-1})	Shoal Density (ad ha^{-1})
		1996	
Fawn			
May	669 (37)	21.5	29.9
June	1 305 (45)	40.8	58.3
July	1 350 (55)	42.2	60.3
August	925 (49)	28.9	41.3
September	775 (48)	24.2	34.6
Total	5 044 (235)	157.6	225.2
Pillar			
May	1 013 (62)	25.3	63.3
June	1 273 (64)	31.8	79.6
July	1 018 (52)	25.4	63.6
August	698 (31)	17.4	47.6
September	568 (38)	14.2	35.5
Total	4 567 (247)	114.2	285.5
Hardcastle			
May	-	-	-
June	101	5.6	6.2
July	87	4.8	5.4
August	79	4.4	4.8
September	59	3.3	3.6
Total	326	18.1	20.1
Rock Island			
May	-	-	-
June	218	4.0	4.4
July	274	5.0	5.5
August	189	3.4	3.8
September	59	1.1	1.2
Total	740	13.4	13.8

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Table A1 (continued). Monthly fishing effort for 1997.

Lake	Angler Days	Total Density (ad ha^{-1})	Shoal Density (ad ha^{-1})
		1997	
Fawn			
May	424 (21)	13.2	16.5
June	1 433 (139)	44.8	55.9
July	847 (36)	26.4	33.1
August	738 (28)	23.0	28.8
September	730 (28)	22.8	28.5
Total	4 170 (252)	130.3	162.9
Hardcastle			
May	-	-	-
June	147	8.2	8.6
July	76	4.2	4.5
August	74	4.1	4.3
September	40	2.2	2.3
Total	337	18.7	19.7
Rock Island			
May	-	-	-
June	194	3.5	3.9
July	319	5.6	6.4
August	173	3.1	3.5
September	16	0.3	0.3
Total	700	12.7	14.1
Crystal			
May	175	3.2	6.4
June	378	6.9	13.7
July	562	10.2	20.4
August	478	8.7	17.4
September	427	7.8	15.5
Total	2020	36.7	73.4
Roche			
May	2 965 (108)	21.2	46.0
June	6 347 (188)	45.3	98.6
July	2 854 (100)	20.4	44.3
August	2 175 (82)	15.5	33.8
September	1 739 (85)	12.4	27.0
Total	16 079 (563)	114.8	249.7

Table A1 (continued). Monthly fishing effort for 1998.

Lake	Angler Days	Total Density (ad ha⁻¹)	Shoal Density (ad ha⁻¹)
		1998	
Hardcastle			
May	-	-	-
June	131	7.3	8.1
July	36	2.0	2.2
August	65	3.6	3.9
September	44	2.5	2.7
Total	276	15.3	17.0
Rock Island			
May	-	-	-
June	307	5.6	6.2
July	149	7.7	3.0
August	157	2.9	3.2
September	45	0.8	0.9
Total	657	12.0	13.3
Crystal			
May	557 (115)	10.1	20.2
June	742 (169)	13.5	27.0
July	570 (188)	10.4	20.7
August	421 (150)	7.7	15.3
September	-	-	-
Total	2 290 (622)	41.6	83.3
Roche			
May	2 906 (620)	20.8	44.9
June	4 477 (936)	32.0	69.2
July	3 181 (831)	22.7	49.2
August	1 991 (447)	14.2	30.8
September	-	-	-
Total	12 555 (2 054)	89.7	194.0
Dairy [A]			
May	457 (159)	16.0	33.4
June	651 (274)	25.7	53.5
July	415 (163)	16.5	34.5
August	31 (12)	1.5	3.2
September	-	-	-
Total	1 554 (608)	59.8	124.5
Duffy [A]			
May	200 (102)	8.8	14.6
June	141 (67)	7.4	12.3
July	198 (97)	9.3	15.6
August	27 (8)	1.4	2.4
September	-	-	-
Total	566 (274)	27.0	44.9

A - both Dairy and Duffy lakes were not fished during most of August due to a large-scale forest fire.

Table A2. Harvest per effort (HPE) and catch per effort (CPE) results from 1996 creel surveys on the study lakes. Total number of interviews (n) and the fraction of catch that is retained by anglers (Retention Rate)..

Lake	n	Sampling Rate	HPE (estimate and std. error)	CPE (estimate and std. error)
			1996	
Fawn				
May	107	0.25	0.33 (0.04)	1.21 (0.10)
June	50	0.05	0.34 (0.07)	2.65 (0.41)
July	46	0.04	0.62 (0.13)	2.81 (0.42)
August	160	0.24	0.46 (0.06)	2.09 (0.22)
September	8	0.01	-	-
Mean		0.12	0.44 (0.07)	2.19 (0.36)
Pillar				
May	72	0.10	0.96 (0.12)	2.12 (0.25)
June	209	0.24	1.54 (0.09)	2.77 (0.16)
July	211	0.31	0.91 (0.07)	1.55 (0.12)
August	90	0.24	0.58 (0.07)	1.55 (0.17)
September	58	0.15	0.84 (0.15)	1.49 (0.23)
Mean		0.21	0.97 (0.16)	1.90 (0.25)
Hardcastle				
May	-	-	-	-
June	49	> .9	3.02 (0.07)	8.22 (0.24)
July	36	> .9	2.22 (0.08)	4.40 (0.13)
August	38	> .9	2.54 (0.07)	4.54 (0.14)
September	37	> .9	2.22 (0.06)	3.86 (0.11)
Mean		> .9	2.50 (0.19)	5.26 (1.00)
Rock Island				
May	-	-	-	-
June	156	> .9	2.44 (0.05)	4.88 (0.10)
July	181	> .9	2.25 (0.05)	3.97 (0.07)
August	122	> .9	1.69 (0.04)	2.59 (0.05)
September	33	> .9	1.19 (0.06)	2.06 (0.11)
Mean		> .9	1.89 (0.28)	3.38 (0.64)

Table A2 (continued). Harvest per effort (HPE) and catch per effort (CPE) results from 1997 creel surveys

Lake	n	Sampling Rate	HPE (estimate and std. error)	CPE (estimate and std. error)
			1997	
Fawn				
May	357	0.92	0.82 (0.02)	1.80 (0.05)
June	600	0.46	0.70 (0.03)	2.03 (0.08)
July	298	0.45	0.58 (0.05)	1.02 (0.09)
August	241	0.31	0.55 (0.05)	1.13 (0.08)
September	233	0.26	0.87 (0.06)	2.67 (0.14)
Mean		0.49	0.70 (0.06)	1.73 (0.30)
Hardcastle				
May	-	.-	-	-
June	61	> .9	1.79 (0.07)	6.82 (0.22)
July	45	> .9	2.51 (0.07)	6.70 (0.24)
August	26	> .9	1.91 (0.09)	3.81 (0.16)
September	26	> .9	2.20 (0.08)	4.40 (0.17)
Mean		> .9	2.10 (0.16)	5.43 (0.78)
Rock Island				
May	-	-	-	-
June	124	> .9	1.85 (0.05)	4.63 (0.09)
July	217	> .9	2.39 (0.03)	4.14 (0.06)
August	112	> .9	2.00 (0.04)	3.61 (0.08)
September	42	> .9	1.18 (0.07)	2.74 (0.12)
Mean		> .9	1.86 (0.25)	3.78 (0.40)
Crystal				
May	36		0.57 (0.12)	1.56 (0.25)
June	48		0.90 (0.13)	1.10 (0.18)
July	94		0.46 (0.08)	1.49 (0.15)
August	87		0.75 (0.13)	1.89 (0.24)
September	66		0.57 (0.12)	1.03 (0.17)
Mean			0.65 (0.08)	1.41 (0.16)
Roche				
May	326	0.17	0.55 (0.03)	1.72 (0.12)
June	623	0.15	0.37 (0.02)	1.46 (0.07)
July	588	0.28	0.27 (0.02)	0.88 (0.05)
August	600	0.37	0.25 (0.02)	0.69 (0.04)
September	75	0.07	0.35 (0.05)	0.92 (0.14)
Mean		0.21	0.36 (0.05)	1.13 (0.19)

Table A2 (continued). Harvest per effort (HPE) and catch per effort (CPE) results from 1998 creel surveys

Lake	n	Sampling Rate	HPE (estimate and std. error)	CPE (estimate and std. error)
			1998	
Hardcastle				
May	-	-	-	-
June	52	> .9	2.14 (0.07)	7.15 (0.19)
July	16	> .9	1.92 (0.07)	4.89 (0.23)
August	32	> .9	1.88 (0.06)	3.67 (0.16)
September	32	> .9	1.67 (0.07)	3.16 (0.14)
Mean		> .9	1.90 (0.10)	4.72 (0.89)
Rock Island				
May	-	-	-	-
June	210	> .9	2.22 (0.04)	4.23 (0.08)
July	137	> .9	2.10 (0.05)	3.58 (0.09)
August	78	> .9	1.25 (0.05)	1.78 (0.07)
September	53	> .9	1.37 (0.10)	2.20 (0.14)
Mean		> .9	1.74 (0.25)	2.95 (0.57)
Crystal				
May	28	0.09	1.13 (0.21)	2.59 (0.56)
June	31	0.14	1.73 (0.19)	2.20 (0.24)
July	42	0.23	0.65 (0.10)	1.06 (0.14)
August	47	0.38	0.50 (0.07)	1.11 (0.14)
September	25	-	0.98 (0.21)	2.12 (0.36)
Mean		0.21	1.00 (0.21)	1.82 (0.31)
Roche				
May	35	0.03	0.32 (0.07)	0.96 (0.31)
June	348	0.12	0.25 (0.02)	1.30 (0.11)
July	315	0.12	0.31 (0.03)	1.05 (0.08)
August	257	0.17	0.36 (0.04)	0.90 (0.09)
September	-	-	-	-
Mean		0.11	0.31 (0.02)	1.05 (0.09)
Dairy				
May	93	0.32	0.44 (0.07)	2.29 (0.20)
June	127	0.23	1.32 (0.14)	5.14 (0.43)
July	109	0.32	0.93 (0.14)	2.22 (0.21)
August	5	-	1.06 (0.95)	1.65 (1.56)
September	-	-	-	-
Mean		0.29	0.90 (0.25)	3.22 (0.96)
Duffy				
May	95	0.54	0.44 (0.06)	0.81 (0.10)
June	60	0.33	0.50 (0.10)	1.57 (0.29)
July	69	0.41	0.46 (0.07)	0.69 (0.12)
August	10	-		0.27 (0.28)
September	-	-	-	-
Mean		0.42	0.47 (0.02)	0.84 (0.27)

Table A3. Monthly harvest and total catch statistics from 1996 creel surveys.

Lake	Harvest (estimate and std. error)	Catch (estimate and std. error)	Retention Rate
	1996		
Fawn			
May	220 (29)	809 (81)	0.27
June	443 (93)	3 458 (548)	0.13
July	837 (179)	3 793 (587)	0.22
August	425 (60)	1 933 (228)	0.22
September	-	-	-
Total	1 926 (361)	9 994 (1 444)	0.21 (0.06)
Pillar			
May	972 (135)	2 147 (285)	0.44
June	1 960 (151)	3 526 (270)	0.55
July	976 (86)	1 578 (146)	0.59
August	405 (52)	1 082 (128)	0.38
September	477 (91)	846 (142)	0.56
Total	4 741 (515)	9 180 (972)	0.50 (0.15)
Hardcastle			
May	-	-	-
June	305 (7)	830 (24)	0.37
July	193 (7)	383 (11)	0.50
August	201 (50	359 (11)	0.56
September	13 (4)	228 (60	0.57
Total	830 (23)	1 799 (53)	0.50 (0.13)
Rock Island			
May	-	-	-
June	532 (11)	1 064 (22)	0.50
July	616 (14)	1 088 (19)	0.57
August	319 (8)	490 (9)	0.67
September	70 (4)	121 (6)	0.57
Total	1 538 (36)	2 763 (57)	0.58 (0.19)

Table A3 (continued). Monthly harvest and total catch statistics from 1997 creel surveys.

Lake	Harvest (estimate and std. error)	Catch (estimate and std. error)	Retention Rate
	1997		
Fawn			
May	348 (19)	763 (43)	0.45
June	1 003 (106)	2 909 (304)	0.34
July	491 (47)	864 (85)	0.57
August	406 (40)	834 (67)	0.49
September	635 (50)	1 949 (127)	0.32
Total	2 883 (263)	7 319 (626)	0.43 (0.11)
Hardcastle			
May	-	-	-
June	263 (11)	1 003 (32)	0.26
July	191 (5)	509 (18)	0.37
August	141 (7)	282 (12)	0.50
September	88 (3)	176 (68)	0.50
Total	683 (25)	1 970 (69)	0.41 (0.08)
Rock Island			
May	-	-	-
June	359 (10)	898 (17)	0.40
July	762 (10)	1 321 (19)	0.58
August	346 (7)	625 (14)	0.55
September	19 (1)	44 (2)	0.43
Total	1 486 (27)	2 887 (52)	0.49 (0.12)
Crystal			
May	100 (21)	273 (44)	0.36
June	340 (49)	416 (68)	0.82
July	259 (45)	837 (84)	0.31
August	358 (62)	903 (115)	0.40
September	243 (51)	440 (73)	0.56
Total	1 300 (228)	2 869 (383)	0.49 (0.11)
Roche			
May	1 631 (107)	5 100 (401)	0.32
June	2 348 (145)	9 667 (522)	0.25
July	799 (64)	2 511 (168)	0.30
August	544 (48)	1 501 (104)	0.37
September	609 (92)	1 600 (256)	0.38
Total	5 931 (455)	19 979 (1 451)	0.32 (0.10)

Table A3 (continued). Monthly harvest and total catch statistics from 1998 creel surveys.

Lake	Harvest (estimate and std. error)	Catch (estimate and std. error)	Retention Rate
		1998	
Hardcastle			
May	-	-	-
June	280 (9)	934 (25)	0.30
July	69 (3)	176 (8)	0.39
August	122 (4)	238 (10)	0.51
September	73 (3)	139 (6)	0.53
Total	545 (19)	1 490 (50)	0.43 (0.10)
Rock Island			
May	-	-	-
June	682 (12)	1 299 (25)	0.52
July	313 (7)	533 (13)	0.59
August	196 (8)	179 (11)	0.70
September	62 (4)	99 (6)	0.62
Total	1 252 (32)	2 210 (55)	0.61 (0.20)
Crystal			
May	629 (175)	1 443 (431)	0.38
June	1 284 (325)	1 632 (412)	0.79
July	371 (135)	604 (215)	0.61
August	211 (80)	467 (177)	0.45
September	-	-	0.46
Total	2 494 (715)	4 146 (1 235)	0.54 (0.21)
Roche			
May	930 (284)	2 790 (1080)	0.33
June	1 119 (250)	5 820 (1313)	0.19
July	986 (275)	3 340 (909)	0.29
August	717 (179)	1 792 (440)	0.40
September	-	-	-
Total	3 752 (999)	13 742 (3 742)	0.30 (0.05)
Dairy			
May	201 (77)	1 047 (375)	0.19
June	859 (373)	3 346 (1 436)	0.26
July	3 86 (162)	921 (372)	0.42
August	33 (32)	51 (52)	0.64
September	-	-	-
Total	1 479 (644)	5 365 (2 236)	0.29 (0.16)
Duffy			
May	88 (46)	162 (85)	0.55
June	71 (36)	221 (113)	0.32
July	91 (47)	137 (71)	0.67
August	-	7 (8)	0.00
September	-	-	-
Total	250 (130)	527 (227)	0.51 (0.20)

Appendix 2: Analytical solution to the model equations for total catch and fishing effort as a function of initial stock size using the ideal free distribution assumption that anglers attempt to equalize CPE among lakes.

In this section, I derive the equations for total catch and effort as a function of initial stock size. The starting point I use here is the relationship between stock size and instantaneous fishing effort assuming the IFD applies. Assuming that anglers attempt to maintain the CPE on any lake at to some regional, access class, or lake-specific average CPE is equivalent to assuming that CPE will remain constant during the fishing season, and effort will vary so that CPE $= c_0$ at all times. If this holds, then the effort at any moment can be expressed as

$$e = \frac{v_1 N}{c_o} - \frac{(v_1 + v_2)}{q} \qquad\qquad \text{A2.1}$$

I suppress the time subscripts for most of the derivation to avoid notational clutter, except for seasonal totals where I use the subscript, T to denote the full length of the fishing season. Since CPE will remain constant, total effort for the season can be written as

$$E_T = \frac{C_T}{c_o} \qquad\qquad \text{A2.2}$$

where C_T is the total annual catch. Assuming that fishing mortality is the sole source of population change, the total catch is obtained by integrating the differential equation

$$dN / dt = -c_o e \qquad\qquad \text{A2.3}$$

over the season. Substituting (A2.1) for e and multiplying by c_0 gives the expression for population change as a function of the current population, N, and time, t

$$dN / dt = -v_1(N - N_\infty)$$ A2.4

where $N_\infty = c_0(v_1 + v_2)/q$ is a constant that represents a minimum population size to give c_0 when effort is low. Separating variables in (A2.4) gives

$$dN /(N - N_\infty) = -v_1 dt$$ A2.5

Integrating both sides

$$\int dN /(N - N_\infty) = \int -v_1 dt$$

A2.6.

$$\ln(N - N_\infty) + C_1 = -v_1 T + C_2$$

C_1 and C_2 can be combined into a single integration constant $C = C_2 - C_1$. Exponentiating both sides and solving for N

$$N(t) = C * e^{-v_1 T} + N_\infty$$ A2.7

where $C^* = e^C$. Evaluating C^* at $t = 0$ gives

$$C^* = N_0 - N_\infty$$ A2.8.

Now, since the total annual catch is

$$C_T = N_0 - N_T$$ A2.9

equation (A2.7) is solved at $t = 0$ and $t = T$ giving

$$N_0 = C * + N_\infty$$
$$N(T) = C * e^{-v_1 T} + N_\infty$$ A2.10.

Now the catch equation (A2.9) becomes

$$C_T = (N_0 - N_\infty)(1 - e^{-v_1 T})$$ A2.11

which, when substituted into (A2.2) gives the total annual effort as

$$E_T = \frac{(N_0 - N_\infty)(1 - e^{-v_1 T})}{c_o}$$ A2.12.

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Appendix 3: Derivation of the Jacobian matrix for the effort dynamics model.

Non-linear estimation of effort model parameters requires a Jacobian matrix, J, whose elements, J_{ij} represent the sensitivity, i.e.,partial derivative, of the ith predicted data point with respect to the jth parameter value. In this section, I derive these sensitivities analytically using partial derivatives of the model equations with respect to the parameters c_o and N_0. The necessary equations are (*i.*) total effort equation written as a function of fish abundance in year t

$$E_t = \frac{(N_t - c_o/q)u_{max}}{c_o} \qquad \text{A3.1}$$

and (*ii.*) fish abundance at time t written as a function of past abundance, N_{t-1}

$$N_t = s_a N_{t-1}(1 - U_{t-1}) + s_j S_{t-1} \qquad \text{A3.2}$$

This equation can be rewritten exclusively in terms of N_{t-1}, S_{t-1} and constant terms by first noting that the exploitation rate, U_{t-1} can be rewritten as $c_o E_t/N_t$. Substituting A3.1 for E_t and expanding the density dependent survival term, s_j, yields

$$N_t = s_a N_{t-1}\left(1 - \frac{(N_{t-1} - c_o/q)u_{max}}{N_{t-1}}\right) + \frac{S_{t-1}s_{max}}{1 + s_1 N_{t-1}} \qquad \text{A3.3.}$$

The sensitivities are then derived by taking partial derivatives of A3.1 and A3.3 with respect to the parameters

$$\frac{\delta E_t}{\delta c_o} = \frac{\delta E_t}{\delta c_o} + \frac{\delta E_t}{\delta N_t}\frac{dN_t}{dc_o} \qquad \text{A3.4}$$

and

$$\frac{\delta E}{\delta N_0} = \frac{\delta E_t}{\delta N_0} + \frac{\delta Et}{\delta N_t}\frac{dN_t}{dN_0}$$

A3.5.

The first two terms on the right hand side of A3.4 are, respectively

$$\frac{\delta E_t}{\delta c_o} = \frac{-u_{max}}{c_o q} - \frac{(N_t - c_o/q)u_{max}}{c_o^2}$$

A3.6

$$\frac{\delta E_t}{\delta N_t} = \frac{u_{max}}{c_o}$$

A3.7

and the last term dN_t/dc_o requires taking the partial derivative

$$\frac{\delta N_t}{\delta c_o} = \frac{\delta N_t}{\delta c_o} + \frac{\delta N_t}{\delta N_{t-1}}\frac{dN_{t-1}}{dc_o}$$

A3.8

where $\delta N_t/\delta N_{t-1}$ is

$$\frac{\delta N_t}{\delta N_{t-1}} = s_a(1 - u_{max}) - \frac{s_{max}s_1 S_{t-1}}{(1 + s_1 N_{t-1})^2}$$

A3.9.

The result for A3.8 is

$$\frac{\delta N_t}{\delta c_o} = \frac{s_a u_{max}}{q} + s_a(1 - u_{max})\frac{dN_{t-1}}{dc_o} - \frac{s_1 s_{max} S_t}{(1 + s_1 N_{t-1})^2}\frac{dN_{t-1}}{dc_o}$$

A3.10.

Note that A3.10 is recursive in dN_{t-1}/dc_o: dN_1/dc_o is calculated for the first data point and the result is then used to calculate dN_2/dc_o which is used to calculate dN_3/dc_o and so forth (Walters 1986).

Equation A3.5 is solved in a similar fashion where the last term on the right hand side, dN_t/dN_1 is

$$\frac{dN_t}{dN_1} = \frac{\delta N_t}{\delta N_{t-1}}\frac{dN_{t-1}}{dN_1}$$

A3.11

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where the recursion in dN_{t-1}/dN_1 causes a linear damping effect of N_1 on future effort predictions; that is, model predictions become less sensitive to N_1 as we move away from the first few data points and the degree of damping effects will be related to the choice of constant terms, i.e., adult survival, s_a, u_{max}, s_{max}, in A3.9. Because $N_t = N_1$ for $t = 1$, we have the following condition for solving A3.4 and A3.5 over time: for $t=1$,

$$\frac{\delta E_1}{\delta c_o} = \frac{\delta E_1}{\delta c_o} + \frac{\delta E_1}{\delta N_t} \cdot 0 = \frac{\delta E_1}{\delta c_o}$$

$$\frac{\delta E_1}{\delta N_1} = \frac{\delta E_1}{\delta N_1} \cdot 1 = \frac{\delta E_1}{\delta N_1}$$

(i.e., c_o has no effect on N_1 and $dN_1/dN_1=1$) and for $t > 1$ equations A3.4 and A3.5 are applied directly. The resulting Jacobian is

$$\mathbf{J} = \begin{bmatrix} \dfrac{\delta E_1}{\delta c_o} & \dfrac{\delta E_1}{\delta N_1} \\ \dfrac{\delta E_2}{\delta c_o} & \dfrac{\delta E_2}{\delta N_1} \\ \cdot & \cdot \cdot \\ \cdot & \cdot \\ \cdot & \cdot \\ \dfrac{\delta E_n}{\delta c_o} & \dfrac{\delta E_n}{\delta N_1} \end{bmatrix}.$$

Appendix 4. Derivation of the joint posterior distribution for the hierarchical model parameters

The purpose of this section is to show the sequence of derivations required to construct the joint posterior distribution $p(\theta,\mu,\tau \mid y)$ required for the hierarchical analysis. For the Gaussian or normal model, the analytical formulae are relatively simple, so it is easy to see where the hierarchical analysis is more powerful compared to typical analysis of variance methods, when results from multiple studies are combined.

Constructing the joint prior distribution of all parameters

If we consider each of the J values y_j as estimates of the true lake-specific parameters, θ_j, with sampling variances, σ^2_j, then a sampling distribution for each y_j can be written as

$$y_j \mid \theta_j \approx N(\theta_j, \sigma^2_j).$$

If we assume further that the θ_j's are just a random sample from a normal population distribution with hyperparameters μ and τ, then the joint likelihood of all θ_j's can be written as

$$p(\theta_1,...\theta_J \mid \mu,\tau) = \prod_{j=1}^{J} N(\theta_j \mid \mu,\tau)$$

which gives the joint prior distribution

$$p(\theta_1,...\theta_J) = \int \prod_{j=1}^{J}[N(\theta_j \mid \mu,\tau^2)]p(\mu,\tau)d(\mu,\tau).$$

That is, the θ_j's are considered conditionally independent in their priors given (μ,τ).

Because the data are typically informative about (μ,τ) I assigned a uninformative uniform hyperprior on μ given τ, as

$$p(\mu,\tau) = p(\mu \mid \tau)p(\tau) \propto p(\tau)$$

where $p(\tau) = 1$.

The joint posterior distribution

Combining the sampling distribution of the y_j's and the prior distribution gives the joint posterior of all parameters as

$$p(\theta,\mu,\tau \mid y) \propto p(\mu,\tau)p(\theta \mid \mu,\tau)p(y \mid \theta)$$

$$\propto p(\mu,\tau)\prod_{j=1}^{J} N(\theta_j \mid \mu,\tau^2)\prod_{j=1}^{J} N(y_j \mid \theta_j,\sigma^2_j).$$

Conditional posterior distribution of θ given the hyperparameters

Conditional on the hyperparameters, there are have J independent normal estimates

$$\theta_j \mid \mu,\tau,y \approx N(\hat{\theta}_j,V_j)$$

which have immediate closed form solutions if μ, τ, and y are fixed. For example, treating the normal models for each θ_j separately gives

$$p(\theta \mid \mu,\tau,y) \propto \exp\left(-\frac{1}{2}\left[\frac{(y_j-\theta_j)^2}{\sigma^2_j} - \frac{(\theta_j-\mu)^2}{\tau^2}\right]\right).$$

Expanding exponents, collecting terms and then completing the square in θ_j results in the marginal posterior of θ_j

$$p(\theta \mid \mu,\tau,y) \propto \exp\left(-\frac{1}{2\tau^2_1}(\theta_j - \hat{\theta}_j)\right)$$

where

$$\hat{\theta}_j = \frac{\frac{1}{\sigma^2_j}y_j + \frac{1}{\tau^2}\mu}{\frac{1}{\sigma^2_j} + \frac{1}{\tau^2}} \quad \text{and} \quad V_j = \frac{1}{\frac{1}{\sigma^2_j} + \frac{1}{\tau^2}} \qquad \text{A4.1}$$

This result has the intuitive appeal that each $\hat{\theta}_j$ is actually a precision-weighted average

of the observed data, y_j, and the B.C.-wide average, or hyperparameter μ. Thus, y_j values

that are relatively precise receive greater weight in estimating θ. Imprecise y_j values

receive lower weight, but will tend to "borrow strength" from more precise y_j values

through the hyperparameters μ and τ. The conditional variance of θ, V_j, behaves in a

similar way: the value of V will be approximately equal to σ^2 when σ^2 is low, and V

approaches τ asymptotically as σ^2 increases (precision decreasing).

Marginal posterior of the hyperparameters, (μ,τ)

The model as specified up to this point remains incomplete because it depends on the

unknown parameters μ and τ. Here, the hierarchical model structure is used to average

over θ and just consider information supplied by the data, y_j about μ and τ. The marginal

distributions of the lake-specific estimates, y_j, averaging over θ are independent normal

$$y_j \mid \mu,\tau \approx N(\mu,\sigma^2_j + \tau^2)$$

so the marginal posterior density $p(\mu,\tau \mid y)$ is

$$p(\mu,\tau \mid y) \propto p(\mu,\tau)\prod_{j=1}^{J} N(y_j \mid \mu,\sigma^2_j + \tau^2) \qquad \text{A4.2.}$$

Factoring this result into

$$p(\mu,\tau \mid y) = p(\mu \mid \tau, y)p(\tau \mid y) \qquad\qquad \text{A4.3}$$

provides the advantage of a closed form solution for μ and leaves only a simple

computation of $p(\tau \mid y)$. With τ assumed known, A4.2 is quadratic in μ so the mean and

variance can be obtained immediately by considering the lake-specific estimates, y_j as J

independent estimates of μ with variances equal to $(\sigma^2_j + \tau^2)$. Combining a uniform prior

density $p(\mu \mid \tau)$ with the data gives

$$\mu \mid \tau, y \approx N(\hat{\mu}, V_\mu) \qquad\qquad \text{A4.4}$$

where, following the derivation for A4.1 above, $\hat{\mu}$ is just the precision weighted average

of the lake-specific estimates and V_μ is the total precision

$$\hat{\mu} = \frac{\sum_{j=1}^{J} \frac{1}{\sigma^2_j + \tau^2} y_j}{\sum_{j=1}^{J} \frac{1}{\sigma^2_j + \tau^2}} \qquad \text{and} \qquad V_\mu^{-1} = \sum_{j=1}^{J} \frac{1}{\sigma^2_j + \tau^2} \qquad \text{A4.5.}$$

That is, the estimates of $\hat{\mu}$ V_μ will depend more strongly on the more precise values of y.

Completing the model requires a posterior distribution for τ, $p(\tau \mid y)$, that depends only

on the data, y. The posterior distribution of τ is obtained analytically by rearranging A4.3

and substituting A4.2 and A4.4 for the numerator and denominator, respectively

$$p(\tau \mid y) = \frac{p(\mu,\tau \mid y)}{p(\mu \mid \tau, y)}$$

$$\propto \frac{p(\tau)\prod_{j=1}^{J} N(y_j \mid \mu, \sigma^2_j + \tau^2)}{N(\mu \mid \hat{\mu}, V_\mu)}.$$

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This expression must hold for all values of μ which it does this if μ is set to $\hat{\mu}$ (Gelman et al. 1994) giving

$$p(\tau \mid y) \propto p(\tau)V_{\mu}^{1/2}\prod_{j=1}^{J}(\sigma_j^2 + \tau^2)^{-1/2} \exp\left(-\frac{(y_j - \hat{\mu})^2}{2(\sigma_j^2 + \tau^2)}\right) \qquad A4.6$$

where $\hat{\mu}$ and V_{μ} are defined as above and the prior $p(\tau) = 1$. The model is now completely specified.

Appendix 5. Solutions to the full limited vulnerability/effort model.

Solving the full model described in Chapter 4 provides predictions of total effort and exploitation while accounting for the effects of partial retention and behavioural changes that may follow catch-and-release. The purpose of this section is to show how partial retention may affect interpretations of asymptotic fishing mortality rates observed on the study lakes. Specifically, partial retention may only explain the observed asymptotic fishing mortality if released fish remain invulnerable to capture during the same fishing season. The sequence of steps leading up to the full solution for total effort are similar to those described in Chapter 4 and Appendix 2, so I do not provide any additional background on the necessary assumptions.

Ignoring natural mortality within the fishing season, the system of ordinary differential equations describing the exchange process between available, unavailable, and refractory states is

$$dV / dt = v_1(N - V - R) - v_2 V - qeV$$
$$dR / dt = (1 - r)qeV - v_3 R$$
$$d(N - V - R) / dt = -v_1(N - V - R) + v_3 R + v_2 V .$$

Proceeding under the assumption that V_t rapidly reaches equilibrium with respect to unavailable fish density ($N_t - R_t$), the short-term equilibrium density of available fish is

$$V_t = \frac{v_1 (N_t - R_t)}{v_1 + v_2 + qe_t}$$

which gives the expected catch rate as

$$c_t = qV_t = \frac{qv_1 (N_t - R_t)}{v_1 + v_2 + qe_t}$$

Applying the "no lake stands out" catch rate $c_t = c_0$ gives the instantaneous effort prediction (compare to Eq. 4.5)

$$e_t = \frac{v_1}{c_o}\left(N_t - R_t\right) - \frac{v_1 + v_2}{q}.$$

Now, total fish density N and the density of fish in a refractory state R will change with retention and recovery as

$$\frac{dN_t}{dt} = -rc_o e_t$$

$$\frac{dR_t}{dt} = (1-r)c_o e_t - v_3 R_t.$$

Solving these equations over time (MapleV Release 5.0) gives the predicted total (N_t) and refractory (R_t) fish densities at time t as

$$N_t = N_\infty + \frac{\left(N_0 - N_\infty\right)}{F_0}\left[\left(v_1 r - F_1\right)e^{-F_2 t} - \left(v_1 r - F_2\right)e^{-F_1 t}\right]$$

and

$$R_t = \frac{v_1(r-1)}{F_0}\left[e^{-F_2 t} - e^{-F_1 t}\right]\left(N_0 - N_\infty\right)$$

where the fishing rate factors F are functions of the form

$$F_0 = \sqrt{v_1^2 + 2v_1 v_3 + v_3^2 - 4v_1 v_3 r}$$

$$F_1 = \frac{1}{2}\left(v_1 + v_3 - F_0\right)$$

$$F_2 = \frac{1}{2}\left(v_1 + v_3 + F_0\right).$$

The solution for effort at time t is then

$$E_t = \frac{N_0 - N_t}{c_o r}.$$

Note that the effort prediction now includes a direct non-linear retention rate effect; as r decreases toward zero (full catch-and-release), effort is predicted to increase at an accelerating rate. This increase is then mediated by the implicit dependence of N_t on the recovery rate v_3 following catch-and-release. When v_3 is high, "recycling" of fish caught and released is rapid and effort increases at the maximum rate with decreases in r, and as v_3 approaches zero, the effect of r is eliminated from the effort prediction. Setting $v_3 = 0$ in the F calculations above, the model for total seasonal effort collapses to the model described in Chapter 4 which is

$$E_T = \frac{N_0 - N_\infty}{c_o}\left(1 - e^{-v_1 T}\right).$$

However, the effect of r is retained for predicted exploitation. When v_3 is approximately equal to zero, the exploitation rate U is of the form

$$U = r\left(1 - e^{-v_1 T}\right)\left(1 + \frac{N_\infty}{N_0}\right) \qquad\qquad \text{A5.1.}$$

If v_1 is high (all fish available at any moment), this model predicts an asymptotic exploitation rate equal to r when fish do not re-enter the available pool following release ($v_3 = 0$). This retention rate effect combined with a fully available stock could potentially explain the asymptotic exploitation rate that I observed on the study lakes (c.f., Chapter 4; Fig. 4.8). There are two reasons why partial retention and full availability are not sufficient to explain the observed asymptotic fishing mortality. First, v_3 cannot be equal to zero because fish that I captured and marked using angling methods were then recaptured by anglers during the same season, sometimes in large numbers. Second, the

apparent density-dependent catchability relationship that I observed on the study lakes indicates that all fish are not fully vulnerable at any moment. Thus, asymptotic fishing mortality may be greater than r, but will always be less than the predicted maximum rate $1 - e^{-v_1 T}$ when $r < 1$. The ultimate effect that r will have on asymptotic exploitation depends on the magnitude of exchange parameters v_1 and v_2, as well as the recovery rate v_3.