Linking Visual Foraging with Temporal Prey Distributions to model Trophic Interactions in Lake Washington

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University of Washington

Abstract

Linking Visual Foraging with Temporal Prey Distributions to model Trophic Interactions in Lake Washington

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Piscivory is often attributed with structuring aquatic fish communities both through direct effects of prey consumption and indirect effects associated with altered prey behavior. However, this assumption is generally made with little understanding of the foraging mechanisms that are mediating piscivore and prey fish interactions at the level of individuals. Because most pelagic piscivores and prey fishes are highly mobile and hunt visually, ambient photic conditions and the spatial-temporal distributions of predators and prey influence interactions. In this study I use a bioenergetically-based food web model to identify the timing and relative strengths of predatory interactions in the fish community. Once important predator-prey interactions are identified, I explore and compare the visual foraging abilities of top salmonine predatory fishes and develop mathematical relationships that describe how piscivorous fishes respond to alterations in their visual environment. Cutthroat trout and prey fish distributions are combined using the developed foraging model to estimate the consumption of piscivorous-size cutthroat trout in Lake Washington. Piscivory was predicted to be most intense during nocturnal and crepuscular periods at depth of 5-10 m in all seasons except summer when piscivory peaked below the thermocline at 15 m. Field measures of horizontal and vertical prey fish distributions were then combined in a spatially-explicit model that uses the foraging ability of predators and their species-specific bioenergetics relationship to estimate growth potential and predation pressure. Simulations indicated that the volume of positive growth habitat was limited to less than 3% of the lake volume during spring and summer of 2002. During fall 2002, recruitment of an abundant year class of longfin smelt to a vulnerable size increased the availability of positive growth habitat to 15% of the lake volume, and this increased availability persisted through fall 2003. Changes in growth potential for cutthroat trout were consistent with annual changes in growth estimated from scale analysis of captured fish and seasonal changes in condition factor. These results emphasize the importance of integrating optical conditions into models of growth for visual feeding fishes and further support the utility of these models for assessing the availability of growth habitat.

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INTRODUCTION

Management of fish populations can be enhanced through examination of food webs and consideration of the community as a whole (Polis and Winemiller 1996; He and Kitchell 1990; Baldwin et al. 2000). Effective management requires knowledge of how food web interactions are influenced by environmental change or human induced perturbations. By quantifying interactions in a food web through time and space, we can identify potential ecological bottlenecks for specific species that might result from limited food supply, competition, predation, or adverse environmental conditions. The food web modeling approach provides a tool to aid managers and researchers in understanding community wide dynamics.

Individuals and species exhibit size-structured interactions that vary spatially and temporally in aquatic food webs (Paine 1966, 1988; Persson et al. 2000). Predation is often directly responsible for the decline or demise of a species (Foerster and Ricker 1941; Zaret and Paine 1974; Griffith 1988; Robinson and Tonn 1989; He and Kitchell 1990; He and Wright 1992). However, indirect effects within a community often have more profound impacts on prey populations (Gliwicz 1994; Brown 1999; Grand and Dill 1999). Examining how individuals interact both directly and indirectly in a food web fosters deeper understanding of how predators influence the structure and function of whole communities.

However, the assumption that predation is capable of structuring fish communities is generally made with little knowledge of the foraging mechanisms that mediate piscivore and prey fish interactions. Knowledge of the mechanisms that structure predator-prey interaction at the level of the individual can help explain community level dynamics (Aksnes et al. 2004). Attempts to apply individual level process across scales to population and community level dynamics have proven to be problematic (Gurney et al. 1995).

Predator-prey interactions in pelagic communities of temperate lakes are characterized by mobile predators and prey that interact visually in a 3 dimensional environment structured by depth gradients in light, temperature, and water chemistry. The mobility of predators and prey result in dynamic seasonal and diel distribution patterns. Because they interact visually, the availability of light often influences fish distributions and foraging behavior. The influence of light on the availability of refuge space structures food webs in many deep pelagic systems through its influence on the prey detection and capture capabilities of predators (Aksnes et al. 2004).

A pelagic predator's ability to successfully encounter, attack, and consume prey depends more on their spatial-temporal overlap, ambient environmental constraints such as light, turbidity, or temperature, and size-dependent vulnerability than on absolute prey abundance. Total prey abundance should be less relevant to the growth of predators than the available or vulnerable fraction of the prey population. Lower densities of prey in some systems could be more vulnerable if spatial-temporal overlap was greater or detection was less constrained. Furthermore, predator-prey models that ignore the effects of behavioral responses, which influence prey vulnerability, produce predictions that deviate markedly from empirical estimates (Brown et al. 1999). Spatially and temporally explicit foraging models can potentially predict how the same abundance of prey could translate into very different consumption rates and growth potentials for predators, given different temporal-spatial distribution patterns or changing environmental conditions. The ability to quantify and predict changes in predation pressure on key prey (e.g. juvenile salmon) or to estimate the carrying capacity of a dynamic environment for top predators is essential for making informed decisions in fisheries management.

Concerns over reductions in juvenile sockeye salmon production in the Lake Washington basin beginning in the early 1980's (Fresh 1994) and the recent listing of chinook salmon under the Endangered Species Act have emphasized the need to identify the factors contributing to the regulation of these stocks. The decline in fish stocks has prompted concerns over the general quality of the lake as a rearing environment and how the growing urbanization in the basin is affecting fish populations and lake transparency. There is a need for developing a process that enables us to understand the current structure and function of this ecosystem and that provides a tool for predicting how different species will respond to changes in environmental conditions or to management manipulations. In complex systems like Lake Washington, examinations of interactions between pairs of species often miss the most important processes that regulate species. A food web approach provides a framework to identify the biotic and abiotic components that are most relevant to the regulation of fish populations of interest and offers the needed structure for identifying possible management solutions.

Historical Background

Lake Washington has undergone a series of perturbations over the past 50 years which have significantly altered the distribution, structure, and trophic dynamics of the limnetic community. Secondary sewage input from expanding urbanization caused the eutrophication of the lake (Edmondson et al. 1956). Lake transparency decreased from the historical average Secchi disk depth of 3.4 m in 1950 to 1.0 m in 1963, and *Oscillatoria rubescens*, a filamentous blue-green algae commonly associated with eutrophication, appeared (Edmondson et al. 1956). Secondary sewage diversion from the lake began in 1963, and was completed by 1968. Lake transparency was restored to the historical average of 3.4 m in 1970 and remained there through 1975. Thus, it was thought that the lake had recovered from eutrophication and had returned to its original trophic equilibrium (Edmondson and Lehman 1981).

However, *Daphnia* appeared in 1972, became the dominant zooplankter in the lake by 1976, and lake transparency doubled (Secchi depth now averaged 7.0 m) in response to the population explosion of this highly efficient grazer (Edmondson and Litt 1982). *Daphnia* only became established after the decline of *Oscillatoria rubescens* and *Neomysis mercedis*, two species that inhibited the survival of *Daphnia* in the lake. *Oscillatoria rubescens* is a cyanobacteria whose filamentous structure disrupted the feeding process of *Daphnia* (Infante and Abella 1985). *Oscillatoria rubescens* disappeared as eutrophication was reversed. *Neomysis mercedis*, a predatory mysid that feeds selectively on *Daphnia* (Murtaugh 1981), both declined in abundance and shifted to a deeper vertical distribution (Eggers et al. 1978). With improved lake transparency, *Neomysis* no longer occupied the upper water column during daylight as it had before the secondary sewage diversion, and its nocturnal distribution shifted from 16 m in 1962 to 20 m in 1975 (Eggers et al. 1978). Thus, a refuge became available in the upper water column, and the density of *Daphnia* became 2-10 times greater in the 0-10 m stratum than in the 10-20 m stratum (Edmondson and Litt 1982).

During the lake's recovery from eutrophication, the planktivorous fish community (longfin smelt *Spirinchus thaleichthys*, juvenile sockeye salmon *Oncorhynchus nerka*, and three-spine stickleback *Gasterosteus aculeatus*) consumed less than 2% of the annual zooplankton production, whereas the *Neomysis* population ate over twice that amount (Eggers et al. 1978).

The major limnetic and bentho-littoral piscivore in the lake during recovery from eutrophication was the northern pikeminnow (*Ptychocheilus oregonensis)*. This predator annually consumed an estimated 30% of the juvenile sockeye salmon production and a slightly lesser quantity of longfin smelt (Eggers et al. 1978). The native predator, cutthroat trout (*Oncorhynchus clarki),* was notably absent from Eggers et al. (1978) discussion of the important species in the Lake Washington food web.

The present Lake Washington food web consists of a complex community of temporally and spatially variable prey fish populations intermixed with a relatively more stable predatory fish assemblage. Wydoski (1972) found 29 resident and semi resident fish species in Lake Washington alone. Of these fish species the seven most abundant were: Prickly sculpin *Cottus asper*, juvenile sockeye salmon, peamouth *Mylocheilus caurinus*, northern pikeminnow, yellow perch *Perca flavescens*, longfin smelt, three-spine stickleback, and largescale sucker *Catostomus machrocheilus.* Longfin smelt are a key prey species in Lake Washington (Beauchamp 1990; 1994; Beauchamp et al 1992) and vary in abundance by 5 – 15 times between high abundant even-numbered year classes and low abundant odd year classes (Moulton 1974; Chigbu et al. 1998). Whereas the top predators northern pikeminnow, cutthroat trout, smallmouth bass (*Micropterus dolomieui*), and rainbow trout (*Oncorhynchus mykiss*) appear to exhibit relatively stable densities among years. Recent increases in cutthroat trout densities in the lake above levels observed by Wydoski (1972) and their role as a native top predator in this system have prompted concerns over their potential impact on the community in general (Fresh 1994, Nowak 2000). Understanding the dynamic structure and function of multiple predators and the highly variable alternate prey resources in Lake Washington requires a broad ecological perspective that can then be related to species of interest for management and research purposes.

Long term analysis of the limnological aspects of Lake Washington combined with more than fifty years of directed fisheries research provides the framework for a food web analysis. Fisheries research during the 1960's and 1970's focused on the large population increases in longfin smelt (Dryfoos 1965; Moulton 1975) and sockeye salmon (Woodey 1972). Focus shifted during the 1980's to include elements of the trout complex, notably studies concerning the rainbow trout (Beauchamp 1990; Warner and Quinn 1995). Major emphasis was directed towards sockeye salmon research throughout the 1990's with an increased emphasis on chinook salmon in the last half of the decade.

Recent research has focused on the important questions surrounding the distribution, movement, and foraging ecology of the diverse predator population in Lake Washington. Smallmouth bass (Fayram 1996), northern pikeminnow (Brocksmith 1999), cutthroat trout (Nowak 2000), and prickly sculpin (Tabor et al 1998) were all investigated within the last decade to determine the impacts that each predator population exert on juvenile salmonids. The recent diet and distribution data for predators, combined with the directed sampling needed to complete a mechanistic food web analysis, will provide an effective tool for determining and understanding bottlenecks influencing the population dynamics of species of interest including sockeye salmon, kokanee, longfin smelt and ESA listed chinook salmon in the Lake Washington drainage.

Study design

In this study I examined interactions among the upper trophic levels in the Lake Washington food web to determine the relative importance of predation as both a direct and indirect structuring force among the primary piscivores and planktivores in the fish community with an emphasis on how these factors affect production of salmonids. I first used a bioenergetically-based food web model with growth, and seasonal diet, distribution, and temperature data for the key fish species to identify the timing and relative strengths of predatory interactions in the fish community. Once important predator-prey interactions were identified, I explored and compared the visual foraging abilities of top salmonine piscivores and developed mathematical relationships to describe how piscivorous fishes respond to alterations in their visual environment. Distribution and movement patterns of cutthroat trout (Nowak and Quinn 2002) and prey fish were combined using the previously developed foraging model to estimate the predation rates by piscivorous-size cutthroat trout in Lake

Washington. Field measures of horizontal and vertical prey fish distributions were then combined in a spatially-explicit model that linked the light-dependent foraging ability of predators with spatial patterns of light and temperature, into a bioenergetics model to estimate spatial variability in growth potential (Brandt et al. 1992) and predation pressure among depths and areas of the lake for each season from spring 2002 to fall 2003.

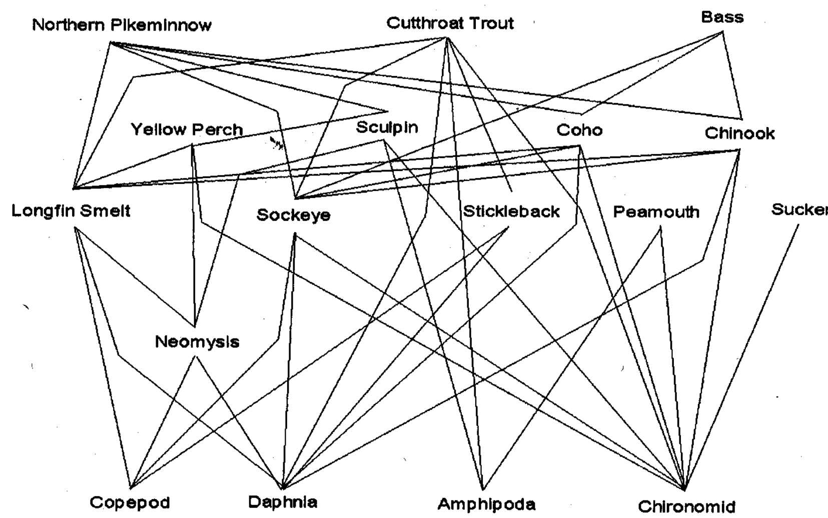

Figure 1. Diagram of the food web of Lake Washington showing some of the important interactions associated with the resident fish community.

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CHAPTER 1

A bioenergetics model of upper trophic-level interactions among fishes in the Lake Washington food web

Synopsis

Size-structured, seasonal predator-prey interactions were quantified for the Lake Washington food web using a bioenergetics model with inputs provided by directed field sampling and existing literature describing the diet, growth, distribution, and thermal experience of key species in the fish community. Cutthroat trout (*Oncorhynchus clarki clarki*) and northern pikeminnow (*Ptychocheilus oregonensis*) were identified as the apex predators in the lake. Annual consumption by a size-structured "unit population" of 1,000 cutthroat trout ≥ 110 mm FL ate twice the biomass of prey (3682 kg/yr) than northern pikeminnow (1850 kg/1,000 northern pikeminnow ≥ 100 mm FL per year). Both cutthroat trout and northern pikeminnow primarily consumed longfin smelt (*Spirinchus thaleichthys*), juvenile sockeye salmon (*O. nerka*), other juvenile salmon, three-spine sticklebacks (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), and lesser quantities of yellow perch (*Perca flavescens*) and other fishes. The abundance of yearling longfin smelt, the primary prey for both cutthroat trout and northern pikeminnow, strongly influenced predation rates on other prey fishes. When yearling smelt were scarce, substantially higher predation rates were imposed on juvenile sockeye salmon, other juvenile salmon, three-spine sticklebacks, and prickly sculpin. Yellow perch fed primarily on *Neomysis mercedis*, zooplankton, benthic invertebrates, and some fish. Annual size-structured consumption rates by 1,000 age 1-7 yellow perch were only 5% of the total biomass consumed by comparable numbers of

cutthroat trout or 11% by northern pikeminnow. Smallmouth bass (*Micropterus dolomieui*) and largemouth bass (*Micropterus salmoides*) consumption was dominated by prey fishes; however, their limited abundance and nearshore distribution minimized their influence on prey fishes in the main basin of the lake. Peamouth (*Mylocheilus caurinus*) fed almost exclusively on benthic invertebrates, and size-structured consumption rates per 1,000 peamouth were only one-third of that eaten by cutthroat trout. The primary uncertainties identified by this analysis included the abundance of consumers, the influence of cyclic abundance by longfin smelt and variable recruitment by sockeye salmon on the food web.

Introduction

Individuals and species exhibit size-structured interactions that vary spatially and temporally in aquatic food webs (Paine 1966, 1988; Persson et al. 2000). Predation has often been directly responsible for the decline or demise of a species (Foerster and Ricker 1941; Zaret and Paine 1974; Griffith 1988; Robinson and Tonn 1989; He and Kitchell 1990; He and Wright 1992); however, indirect effects of predators often have more profound impacts on prey populations (Gliwicz 1994; Brown 1999; Grand and Dill 1999). Examining how individuals interact both directly and indirectly in a food web fosters deeper understanding of how predators influence the structure and function of entire communities.

Management of fish populations can be enhanced through examination of food webs and consideration of the community as a whole (Polis and Winemiller 1996; He and Kitchell 1990; Baldwin et al. 2000). Effective management requires knowledge of how food web interactions are influenced by environmental change or human induced perturbations. By quantifying interactions in a food web through time and space, we can identify potential ecological bottlenecks for specific species that might result from limited food supply, competition, predation, or adverse environmental conditions. The food web modeling approach provides a tool to aid managers and researchers in understanding community wide dynamics.

Long-term analysis of the limnological aspects of Lake Washington combined with more than fifty years of episodic fisheries research provides the framework for this food web analysis. Fisheries research during the 1960's and 1970's focused on the large population increases in longfin smelt (Dryfoos 1965; Moulton 1975) and sockeye salmon (Woodey 1972). Focus shifted during the 1980's to include elements of the trout complex, notably studies concerning potential predation effects by rainbow trout on juvenile sockeye salmon and longfin smelt (Beauchamp 1990; Warner and Quinn 1995). Major emphasis was directed towards sockeye salmon research throughout the 1990's with an increased emphasis on chinook salmon in the last half of the decade.

Recent research has focused on the important questions surrounding the distribution, movement, and foraging ecology of the diverse predator population in Lake Washington. Smallmouth bass (Fayram 1996), northern pikeminnow (Brocksmith 1999), cutthroat trout (Nowak 2000), and prickly sculpin (Tabor et al 1998) were all investigated within the last decade to determine the impacts each population of predators exhibits on juvenile salmonids. The recent analysis of predators combined with the directed sampling needed to complete a mechanistic food web analysis provide an effective tool for determining and understanding bottlenecks influencing the population dynamics of sockeye salmon and ESA listed chinook salmon in the Lake Washington drainage.

Previous studies have used bioenergetics simulations to estimate consumption by cutthroat trout, rainbow trout, and northern pikeminnow during the mid 1980's and early 1990's (Beauchamp 1994), but were hampered by significant gaps in knowledge. More recently diet studies were conducted for cutthroat trout (Nowak et al. in press), northern pikeminnow (Brocksmith 1999), smallmouth bass and largemouth bass (Fayram and Sibley 1999) in Lake Washington; this paper supplemented diet information from the previous studies. Seasonal estimates of distribution, thermal experience, age structure, growth, and diet composition of fishes in Lake Washington were also obtained from published literature, thesis, and field sampling conducted in 2002 and 2003. These data were integrated into a more comprehensive multi-species analysis of seasonal, size-structured trophic interactions in the lake.

We examined interactions among the upper trophic levels in the Lake Washington food web to examine the relative importance of predation and food supply as potentially limiting factors for survival or growth of juvenile salmonids and other key species. The objectives of this study were to construct a bioenergetics-based food web model to quantify size-structured seasonal interactions among species within Lake Washington, identify the strong interactions in the fish community and to determine the relative importance of inter-specific and intra-specific trophic interactions in regulating life stages and populations of fishes.

Methods

Bioenergetics models were used to estimate age-specific seasonal consumption by piscivorous cutthroat trout, northern pikeminnow, yellow perch, smallmouth bass, largemouth bass, and prickly sculpin on different prey within the Lake Washington food web. Size-structured bioenergetics models were also used to quantify trophic interactions of peamouth, a very abundant, but non-piscivorous species in the lake. The bioenergetics model links the physiology of each fish species with the environmental variables available in the system and combines estimates of the consumer's diet, thermal experience, and growth within an energy balance equation to estimate food consumption for individual fish (Hanson et al. 1997). The energy balance equation, in its simplest form, estimates the amount of consumption required to satisfy observed growth after accounting for the costs of waste and metabolism (Hanson et al. 1997).

Population-level consumption rates integrate the effects of changes in the abundance, food habits, and consumption rate among size classes of the consumer. Consumption increases but abundance declines with larger, older fish, and ontogenetic shifts in diet or distribution are common, particularly for piscivorous species. In the absence of reliable population estimates we chose to expand individual level consumption estimates to relative population-level estimates of 1000 fish. The 1000-fish approach accounts for the size-structure and population mortality for each consumer species in our consumption estimate and sets the stage for easily computing true population-level consumption estimates if an abundance estimate becomes available.

The importance of fluctuating prey fish abundances on the consumption of cutthroat trout was explored for strong year classes (spawning in even-numbered years) and weak year classes (spawning in odd-numbered years) of longfin smelt by partitioning seasons into periods when age-1 to adult smelt were abundant or not. From a predator's perspective, smelt become abundant during the fall of even numbered years at fork lengths (FL) $\geq$ 40 mm and then become scarce in the spring of even numbered years, after the adults spawn and die (Dryfoos 1965; Moulton 1970; Chigbu and Sibley 1994). To account for the cyclicity in the abundance of yearling smelt, consumption estimates were produced for a two year period spanning even and odd smelt abundances.

The ecological role of piscivorous northern pikeminnow was compared under three different prey regimes: during 1972 when age 1 smelt were scarce (Olney 1975); during 1997 when age 1 smelt were abundant (Brocksmith 1999); and late summer 2002-2003 when age 1 smelt were abundant. Model inputs for the three periods differed in growth rates of northern pikeminnow and in the proportions of smelt and other prey in the diet. Estimates of annual growth from 1972 (Olney 1975) were used to model 1997 consumption estimates. Olney (1975) collected diet information primarily during 1972, when yearling smelt were relatively scarce; whereas Brocksmith (1999) collected diet information primarily during 1997, when the cyclic abundance of yearling longfin smelt was high (Beauchamp 1994; Chigbu et al. 1998). Sampling effort during 2002-2003 encompassed a strong year class of longfin smelt. The effect of inter-annual variation in longfin smelt and sockeye salmon abundance was explored through comparisons of northern pikeminnow consumption using seasonal diet estimates from all three periods.

Field sampling for fish

Fish sampling was conducted using gill nets, hydroacoustics, midwater trawling, purse seining, and beach seining to acquire information on age, growth, diet, and distribution. Gill nets were deployed monthly during 2001-2003 and were stratified among 4 depth intervals and 5 areas along the north-south axis of the lake with area 1 in the north end of the lake and area 5 in the south, using boundaries defined in previous studies (Figure 1.1; see Chigbu et al. 1998). All areas were sampled within the same week using overnight (≥12 hour) sets of sinking and suspended limnetic net sets. Horizontal sinking gill nets were set parallel to shore to sample depth contours of 7, 15, 30, and 45 m (± 2 m) along the slope zones of the lake. An additional perpendicular net was set with the shallow end starting at 5 m and deep end extending as deep as 15 m. Each depth contour was sampled simultaneously with one 60 m long by 2 m deep multi-mesh experimental net with panels of 25, 31, 38, 50, 63, and 75 mm stretch mesh. Limnetic regions of the lake were sampled using 1 to 10 vertical gill nets, each with a single mesh size, and horizontal multi-mesh nets suspended in the water column using floats. Limnetic nets were grouped within 200 m of each other to minimize navigational hazards, and white anchor lights were affixed to floats. Vertical gill nets were 60 meters long x 2.3 meters wide and were suspended on floating aluminum rollers. Each vertical net consisted of one monofilament panel of a single mesh size. The vertical mesh sizes were 25, 38, 50, 63, 75, 83, 95, 108 mm stretch mesh, and the length of the nets were adjusted to match the bottom depth where they were deployed. Horizontal nets (2 x 60 m with variable mesh sizes of 25, 31, 38, 50, 63, and 75 mm stretch mesh) were suspended in the water column, at depths of 10, 15, 20, and 25 m by surface floats spaced every 7 m. Depth of capture for each fish was recorded.

Monthly hydroacoustic surveys were conducted from October 2001 to November 2003 to describe the distribution of pelagic fishes by area and depth. Hydroacoustic surveys were conducted with a 430-kHz split beam echo sounder (Biosonics DE 6000) mounted on a tow fin. The tow fin was attached to a davit and deployed from the side of a 7 m aluminum hulled boat. Transducers were suspended at a depth of 0.5-1 m below the surface of the water and operated at 1.5-3 pings per second. The transducer was vertically positioned with a 6º full-angle beam. Hydroacoustic settings for collection of data were TVG of 40 Log R, -65 dB threshold, and a pulse width of 0.4 ms. Boat speeds ranged between 6 and 8.5 km/h. Transects were recorded to the hard drive and post processed using SonarData Echoview ® 3.10.129 software.

Transects were echo counted for individual targets and individual target strengths were stratified into 1 m depth bins. Target strengths were converted to total length using Love's equation (Love 1971). Targets between -52 and -42 dB (roughly 4-15 cm), which corresponded to the most frequently observed prey fish sizes in cutthroat trout stomachs, were classified as prey fish, and depth specific densities were calculated by dividing the total count of targets at each depth by the total volume sampled for that depth. The sample volume within each 1 m depth interval was calculated for each transect by multiplying the total number of pings sampled at each depth by the volume of a 1 m high frustrum at each depth. Targets and density estimates for the 6º beam were restricted to a 4º beam (<2º off axis) to increase confidence in target strength estimates and decrease our reliance on beam angle compensations. Targets closer than 1 m to the bottom and were excluded from the analysis. Initial analyses indicated that prey fish abundances in the top 5 meters of water were highly variable and biased due to low sample volumes and were excluded from the analysis.

Concurrent midwater trawl and hydroacoustic surveys were conducted at night during March and October of 2002 and 2003 to provide species-specific abundance estimates of sockeye, smelt and sticklebacks. Depth specific midwater trawls used a Kvichak trawl with a 2.5m x 2.5m cross-sectional opening with mesh sizes grading down to 2 mm mesh in the cod-end. The Kvichak trawl was towed for 10-minutes at depths of 6 m, 15 m, 22 m, 31 m, and 41 m for a total of 24 trawls over a two day period in March and 27 trawls in October. Density estimates were generated for each pelagic species from the nocturnal hydroacoustic transects, based on the depth- and size-specific target densities in five areas stratified across the lake.

A purse seine (600m x 40 m deep; 25 m effective capture depth) was deployed in afternoon, dusk and night sets during June of 2003 and beach seines were conducted during dusk and night in April and May 2003. Weekly beach seines were conducted for a week prior and 3 weeks following the release and migration through Lake Washington of coho (O. kisutch) and chinook salmon (O. tshawytscha) from the Issaquah state fish hatchery in April of 2003. The beach seine was a floating net with the dimensions of 37 m length x 2 m height, and mesh grading from 3 cm in the wings to 6 mm at the cod end. The beach seine was used to supplement the capture of juvenile fishes that were too small to be sampled adequately by gill nets.

All fish captured in the field were counted, and a subset of sizes and species were placed on ice until they could be processed in the laboratory. Fish were measured (mm), weighed (g) and processed for stomach contents, sex, gonad weight, and hard parts (scales, otoliths, and/or operculum) were collected for aging. Stomach samples were initially preserved in 10% buffered formalin and later switched to 50% ethanol (ETOH) prior to examination.

Age and growth

Annual growth estimates were obtained from the literature for smallmouth bass and largemouth bass (Fayram 1996), peamouth (Nishimoto 1972), and prickly sculpin (Rickard 1980) in Lake Washington and were based on back-calculated mean size-at-age from scales or otoliths (Table 1.1). Size-at-age for cutthroat trout, northern pikeminnow, and yellow perch were estimated using 2001-2003 data. The comparative historical model runs used size-at-age information for cutthroat trout (Nowak 2000) and northern pikeminnow (Olney 1975). Nowak (2000) estimated growth of cutthroat trout using scales collected during April 1998 through June 1999 by fitting a von Bertalanffy growth curve to the length-at-age estimates ($r^2 = 0.96$, N = 74).

$$\text{Fork Length} = 1591 \cdot (1 - \exp^{(-0.066(\text{years}))})$$

Weight-at-age information was estimated by applying a length-weight regression ($r^2 = 0.96$, N = 74)

$$\text{Weight (g)} = 5.59 \cdot 10^{-6}\ \text{FL (mm)}^{3.12}$$

to the length-at-age estimates (Nowak 2000).

For 2002-2003, the average length of cutthroat trout in each age class was used in a length-weight regression to compute average weight-at-age to model consumption for 2002-2003 data. Cutthroat trout growth was estimated based on scale samples collected from 58 fish between November 2001 and November

2003. The cutthroat trout were captured in offshore suspended gill net sets (44) and purse seines (14). Scales were removed above the lateral line half way between the dorsal and anal fin insertion. Three to six non-regenerated scales from each fish were pressed on acetate cards and read using a dissecting microscope. The scale radius from the center of the scale to each annulus and to the outer scale margin along the posterior field of the scale were measured and recorded using Image-Pro plus® software (version 4.1; Media Cybernetics). A linear relationship between scale radius and fish length was determined by regressing the distance (R) between focus to posterior scale margin and the fork length (FL in mm) for each fish.

$$FL\ (mm) = 45.1 + 229.6 \cdot R,\ r^2 = 0.72,\ p < 0.001,\ n = 58$$

This regression was then used to back-calculate FL at each age and year for each cutthroat trout to investigate the potential impact of variable smelt abundance on cutthroat trout growth rates. Estimated fork lengths were transformed into body weight at age using the length-weight regression determined from all cutthroat trout captured during 2001 thru 2003.

$$W(g) = 5.0 \times 10^{-6}\ FL\ (mm)^{3.14},\ r^2 = 0.99,\ n = 258$$

Length-at-age for northern pikeminnow was estimated in previous studies separately for males and females using opercles and scales (Olney 1975). In this study, only opercles were used but scales and otoliths were archived. Sex-specific growth by northern pikeminnow was estimated based on opercle samples collected from 172 fish (92 females, 45 male, and 35 of undetermined sex) between November 2001 and November 2003. Northern pikeminnow were captured primarily in sinking gill nets. Weight-at-age information was computed for the previous studies using a length-weight regression (r^2= 0.99, N=933; Olney 1975). For the 2003 data, sex specific length-weight regressions were also calculated and used to estimate weights at age.

$$\text{Weight (g)} = 0.000009 \text{ Fork Length (mm)}^{3.07} \qquad \text{for females}$$

$$\text{Weight (g)} = 0.00001 \text{ Fork Length (mm)}^{2.99} \qquad \text{for males}$$

Length-at-age estimates for yellow perch were estimated using otoliths collected from 33 fish (J. McIntyre, unpublished data). Otoliths were sectioned and burned in a flame to enhance annulus appearance. Yellow perch weights-at-age were calculated using a length-weight regression developed from yellow perch captured in 2003.

$$\text{Weight (g)} = 0.000003 \text{ Fork Length (mm)}^{3.27}$$

Length-at-age for smallmouth bass and largemouth bass were estimated from scale samples collected during 1995 by estimating mean length from each age class sampled (Fayram 1996). For smallmouth bass, weight-at-age was obtained from Fayram and Sibley (2000) and was the arithmetic average for individuals in each age-class.

Mean weight-at-age for largemouth bass was calculated using a length-weight regression developed from reported catch lengths and weights (Fayram 1996; $r^2 = 0.98$, N = 26).

$$\text{Weight (g)} = 0.000003 \text{ TL (mm)}^{3.32}$$

Length-at-age estimates for prickly sculpin were obtained from otolith analysis (Rickard 1980). Weight-at-age was estimated using a length weight regression (r^2=0.967, *N*=2156; Rickard 1980; J. Moss, University of Washington, unpublished data) developed from sculpin captured in minnow traps.

$$\text{Weight (g)} = 0.00000263 \text{ TL(mm)}^{3.32}$$

Length-at-age estimates for peamouth were determined from scales collected between 1970 and 1972 (Nishimoto 1973). Peamouth weight-at-age estimates were then calculated using sex-specific length-weight regressions (Nishimoto 1973).

$$\text{Female Weight (g)} = 0.0000044 \cdot \text{TL(mm)}^{3.14},\ r^2 = 0.988,\ N = 1560$$

$$\text{Male Weight (g)} = 0.0000117 \cdot \text{TL(mm)}^{2.94},\ r^2 = 0.987,\ N = 721$$

For modeling purposes, non sex-specific weight-at-age estimates were produced by averaging male and female weights at each age.

Diet analysis

Stomach contents were separated into prey fish species and invertebrates were sorted into functional taxonomic groups (e.g. *Daphnia*, *Neomysis*, copepod, aquatic and terrestrial insects, benthic inverts). Prey fishes were identified to the lowest possible taxonomic level using skin, bone, tissue, and scales (Hansel et al. 1988). Vertebral, standard, or total lengths were measured for all prey fishes, and lengths were converted to total lengths (Carlander 1969; Nowak 2000). Invertebrates in the stomach samples were sorted by terrestrial and aquatic taxonomic groups and blotted wet weights were recorded to the nearest 0.01 g (Baldwin et al. 2000).

Diet composition was analyzed by season and size class for each species of consumer. Species were separated into size classes based on length frequency modes of the consumers and similarities in prey composition within size classes (e.g. onset of piscivory). For 2002-2003, cutthroat trout were separated into size classes of < 200 mm fork length (FL) corresponding to age 2-3 fish, 200-350 mm FL (age 3-5), and > 350 mm FL (age ≥ 5; Table 1.2). The same size categories were applied to cutthroat trout in earlier data sets (Nowak 2000). For 2002-2003, northern pikeminnow were grouped into three size groupings of <

200 mm FL, 200–300 mm FL, and > 300 mm FL to account for the onset of piscivory and observed changes in prey species selection (Table 1.3). The previous diet study conducted in 1972 grouped northern pikeminnow into > 300 mm TL during a weak smelt year (Table 1.4; Olney 1975) whereas the diet collected in 1997 was grouped into size classes of ≤ 320 mm and > 320 mm FL during a strong smelt year when age 1 to adult smelt were abundant (Brocksmith 1999). The ≤ 320 mm FL size class corresponded to age 2-5 females and age 2-6 males whereas the > 320 mm FL size class corresponded to age 6-13 females and age 7-13 males (Brocksmith 1999). Yellow perch were separated into 100-225 mm fork length (FL) and > 225 mm FL size classes from collections in 2002-2003 (Table 1.5). Smallmouth bass and largemouth bass were grouped together in one size class > 150 mm corresponding to fish ages 2-13 for smallmouth bass and ages 2-11 for largemouth bass (Table 1.6; Fayram and Sibley 2000). Prickly sculpin were separated into two size classes using the differences in seasonal distribution associated with age 1-2 prickly sculpin compared to age 3 and older prickly sculpin (Table 1.7; Rickard 1980; J. Moss, unpublished data). For peamouth diet composition did not differ by body size (Table 1.8; Shanbhogue 1976); therefore all peamouth were modeled using the same temporal diet.

Bioenergetics model simulations

A bioenergetics model (version 3.0, Hanson et al. 1997) was used to estimate seasonal consumption rates using species-specific physiological parameters for cutthroat trout (Beauchamp et al. 1995), northern pikeminnow (Peterson and Ward 1999), yellow perch (Kitchell et al. 1977; Post 1990), smallmouth bass (Shuter and Post 1990), largemouth bass (Rice et al. 1983), and prickly sculpin (Moss 2002). A cyprinid model by Duffy (1998) was used as a surrogate for peamouth. Indigestible fractions of various prey used for the cutthroat trout model were 17% for terrestrial insects, aquatic insects, and zooplankton, and 3% for all prey fish (Hanson et al. 1997). All species and age groups were modeled with January 1 as day 1 and December 31 as day 365 of the bioenergetics simulations.

Thermal experience used in bioenergetics simulations (Table 1.9) was obtained by overlapping vertical movement and distribution patterns from recent ultrasonic tracking studies of cutthroat trout (Nowak and Quinn 2002), smallmouth bass (Fayram 1996), and largemouth bass (Fayram 1996) on vertical temperature profiles. Thermal experience for yellow perch, peamouth chub, and northern pikeminnow were obtained from depth-specific catch per unit effort values calculated from vertical gill nets (Bartoo 1972). Distribution and thermal experience for prickly sculpin were estimated from Rickard (1980).

Energy densities for prey species were estimated using a bomb calorimeter (McIntyre, unpublished data) or taken from previous studies of cutthroat trout and northern pikeminnow in Lake Washington (Nowak 2000; Brocksmith 1999) and standardized for all species in joules per gram (J/g) wet weight. Additional prey energy densities for all species were taken from literature values including: 3800 J/g for *Daphnia* (Luecke and Brandt 1993), 4428 J/g for insects (Cummins and Wuycheck 1971). Gastropoda were arbitrarily assigned an energy content of 1800 J/g. For unidentified fish, an energy density of 5211 - 7445 J/g was assigned and was calculated by averaging the energy density of all fish found in the diets by season. Prey energy densities were also measured with a bomb calorimeter for some prey taxa in Lake Washington: 3826 J/g for copepods, 4868 J/g for *Neomysis*, 3318 J/g for crayfish, 8052 J/g for Trichoptera, 6949 J/g for three-spine stickleback, 4079 J/g for amphipoda, 5211 – 7445 J/g for sockeye salmon fry and pre-smolts, 4316 – 5960 J/g for longfin smelt, 7093 J/g for northern pikeminnow, and 4532 J/g for sculpin (McIntyre, unpublished data). Energy contents were varied by season and size for prey organisms like sockeye salmon, longfin smelt, *Neomysis*, coho salmon, other fish, and unidentified fish (Table 1.10).

Losses associated with spawning were accounted for in the model by estimating the average proportion of gonad loss for both sexes (Hanson et al. 1997). Age 4 and older cutthroat trout were assigned a spawning date of 15 March (day 76) with an 8% average loss of body mass (Beauchamp, unpublished data). Spawning dates and associated weight losses for age 4-13 northern pikeminnow were modeled on June 15 (day 166) incurring a 4.1% weight loss (Brocksmith 1999). Prickly sculpin were modeled to spawn at age 3 on June 1 (day 153) and lose 5.4% body weight (Rickard 1980; J. Moss unpublished data). Peamouth incurred a weight loss of 6.8% on May 1 (day 122) for ages $\geq$ 4 (Shanbhogue 1976). For yellow perch, weight loss of 14% was modeled on June 1 for ages 2-5. Spawning energy loss was not simulated for smallmouth bass, or largemouth bass. The model interpolated values for thermal experience, growth, and diet composition between sampling dates for all modeled species.

Consumption Estimates

We used bioenergetics model simulations to estimate seasonal consumption for individuals from each age class of cutthroat trout, northern pikeminnow, yellow perch, smallmouth bass, largemouth bass, prickly sculpin, and peamouth chub in Lake Washington. Estimates of prey biomass consumed by individual fish for each species and size class were expanded to a standardized, size-structured population of 1,000 fish of each species (here after called unit population). Each unit population was structured using the observed proportion of each size class captured. We determined the age class contribution by applying an annual survival rate of 76.2% for northern pikeminnow (Olney 1975; and iteratively fit by Brocksmith 1999), and 24% for prickly sculpin

(Rickard 1980; Moss 2002). Unit populations of 1,000 fish for cutthroat trout (Nowak 2000), yellow perch (Nelson 1977), smallmouth bass (Fayram 1996), largemouth bass (Fayram 1996), and peamouth (Nishimoto 1973) were determined using size-at-age estimates and length frequencies from catches during each study (Table1.11). The proportion of each size class in catch samples was assumed to represent the size structure of each species' population in Lake Washington, and the size frequency for each species represented the proportion of each modeled age class in the unit population of 1,000 fish. Because size-selectivity varied among capture methods and species, the estimated size structure of these populations might require adjustments in the future to correct for size-selective biases. However, the purpose of this study was to provide an initial evaluation of the relative strength of interactions among species. Based on these results, adjustments could be identified and prioritized based on their relative importance in the food web (e.g. sensitivity of system responses).

The size-structured consumption estimates provided a useful index for comparing the relative impact of predation by different species. However, the predation rates per 1,000 fish artificially elevated the relative importance of larger bodied, but potentially less abundant species within the community, and should be considered within the context of the relative population sizes of these consumers. For example, populations of smallmouth and largemouth bass probably numbered in the 1,000's to 10,000's, whereas cutthroat trout ≥ 110 mm FL and northern pikeminnow ≥100 mm FL populations numbered in the 100,000's, yellow perch in the millions, and prickly sculpin abundance probably ranged in the 10-100 millions. Because of the large disparity in the abundance among populations of consumers, the size-structured consumption estimates per 1,000 fish were expanded to the corresponding order of magnitude for each population (reported above) to examine the importance of each consumer on key prey populations.

Results

Bioenergetics consumption simulations

Model simulations for 2002-2003 indicated that consumption peaked during summer when a variety of prey types were available and temperatures enabled cutthroat trout, northern pikeminnow, and black bass species to forage at or near their maximum consumption. Both the magnitude of consumption and composition of prey varied seasonally by the size and species of consumers (Figure 1.2; Table 1.11). Prey fish species were predominantly consumed during the summer when juvenile fishes were most abundant. Zooplankton, insects and other invertebrates were also consumed most heavily during the summer; however, consumers consisted of a wide range of sizes and species of fishes.

Cutthroat trout consumption

When age-1 smelt were abundant in 2002-2003 consumption by cutthroat trout shifted ontogenetically from smaller, more benthic prey to larger, more pelagic prey (Table 1.11). Size-structured predation on smelt (1121.3 kg/1000 predators) was most intense during the spring and summer of 2003, especially by cutthroat trout > 200 mm. Whereas, consumption of sockeye salmon (321.3 kg/1000 predators) was much lower and was most prevalent in the fall and winter by cutthroat trout > 200 mm. Consumption of three-spine sticklebacks (741.8 kg/1000 predators) was more than double sockeye salmon consumption and was heaviest during the spring and summer by the large cutthroat trout > 350 mm FL. Consumption of all species of sculpin, yellow perch, peamouth, and other salmonids represented the rest of the prey fish consumed by cutthroat trout.

Limited diet information for cutthroat trout in limnetic regions of the lake during the spring and summer when yearling smelt were scarce in even-numbered years hindered attempts to evaluate how predation rates on different prey fish would change in response to fluctuating longfin smelt abundance. Limited diet data were collected during late summer in 2002, and this information was supplemented with diet data from 1984 (Beauchamp et al. 1992). Consumption of three-spine stickleback, sockeye salmon, yellow perch, and cyprinid species all increased during the spring, summer, and fall during even years when yearling smelt were scarce compared to odd-numbered years when yearling smelt were abundant (Figure 1.3). Similarly, cutthroat trout consumed more aquatic insects and zooplankton when yearling smelt were scarce.

Northern pikeminnow consumption

When age-1 smelt were abundant during 2002-2003, predation on smelt (762.1 kg/1000 predators predators) was heaviest during the spring and summer especially by northern pikeminnow > 300 mm (Table 1.11). Predation on juvenile sockeye salmon was much lower (77.1 kg/1000 predators predators) and was most prevalent during winter, spring, and summer by northern pikeminnow > 200 mm. Three-spine stickleback, sculpin, and other juvenile salmonids represented the majority of other fish prey. In contrast, when densities of age 1-2 smelt were low in 1972 annual predation on smelt (198 kg/1000 predators) was 3-4 times lower, sockeye predation (349.9 kg/1000 predators) was 5 times greater, and prickly sculpin (659.6 kg/1000 predators), other fishes (337.7 kg/1000 predators), and crayfish (405.1 kg/1000 predators) dominated the annual consumption of northern pikeminnow.

Similar to cutthroat trout, limited diet information for northern pikeminnow during the spring and summer of even-numbered years hindered attempts to explore the influence of fluctuating longfin smelt abundances on northern pikeminnow consumption. Comparison between even-numbered and odd-numbered year consumption from 1972 and 2003 indicated that longfin smelt consumption has increased dramatically (Figure 1.3). However, conclusions concerning the influence of even and odd smelt year classes from this analysis are burdened with uncertainties associated with background levels of alternative prey and the influence of the lakes recovery from eutrophication on fish dynamics.

Yellow perch consumption

When age-1 smelt were abundant during 2002-2003, predation on smelt (10.4 kg/1000 predators) was greatest during summer by large yellow perch > 225 mm TL (Table 1.11). Large yellow perch (> 225 mm TL) made up only 10% of the simulated 1000 fish population but were responsible for the majority of consumption of prey fishes. Consumption of juvenile sockeye salmon (5.6 kg/1000 predators) was nearly half that of smelt and primarily consisted of fry during the spring and summer. Sculpin species (25.4 kg/1000 predators) were the most consumed prey fish by yellow perch during the spring and summer, doubling the consumption of smelt. Juvenile yellow perch (5.4 kg/1000 predators) and fish eggs represented the majority of other fish prey consumed.

Smallmouth bass consumption

Smallmouth bass captured during 1995, when age-1 smelt were abundant, primarily consumed prey fish through spring, summer and early fall with over half (68%) of the consumption consisting of non-salmonid prey fishes (627.4 kg/1000 predators; Table 1.11). Salmonids accounted for only 24.7 kg/1000 predators and crayfish composed 263.6 kg/1000 predators of the total consumption. Sculpin species and three-spine stickleback composed the majority of the "non-salmonid" other fish prey category, but the available information did not allow consumption of non-salmonid prey to be partitioned to specific species. Size-specific differences in consumption were also not determined because of limited data on diet ontogeny.

Largemouth bass consumption

Consumption estimates for largemouth bass during 1995 were similar to smallmouth bass with the main prey being other fish (467.3 kg/1000 predators), salmonids (114.3 kg/1000 predators), and crayfish (245.4 kg/1000 predators; Table 1.11). Largemouth bass sample sizes were low (Fayram 1996), and were only available during the spring and summer. Therefore, consumption estimates may not accurately reflect the largemouth bass population in Lake Washington.

Prickly sculpin consumption

Consumption estimates for prickly sculpin during 1975, when age-1 smelt estimates are not well known, indicated that prey fish (3 kg/1000 predators) were only 5% of the total sculpin consumption (Table 1.11) and was primarily restricted to sculpin > 87 mm TL. Sculpin of all sizes primarily consumed chironomids (36.4 kg/1000 predators), *Neomysis* (7.5 kg/1000 predators), and aquatic insects (8.2 kg/1000 predators). The oldest prickly sculpins (age 4-6) annually consumed 33% prey fishes, consisting mostly of smaller sculpin and seasonally-available larval and post-larval fishes.

Peamouth consumption

Consumption estimates for peamouth during 1973-1975 were dominated by benthic invertebrates through all seasons and across all size classes (Table 1.11) and no prey fish were observed in the diets. Gastropods represented 35% of the total annual consumption followed by 22% oligochaeta, and 19% chironomids. Differences in consumption associated with the size structure of peamouth were not apparent from the available data.

Consumption by relative populations of consumers

The relative abundances of 10,000 smallmouth and largemouth bass, 100,000 cutthroat trout, 100,000 northern pikeminnow, and 1,000,000 yellow perch were used to examine the relative importance of each consumer on its prey, and were believed to be within the correct order of magnitude for the populations in the lake during 2003, an odd-numbered year when yearling smelt were abundant. Prickly sculpin were not included in this analysis because of large uncertainties in their relative abundance. Cutthroat trout consumed three times more biomass of sockeye salmon than northern pikeminnow and nearly 11 times more than yellow perch (Table 1.12). However, when the biomass consumed was converted into numbers of individuals using monthly mean prey species weights (Table 1.13), cutthroat trout consumed only 1.5 times more sockeye salmon than northern pikeminnow and only four times more than yellow perch, because cutthroat trout consumed more of the larger, older prey (Table 1.14). All piscivores consumed 2-8 times more longfin smelt and slightly more three-spine stickleback than sockeye salmon during 2003.

Discussion

Model simulations suggested that among all the predatory fishes in the Lake Washington food web, cutthroat trout had the most potential to act as a keystone predator (Paine 1966, 1988). The movement and distribution patterns of a cruising predator like cutthroat trout enabled them to interact with the key pelagic prey fishes throughout the year. Rapid growth by cutthroat trout also resulted in higher per capita consumption demand than the other cruising bentho-pelagic predator, northern pikeminnow, a slower-growing, longer-lived species. The extent to which cutthroat trout or northern pikeminnow regulated prey populations in Lake Washington is still unclear, primarily because of uncertainties associated with predator population levels. However, relative CPUE from bottom gill net sets suggests that northern pikeminnow are more abundant than previously thought (Olney 1975; Bartoo 1977; Brocksmith 1999). In this study, northern pikeminnow were captured 5 times more frequently than cutthroat trout during the winter near shore, while cutthroat trout were staging to spawn and capture efficiency was assumed to be most similar between the two species.

Given our current understanding of the visual foraging capabilities of piscivores (Beauchamp et al. 1999; Vogel and Beauchamp 1999; Mazur and Beauchamp; 2003) and the available thermal and optical environment in Lake Washington, piscivores were capable of structuring the prey fish community (Beauchamp 1994; Beauchamp et al. 1999). Similarly, the large size and availability of zooplankton throughout the year, even after the consumptive demand of zooplanktivorous fishes had been accounted for (Beauchamp 1996; Beauchamp et al. in press), suggests that prey fishes are limited more by predation mortality than by food. Top down control of the planktivore community in Lake Washington was suggested in the 1970's during recovery from eutrophication (Eggers et al. 1978). Despite apparent dramatic shifts in the prey fish assemblage in terms of increases in abundance and species composition (Chigbu and Sibley 1994; Beauchamp 1994; Chigbu et al. 1998), piscivores appear to maintain the ability to structure the fish community. Thus, identifying shifts in species composition, size structure, and abundance of predators will be critical to understanding the temporal and spatial dynamics of prey fish in Lake Washington. Bioenergetics modeling enabled us to identify uncertainties associated with predator-prey interactions in the Lake Washington food web and to identify critical information needs necessary to further our understanding of the structure and function of the entire fish community.

This modeling exercise suggested that potential top down regulatory effects on prey fishes in Lake Washington varied predictably by season but in less predictable, complex inter-annual cycles for all prey species. Many of the studies referenced in this work pooled salmonid prey fishes such as juvenile sockeye salmon, chinook salmon, coho salmon, kokanee, rainbow trout, and cutthroat trout into one prey category. Because estimates of predation losses are necessary to investigate which interactions are critical to the recruitment and growth of each prey species, more specific prey identification was acquired during 2002 and 2003. The remaining uncertainty associated with direct consumption estimates and recruitment dynamics of prey fishes resulted from an absence of predatory fish abundance estimates. Although our relative estimates of population-level consumption provided some indication of the relative importance of each consumer on its prey population, they should not way be substituted for consumption estimates produced using statistically sound abundance estimates of piscivores.

Sockeye salmon and other salmonids were consumed during all seasons, with peak predation by large cutthroat trout occurring during the fall and winter, in terms of biomass, and during spring in terms of peak numbers of salmonids consumed. Consumption of larger juvenile sockeye salmon and other salmonids by piscivorous cutthroat trout increased during the fall, coinciding with declining epilimnetic temperatures and increased overlap between piscivores and their prey. The loss in body weight for pre-smolt sockeye salmon over the winter and availability of newly hatched sockeye fry in winter and spring resulted in higher numbers of sockeye consumed by cutthroat trout during spring. The relatively low weight of individual sockeye during spring and summer increased the numerical consumption of sockeye salmon by northern pikeminnow and yellow perch compared to cutthroat trout. Relative population estimates of consumption suggested that cutthroat trout were the most significant source of mortality for sockeye salmon during 2003, consuming more biomass and larger sized individuals than other piscivores. However, spring and summer predation by northern pikeminnow and yellow perch on smaller-bodied sockeye salmon could be significant during even-numbered years when abundant yearling smelt are not available as an alternative prey.

Both of the abundant longfin smelt year classes of 1996 and 2002 were consumed 10 times more frequently by northern pikeminnow than sockeye salmon during the summers of 1997 and 2003. Coho salmon smolts migrating through Lake Washington in the spring of 2003 were eaten by larger northern pikeminnow, but the relative importance of this interaction to coho population dynamics was unclear largely due to unknown northern pikeminnow abundance. Consumption of migrating coho and chinook salmon within the system could be elevated during even years when longfin smelt are scarce.

Large uncertainties surround the effect of variable recruitment of longfin smelt and sockeye salmon and how the inter-annual variability in abundance influences predator consumption and predator-prey size interactions. Developing an understanding of the temporal and spatial overlap of predators and prey, and the extent to which variable prey abundance alters encounter rates and vulnerability of different prey fishes to predators should greatly increase our understanding of the role of predators in structuring the Lake Washington pelagic community.

Three-spine sticklebacks were consumed by all piscivorous species, primarily during late spring and summer as the sticklebacks grew from larval to about 40 mm TL. By fall, consumption of three-spine stickleback was infrequent except by the large northern pikeminnow and cutthroat trout. The ontogeny of sticklebacks combined with the thermal structure of the lake appeared to limit the size and species of piscivores that were capable of consuming three-spine sticklebacks. Three-spine sticklebacks were the most important prey item for cutthroat trout larger than 350 mm FL during fall and the second most consumed prey during the summer of 2003 (Table 1.10). Increased size of three-spine stickleback limited predation by all but the largest piscivores. Stickleback were numerically, the most consumed prey fish by cutthroat trout during 2003, suggesting that sticklebacks are an important alternate prey source for cutthroat trout when smelt are scarce or sockeye salmon are not available.

The relatively abundant yellow perch were primarily consumed by piscivores in the spring and early summer of their first year in the lake. Yellow perch were not consumed in large quantities by cutthroat trout, northern pikeminnow, or black bass suggesting that yellow perch recruitment was more dependent on available spawning habitat, egg survival, and larval fish dynamics such as cannibalism or predation by smaller body-sized predators such as smelt. Cutthroat trout and cannibalism accounted for the majority of predation mortality experience by yellow perch during 2003. Similarly, peamouth and sculpin were underutilized by piscivores in relation to their abundance. Consumption of peamouth and sculpin was generally low in all information collected after the 1980's, following the recovery of the lake from eutrophication and the subsequent increase in longfin smelt and sockeye salmon abundances. Yellow perch, peamouth, and sculpin could provide alternative forage to piscivore species during the spring and summer of even-numbered years when yearling longfin smelt abundance is low. Benthic fishes were previously hypothesized to provide the Lake Washington piscivore population with an alternative forage base during periods of low planktivore abundance (Eggers et al. 1978).

Since rainbow trout stocking was terminated in the mid-1990's, cutthroat trout and northern pikeminnow have become the major consumers and potential regulators of longfin smelt in Lake Washington. For longfin smelt, potentially important interactions occur in the summer with northern pikeminnow and throughout the year with cutthroat trout. When yearling longfin smelt were abundant in summer 1997, predation per 1,000 northern pikeminnow was double that of the combined summer consumption on longfin smelt/1,000 predators by all other predators. Similar patterns were observed when longfin smelt were abundant in 2003, but summer consumption by cutthroat trout was slightly higher than by northern pikeminnow. Predation on longfin smelt by northern pikeminnow during the summers in 1997 and 2003 was relatively high, whereas longfin smelt were absent from pikeminnow diets during the summer when abundance was lower in 1972 (Olney 1975). Critical uncertainties surrounding longfin smelt interactions with their predators hinge on the timing and size of recruitment classes and how they interact with variable sockeye salmon recruitment to the lake. The potential regulation of longfin smelt by predators could play a critical role in the Lake Washington food web. Longfin smelt are believed to be a regulating force on the zooplanktivorous *Neomysis* and could indirectly influence the presence and abundance of *Daphnia* in the lake (Edmondson and Litt 1982; Edmondson and Abella 1988; Beauchamp 1994).

It remains unclear what processes regulate the population dynamics of longfin smelt and maintain the strong cyclic odd-even year class pattern. Differences in spawning time and Cedar River hydrology between even and odd years was hypothesized as a possible mechanism that initiated cyclicity (Chigbu 2000). Cannibalism of the weak odd year class by the strong even year class is a potential mechanism for perpetuating the longfin smelt cycles as is depensatory predation mortality on weak year classes (Beauchamp 1994). An understanding of the interaction between longfin smelt and sockeye salmon abundance and how variable prey densities influence prey selection and consumption by piscivores in Lake Washington is still unresolved. Did abundant longfin smelt year classes reduce the predation pressure on sockeye salmon and other salmonids, or did the system wide increase in longfin smelt abundance since the 1960s (Moulton 1970) result in increased predator abundance?

Prickly sculpin were an important prey resource for northern pikeminnow during 1972 when yearling longfin smelt abundance was relatively low (Olney 1975); however, consumption was reduced during years when yearling longfin smelt were abundant in more recent investigations (Brocksmith 1999; this study). The nature of prickly sculpin interactions with their predators is confounded by our limited understanding of the effect of alternate prey species and how shifts in prey abundance alter predator-prey interactions within Lake Washington. This analysis suggests that prickly sculpin are an underutilized prey resource in relation to their historical abundance (Rickard 1980), and consumption of prickly sculpin may depend more on the abundance of longfin smelt and sockeye salmon than on seasonal shifts in feeding. Or the abundance of prickly sculpin has declined dramatically since the 1970's. When longfin smelt were abundant, predation on prickly sculpin by northern pikeminnow was limited and occurred primarily during the spring and summer, whereas adult yellow perch ate prickly sculpin at a constant low level throughout all seasons. The potential for predators to regulate prickly sculpin abundance has yet to be determined. More research on cannibalistic relationships of prickly sculpin and yellow perch interactions is needed.

The potential for longfin smelt to regulate *Neomysis* through predation has been alluded to by a number of investigators (Edmondson and Abella 1988;

Chigbu and Sibley 1998; Chigbu et al. 1998; Beauchamp 1994, 1996; Chigbu 2004), with the impact on *Neomysis* varying annually. Annual consumption of *Neomysis* by longfin smelt was estimated to be almost three times as high during an odd-numbered year (1989) when abundance of age-1 smelt was high compared to an even-numbered year (1990) when age-1 abundance was low (Beauchamp 1996). In addition to longfin smelt many other fishes consumed *Neomysis* throughout the year, most notably during spring-summer by yellow perch, summer-fall by cutthroat trout, fall-winter by prickly sculpin, and during the winter by peamouth. The relative importance of these interactions in the regulation of *Neomysis* is unknown primarily because reliable abundance estimates do not exist for most predators and prey. However, our findings further strengthen the hypothesis that *Neomysis* abundance is regulated by predation (Chigbu 1993; Chigbu and Sibley 1998).

A major objective of this analysis was to identify strong interaction in the food web and determine how the existing uncertainties limit our understanding of how the abiotic and biotic environment influences trophic interactions of fishes in Lake Washington. This study quantified per-capita and size-structured consumption rates by the upper trophic level consumers on key prey. This focused the uncertainty onto predator abundance and trophic response to low smelt abundance. This study set the stage for producing population level consumption rates via simple multiplication if abundance estimates become available. The primary uncertainties identified by this study include: unknown predator and prey abundance, how highly variable longfin smelt, *Neomysis*, and sockeye salmon abundance influence food web dynamics, and the effect of space and time on data acquisition and perception of food web dynamics.

Table 1.1. Length-at-age (mm TL or FL), the associated weights (g), and relative abundance (as a proportion of 1,000 fish for each species) used in bioenergetics modeling for cutthroat trout, yellow perch, peamouth chub, male and female northern pikeminnow, largemouth bass and smallmouth bass. The years fish were collected for each estimates are located in the column heading.

	Cutthroat trout (2003)			**Yellow perch (2003)** [1]		
Age	FL	Weight	Nt	TL	Weight	Nt
1				130	25.0	603
2	167	47	210	209	118.0	300
3	225	120	260	242	191.0	93
4	334	420	140	275	290.0	85
5	369	570	180	275	288.0	9
6	397	722	140			
7	459	1137	70			1,000
8	515	1629				
9			1,000			

	Peamouth (1972) [2]			**Prickly sculpin (1975)** [3]		
Age	TL	Weight	Nt	TL	Weight	Nt
1	102	95.6	18	47	1.0	760
2	163	158.8	92	87	7.2	182
3	210	208.0	271	110	15.7	43
4	248	246.2	300	128	26.1	11
5	281	282.1	211	147	40.7	3
6	307	309.4	86	165	59.7	1
7	325	326.1	22	182	80.6	
8	339	339.0				1,000
			1,000			

1 Mean weight-at-age and length-at-age (McIntyre, unpublished).
2 Mean weight-at-age and length-at-age (Nishimoto 1973).
3 Mean length-at-age and weight-at-age (Rickard 1980).

Table 1.1. Continued.

	Northern pikeminnow Female (2003)			Northern pikeminnow Male (2003)		
Age	TL	Weight	Nt	TL	Weight	Nt
1		28.3			28	
2	190	89	124	184	58	136
3	261	233	96	251	145	107
4	316	423	74	290	225	85
5	342	539	57	324	314	69
6	421	1014	45	377	491	56
7	440	1165	35	385	522	47
8	453	1274	28			
9	452	1265	22			500
10	495	1672	18			
			500			

	Northern pikeminnow female (Olney 1975)			Northern pikeminnow male (Olney 1975)		
Age	TL	Weight	Nt	TL	Weight	Nt
1		28.3			30	
2	64	99	120	64	103	120
3	152	195	91	154	190	91
4	227	301	70	230	266	70
5	282	417	53	279	334	53
6	323	534	40	311	394	40
7	359	646	31	334	456	31
8	388	777	23	352	517	23
9	412	902	18	369	567	18
10	437	1031	14	384	622	14
11	459	1144	10	396	681	10
12	479	1258	29	408	726	29
13	495			419		
			500			500

Table 1.1. Continued.

	Largemouth bass (1995)[4]			Smallmouth bass (1995)[4]		
Age	TL	Weight	Nt	TL	Weight	Nt
1	138	38.0	0	103	35.0	0
2	160	62.0	0	145	70.0	0
3	218	174.0	154	228	223.0	236
4	276	381.0	154	278	367.0	251
5	315	590.0	154	308	470.0	154
6	354	870.0	77	348	680.0	215
7	384	1,139.0	115	391	1,038.0	97
8	438	1,763.0	192	418	1,260.0	21
9	446	1,872.0	77	450	1,250.0	26
10	485	2,473.0	77	478	1,950.0	
	495	2,646.0				1,000
			1,000			

4 Mean length-at-age (Fayram 1996) converted to mean weight-at-age using a length-weight regression.

Table 1.2. Diet composition for cutthroat trout ages 2, 3-4, and 5-7 used in bioenergetics modeling for annual comparison.

Cutthroat trout diet

Date	Model day	N	Sockeye salmon	Salmonid	Longfin smelt	Stickleback	Yellow perch	Sculpin	Other fish	*Neomysis*	*Daphnia*	Chironomid pupae	Aquatic insect	Benthic invertebrates
Age 2, Fork length < 200 mm.														
1/1	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
3/1	61	5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.48	0.02	0.00
5/1	122	9	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.01	0.33	0.53	0.01
6/1	153	7	0.00	0.00	0.03	0.19	0.05	0.00	0.00	0.03	0.34	0.31	0.07	0.00
9/8	252	56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
12/30	365	2	0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Age 3 & 4, Fork length 200 - 350 mm.														
1/1	1	2	0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3/16	76	6	0.05	0.01	0.00	0.00	0.12	0.18	0.11	0.11	0.00	0.23	0.17	0.00
3/23	83	3	0.16	0.00	0.73	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00
4/20	111	8	0.17	0.00	0.76	0.00	0.00	0.05	0.00	0.00	0.00	0.02	0.00	0.00
6/22	174	39	0.06	0.00	0.23	0.16	0.03	0.02	0.00	0.03	0.34	0.07	0.07	0.00
8/4	217	3	0.00	0.00	0.51	0.00	0.00	0.00	0.00	0.00	0.49	0.00	0.00	0.00
8/18	231	4	0.00	0.00	0.25	0.25	0.00	0.00	0.00	0.24	0.26	0.00	0.00	0.00
8/25	238	3	0.00	0.00	0.07	0.60	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00
9/7	251	3	0.00	0.00	0.62	0.00	0.00	0.05	0.00	0.00	0.33	0.00	0.00	0.00
9/21	265	7	0.11	0.00	0.46	0.00	0.00	0.14	0.00	0.00	0.29	0.00	0.00	0.00
12/30	365	4	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.73	0.00	0.00
Age 5-7, Fork length > 350 mm.														
1/1	1	4	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.73	0.00	0.00
3/16	76	5	0.59	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.20	0.00
3/23	83	2	0.50	0.00	0.00	0.45	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00
4/6	97	1	0.15	0.06	0.41	0.06	0.07	0.13	0.00	0.06	0.00	0.00	0.06	0.00
6/22	174	2	0.14	0.08	0.38	0.08	0.09	0.15	0.00	0.08	0.00	0.00	0.00	0.00
8/4	217	1	0.00	0.00	0.55	0.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8/18	231	13	0.00	0.00	0.25	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8/25	238	2	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10/1	275	4	0.33	0.04	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
12/30	365	3	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.73	0.00	0.00

Table 1.3. Northern pikeminnow diets estimated during an abundant longfin smelt year (2003). Diet composition for 100-200 mm Fork Length, 200-300 mm FL, and > 300 mm FL northern pikeminnow used in bioenergetics modeling.

Northern pikeminnow diet

Date	Model day	N	Sockeye salmon	Salmonid	Longfin smelt	Stickleback	Yellow perch	Sculpin	Other fish	*Neomysis*	*Daphnia*	Chironomid pupae	Aquatic insect	Benthic invertebrates
Age 1-2, Fork lengths 100 - 200 mm.														
1/1	1	11	0.00	0.00	0.27	0.00	0.0	0.00	0.4	0.09	0.00	0.18	0.09	0.00
3/16	76	17	0.00	0.00	0.26	0.00	0.0	0.00	0.1	0.08	0.04	0.03	0.40	0.02
4/20	111	2	0.02	0.00	0.29	0.00	0.0	0.00	0.1	0.00	0.00	0.12	0.30	0.02
5/20	141	2	0.00	0.00	0.20	0.00	0.0	0.00	0.2	0.00	0.00	0.40	0.08	0.11
6/22	174	40	0.00	0.00	0.00	0.00	0.0	0.00	0.0	0.00	0.50	0.00	0.25	0.25
8/3	216	5	0.00	0.00	0.00	0.00	0.0	0.00	0.3	0.00	0.00	0.00	0.67	0.00
8/17	230	4	0.00	0.00	0.00	0.25	0.0	0.00	0.0	0.00	0.00	0.00	0.00	0.10
9/7	251	3	0.00	0.00	0.00	0.00	0.0	0.00	0.1	0.00	0.55	0.19	0.15	0.00
9/21	265	4	0.00	0.00	0.00	0.00	0.0	0.00	0.0	0.00	0.33	0.33	0.17	0.17
10/26	300	18	0.00	0.14	0.00	0.00	0.0	0.00	0.3	0.00	0.57	0.00	0.00	0.00
12/30	365	10	0.27	0.00	0.13	0.00	0.25	0.25	0.10	0.00	0.00	0.00	0.0	0.00
Age 3-4, Fork lengths 200 - 300 mm.														
1/1	1	10	0.27	0.00	0.13	0.00	0.25	0.25	0.10	0.00	0.00	0.00	0.0	0.00
3/16	76	13	0.20	0.00	0.55	0.00	0.07	0.04	0.14	0.00	0.00	0.00	0.0	0.00
4/20	111	1	0.03	0.00	0.90	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.0	0.00
5/20	141	2	0.08	0.00	0.39	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.4	0.00
6/22	174	27	0.18	0.01	0.62	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.1	0.07
8/3	216	12	0.00	0.00	0.35	0.13	0.00	0.00	0.07	0.00	0.00	0.00	0.4	0.01
8/17	230	21	0.03	0.00	0.61	0.01	0.03	0.00	0.00	0.00	0.00	0.07	0.1	0.10
9/7	251	14	0.04	0.00	0.32	0.04	0.00	0.00	0.04	0.00	0.51	0.00	0.0	0.00
9/21	265	29	0.00	0.05	0.71	0.05	0.00	0.05	0.00	0.00	0.10	0.00	0.0	0.00
10/26	300	24	0.00	0.00	0.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.20
12/30	365	21	0.50	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00
Age 5-11, Fork lengths > 300 mm.														
1/1	1	3	0.50	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00
3/16	76	10	0.50	0.00	0.10	0.00	0.00	0.25	0.08	0.00	0.00	0.00	0.00	0.07
3/23	83	5	0.55	0.00	0.35	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4/20	111	1	0.13	0.00	0.77	0.00	0.00	0.04	0.00	0.00	0.00	0.05	0.00	0.00
5/20	141	20	0.00	0.10	0.30	0.00	0.00	0.10	0.08	0.00	0.00	0.03	0.23	0.17
6/22	174	10	0.10	0.01	0.43	0.15	0.00	0.06	0.00	0.00	0.00	0.08	0.00	0.09
8/3	216	13	0.00	0.00	0.55	0.29	0.00	0.00	0.00	0.00	0.00	0.03	0.13	0.00
8/17	230	12	0.18	0.01	0.64	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00
9/7	251	15	0.00	0.06	0.65	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.00	0.00
9/21	265	7	0.00	0.00	0.83	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10/26	300	6	0.11	0.01	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00
12/30	365	8	0.50	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00

Table 1.4. Northern pikeminnow diet estimated during a weak longfin smelt year (1972) used in bioenergetics modeling (Olney 1975).

Simulation Date	N	Day	Sculpin	Sockeye	Longfin smelt	Stickle-back	Other Fish	Cray-fish	Chiro-nomids	Inverte -brates
1/1	75	1	0.40	0.14	0.19	0.02	0.22	0.03	0.00	0.00
3/1	89	61	0.42	0.12	0.02	0.02	0.35	0.06	0.00	0.00
5/31	42	152	0.58	0.09	0.00	0.00	0.19	0.13	0.01	0.01
8/31	28	244	0.12	0.26	0.17	0.00	0.13	0.31	0.02	0.00
11/30	75	335	0.40	0.14	0.19	0.02	0.22	0.03	0.00	0.00
12/30	75	365	0.40	0.14	0.19	0.02	0.22	0.03	0.00	0.00

Table 1.5. Diet composition for 100-225 mm and >225 mm FL size classes of yellow perch during 2003 used in bioenergetics modeling.

Yellow perch diet

Date	Model day	N	Sockeye salmon	Salmonid	Longfin smelt	Stickleback	Yellow perch	Sculpin	Other fish	*Neomysis*	*Daphnia*	Chironomid pupae	Aquatic insect	Benthic invertebrates
Age 1-2, Fork length 100 - 225 mm.														
1/1	1	14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.00	0.08	0.25	0.02
3/16	76	14	0.00	0.00	0.07	0.00	0.00	0.00	0.09	0.53	0.01	0.15	0.06	0.09
4/20	111	15	0.00	0.00	0.06	0.12	0.07	0.00	0.15	0.10	0.00	0.42	0.07	0.00
5/18	139	15	0.00	0.00	0.00	0.00	0.00	0.07	0.13	0.25	0.00	0.06	0.50	0.00
6/22	174	14	0.07	0.00	0.00	0.00	0.00	0.14	0.07	0.25	0.28	0.00	0.18	0.00
8/3	216	7	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.14	0.00	0.29	0.43
9/1	245	59	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.04	0.79	0.04	0.09	0.02
10/20	294	18	0.00	0.00	0.00	0.06	0.00	0.00	0.11	0.55	0.22	0.07	0.00	0.00
11/17	322	10	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.90	0.00	0.00	0.00	0.00
12/30	365	4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.00	0.08	0.25	0.02
Age 3-5, Fork length > 225 mm.														
1/1	1	4	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.25	0.00	0.27	0.0	0.18
3/16	76	2	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.5	0.00
4/20	111	2	0.00	0.00	0.61	0.00	0.00	0.39	0.00	0.00	0.00	0.00	0.0	0.00
5/18	139	2	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.0	0.50
6/22	174	10	0.29	0.00	0.00	0.00	0.00	0.68	0.03	0.00	0.00	0.00	0.0	0.00
8/3	216	3	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.33	0.00	0.0	0.53
9/1	245	3	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00
10/20	294	4	0.00	0.00	0.25	0.25	0.00	0.00	0.00	0.00	0.00	0.25	0.2	0.02
11/17	322	2	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00
12/30	365	4	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.25	0.00	0.27	0.0	0.18

Table 1.6. Diet composition from an abundant longfin smelt year in 1995 a) for smallmouth bass and b) for largemouth bass used for bioenergetics modeling (Fayram and Sibley 2000).

a) Smallmouth bass > 150 mm TL.

Date	Model Day	N	Salmonid	Other Fish	Crayfish	Zooplankton	Other invertebrates
4/1	92	28	0.28	0.51	0.13	0.00	0.07
7/1	183	22	0.00	0.70	0.30	0.00	0.00
10/1	275	22	0.00	0.70	0.30	0.00	0.00

b) Largemouth bass > 150 mm TL.

Date	Model day	N	Salmonid	Other Fish	Crayfish	Zooplankton	Other invertebrates
5/1	122	8	0.18	0.52	0.10	0.10	0.10
6/1	153	4	0.55	0.25	0.00	0.00	0.20
7/1	183	7	0.00	0.81	0.00	0.00	0.19
9/1	245	13	0.00	0.18	0.77	0.05	0.00

Table 1.7. Prickly sculpin diet composition for age 1, age 2-3, and age 4-6 sculpin used for bioenergetics modeling (Recomputed from Rickard 1980 by Moss, unpublished).

Prickly sculpin diet age 1 (total length < 87 mm)

Simulation Date	Day	Fish	*Neomysis*	Chironomid	Trichoptera	Mollusca	Misc. Invertebrate
1/1	1	0.00	0.23	0.69	0.00	0.00	0.08
3/30	90	0.00	0.05	0.87	0.00	0.00	0.08
6/28	180	0.00	0.06	0.88	0.00	0.00	0.06
9/26	270	0.00	0.13	0.77	0.00	0.00	0.10
12/30	365	0.00	0.13	0.77	0.00	0.00	0.10

Prickly sculpin diet age 2-3 (total length 87-128 mm)

Simulation Date	Day	Fish	*Neomysis*	Chironomid	Trichoptera	Mollusca	Misc. Invertebrate
1/1	1	0.05	0.34	0.30	0.05	0.08	0.18
3/30	90	0.03	0.06	0.38	0.28	0.07	0.18
6/28	180	0.05	0.12	0.50	0.14	0.03	0.16
9/26	270	0.13	0.18	0.31	0.03	0.15	0.20
12/30	365	0.13	0.18	0.31	0.03	0.15	0.20

Prickly sculpin diet age 4-6 (total length >129 mm)

Simulation Date	Day	Fish	*Neomysis*	Chironomid	Trichoptera	Mollusca	Misc. Invertebrate
1/1	1	0.22	0.34	0.09	0.01	0.05	0.29
3/30	90	0.20	0.09	0.16	0.09	0.06	0.40
6/28	180	0.29	0.15	0.18	0.04	0.02	0.32
9/26	270	0.45	0.14	0.07	0.01	0.08	0.25
12/30	365	0.45	0.14	0.07	0.01	0.08	0.25

Table 1.8. Diet composition for all size classes of peamouth chub used in bioenergetics modeling (Shanbhogue 1976).

Peamouth diet

Date	Model day	N	Oligochaetes	Chironomid larvae	Chironomid pupae	Bivalve	Gastropod	Trichoptera larvae	Coleoptera	Odonate	*Neomysis*	Amphipoda	Other diptera	Hirudinea	Nemerteans	Plant
1/1	1	6	0.03	0.04	0.08	0.00	0.42	0.00	0.10	0.00	0.20	0.12	0.00	0.00	0.00	0.01
4/1	92	43	0.32	0.19	0.00	0.27	0.01	0.02	0.01	0.00	0.00	0.01	0.02	0.03	0.02	0.10
5/1	122	59	0.37	0.31	0.01	0.22	0.03	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.04
6/1	153	119	0.31	0.16	0.00	0.27	0.02	0.06	0.02	0.02	0.01	0.01	0.01	0.00	0.00	0.11
7/1	183	111	0.21	0.10	0.27	0.01	0.23	0.09	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.05
8/1	214	74	0.21	0.07	0.05	0.05	0.50	0.06	0.04	0.01	0.00	0.01	0.00	0.00	0.00	0.00
9/1	245	36	0.18	0.04	0.02	0.00	0.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
11/1	306	25	0.19	0.03	0.18	0.00	0.48	0.00	0.01	0.00	0.01	0.06	0.00	0.00	0.00	0.04
12/1	336	6	0.03	0.04	0.08	0.00	0.42	0.00	0.10	0.00	0.20	0.12	0.00	0.00	0.00	0.01
12/30	365	6	0.03	0.04	0.08	0.00	0.42	0.00	0.10	0.00	0.20	0.12	0.00	0.00	0.00	0.01

Table 1.9. Thermal exposure in degrees centigrade used for bioenergetics models of cutthroat trout, northern pikeminnow, yellow perch, peamouth chub, largemouth bass, smallmouth bass, and prickly sculpin.

Date	Model day	**Cutthroat trout [1]** all ages	Date	Model day	**Y. perch, peamouth, & N. pikeminnow [2]** all ages
1/1	1	8.0	1/1	1	6.6
2/1	32	7.0	2/1	32	6.5
3/11	71	7.0	3/1	61	6.2
3/23	83	8.0	4/1	92	8.7
4/6	97	8.0	5/1	122	11.6
4/20	111	9.0	6/1	153	16.6
5/4	125	11.0	7/1	183	22.7
5/19	140	13.0	8/1	214	23.0
10/31	305	13.0	9/1	245	21.0
11/16	321	12.0	10/1	275	10.0
11/29	334	10.0	11/1	306	10.1
12/13	348	9.0	12/1	336	6.8
12/30	365	8.0	12/30	365	6.8

Date	Model day	**Largemouth & smallmouth bass [3]** all ages	Date	Model day	**Prickly sculpin [4]** all ages
	1	6.9	1/1	1	8.3
1/19	19	6.9	1/30	30	7.0
2/6	37	7.8	2/29	60	7.0
3/6	66	7.2	3/30	90	8.3
3/20	80	8.5	4/29	120	11.0
4/3	94	11.5	5/29	150	13.8
4/17	108	10.2	6/28	180	7.5
5/1	122	13.9	8/17	230	7.5
5/15	136	16.1	9/16	260	7.5
6/6	158	18.9	10/16	290	7.5
7/11	193	21.3	11/15	320	8.0
8/2	215	22.4	12/30	365	9.0
9/11	255	20.4			
10/4	278	18.5			
11/6	311	11.9			
12/4	339	10.0			
12/30	365	6.9			

1 Thermal experience for cutthroat trout (Nowak 2000)
2 Thermal experience for benthic species (Bartoo 1977)
3 Thermal experience estimated from King County temperature profiles using 1 meter readings conducted in 1995
4 Thermal experience estimated from thermal profiles and prickly sculpin distributional movement (Moss, unpublished data).

Table 1.10. Seasonal prey energy densities (J/g wet weight) used in bioenergetics modeling (Cummins and Wuycheck 1971; Luecke and Brandt 1993; Jen McIntyre, unpublished data).

Prey Species	Winter	Spring	Summer	Fall
Amphipod	4079	4079	4079	4079
Aquatic insects	4428	4428	4428	4428
Bivalve	1800	1800	1800	1800
Chironomid pupae	4428	4428	4428	4428
Chironomid larvae	4428	4428	4428	4428
Coho	5211	7445	7287	7129
Coleoptera	4428	4428	4428	4428
Cottid	4178	4514	4267	4380
Crayfish	3318	3318	3318	3318
Cyprinid	7093	7093	7093	7093
Daphnia	3800	3800	3800	3800
Ephemoptera	4428	4428	4428	4428
Gastropod	1800	1800	1800	1800
Neomysis	4337	4196	3817	4337
Peamouth	7093	7093	7093	7093
Smelt	5960	5960	5138	4316
Sockeye	5211	7445	7287	7129
Stickleback	6949	6949	6949	6949
Terrestrial insects	4428	4428	4428	4428
Tricoptera	8052	8052	8052	8052
Unidentified/other fish	6040	6785	6458	6131
Unidentified salmonid	5211	7445	7287	7129
Yellow perch	6332	6332	6337	6337

Table 1.11. Size-structured, seasonal consumption estimates (kg) for different sizes/age groups of cutthroat trout, northern pikeminnow, and yellow perch based on data collected in 2003 and for largemouth bass and smallmouth bass collected during 1995 (Fayram and Sibley 2000), prickly sculpin collected during 1975 (Rickard 1980), and peamouth chub collected during 1972-1974 using relative population densities of 1,000 fish for each species. Population age-structure was determined from proportions observed in sample catches for each consumer. Northern Pikeminnow population structure was estimated by applying an annual survival rate, s. Consumption patterns pertain to the main basins of the lake and exclude the ship canal.

Cutthroat trout, (High smelt year)

Season	N	Sockeye salmon	Salmonid	Longfin smelt	Stickleback	Yellow perch	Sculpin	Other fish	*Neomysis*	*Daphnia*	Aquatic insect	Total
					age 2, FL < 200 mm							
spring	210	0.0	0.0	0.2	2.3	1.1	0.0	1.1	1.1	6.5	13.7	25.9
summer	210	0.0	0.0	0.2	1.7	0.4	0.0	0.4	0.3	32.1	4.9	39.9
fall	210	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	17.2	25.0	42.6
winter	210	0.0	0.0	0.0	0.0	0.1	0.0	0.1	2.9	0.0	6.7	9.8
					age 3 & 4, FL 200-350 mm							
spring	400	19.4	2.4	94.6	14.5	2.4	5.5	2.6	2.8	32.8	16.2	193.2
summer	400	6.3	0.9	93.1	27.4	0.9	8.1	0.1	7.4	84.9	5.1	234.3
fall	400	74.1	0.0	111.6	0.0	0.0	15.3	0.0	0.0	30.7	0.3	232.1
winter	400	22.2	2.5	29.9	0.0	5.1	7.7	10.9	4.8	0.0	19.5	102.5
					age 5-7, FL ≥ 350 mm							
spring	390	24.3	115.9	288.8	53.7	49.5	89.1	2.1	43.0	17.7	26.5	710.6
summer	390	3.3	73.0	389.1	264.5	9.8	19.9	0.1	11.9	45.0	3.1	819.7
fall	390	38.4	132.4	57.9	318.6	0.4	8.0	7.2	0.0	16.0	249.7	828.6
winter	390	133.4	3.5	55.9	59.1	3.8	6.1	15.5	3.5	0.0	163.1	443.8
total	1000	321.3	330.7	1121.3	741.8	73.4	159.8	40.4	77.7	282.9	533.7	3682.8

Table 1.11. Continued.

Northern pikeminnow (2003, high smelt year), s = 76%

Season	N	Sockeye salmon	Salmonid	Longfin smelt	Stickleback	Yellow perch	Sculpin	Other fish	*Neomysis*	*Daphnia*	Aquatic insect	Total
< 200 mm FL												
spring	463	0.7	0.0	25.6	0.0	0.0	0.0	0.0	0.0	27.7	66.8	120.8
summer	463	0.0	0.8	0.0	41.5	0.0	0.0	0.0	0.0	58.5	140.9	241.7
fall	463	0.0	11.3	6.3	0.0	0.0	0.0	4.2	0.0	24.2	8.9	54.9
winter	463	0.0	0.0	3.3	0.0	0.0	0.0	0.8	0.0	1.0	4.3	9.5
201-300 mm FL												
spring	286	24.8	0.9	117.0	0.5	0.2	0.1	0.4	0.0	0.0	29.0	172.9
summer	286	13.2	2.6	155.4	18.4	2.3	1.8	0.0	0.0	34.7	73.2	301.6
fall	286	2.9	0.5	37.9	0.5	2.6	3.1	0.0	0.0	0.9	7.7	56.1
winter	286	3.4	0.0	6.7	0.0	2.1	1.8	1.3	0.0	0.0	0.0	15.3
> 300 mm FL												
spring	251	23.3	13.2	135.2	21.8	0.6	22.8	0.0	0.0	0.0	72.1	289.1
summer	251	26.9	6.2	287.3	75.9	0.0	4.7	0.0	0.0	28.1	44.4	473.5
fall	251	12.6	0.8	58.7	2.6	0.0	5.8	0.0	0.0	0.0	7.1	87.6
winter	251	14.4	0.0	4.4	0.0	0.7	7.4	0.0	0.0	0.0	0.9	27.7
total	1000	110.4	27.6	762.1	125.7	8.0	43.7	4.1	0.0	175.1	455.2	1850.4

Northern Pikeminnow (1972, low smelt year *), s = 76%

Season	N	Sockeye salmon	Crayfish	Longfin smelt	Stickleback	Yellow perch	Sculpin	Other fish	Neomysis	Daphnia	Aquatic insect	Total
TL < 300 mm												
spring	708	12.3	13.8	0.6	0.6		67.5	28.8			1.2	124.9
summer	708	102.5	127.7	52.5	0.0		189.0	90.6			8.0	570.4
fall	708	56.5	58.5	44.8	1.4		49.8	39.3			2.7	253.2
winter	708	2.6	0.7	2.9	0.4		7.6	4.7			0.0	18.9
TL > 300 mm												
spring	292	16.2	18.0	0.8	0.8		88.3	37.8			1.6	163.6
summer	292	106.8	133.3	53.7	0.0		205.4	96.7			8.5	604.3
fall	292	50.3	52.3	39.7	1.2		43.7	34.7			2.4	224.4
winter	292	2.7	0.8	2.9	0.4		8.2	5.1			0.0	20.1
total	1000	349.9	405.1	197.9	4.9		659.6	337.7			24.5	1979.7

Table 1.11. Continued.

Yellow Perch

Season	N	Sockeye salmon	Benthic Invert.	Longfin smelt	Stickleback	Yellow perch	Sculpin	Other fish	*Neomysis*	*Daphnia*	Aquatic insect	Total
						100 - 225 mmTL						
spring	900	1.3	0.4	0.6	1.0	0.6	3.7	4.6	9.9	5.4	16.6	44.2
summer	900	0.9	14.9	0.0	0.3	0.0	7.1	1.5	7.4	33.0	16.1	81.2
fall	900	0.0	0.2	0.0	2.2	0.0	0.0	1.5	26.3	4.5	3.8	38.5
winter	900	0.0	0.9	0.7	0.1	0.1	0.0	0.9	9.5	0.1	4.5	16.9
						> 225 mmTL						
spring	100	2.1	3.5	2.5	0.0	0.0	9.9	0.6	0.0	0.1	0.4	19.0
summer	100	1.3	6.2	10.4	2.1	0.0	3.0	0.1	0.0	3.8	0.9	27.9
fall	100	0.0	0.3	1.7	1.1	4.8	0.7	0.0	0.7	0.0	3.0	12.3
winter	100	0.0	0.4	0.2	0.0	0.0	1.0	2.4	0.9	0.0	3.5	8.4
total	1000	5.6	26.9	16.2	6.9	5.4	25.4	11.7	54.6	47.0	48.8	248.6

Smallmouth bass, > 150 mm FL

Season	N	*Daphnia*	Crayfish	Aquatic insect	Salmonid	Other fish	Total
spring	1000	0.1	22.8	4.7	18.1	65.9	111.6
summer	1000	0.0	182.1	1.7	6.7	425.7	616.2
fall	1000	0.0	58.7	0.0	0.0	135.8	194.5
total	1000	0.2	263.6	6.4	24.7	627.4	922.3

Largemouth bass, > 150 mm FL

Season	N	*Daphnia*	Crayfish	Aquatic insect	Salmonid	Other fish	Total
spring	1000	6.9	6.9	22.6	55.5	55.6	147.5
summer	1000	15.5	238.5	97.4	58.8	411.7	821.8
total	1000	22.4	245.4	119.9	114.3	467.3	969.3

Table 1.11. Continued.

Prickly Sculpin

Season	N	*Neomysis*	Chironomid	Aquatic insect	Trichoptera	Mollusca	fish	Total
				age 1, TL < 87 mm				
spring	760	0.3	4.9	0.4	0.0	0.0	0.0	5.6
summer	760	0.8	8.8	0.7	0.0	0.0	0.0	10.3
fall	760	1.4	8.6	1.1	0.0	0.0	0.0	11.1
winter	760	0.8	4.4	0.5	0.0	0.0	0.0	5.8
				age 2 - 3, TL 87 - 128 mm				
spring	225	0.5	2.3	1.0	1.3	0.3	0.2	5.5
summer	225	1.0	3.3	1.3	0.9	0.5	0.5	7.4
fall	225	1.3	2.2	1.4	0.2	1.0	0.9	7.1
winter	225	1.0	1.5	0.9	0.4	0.5	0.4	4.7
				age 4 - 6, TL >128 mm				
spring	15	0.1	0.1	0.3	0.1	0.0	0.2	0.8
summer	15	0.1	0.1	0.2	0.0	0.0	0.2	0.7
fall	15	0.1	0.1	0.2	0.0	0.1	0.3	0.7
winter	15	0.1	0.1	0.2	0.0	0.0	0.2	0.7
total	1000	7.5	36.4	8.2	2.9	2.5	3.0	60.5

Peamouth Chub, > 100 mm TL

Season	N	*Neomysis*	Chironomid	Aquatic insect	Benthic Invert.	Gastropod	Plant	Total
spring	1000	2.3	56.3	14.6	133.3	8.2	17.8	232.4
summer	1000	0.9	122.7	62.1	168.2	226.0	22.7	602.4
fall	1000	6.8	34.1	14.2	43.4	151.8	8.3	258.6
winter	1000	21.8	18.8	25.9	19.8	46.1	3.8	136.3
total	1000	31.8	231.9	116.7	364.7	432.1	52.5	1229.7

Table 1.12. Relative population-level consumption (kg) of major prey fishes and *Neomysis* by a) cutthroat trout, b) northern pikeminnow, c) yellow perch and d) black bass during an odd-numbered year when yearling smelt were abundant (2003).

a) Cutthroat trout, N = 100,000

Season	Sockeye	Other Salmonids	Smelt	Stickleback	Sculpin	Yellow perch	Neomysis	Other fish	Coho
Winter	19,913	66	10,592	7,286	1,695	1,101	1,025	-	78
Spring	13,440	957	42,689	7,552	10,661	5,836	5,146	-	3,774
Summer	7,599	737	51,849	31,697	2,986	1,181	2,043	-	708
Fall	24,169	1,437	16,950	34,604	2,336	40	-	-	-
Total	65,121	3,198	122,079	81,137	17,678	8,157	8,213	-	4,560

b) Northern pikeminnow, N = 100,000

Season	Sockeye	Other Salmonids	Smelt	Stickleback	Sculpin	Yellow perch	Neomysis	Other fish	Coho
Winter	3,064	0	2,691	-	1,640	579	176	-	-
Spring	8,994	291	50,723	3,890	4,195	141	27	-	2,366
Summer	7,606	332	84,307	20,340	1,235	475	-	-	1,379
Fall	3,088	137	19,745	561	1,918	647	237	-	1,264
Total	22,752	760	157,466	24,790	8,988	1,842	440	-	5,009

c) Yellow perch, N = 1,000,000

Season	Sockeye	Other Salmonids	Smelt	Stickleback	Sculpin	Yellow perch	Neomysis	Other fish	Coho
Winter	-	-	978	92	1,112	51	10,468	3,564	-
Spring	3,637	-	3,345	1,045	14,495	560	9,913	5,273	-
Summer	2,307	-	11,291	2,566	10,370	-	7,379	1,664	-
Fall	-	-	1,866	3,464	754	5,134	26,999	1,533	-
Total	5,944	-	17,480	7,167	26,731	5,745	54,758	12,035	-

d) Smallmouth and Largemouth bass, N = 10,000

Season	Sockeye	Other Salmonid	Smelt	Stickleback	Sculpin	Yellow perch	Neomysis	Other fish	Coho
Spring	-	730	-	-	-	-	-	1,765	-
Summer	-	-	-	-	-	-	-	3,771	-
Fall	-	-	-	-	-	-	-	36	-
Total	-	730	-	-	-	-	-	5,572	-

Table 1.13. Average monthly weights (g) of individual prey fishes, used to convert relative population estimates of consumed biomass of prey fish (kg) into numbers of prey consumed. Weights for three-spine stickleback were from Chigbu (2000). March and October weights for sockeye salmon and longfin smelt were means observed during 2003 (Beauchamp et al. 2003). Other months were estimated using lengths reported in Chigbu (2000) and a length-weight regression to estimate weight, or were the geometric mean weight of the previous and following months.

Month	Sockeye	Other Salmonids	Longfin Smelt	Three-spine Stickleback
Jan	16.0	16.0	6.8	3.0
Feb	12.9	12.9	9.3	3.0
Mar	10.4	10.4	8.8	3.0
Apr	10.4	10.4	8.8	3.0
May	8.0	8.0	2.0	3.0
Jun	3.5	3.5	2.5	3.0
July	3.7	3.7	3.0	0.5
Aug	5.0	5.0	3.5	1.0
Sept	8.7	8.7	5.0	1.5
Oct	13.2	13.2	5.4	2.0
Nov	14.5	14.5	5.8	2.3
Dec	16.0	16.0	6.2	2.5

Table 1.14. Relative population-level consumption of sockeye salmon, other salmonids, longfin smelt, and three-spine stickleback (number of individuals) by a) cutthroat trout, b) northern pikeminnow, c) yellow perch and d) black bass during 2003, an odd-numbered year when yearling smelt were abundant.

a) Cutthroat trout, N = 100,000

Season	Sockeye	Other Salmonids	Smelt	Stickleback
Winter	1,647,258	5,798	1,300,267	2,428,619
Spring	2,201,227	173,037	14,824,356	2,517,189
Summer	1,172,927	114,951	14,185,758	36,551,782
Fall	1,720,279	105,227	2,950,641	15,922,721
Total	6,741,691	399,013	33,261,022	57,420,311

b) Northern pikeminnow, N = 100,000

Season	Sockeye	Other Salmonids	Smelt	Stickleback
Winter	248,081	14	320,937	-
Spring	1,961,622	78,027	19,887,515	1,296,564
Summer	1,693,472	73,475	23,104,131	28,504,621
Fall	214,443	10,097	3,574,024	280,553
Total	4,117,619	161,613	46,886,607	30,081,738

c) Yellow perch, N = 1,000,000

Season	Sockeye	Other Salmonids	Smelt	Stickleback
Winter	-	-	113,032	30,624
Spring	993,342	-	673,080	348,412
Summer	622,600	-	2,685,711	3,197,201
Fall	-	-	345,470	1,621,995
Total	1,615,942	-	3,817,294	5,198,233

d) Smallmouth and Largemouth bass, N = 10,000

Season	Sockeye	Other Salmonid	Smelt	Stickleback
Spring	-	141,811	-	-
Summer	-	-	-	-
Fall	-	-	-	-
Total	-	141,811	-	-

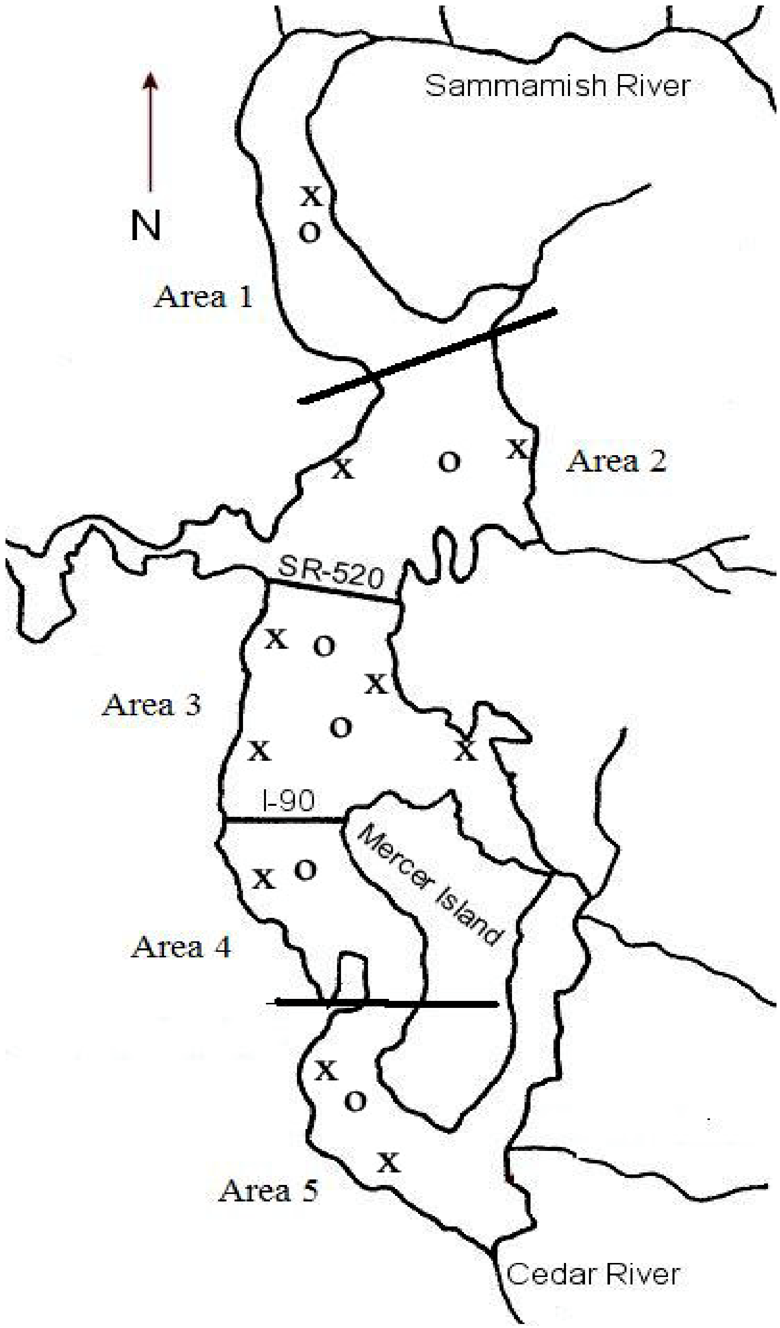

Figure 1.1. Lake Washington showing the five sampling areas, limnetic sampling sites (O), and sites where bottom nets were deployed (X).

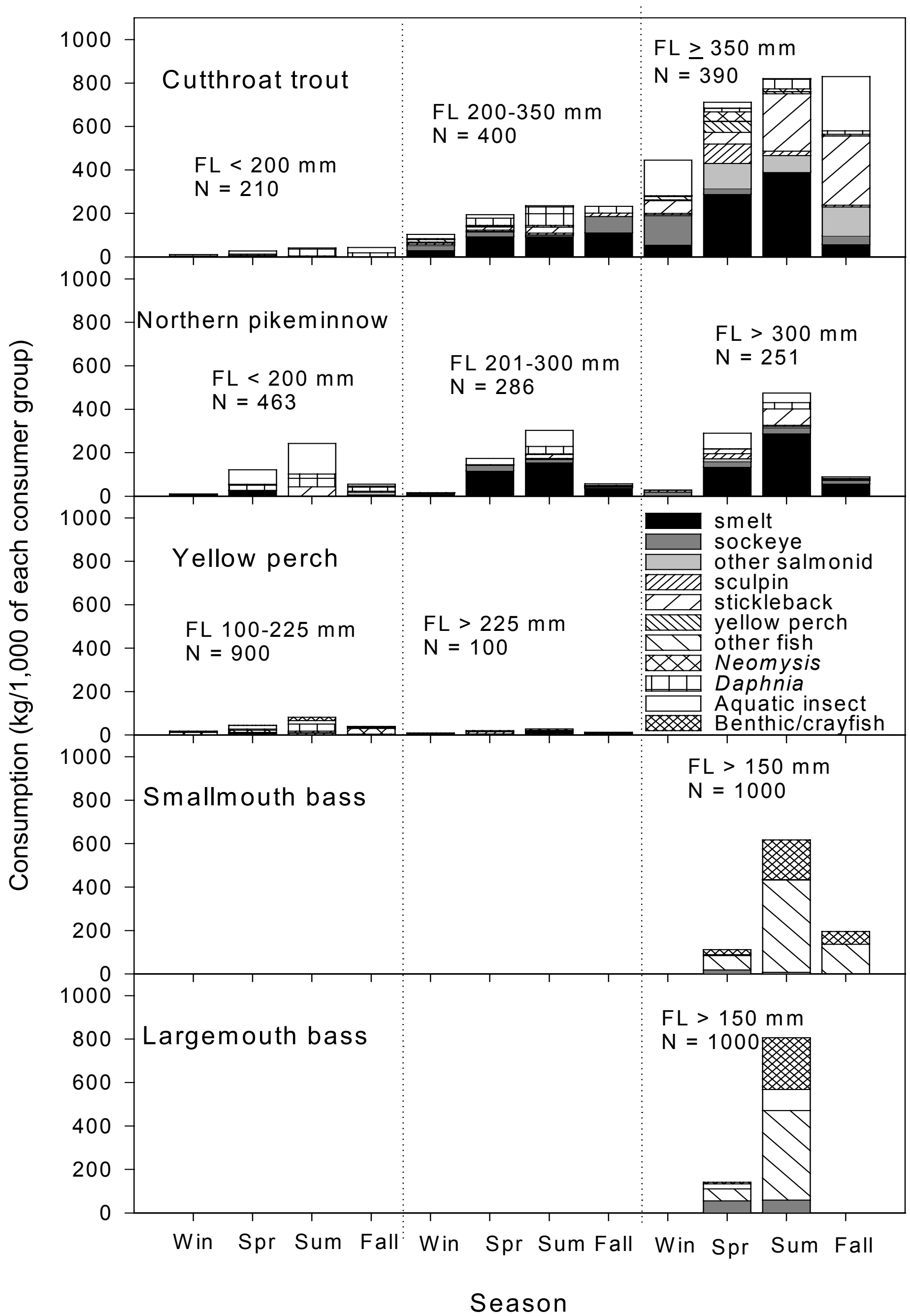

Figure 1.2. Estimated seasonal prey consumption by size-structured unit populations of 1,000 piscivores in Lake Washington (kg/1,000 of each consumer species) during odd years when yearling smelt were abundant. N represents the number of individuals from each size group that was modeled as part of the 1,000 fish population.

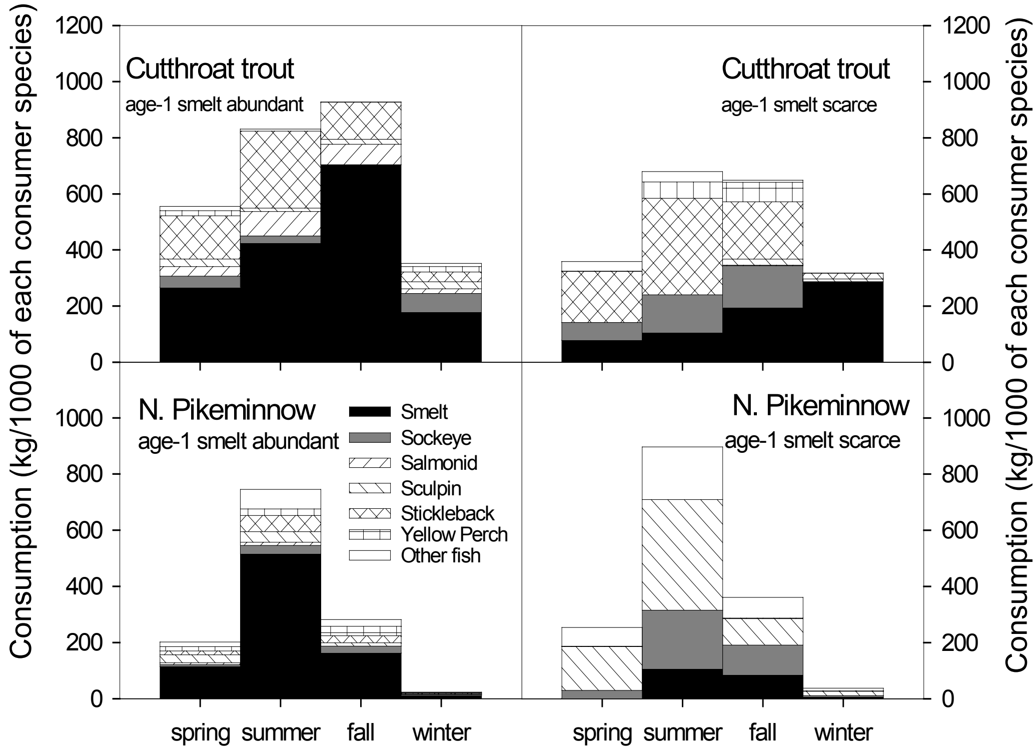

Figure 1.3. Estimated seasonal consumption of longfin smelt, sockeye salmon, unidentified salmonid, sculpin, three-spine stickleback, yellow perch, and other fish (kg/1,000) by cutthroat trout (top panels) and northern pikeminnow (bottom panels) for an abundant longfin smelt year (odd year) and less abundant longfin smelt year (even year). Odd year diets were from 2003 and even year diets combined data from 2002 with 1984 for cutthroat trout (Beauchamp 1992) and 1972 for northern pikeminnow (Olney 1975).

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CHAPTER 2

A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities

Synopsis

Differences in reaction distance to prey fish by piscivorous salmonids can alter predator–prey interactions under different visual conditions. We compared reaction distances of three piscivorous salmonids commonly found in western lakes: cutthroat trout (*Oncorhynchus clarki utah)*, rainbow trout (*O. mykiss)*, and the nonnative lake char (*Salvelinus namaycush)*. Reaction distances to salmonid prey were measured as functions of light and turbidity in a controlled laboratory setting. In addition, predation rates and swimming speeds of lake char preying on juvenile cutthroat trout were measured experimentally under a range of light levels. Reaction distances for cutthroat trout and rainbow trout increased rapidly as light levels increased, reaching relatively constant reaction distances at higher light levels. Reaction distances for lake char were similar to cutthroat trout and rainbow trout at the lower light levels; however, lake char reaction distances continued to increase with increasing light intensity to asymptote at distances 65% higher than those for both cutthroat and rainbow trout. Predation rates by lake char were low for the darkest light levels, increased rapidly under low light levels (0.50-0.75 lux), and then declined to an intermediate rate at all higher light levels. Swimming speeds by lake char also increased rapidly from extremely low light conditions to a peak and declined to an intermediate level at light levels above 1.00 lux. These results suggest that, above the saturation intensity threshold, piscivorous lake char react to fish prey at greater distances than do cutthroat trout and rainbow trout. These differences may help explain the decline of native trout following the introductions of nonnative lake char in lakes and reservoirs of western North America.

Introduction

Predation can affect the structure of aquatic communities (Paine 1966, Carpenter et al. 1985, Kerfoot & Sih 1987, Persson et al. 1991, Strong 1992, Carpenter & Kitchell 1993), and has been implicated in the decline or localized extinctions of fish populations following the introduction or invasion of exotic species (Zaret & Paine 1973, Robinson & Tonn 1989, Donald & Alger 1993, Kitchell et al. 1997). However, because predation effects vary considerably among communities with similar assemblages, a closer examination of the underlying mechanisms of these interactions is required to determine conditions under which predation will regulate prey populations. Insight into the mechanisms governing predatory and competitive interactions among piscivorous species, and an understanding of how these interactions are mediated by changes in the physical environment, should enhance our ability to predict how key species will respond to differences in environmental conditions and prey availability.

Pelagic salmonids are primarily visual feeders (Ali 1959). Knowing how light and turbidity affect prey detection and temporal-spatial foraging success of different species (Beauchamp et al. 1999) will be important for defining the spatial and temporal dimensions of each species' niche and for determining which species may have a competitive or predatory advantage under different environmental conditions. Additionally, differences in visual feeding due to ontogeny and hierarchical interactions can also exist between individuals of the same species and may influence fine scale habitat use and distributional patterns. Some aspects of visual feeding by piscivores have been examined for cyprinids (Cerri 1983), centrarchids (Howick & O'Brien 1983, Miner & Stein 1996), and salmonids (Savitz & Bardygula unpublished, Vogel & Beauchamp 1999). Reaction distances to zooplankton differ considerably between cutthroat trout and Dolly Varden char (*S. malma),* and the advantage shifts from char under low light conditions to trout at higher light intensities (Henderson & Northcote 1985). These results suggest that ecologically significant differences in visual capabilities exist between genera, and perhaps among finer taxonomic groups of salmonids. However, reaction distances have not been compared among different species of piscivorous salmonids under different optical conditions. Nor have predation rates or swimming speeds been examined for piscivorous salmonids across a range of light levels that would be experienced by predators during nocturnal and crepuscular periods or during daylight in deep water. Because pelagic prey fishes often seek refuge in darker waters and minimize predation risk by feeding during crepuscular periods (Eggers 1978, Clark & Levy 1988), it is particularly important to understand the piscivores' visual foraging capabilities under these conditions when prey are most available to them.

Vogel & Beauchamp (1999) reported that reaction distances for lake char increased rapidly with light intensity then remained constant or declined gradually above a threshold light level. Reaction distances were unaffected by prey size over the range examined (55-130 mm TL), but declined with increasing turbidity (Vogel & Beauchamp 1999). Reaction distances also declined exponentially with increasing turbidity for largemouth bass (*Micropterus salmoides)* reacting to small bluegills (*Lepomis macrochirus)* (Miner & Stein 1996). When this exponential relationship was applied in a visual foraging model to natural systems, prey encounter rates were quite sensitive to small changes in turbidity over a range corresponding to levels (≤ 3 NTU) generally found in ultra-oligotrophic to mesotrophic lakes and reservoirs. The few turbidity studies involving piscivore-prey detections covered a very broad range of turbidities (e.g., 0.3-100 NTU in Miner & Stein 1996) and were not designed to detect thresholds or other fine-scale responses over the range most relevant to lacustrine salmonid systems. Therefore, experimentation at low turbidity (≤ 3 NTU) and light levels (< 1.00 lux) was necessary to determine the appropriate relationship between reaction distance, light, and turbidity over a low range of turbidities. Nocturnal feeding of salmonids has been documented primarily from diet studies (see review by Helfman 1978). Laboratory experimentation has shown the importance of low light foraging by piscivorous northern pikeminnow (*Ptychocheilus oregonensis;* Petersen & Gadomski 1994). Similar experiments are required to examine how relative prey capture rates and swimming speeds change as a function of light for piscivorous salmonids.

In this paper we refine the existing reaction distance relationships of Vogel & Beauchamp (1999) with higher-resolution experimental data at low light and turbidities. We then develop and compare reaction distance relationships for cutthroat and rainbow trout to those for lake char over similar ranges of light and turbidity. For lake char, we also examined how relative predation rates and swimming speeds changed over a range of light levels.

Methods

Predators and Prey

Reaction distance and predation rate experiments were conducted on lake char (size range 330-496 mm total length TL), cutthroat trout (size range 328-502 mm TL), and rainbow trout (size range 377-412 mm TL) in a 4.5 m long x 1 m wide x 1 m high laboratory trough following the methods of Vogel & Beauchamp (1999). Lake char were obtained from a hatchery and were first-generation offspring of wild brood stock. Cutthroat trout and rainbow trout were captured from the outflow channels below two hatcheries. The cutthroat trout were also first-generation wild stock from the hatcheries. Lake char were pre-conditioned from previous experiments to feed on live prey (Vogel & Beauchamp 1999), whereas piscivorous cutthroat trout and rainbow trout were conditioned to feed on live prey fish for a period of 2–4 weeks prior to experimentation. Prey fish consisted of cutthroat trout and rainbow trout obtained from local hatcheries. Only one size of prey (TL = 75 mm; SD = 5 mm) was used because no effect of prey size on reaction distances of lake char was evident for prey 55–139 mm TL (Vogel & Beauchamp 1999). All prey fish exhibited similar coloration (dark with parr marks) and morphology. Institutional animal care and use committee protocols were followed.

Fish were held indoors with partial natural lighting conditions, through windows with a northern exposure, to reduce potential effects of light shock stress (Heinen 1998). Natural light was supplemented with fluorescent ceiling lights during the day. Fish experienced approximately 11 hours of daylight and 13 hours of darkness $\pm$ 1.5 hours. Between experiments, piscivores were held in circular (2 m diameter) or rectangular (0.5 m x 1 m x 3 m) tanks in groups of 1–6 fish of the same species per tank. Prey fish were held in groups of approximately 500 fish within (150 liter) tanks. All fish were supplied with well water at 10–12 °C.

Experimental Arena

We used the same experimental arena as in Vogel & Beauchamp (1999), with minor alterations to lighting sources, tank shape, and the number and positioning of video cameras. Reaction distance and predation rate experiments were conducted within a rectangular tank (4.5 m long x 1 m wide x 1 m high) modified with rounded plastic corners. The experimental arena was shrouded with 2-4 layers of black plastic to minimize intrusion of external light. Three overhead fluorescent light fixtures with two light tubes per fixture (Philips® 50 watt fluorescent tubes) were suspended 1 m above water level and aligned diagonally with the sides of the arena, to provide uniform light distribution to the entire tank. Light levels were controlled with layers of fiberglass window screen over light fixtures (Neverman & Wurtsbaugh 1992, Vogel & Beauchamp 1999). Light declined exponentially (r^2 = 0.998, DF = 5, P < 0.001) as layers of window screen were added:

(1) $\text{lux} = 81.944\, e^{(-0.5151 \,\bullet\, \text{number of screens})}$

Light levels ranged from 0.00 to 50.70 lux and were measured to the nearest 0.10 lux at the water surface with a Spur Scientific (model 840006C) light meter. Because the 0.01 lux light level was below the detectable limit of the light meter, it was estimated using equation 1. The 0.00 lux experiments were conducted at night with all room lighting extinguished to ensure no intrusion from external sources of light.

A narrow range of turbidities were used in our experiments because the highest variability in reaction distances of lake char were observed between the two lowest levels of turbidity used by Vogel & Beauchamp (1999), and because most western lakes with salmonids have low turbidity. Turbidities were controlled by adding powdered bentonite clay to obtain levels of 0.08, 0.55, and 1.50 nephelometric turbidity units (NTU; Miner & Stein 1996, Vogel & Beauchamp 1999). Turbidities were measured with a LaMotte (model 2008) nephelometer turbidimeter to the nearest 0.01 NTU. Nephelometer turbidimeters measure the amount of light scattered at right angles from a light source by suspended particles in the water (Renn 1992). Bentonite clay remained in suspension for the duration of all experiments (Miner & Stein 1996, Vogel & Beauchamp 1999).

Reaction Distance Experiments

The handling and acclimation protocols used were described in Vogel & Beauchamp (1999). Two to six cutthroat and rainbow trout were tested individually at each combination of light and turbidity. To compare the supplementary lake char experiments to existing data from Vogel & Beauchamp (1999), two to five lake char were tested individually at selected light levels (0.63, 2.59, 4.97, 17.50, and 20.78 lux) under clear water conditions (0.08 NTU). The slope of the ascending limb of the reaction distance curve from these new data (slope = 3.68, $r^2 = 0.85$) was slightly, but significantly different from the slope of the combined data (slope = 3.54, $r^2 = 0.87$, $P = 0.049$).

However, because these differences only represented a maximum difference of 2 cm (≤ 3%) in reaction distance across the ascending limb of the curve, we combined the two data sets for further analysis. Lake char were subjected to all light levels at turbidities of 0.55 and 1.50 NTU; at 0.08 NTU lake char were tested at all light levels less than 0.17 lux, 50.70 lux, plus the selected five levels (0.63-20.78 lux) listed above.

To prevent potentially confounding stimuli to non-visual sensory systems during the reaction distance trials, prey were held in a 38-L glass aquarium inside the experimental tank. Prey fish were restricted to a small region of the aquarium (80.8 cm long x 2.5 cm wide x 30.5 cm deep) by a rigid gray plastic sheet limiting prey movement and providing a constant prey profile to the predator (Vogel & Beauchamp 1999). Trial times were reduced from the 1-4 hours used by Vogel & Beauchamp (1999) to 0.5-1 hour trials, because review of videotapes showed that sufficient reactions occurred during shorter periods, and reaction distances did not change with duration of the experiment.

Reaction distances of all predators to prey fish were recorded using black and white surveillance cameras (3-4 Polaris® CCD model VT-90D, oriented vertically toward the tank), a multiplexing processor (Sanyo® 8-channel model MVP-8), and a videocassette recorder (four head Magnavox® model VRT 242). Video images were recorded after the multiplexing step so that all cameras were synchronized and recorded on one tape for analysis of reaction distances (Vogel & Beauchamp 1999). Light levels below the normal detectible range of the cameras (approximately <1 lux) were recorded with the addition of infrared (IR) lighting (>880 nm) using illuminators (4-6 Polaris IR model IL101, 14 Watts). IR illuminators bathed the experimental tank in IR light detectable by the cameras, but not by human eyes. IR light has been used in foraging experiments on walleye Pollock, *Theragra chalcogramma* and sablefish, *Anaplopoma fimbria* with no perceived effect on fish foraging behavior (Ryer & Olla 1999).

Fishes in general appear to be insensitive to light in the IR range (Douglas & Hawryshyn 1990).

We tested for potential sensitivity of the fish to IR illumination by conducting IR and non-IR trials in clear water at light levels of 0.63, 2.56, and 4.98 lux for all predators. No significant effects of IR illumination on reaction distances (2-way ANOVA) were found for lake char ($P = 0.116$, n = 27), cutthroat trout ($P = 0.346$, n = 29), or rainbow trout ($P = 0.573$, n = 25) at these light levels. We therefore assumed that IR illumination did not affect reaction distance measurements, and all further low light trials (<0.1 lux) were recorded using IR illumination.

Reaction distances measured from video recordings followed the methods of Vogel & Beauchamp (1999). Reaction distance was defined as the linear distance between the fish and its prey at the point where the fish first orients toward the prey (Vinyard & O'Brien 1976, Vogel & Beauchamp 1999). Mean reaction distances of individual predators were used as the experimental unit for analysis.

Effect of Light on Relative Predation Rate and Swimming Speed

Consumption rates and swimming speeds of lake char were obtained from trials consisting of 15 cutthroat trout prey fish (75 mm) and two lake char predators (mean TL = 469 mm; SD = 28 mm) in a 4.5 x 1 x 1 m trough. Prey fish were exposed to lake char within a week prior to experimentation, and were naive to the experimental arena. Predators and prey were acclimated to the experimental tank conditions for one hour prior to initiation of a trial, and survivors were not used in future experiments. Trials were initiated by the introduction of two lake char predators into the experimental tank and lasted for four hours. Predation rates were measured at light levels of < 0.10, 0.10, 0.25, 0.38, 0.50, 0.75, 1.00, and 276.00 lux in clear water with a turbidity of 0.08 NTU. Swimming speeds were measured from individual lake char recorded during predation trials at light levels of 0.25, 0.50, 1.00, 10.00, and 276.00 lux. Twelve to sixteen samples were randomly selected from recorded predation rate trials and measurements of swimming distance during a 10-second period were determined from the grid on the bottom of the tank.

Results

Reaction distances increased rapidly with increasing light intensity up to a saturation intensity threshold (SIT; Henderson & Northcote 1985), above which reaction distances remained relatively constant (Figure 1). Above 5.00 lux, reaction distances were greater for lake char than for cutthroat and rainbow trout, but reaction distances declined at similar rates below 5.00 lux for all three species (Figure 1). Reaction distances across all light and turbidity levels were similar between cutthroat trout and rainbow trout. Above SIT, reaction distances were significantly higher for lake char (RD = 96.7 cm) than for cutthroat (RD = 58.4 cm) and rainbow trout (RD = 56.5 cm; ANOVA, multiple comparison test, P<0.005), but there were no differences between cutthroat and rainbow trout (ANOVA, Tukey test, P= 0.782). For all three species, reaction distances did not differ between turbidities 0.08 NTU and 0.55 NTU (ANOVA, Tukey test, P=0.14 to 0.97). At 1.50 NTU, reaction distances above SIT declined 17% to 80 cm for lake char (ANOVA, Tukey test, P=0.006), declined 9% to 53 cm for cutthroat trout (ANOVA, Tukey test, P=0.014), and declined 13% to 49 cm for rainbow trout (ANOVA, Tukey test, P=0.131; Table 1). No significant effect of predator length on reaction distance was evident for lake char (r^2 = 0.048, P= 0.317) and cutthroat trout (r^2 = 0.024, P= 0.741) over the size range of 330-502 mm TL; however, reaction distance differed significantly with length for rainbow trout (r^2 = 0.50, P= 0.034; Table 2) despite the relatively narrow range of predator sizes (377-412 mm TL) tested.

A single function could not adequately fit the sharp threshold effect of light on reaction distance for any of the predators; therefore, piecewise functions were applied to different light levels. For lake char, we used a three-piece model because it produced the best fit at the ecologically important low light levels (0.00-1.00 lux) and regions near the threshold light levels (10.00-25.00 lux). Equations 1a and 1b (Table 1) represented the dynamic response of reaction distances by lake char to low light conditions, whereas equation 1c accounted for the observed reaction distance threshold or saturation (SIT) effect. The alternative two-piece model would have overestimated encounters under low light conditions because of a relatively large intercept value for the linear ascending limb of the reaction distance function.

Predation Rate and Swimming Speed Experiments

Predation rates of lake char varied significantly among light levels (ANOVA $F = 5.421$, $P = 0.041$; Figure 2). Predation rates were low (0-3 prey eaten/trial) and did not differ significantly among the lowest light levels (0.00-0.40 lux), but peaked at 0.50-0.75 lux (8.0-8.5 prey/trial), then declined to an intermediate rate at all higher light levels (4 prey/trial at 1.00-276.00 lux). Swimming speeds by lake char followed a similar pattern to predation rates (Figure 2), increasing from a low level (19.40 cm/s, 0.46 body lengths/s) at 0.25 lux, peaking at 0.50 lux (32.6 cm/s, 0.77 body lengths/s), then declining at 1.00 lux (19.5 cm/s, 0.46 body lengths/s) and increasing to an intermediate level at higher light levels (27-27.1 cm/s, 0.63 body lengths/s at 10.00 and 276.00 lux).

Discussion

All three species shared a common SIT centered around 20.00 lux under clear water conditions (0.08-0.55 NTU); however, the increase in reaction distances for cutthroat and rainbow trout began to decelerate and diverge from lake char at light levels above 5.00 lux, and reaction distances for lake char were approximately 65% longer than those for both cutthroat and rainbow trout when light levels exceeded SIT (>20.00 lux). The different threshold reaction distances among these piscivores implies that lake char can detect prey fish and react to them at greater distances under moderate to high light intensities.

Contrary to our findings, Henderson & Northcote (1985) found that reaction distances to copepods and small artificial prey (1 x 3 mm cylinders) were considerably higher for cutthroat trout than Dolly Varden (18.1-24.3 cm FL) at light levels above SIT. The difference between our findings and those of Henderson & Northcote (1985) suggests either a age specific difference in visual performance, a difference between a species' ability to detect prey using acuity versus contrast-based vision (Douglas & Hawryshyn 1990; Breck 1993), or that the two char species (Dolly Varden and lake char) have different prey detection capabilities. Differences between acuity- and contrast-based vision or between prey detection capabilities among species of char should be readily discernable from an analysis of the species' retinal rod and cone composition (Douglas & Hawryshyn 1990).

Our laboratory results demonstrated that lake char reacted to prey fish at greater distances than cutthroat and rainbow trout under moderate to high light intensities, and that these differences could not be attributed to the size of the predator in these experiments. This suggests that lake char could both eat younger trout and out-compete larger piscivorous cutthroat trout or rainbow trout for prey in lacustrine environments (Ruzycki et al. 2001, Ruzycki et al. 2003), and might replace them if suitable spawning and rearing habitat for lake char were available. Low productivity lakes in western North America with relatively deep, oxygenated hypolimnia offer conditions for the displacement of native salmonine piscivores by nonnative lake char.

The similarity in maximum reaction distances between cutthroat and rainbow trout, and the large difference between these two species and lake char indicates that further examination of inter-generic differences in reaction distances would be fruitful (e.g. among *Salvelinus*, *Oncorhynchus*, and *Salmo*). Comparisons among piscivorous rainbow and cutthroat trout and Pacific salmon *Oncorhynchus spp.* may also yield important insights into the relationships between visual foraging capabilities of these species and their ecological role under different environmental conditions.

Previous work suggests that reaction distances decline as a decaying power function of turbidity (Miner & Stein 1996). However, the lack of a turbidity effect on reaction distance over a 7-fold increase in turbidity (0.08-0.55 NTU), followed by a measurable decline in reaction distance from 0.55 NTU to 1.50 NTU suggests that a threshold turbidity exists between those levels.

Pelagic piscivore-prey interactions occur across large 3-dimensional scales that are not conducive to laboratory experimentation. Our tank experiments were designed to examine how these piscivores responded to changes in the light environment over a low range of turbidities. The piscivores typically cruised continuously around the entire arena, and maximum reaction distances were consistently less than 20-25% of the maximum dimension of the arena for lake char and were only 10-15% for cutthroat and rainbow trout. These considerations increase our confidence that reaction distances can be modeled directly from experimental results. However, tank effects on predation rates and swimming speeds (Tang & Boisclair 1993) were unavoidable in these experiments and were not intended to represent the actual rates for lake char in nature, but rather the relative change in rates by these fish in response to alterations in their visual environment. Predation rate and swimming speed experiments were conducted under controlled conditions where the only variable was light level. Our swimming speed and foraging rate studies suggest that lake char more than doubled their foraging rate under extremely reduced light conditions (0.50-0.75 lux) compared to their foraging rates under daylight conditions (10.00-276.00 lux). Similarly, lake char increased their swimming speed in low light environments, and this coincided with increased prey consumption. A similar pattern of peak predation rates on juvenile salmon under extremely low light conditions (<0.03 lux) compared to lower and higher light levels was also noted for northern pikeminnow (Petersen & Gadomski

1994). Similar results among such disparate taxa could suggest that these peaks represent conditions where the net difference in detection abilities between piscivores and their prey may be most favorable for the predators and capture success, given a prey encounter is maximized.

Table 2.1. Species-specific reaction distance equations developed for lake char, cutthroat trout, and rainbow trout. I is the ambient light level (lux).

Lake char at 0.08-0.55 NTU:

(1a)	$RD = 67.714\, I^{0.36825}$	for I 0.00-0.01 lux ($r^2 = 0.74$; $P < 0.001$)
(1b)	$RD = 32.514 + 3.545\, I$	for I 0.10-18.10 lux ($r^2 = 0.86$; $P < 0.001$)
(1c)	$RD = RD_{max} = 96.68$ cm	for $I > 18.10$ lux

Lake char at 1.50 NTU:

(2a)	$RD = 28.73 + 3.16\, I$	for I 0.00-16.20 lux ($r^2 = 0.95$; $P < 0.001$)
(2b)	$RD = RD_{max} = 80.00$ cm	for $I > 16.20$ lux

Cutthroat trout at 0.08-0.55 NTU:

(3a)	$RD = 33.70\, I^{0.194}$	for I 0.00-17.00 lux ($r^2 = 0.88$; $P < 0.001$)
(3b)	$RD = RD_{max} = 58.38$ cm	for $I > 17.00$ lux

Cutthroat trout at 1.50 NTU:

(4a)	$RD = 36.99\, I^{0.118}$	for I 0.00-21.40 lux ($r^2 = 0.93$; $P < 0.001$)
(4b)	$RD = RD_{max} = 53.16$ cm	for $I > 21.40$ lux

Rainbow trout at 0.08-0.55NTU:

(5a)	$RD = 34.80\, I^{0.1651}$	for I 0.00–18.75 lux ($r^2 = 0.86$; $P < 0.001$)
(5b)	$RD = RD_{max} = 56.45$ cm	for $I > 18.75$ lux

Rainbow trout at 1.50 NTU:

(6a)	$RD = 36.03\, I^{0.133}$	for I 0.00–10.02 lux ($r^2 = 0.93$; $P < 0.001$)
(6b)	$RD = RD_{max} = 49.02$ cm	for $I > 10.02$ lux

Table 2.2. Species-specific relationship between body length (mm TL) and reaction distance above the saturation intensity threshold (SIT).

Species	Size range (mm TL)	n	Regression equation	r^2	*P*
Lake char	330-496	22	RD = 0.056 TL + 71.9	0.048	0.317
Cutthroat trout	328-502	7	RD = 0.007 TL + 56.6	0.024	0.741
Rainbow trout	377-412	9	RD = 0.216 TL – 27.7	0.497	0.034

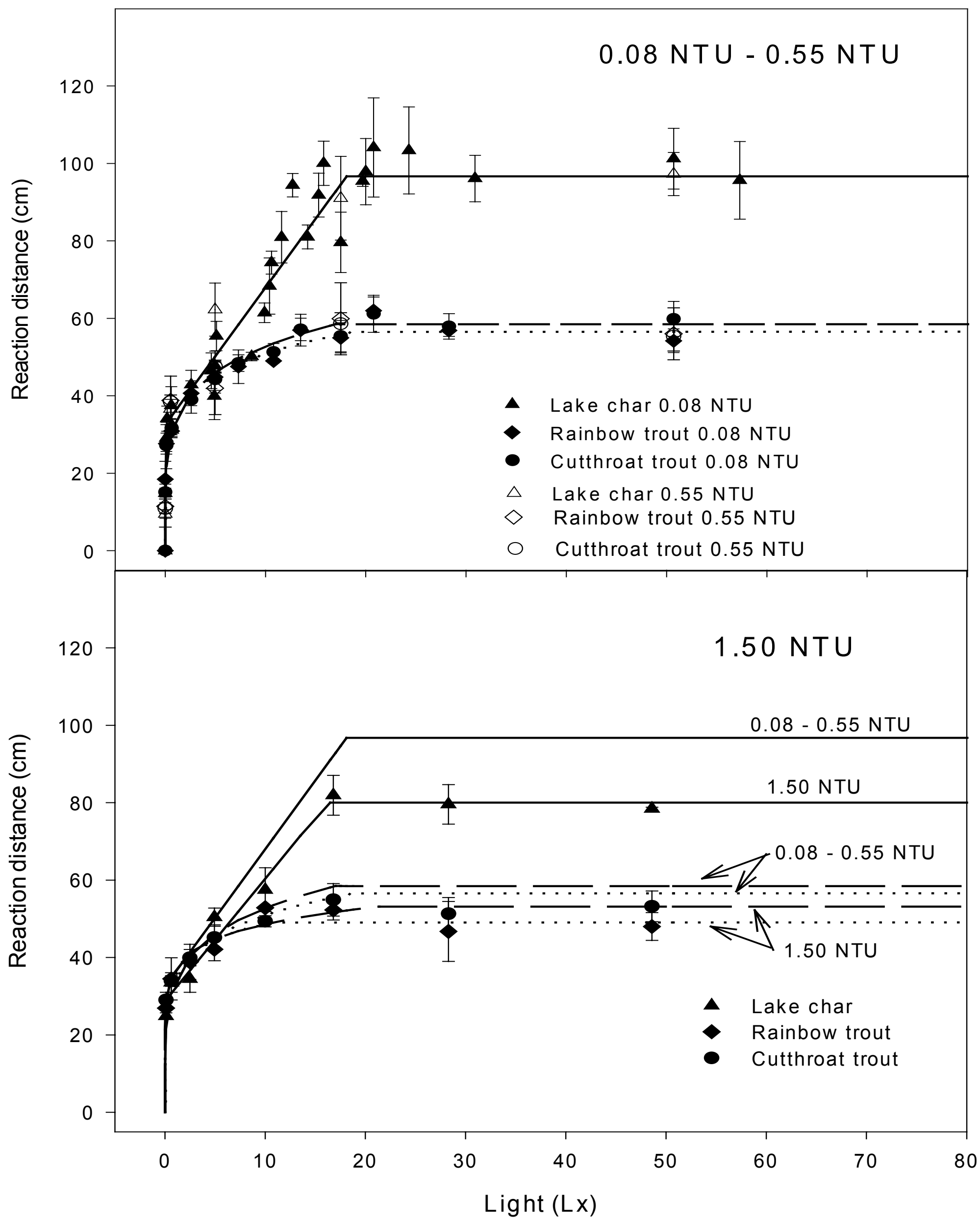

Figure 2.1. Reaction distances of lake char, cutthroat trout, and rainbow trout to 75 mm prey fish as a function of light (0.00-50.00 lux) and turbidity (0.08 NTU, 0.55 NTU top, and 1.50 NTU bottom). Data points represent the means $\pm$ 2 SE of individual average reaction distances and lines represent “best fit” reaction distance models for lake char (solid line), cutthroat trout (dashed line), and rainbow trout (dotted line) at each discrete turbidity level. Lines for all turbidity models are drawn on the bottom panel for comparison.

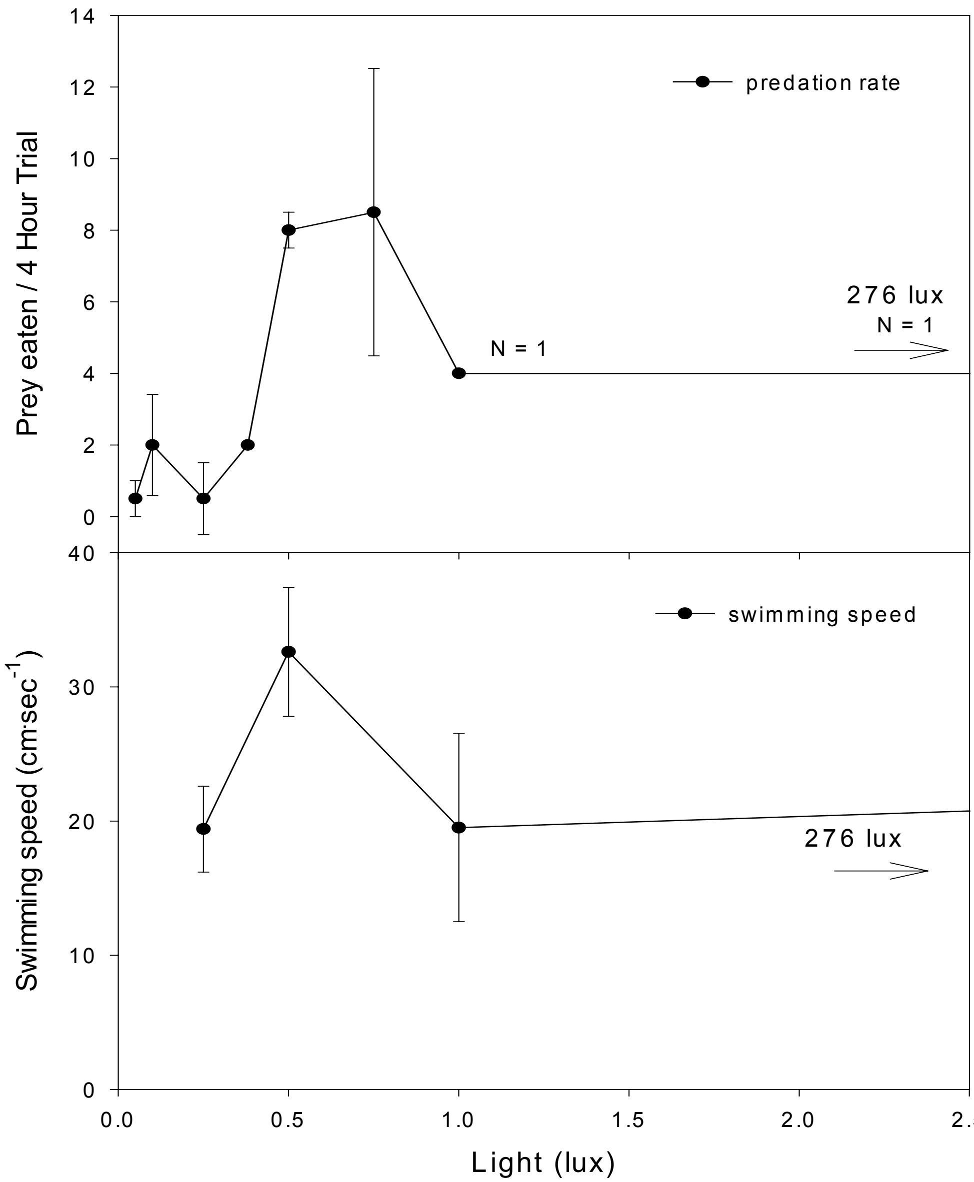

Figure 2.2. Observed number of rainbow trout (75 mm total length) eaten (top panel) during a 4-hour predation trial by 2 randomly selected lake char predators (330-456 mm total length, N = 19) as a function of light (0.01-276.00 lux). Mean swimming speeds (cm/s; bottom panel) of lake char predators as a function of light during foraging experiments. Swimming speed and predation trials extend to 276.00 lux. Predation rate data points represent the means + 2 SE of two trials at each light level (0.01-0.75 lux) and one trial at 1.00 lux and 276.00 lux. Swimming speed data points represent the means + 2 SE of 12-16 samples at each light level (0.25-276.00 lux).

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CHAPTER 3

Using a visual foraging model to link temporal distribution and abundance of limnetic prey fish to consumption by pelagic piscivores

Synopsis

Because most pelagic piscivores hunt visually, ambient photic conditions and the spatial distributions of predators and prey influence prey encounters. A light-dependent encounter rate model with a species-specific reaction distance function was used to link observed prey fish abundance and distribution in Lake Washington to predation rates and the foraging performance of piscivorous cutthroat trout (*Oncorhynchus clarki*). Field estimated consumption of prey (prey fish/piscivore) was compared to model-derived estimates of prey consumption (prey fish/average piscivore). Total prey fish density did not correlate with the consumption potential estimated for cutthroat trout by the foraging model because prey were rarely distributed in optically optimal conditions for visual detection by piscivores. Visual foraging model estimates of prey fish consumption fell within the range of prey fish consumed in diel stomach samples of cutthroat trout. Similarly, predictions of the depth-specific distribution and timing of cutthroat trout foraging were qualitatively similar to diel stomach fullness observed in field samples. Nocturnal foraging accounted for 53% to 75% of all prey fish consumption in simulations for 2002 and 2003. These results suggest that visual foraging models are useful tools for converting observed prey fish density into predictions of predator consumptions and behavioral responses of predators to environmental change.

Introduction:

Prey abundance in aquatic habitats is often a poor predictor of consumption and growth performance for predatory fishes (Mittelbach and Osenberg 1994), therefore foraging models are useful in converting prey abundances into prey availabilities to predators. The non-linear processes associated with encountering, attacking, and consuming prey complicate how predators and prey interact. Foraging theory offers predictions about prey selection and diet breadth given the encounter rate and rate of net energy return from different prey (Stephens and Krebs 1986; Mittelbach and Osenberg 1994). Encounter rate models (Beauchamp et al. 1999) convert measured prey densities to the density perceived by a predator in a particular environment by incorporating relevant sensory capabilities of the predator, and can be explicitly applied to the spatial and temporal distribution of predators and prey. Visual encounter rate models can quantify the strength of predator-prey interactions under different conditions, and provide insight into spatial and temporal trade-offs in foraging opportunity and predation risk at multiple trophic levels (Beauchamp et al. 1999; Hardiman et al. in press).

A pelagic predator's ability to successfully encounter, attack, and consume prey depends more on their spatial-temporal overlap, ambient environmental constraints such as light, turbidity, or temperature, and size-dependent vulnerability than on absolute prey abundance. Total prey abundance should be less relevant to the growth of predators than the available or vulnerable fraction of the prey population. Lower densities of prey in some systems could be more vulnerable if spatial-temporal overlap was greater or detection was less constrained. Furthermore, predator-prey models that ignore the effects of behavioral responses, which influence prey vulnerability, produce predictions that deviate markedly from empirical estimates (Brown et al. 1999). Spatially and temporally explicit foraging models can potentially predict how the same abundance of prey could translate into very different consumption rates and growth potentials for predators, given different temporal-spatial distribution patterns or changing environmental conditions. The ability to quantify and predict changes in predation pressure on key prey (e.g. juvenile salmon) or to estimate the carrying capacity of a dynamic environment for top predators is essential for making informed decisions in fisheries management.

This study applied a visual foraging model developed for piscivorous cutthroat trout (Mazur and Beauchamp 2003) to field estimates of diel and seasonal distributions and abundances of pelagic prey fishes in Lake Washington to estimate spatially and temporally explicit predation rates and growth potential for piscivorous cutthroat trout. Cyclic longfin smelt (*Spirinchus thaleichthys*) abundance patterns (Chigbu and Sibley 1994) and seasonal shifts in vertical distribution provided the opportunity to simulate predator-prey interactions over a broad range of prey fish densities and distributions and to compare model predictions to observed predation rates. The foraging model along with a diel stomach content analysis was used to predict where and when cutthroat piscivory was occurring. Additionally, we investigated how predictions of diel prey fish consumption from the visual foraging model compared to independent estimates of prey consumption derived from a bioenergetics model and field observations of diet content.

Methods

Prey fish distribution and abundance

Distributions of prey fish were collected monthly from February 2002 thru November 2003 using one diel hydroacoustic surveys per month (Figure 3.1). Hydroacoustic surveys were conducted with a BioSonics split beam echosounder (DE6000) with a 430-kHz transducer mounted on a tow fin. The tow fin was deployed from the side of a 7 m boat and suspended at a depth of 0.5 - 1 m. The transducer was operated at 1.5 pings per second with a vertically positioned 6º full-angle beam. Samples were collected using a TVG of 40 Log R, threshold of -65 dB, and a pulse width of 0.4 ms. The boat speed ranged between 6 and 8.5 km/h. Transects were recorded to the hard drive and post processed using SonarData Echoview ® 3.10.129 software.

Transects were echo counted for individual targets and individual target strengths were stratified into 1 m depth bins. Target strengths were converted to total length using Love's equation (Love 1971). Targets between -52 and -42 dB (roughly 4–15 cm), which corresponded to the most frequently observed prey fish sizes in cutthroat trout stomachs (Figure 3.2), were considered prey fish and depth specific densities were calculated by dividing the total count of returned targets at that depth by the total volume sampled for that depth. The sample volume within each 1 m depth interval was calculated for each transect by multiplying the total number of pings sampled at each depth by the volume of a 1 m high frustrum at each depth. Targets and density estimates from the 6º beam were restricted to a 4º beam (< 2º off axis) to increase confidence in target strength estimates and decrease our reliance on beam angle compensations. Targets closer than 1 m to the bottom were excluded from the analysis to avoid potential contamination from bottom structure. All transects were conducted in the pelagic portions of the lake, defined as areas with water depths 15 m or greater (Beauchamp 1992). Initial analyses indicated that prey fish abundances in the top 5 meters of water were highly variable and biased due to low sample volumes. Subsequently, prey fish density estimates collected at 6-8 meters were used in the 0-5 meter range for the foraging model.

Visual foraging model

Predation rates were estimated from time- and depth-specific prey densities (from hydroacoustics), and time- and depth-dependent functions of search volume and capture success. A visual encounter rate modeling approach (Beauchamp et al. 1999) was used to evaluate how differences in reaction distances and the depth distribution of cutthroat trout and prey fishes would translate into predation rates in Lake Washington. An experimentally derived reaction distance equation for cutthroat trout (chapter 2; Mazur and Beauchamp

2003) was applied to monthly diel hydroacoustic measurements of depth-specific prey fish densities from February 2002 through November 2003 in Lake Washington. Model predictions for each hydroacoustic transect were averaged to produce mean estimates of encounter rates (prey fish/predator/hr), consumption rates (prey fish/predator/hr; grams prey fish/predator/hr), and total consumption (prey fish/predator/hr; grams prey fish/predator/hr) for each month or season of interest.

Prey encounter rates were modeled using Beauchamp et al. (1999) equation 1 for temporally and depth-explicit search volumes and prey densities:

$$ER_{z,t} = SV_{z,t}\,PD_{z,t}$$

Where $ER_{z,t}$ is the prey encounter rate per hour at depth *z* and diel time *t* estimated by multiplying search volume SV by the prey density PD at each depth and time obtained from hydroacoustic surveys. Search volume was modeled as a cylinder:

$$SV_{z,t} = \pi RD^2_{z,t} SS_t\, T_t$$

with radius $RD_{z,t}$ representing reaction distance of the piscivore at depth *z* and time *t*, and *SS* a cylinder length of the swimming speed of the piscivore within diel period *t*, multiplied by T_t, the duration in hours of each diel period. Reaction distances $RD_{z,t}$ (cm) was a light- and turbidity-dependent function (Mazur and Beauchamp 2003). In clear water (e.g. ≤ 1.0 NTU) $RD_{z,t}$ increases rapidly until reaching a light threshold of 17 lux:

$$RD_{z,t}\,(\text{cm}) = 33.7 \cdot I_{z,t}^{\;0.194} < 17 \text{ lux}$$

$$RD_{z,t} = 58.4 \text{ cm} \geq \text{lux}$$

Field estimates of *in situ* diel swimming speeds for large cutthroat trout were borrowed from an ultrasonic telemetry study conducted on Strawberry Reservoir, Utah (Baldwin et al. 2002) and were very similar (21 $cm \cdot s^{-1}$) to average swimming speeds (22 $cm \cdot s^{-1}$) from Lake Washington during 1998-1999

(Nowak and Quinn 2002). Swimming speeds of 14 ± 6 $cm \cdot s^{-1}$ for night, 22.5 ± 12 $cm \cdot s^{-1}$ for crepuscular, and 30 ± 9 $cm \cdot s^{-1}$ for day periods were used.

A light-dependent capture probability was computed from Mazur and Beauchamp (2003) to convert daily encounter rates into estimates of consumption:

$$C_{z,t} = ER_{z,t}\, PC(I_{z,t})$$

The probability of a successful capture was modeled as a step function of light (Table 3.1) where consumption $C_{z,t}$ at depth z(m) and time t is equal to the encounter rate $ER_{z,t}$ multiplied by the light-dependent probability of capture given an encounter $PC(I_{z,t})$ at that depth and time.

Predation rate estimates from controlled laboratory experiments with lake trout (Chapter 2; Mazur and Beauchamp 2003) were used as an approximation for PC ($I_{z,t}$). We assumed that cutthroat trout captured every prey encountered (PC = 1.0) under light conditions when predation rates were maximized, then PC was reduced for any encounters at light levels above the observed peak in predation rate for lake trout. Prey sized bluegill (*Lepomis gibbosus*) were able to detect predatory bass before being detected themselves under high light conditions (Howick and Obrien 1983). Prey detecting predators prior to being attacked should result in fewer predator encounters resulting in a prey capture. The mean observed predation rates rose from 0.125 prey fish/predator/h at <0.01 lux to a peak at 0.5-0.75 lux with 1.03 prey fish/predator/h, then declined to 0.5 prey fish/predator/h at higher light levels up to the maximum experimental level of 276 lux (Chapter 2; Mazur and Beauchamp 2003). The reduction in predation rates at light levels less than 0.75 lux were assumed to be limited exclusively by reduced encounter rates rather than by prey behavior; therefore we assigned PC modeled as 1 and the PC for encounters at light levels greater than 0.75 was modeled as 0.49. The assumption that peak capture probability given an encounter = 1.0 should be considered a first approximation that should be explored via sensitivity analysis and tested in the future under appropriate experimental conditions. Other investigations have suggested that average capture probabilities are considerably less than 1.0 based on experimental (Savitz and Bardygula 1989; Christensen 1996; De Robertis et al. 2003) and model simulations (Mason et al. 1995). Any bias from our assumption of peak capture probability of 1.0 should result in a consistent overestimate of predation rates. Despite this potential bias, the important feature is that PC at higher light levels should be 49% of the peak probability of capture. Therefore, if peak PC was reduced, then PC at higher light levels would be reduced accordingly to 49% of the new peak PC.

The diel and seasonal variability in the depth distribution of cutthroat trout was accounted for by multiplying the model estimates of depth specific encounter and consumption rates by the corresponding proportion of cutthroat trout observed at each depth in the environment. Estimates from Nowak and Quinn (2002) for diel depth-specific distributions of cutthroat trout were used to estimate proportions of time spent at different depths during each season. Daily consumption estimates were produced by summing the time-weighted, diel, depth-specific consumption rates for a 24 hour sequence.

The daily consumption of prey fishes was estimated with the visual foraging model for months when day, crepuscular, and night estimates were available, and were compared to the average number of prey fish found in the diet of trout captured with gill nets and purse seines. Overnight vertical and horizontal gill net sets were deployed monthly (Chapter 1) from September 2002 –November 2003 and a purse seine (600m x 40 m deep; 25 m effective capture depth) was deployed in afternoon, dusk and night sets during June of 2003. Vertical gill nets were 60 meters long x 2.3 meters wide and were suspended on floating aluminum rollers. Each vertical net consisted of one monofilament panel of a single mesh size. The available vertical mesh sizes were 25, 38, 50, 63, 75, 83, 95, 108 mm stretch mesh and nets were adjusted to match the bottom depth where they were deployed. Horizontal nets (3 x 60 m with variable mesh sizes of 25, 31, 38, 50, 63, and 75 mm stretch mesh) were suspended in the water column, at depths of 10, 15, 20, and 25 m by surface floats spaced every 7 m. Depth of capture for each piscivore was recorded.

Surface light intensities were recorded for Lake Washington ($I_{0,t}$) in 2001-2002 using a LI-COR radiation sensor (terrestrial type photometric sensor) and were used to estimate night specific seasonal profiles. The sensor malfunctioned in October of 2002 and subsequent estimates of day and crepuscular surface light intensities were generated by a computer program (Janiczek and De Young 1987) to coincide with the dates and times of hydroacoustic surveys (Table 3.2). Model estimates of light were consistently within 10% of those observed during the day and crepuscular periods during 2001, and differences were associated with variable cloud coverage during surveys. Spring, summer, and fall light extinction coefficients were estimated from depth specific light recordings acquired 1000-1400 hours. The winter light extinction coefficient was generated using light profile data from January 2003 (J. Scheuerell and Schindler unpublished data). Surface light intensities from each diel period were used to estimate ambient light at each depth in the lake.

$$I_{z,t} = I_{0,t}e^{zk}$$

The light level (I) at depth *z*(m) and time *t* was calculated using the surface light ($I_{0,t}$) multiplied by the exponential decline of light with depth *z*(m), based on the light extinction coefficient k (Table 3.2).

Turbidity samples were collected biweekly from March, April, and early May 2002 at 11 sampling stations around the southern half of Lake Washington (Beauchamp et al. in press). Turbidity samples were collected with a 5 meter long lead weighted nalgene tube that was lowered vertically through the water column. Turbidity samples were taken from water contained within the 2-4 meter interval of the integrated tube sampler. Three sub-samples were taken from each sub surface water sample and measured with a LaMotte (model 2008) turbidity meter to the nearest 0.1 NTU. Turbidities did not exceed 1.5 NTU the level of turbidity that would necessitate shifting to a higher turbidity reaction distance model for cutthroat trout. Additionally, monthly depth-specific mean turbidities, measured from 1993 through 2000 in the center of the lake, peaked in April and May but did not exceed 1.5 NTU (Table 3.2). The consistently low turbidities (0.97 NTU, 0.48 SD) justified the use of the low-turbidity reaction distance model for cutthroat trout from Mazur and Beauchamp (2003; Chapter 2).

Bioenergetics and Gastric Evacuation Model-based Estimates of Consumption

A Wisconsin bioenergetics model (version 3.0; (Hanson et al. 1997) was used to estimate consumption of prey fishes by large piscivorous cutthroat trout in Lake Washington (Chapter 1). The bioenergetics model, parameterized for cutthroat trout (Beauchamp et al. 1995; Cartwright et al. 1998) was used to estimate consumption from a balanced energy budget where energy consumed equals energy allocated to somatic and reproductive growth, waste, activity, and respiration (Hanson et al. 1997). Estimates of annual growth (Chapter 1; Table 3.3), size-specific annual and seasonal diets (Chapter1; Table 3.4), energy content of the diet, and thermal experience were collected during 1995-1999 (Nowak 2000) and during this study in 2002-2003 (Chapter 1).

Daily consumption of prey fishes by cutthroat trout was estimated for December 1, 1998, March 23, 1999, April 24 1999, and October 28, 1999 using the bioenergetics model and a diel gastric evacuation rate model, when comparable data was available. Information on the diet, size, and capture time of cutthroat trout acquired from purse seine captures during a predation study in 1998-1999 on Lake Washington (Nowak 2000) were used in a gastric evacuation model to estimate daily consumption rates (Ney 1990). Consumption estimates were only estimated for cutthroat trout larger than 350 mm FL, because they were highly piscivorous and could feed on all sizes of longfin smelt, sockeye salmon (*Oncorhynchus nerka*), and three-spine sticklebacks (*Gasterosteus aculeatus*) available in Lake Washington (Figure 2; (Beauchamp et al. 1992; Nowak 2000). Purse seine samples collected within a week of the target date were grouped into 2-h diel periods. Consumption was estimated using the modified Bajkov (1935) equation (Ney 1990).

$$C_D = 24SR$$

Daily consumption C_D (g/d^{-1}) was estimated from S, the mean mass of all food types in the stomach and R, the gastric evacuation rate in percent per hour for a 24 hour period. We used the instantaneous gastric evacuation rate developed for brown trout feeding on rainbow trout (He and Wurtsbaugh 1993).

$$R_e = 0.053\ e^{0.073(T)},$$

where the gastric evacuation rate R_e is expressed as an exponential function dependent on the water temperature T (ºC). Daily consumption estimates were only estimated if cutthroat trout were captured in at least four different 2-hour sampling events spaced across a diel period.

Consumption estimates produced from the bioenergetics and gastric evacuation models for December 1998, and March, April, and October 1999 (data from Nowak et al. unpublished) were compared to visual foraging model estimates and bioenergetics estimates for model runs using data from December 2002, March, April, and October of 2003 data. The bioenergetics estimates were used as a common reference for inter-annual variability between the two data sets. Bioenergetics estimates were scaled to the gastric evacuation estimates by using the observed size structure from the cutthroat trout captured in purse seines. Because consumption is dependent on fish size, the proportion of each size class of cutthroat trout used in the gastric evacuation model was applied to the bioenergetics model outputs to produce a standard size for comparison among models.

Selectivity indices

The selection of prey fish species by cutthroat trout in relation to availability in the habitat was investigated using the Strauss index (Strauss 1979).

$$L = r_i - p_i,$$

L is a linear food selection index calculated from the relative abundance (proportion) of a prey item in the diet r_i, and p_i is the proportion of that diet item in the environment. Values for the index range between -1 to +1, with negative values indicating prey avoidance or inaccessibility and positive values indicating preference for a prey item. Variances for the index were calculated as suggested by Strauss (1979).

$$S^2(L) = \frac{r_i(1-r_i)}{n_r} + \frac{p_i(1-p_i)}{n_p}$$

Where n_r is the total number of available diets and n_p is the total number of potential prey collected from the lake.

Depth specific diets were stratified during March 2003 for cutthroat trout into 3 depth regions, 0-10 m, 11-20 m, and 21+ m. The number of three-spine stickleback, sockeye salmon, and longfin smelt were enumerated and the proportions of these prey fishes in the diet were compared to the estimated proportional abundance of these fishes determined from a hydroacoustic and midwater trawl survey (Beauchamp et al. 2003). The hydroacoustic survey consisted of 19 transects stratified horizontally similar to the SE survey design (Figure 3.1) and was post processed using echo counting as described previously.

Parallel midwater trawl and hydroacoustic surveys were conducted during the winter during March and October for the fall season of 2003. Depth specific trawls used a Kvichak trawl with a 2.5m x 2.5m cross-sectional opening with mesh sizes grading down to 2 mm mesh in the cod-end. The midwater trawl survey deployed the Kvichak trawl for 10-minutes at depths of 6 m, 15 m, 20-24 m, 31 m, and 41 m for a total of 24 trawls over a two night period in March and

27 trawls in October. Density estimates were generated for each pelagic species from the nocturnal hydroacoustic transects, based on the depth- and size-specific target densities in five areas stratified across the lake (Figure 3.1). The five sample areas of the lake were consistent with those developed in previous studies of Lake Washington (e.g. Chibu and Sibley 1994). Densities were partitioned into different species based on the midwater trawl samples from the corresponding depth x area cell. Area specific estimates were combined to produce a lake wide estimate for depth bins of 0-10 m, 11-20 m, and >20 m during March for use in generating a depth specific Strauss index. Depth-specific cutthroat trout stomach contents were integrated within the depth bins throughout the month of March 2003. Ten individual cutthroat trout were partitioned by depth, based on depth bins used in prey fish abundance estimates, with 6 in 0-10 m, 2 in 10-20m, and 2 > 20 m. A total of 24 prey fish were observed in the stomach samples with 12 in 0-10m, 4 in 10-20, and 8 > 20m. All trawls and hydroacoustic transects used in the abundance estimate were conducted at night when the prey fish were most vulnerable to both gear types (Eggers 1978).

Monte Carlo Error Analysis

A Monte Carlo analysis was performed to determine the relative influence and contribution of the key model inputs of prey density, swimming speed, and capture success to estimates of cutthroat trout consumption for a night transect measured in May 2003. The Monte Carlo simulation consisted of 1000 runs of random prey densities for depths between 6 and 15 m, cutthroat trout nocturnal swimming speeds (Baldwin et al. 2002), and capture success above and below 0.75 lux (De Robertis et al. 2003). All inputs were assumed to be normally distributed and random values were generated from the mean and standard deviation of each of the 13 model inputs being tested (Table 3.5). Negative random values for prey densities and swimming speed were assigned a zero value. Capture success values above the maximum of 1 were redrawn from the random number generator.

Foraging model sensitivity to reaction distances

Reaction distance is a behavioral response by a predator to its prey, and represents the distance that an average piscivorous cutthroat trout initiates an attack on a highly mobile, low contrast, prey fish. Reaction distances as a behavior may underestimate the distance a predator can detect a prey. Because previous sensitivity analysis (Beauchamp et al. 1999) indicated that encounter rate models were sensitive to reaction distance estimates, we applied estimates of light-dependent human detection distances to daytime model runs from May 2003. Under degraded optical conditions, human detection distances to 75-139 mm prey fishes converged with reaction distances of large piscivorous lake trout, in both laboratory and natural lake conditions (Vogel 1998). Thus we applied the maximum human detection distances of 3-m as a surrogate for cutthroat detection distance to daytime model runs when high light intensities saturate reaction distances in the upper water column (Henderson and Northcote 1985; Vogel and Beauchamp 1999; Mazur and Beauchamp 2003). In model runs where prey fish were found in the top 20 m of water, the 3-m detection distances increased unweighted encounter rates by four orders of magnitude. However, encounter rates that were weighted by the observed depth distribution of the piscivore's were much less affected, and inflated encounters occurred in only two of seven daytime model runs. In these two model runs the potential consumption rates achieved exceeded the bioenergetically-determined maximum daily consumption rate.

Results

Diel and seasonal prey fish distributions and associated reaction distances by cutthroat trout

The abundance and distribution of prey fish varied among seasons and across diel periods as did depth-specific reaction distances for predators (Figure 3.3). Prey fish targets were rare in the water column during the day with observed peak density within 5-10 m of the bottom in water depths of 55-65 meters in all seasons. Prey fish schools were rarely observed with most occurred in the water column during daylight and may have been associated with juvenile sockeye salmon and three-spine sticklebacks during the fall. Crepuscular prey fish densities remained deep during winter, but peaked at 10 m during spring, summer, and fall seasons. Nocturnal prey fish densities peaked at 10 m when the lake was not thermally stratified or weakly stratified in winter and spring. Thermal stratification during summer and fall resulted in peak nocturnal prey fish densities at 15 m. Summer and fall night time prey fish densities were slightly bimodal with the 15 m mode composed predominantly of age 0-1 longfin smelt and three-spine stickleback, and the second peak at 30 m in summer and 40 m in fall composed of juvenile sockeye salmon and age-1 longfin smelt.

Daytime reaction distances for cutthroat trout remained constant at 58.4 cm down to 18 m in winter, 21 m in spring, 25 m in summer, and 23 m in fall. Crepuscular reaction distances were similarly saturated near the surface at 58.4 cm, but reaction distances declined exponentially below 2-3 m for all seasons. Night reaction distances ranged from 42.8 to 43.1 cm at the surface during all seasons, with reaction distances from 23.7 cm at 10 m depth to 16.7 cm at 15 m depth where peak prey fish densities were observed.

Visual foraging model application

If spatial and temporal overlap of predators and prey were unconstrained (i.e. cutthroat trout foraged freely across all depths), then unweighted encounter rates (encounter rates not weighted by predator distributions) would generally have been highest in 0-15 m, during crepuscular and night periods, and lower during daylight (Figure 3.4). Night unweighted encounters would peak at 5 m depth during fall, winter, and spring (1.56-3.23 prey fish/h) with prey fish distributions less thermally constrained and ample available light for visual foraging for both predators and prey fish (Figure 3.3). Night encounters during summer would peak at 15 m depth with 2.16 prey fish/h reflecting possible thermal constraints for prey fishes or the availability of adequate zooplankton densities at deeper depths for foraging. Crepuscular encounters would be similar to night encounters, peaking at depths of 5-10 m during all seasons, summer included, due to the absence of hydroacoustics data in the middle of summer for the crepuscular period (Figure 3.3). Daytime encounter rates were maximized deep in the water column during thermally unstratified seasons (0.42-0.53 prey fish/h) at 25 m during winter and spring and near the surface during stratified seasons (0.7-1.72 prey fish/h) at 5 m during summer and fall. Deeper maximum encounter rates during daylight prior to thermal stratification resulted from deeper prey fish distributions during these times (Figure 3.3).

However, because the vertical distribution of predators was restricted to a limited range of depths, affecting prey encounter rates, the weighted mean encounter rates provided a more realistic view of the predator-prey interaction. Weighted peak encounter rates, based on the depth distribution pattern of cutthroat trout, occurred at similar depths to unweighted peak encounters, but were concentrated into much narrower depth intervals (Figure 3.5) and peak weighted encounter rates were generally 2-3 times lower than the unweighted encounters (Figure 3.4). Weighted encounter rates were highest during crepuscular and night periods in depths 5-10 m during winter, spring, and fall; however during summer stratification weighted encounters peaked around 15 m because cutthroat trout avoided the warmer epilimnetic waters (Figure 3.5). Consequently cutthroat trout did not exploit the relatively high theoretical prey encounter rates available in the epilimnion during summer (Figure 3.4). Daylight encounter rates were always much lower than for crepuscular and night periods.

Seasonally, the highest daily prey fish encounter rates occurred during fall (21.7 encounters/24 hr) and spring (20.1 encounters/24 hr), compared to winter (18.4 encounters/24 hr) and summer (11.3 encounters/24 hr), and the total number of encounters per period were consistently much higher at night (6.7-13.9 encounters/period) than during the other diel periods (1.7-6.0 encounters/period; Table 3.6). Even though there were many more daylight hours than crepuscular hours, the total number of prey encounters were generally higher from the shorter crepuscular periods than during daylight. When light-dependent capture success rates were applied to the depth-specific diel encounter rates to produce predation rates, the foraging model predicted that cutthroat trout consume over half of all prey fish consumed during night periods (Table 3.6). Nocturnal consumption represented 75% of all consumption in winter, 59% in spring, 71% in summer, and 53% in the fall. Despite the short 3-h (0.125 proportion of a 24 h day) duration of the crepuscular period, consumption estimates for dawn and dusk accounted for 16-23% of the total consumption for a 24 hour period. Daytime consumptions were lower than night and crepuscular for all seasons (9-23 %).

Consumption rate estimates, adjusted for light-dependent capture probabilities and weighted to the observed depth distribution of cutthroat trout, showed the same seasonal and diel patterns as observed in the weighted prey fish encounter rates (Figure 3.6). As expected, peak consumption rates occurred at the same depths as those observed for peak weighted encounter rates, but the effect of light-dependent capture success altered the magnitude of consumption at deeper depths. In general consumption rates during winter and spring for all diel periods occurred at shallow enough depth (≤ 15 m) that ambient light conditions were above 0.75 lux, thus all consumptions were discounted by the light dependent consumption probability (PC = 0.49). Thermal stratification during summer and fall resulted in a deeper distribution for both predators and prey fishes and consumption rates occurred deeper under reduced ambient light conditions. Daytime and crepuscular consumption rates during stratified seasons still resulting in a discounted consumption probability of 49%; however, night encounters during fall were only reduced by 34% and during summer encounters were deep enough that no discounts were applied.

Consumption comparison

Although predation rates from the model loosely reflected the general temporal trends in prey abundance and evidence of predation from stomach samples, monthly estimates of prey fish density were not significantly correlated with foraging model estimates of prey fish consumption in terms of biomass (r^2 = 0.38, p = 0.19) or numbers of individual prey fish (r^2 = 0.11, p = 0.25; Figure 3.7). Increases in prey fish density generally produced increases in foraging model estimates of consumption. Low prey densities from February 2002 through October 2002 produced the lowest estimates of consumption from the foraging model, while high prey densities present from December 2002 through November 2003 produced the highest prey consumptions. Although the average numbers of prey fish observed in stomach samples of large cutthroat trout were generally lower than the visual foraging model predictions, the model predictions fell within a reasonable range of observed predation (Figure 3.8).

Bioenergetics model and gastric evacuation model output produced similar results for cutthroat trout captured in 1998 and 1999 (Chapter 1; Figure 3.9). Consumption estimates for both the bioenergetics model and the gastric evacuation model were very similar for three of four months, where comparable information existed. Because the bioenergetics model was operated on an annual time step for growth it was unable to capture the March decrease in consumption associated with cutthroat trout spawning and recovery in Lake Washington. Despite the disparity in March, the similarity between consumption estimates corroborate that the bioenergetics model predictions of consumption are consistent with those produced directly from field estimates combined with a commonly excepted gastric evacuation model.

Consumption estimates from the visual foraging model were generally 2-3 times larger than comparable bioenergetics estimates (Figure 3.9). However, this was not unexpected because foraging model estimates were produced without reasonable knowledge concerning feeding chronology, the influence of partial satiation and satiation on foraging motivation, differing prey catchabilities, and limited understanding of how optical conditions influence the capture success of piscivores. Thus foraging model estimates represent a maximum foraging potential more than a predictor of prey fish consumption. Exploratory foraging model runs that used the capture success observed for sablefish (*Anoplopoma fimbria*) foraging on chum salmon (*O. keta*) at light levels between 60-70 lux (De Robertis et al. 2003) to discount capture success rates were very similar to bioenergetics model estimates of fish consumption. Similarity between bioenergetics model estimates of consumption and the discounted foraging model runs (Figure 3.9) suggests that appropriate light-dependent capture success information for cutthroat trout would greatly improve foraging model estimates.

Existing data on diel feeding chronology (Figure 3.10) indicated that cutthroat trout consumed most fish prey during crepuscular and night periods during spring and fall. These results correspond to model predictions where the majority of prey fish in spring and fall are consumed at night, and crepuscular foraging is characterized by high rates, or peaks of consumption occurring over short time intervals. Shifts in prey fish species composition also occurred between winter and spring of 1999 and fall 1999 and can be observed by the shift in cutthroat trout diet content.

Prey fish distribution

The midwater trawl and hydroacoustic surveys were combined to estimate depth-and species-specific prey fish densities (Figure 3.3) for both the winter and fall periods of 2003 in pelagic regions of Lake Washington. Three-spine sticklebacks, sockeye salmon fry, and 0+ longfin smelt were the most abundant prey fish species during the winter and were distributed throughout the top 10 meters of the water column, while 1+ longfin smelt and sockeye salmon parr were less abundant and generally distributed deeper. Three-spine sticklebacks were abundant in the 0-5 m depths representing 50% (251/501) of prey fish and had densities of 3.0-4.0/1000 m^3 between 0 and 10 m. The abundant even year class of longfin smelt (0+ winter 2003, 1+ fall 2003) made up greater than 33% (1876/5686) of all prey fish at all depths and were 56-78% of prey fish between 15 and 35 m. Peak longfin smelt densities of 2.5–5.6/1000 m^3 were in the top 20 m. Sockeye salmon fry migrate to the lake from January – May and made up 10-22% of prey fishes through all depths in winter and were proportionally highest making up 20-22% of prey fish between 20 and 25 m. Sockeye salmon parr were 3-10 % of prey fish at all depths making up 10% of prey fish below 40 m.

By fall 2003 the abundant even year class of longfin smelt composed the majority of the available prey fish in Lake Washington (Figure 3.3). Longfin smelt accounted for 75-95% of all prey fish species in the top 25 m with densities of 3.5-9.0/1000 m^3 compared to 34-46% of prey below 25 m in October 2003. Sockeye salmon parr were distributed deeper than longfin smelt making up less than 2% of prey fishes in the upper 15 m, 8-14% between 15 and 30 m, and 41-65% of prey fishes below 30 m. Peak densities of sockeye salmon parr were located at 35-40 m with 2.05-2.65/1000 m^3. Three-spine sticklebacks were distributed throughout the top 40 m, peaking at 30 m of water, but did not account for more than 11% of prey fish in any depth strata. Peak densities of stickleback did not exceed 0.5/1000 m^3 during the fall of 2003.

Selectivity Indices

Sockeye salmon parr (mean FL = 102 mm; SD = 9) were selected for by cutthroat trout in all depth strata during March 2003 while longfin smelt (mean FL = 73 mm; SD = 8) and three-spine stickleback (mean FL = 68 mm; SD = 3) were selected against in all depth strata (Figure 3.11). Sockeye parr were highly selected for in the 10-20 m depth range with a Strauss index value of 0.78. The 10-20 m depth range is associated with a deeper mode in cutthroat trout distribution during winter (Figures 3.5 and 3.6) and corresponds with reaction distance estimates of 10-20 cm. At depth of 0-10 m sockeye parr had their lowest Strauss index of 0.23 while longfin smelt were almost neutral with an index of -0.02. Similarly, three-spine sticklebacks were increasingly avoided nearer to the surface with -0.22 at 0-10 m, -0.19 at 10-20 m and -0.11 at > 20 m. This pattern is consistent with increased incident light higher in the water column. Longfin smelt had the opposite response to changes in incident light with the two lowest Strauss index of -0.59 and -0.44 in the 10-20 and > 20 m depth strata respectively. The different response in selectivity by depth for stickleback and smelt suggest that increased light results in increased avoidance of the armored stickleback while the cryptic coloring of smelt reduces their vulnerability under darker incident light levels (< 0.5 lux below 10 m).

Monte Carlo Error Analysis

The Monte Carlo analysis indicated that, of the input variables tested, the majority of variations with foraging model predictions of consumption were associated with the estimation of prey densities in the top 8 meters of the water column (Figure 3.12). A multiple linear regression analysis indicated that prey density inputs in the top 8 m of water explained 90% ($p < 0.001$) of the variation associated with consumption estimates. The error associated with estimates of swimming speed was not significant and the light-dependent probabilities of capture only accounted for 7% of the variation ($p < 0.001$). We estimated prey fish densities for each transect by integrating prey fish density horizontally within each transect. The conical geometry of the acoustic beam and the natural variability associated with prey fish distributions resulted in large variance around prey density estimates and was the main contributor to the variation observed in the Monte Carlo analysis. These results suggest that the scale at which prey fish abundance is estimated is a critical component for pelagic piscivore foraging models.

Discussion

Similar to other analysis (Mittelbach and Osenberg 1994) we demonstrated that prey fish abundance alone was a poor predictor of cutthroat trout prey fish consumption. Rather it was the interplay between light dependent reaction distances and the available density of prey fish sized targets in the water column that influenced the amount of prey that were vulnerable to consumption by cutthroat trout. Accounting for the influence of light on the foraging ability of the visual feeding cutthroat trout enabled us to convert observed depth specific prey fish densities into encounter rates and ultimately into consumption rates based on the depth distribution of piscivorous cutthroat trout.

Visual foraging model estimates of the number of prey fish consumed across time and under different abundances of prey fish were within the range of observed counts of prey fish in individual cutthroat trout stomachs. The mean numbers of prey fish in cutthroat trout captured in the same month were consistently lower than the visual foraging model estimate, but we did not attempt to correct for digestion and other losses that influenced stomach contents. Digestion and handling of cutthroat trout captured in night gill net sets and potential regurgitation should result in reduced observed numbers of prey fish. Similarly, the vulnerability of cutthroat trout to passive fishing gear may be dependent on gut fullness with satiated predators being less active and thus less susceptible to capture. Alternatively, cutthroat trout may actually consume fewer fish than they are capable of based on the encounter and capture probabilities. The foraging model may simply over predict mean prey consumption at the spatial resolution of this application.

Diel predictions of consumption for cutthroat trout qualitatively agreed with field estimates of the timing of piscivory. The visual foraging model predicted that the majority of consumption of prey fish by cutthroat trout in Lake Washington would occur at night, with significant peaks near dawn and dusk. Similar patterns were observed in the diel diets of cutthroat trout captured in purse seine hauls conducted in the 1980's and 1990's (Beauchamp 1992; Nowak 2000).

The surprisingly high predicted consumption levels at night on Lake Washington compared to previous applications of this model (Beauchamp et al. 1999) resulted from the artificially high levels of light measured at night during this study. Similar light experiences were recorded near the south end of Lake Washington on the Cedar River during 2001 (Tabor et al. 2004). The highly urbanized light levels measured on Lake Washington at night were between 1 and 20 lux, roughly 2,000 to 40,000 times higher than the natural ambient light estimated for this latitude (Janiczcek and DeYoung 1987) or observed in surrounding rural areas. Such high incident light enabled cutthroat trout to maintain sufficient nocturnal encounter rates with vertically migrating planktivorous prey fish.

Urban light contamination appears to influence the predator-prey interactions in Lake Washington by increasing the access of foraging cutthroat trout to vertically migrating prey fish. Planktivorous prey fish often vertically migrate in order to trade off foraging opportunity with the risk of being eaten by predators (Clark and Levy 1988; Scheuerell and Schindler 2003); Hardiman and

Johnson in press). Increased levels of light at night would both increase the risk of predation and increase the foraging ability of visual feeding planktivores in Lake Washington, resulting in temporally and spatially shorter vertical ascents at night. Sockeye salmon in Lake Washington exhibit shorter diel vertical ascents than conspecifics in less urbanized Alaskan lakes (Eggers 1978, Scheuerell and Schindler 2003), and surface light estimates recorded during 1974 were comparable to levels observed in this study (Eggers 1978).

Telemetered cutthroat trout (Nowak and Quinn 2002) occupied depths in the lake that corresponded to depths where peak unweighted encounter rates at night were predicted during all seasons of the year. It is interesting to note that cutthroat trout were observed during the day either in the surface water or at depths of 20-25 m under thermally mixed conditions (Nowak and Quinn 2002). Depths of 20-25 m were predicted to have the highest unweighted encounter rates during daylight in the winter. The visual foraging model was less successful in predicting daytime distributions of cutthroat trout when the lake was thermally stratified. Vertical distributions of large cutthroat trout during the day peaked at much deeper depths than the estimated peak unweighted encounter rates for the summer and fall (Nowak and Quinn 2002), suggesting that thermal regulation took precedence over foraging at these times.

The visual foraging model predicted the timing and vertical position of cutthroat trout piscivory, but the predicted magnitude was consistently higher than the other independent estimates. Because of annual differences associate with highly variable prey fish densities in Lake Washington (Chigbu and Sibley 1994; Chigbu et al. 1998), our data did not allow for direct comparisons of the foraging model to direct field estimates generated from gastric evacuation techniques. However, comparisons to diet data collected during this study and consumption estimates generated using the bioenergetics model suggests that the foraging model produced consumption estimates within the range of other techniques. We expected the foraging model to over estimate consumption by large cutthroat trout due to the assumptions made concerning attack probabilities and capture success given an attack. Additional simulations using the capture success of piscivorous sablefish (De Robertis et al. 2003) foraging on chum salmon, as a surrogate for cutthroat trout capture success, produced consumption estimates within 1-2 times those of the bioenergetics model (Figure 3.9).

Estimates of consumption for cutthroat trout from the visual foraging model also operated under the assumption that cutthroat trout forage for 24 hour periods. A review of diel foraging behavior for fishes (Helfman 1993) suggests that most species of fish do not forage continuously over a 24 hour day. Nowak and Quinn (2002) found that cutthroat trout were less active from noon until 2 pm in the afternoon and we have shown that cutthroat trout are distributed well below depths where unweighted prey encounters are maximized during the day in summer and fall. We infer that larger cutthroat trout might actively reduce foraging during daylight, when potential foraging success would be limited, for other behaviorally motivated purposes, such as thermoregulation. Thus an accurate accounting of the amount of time within a 24 hour period that a piscivorous cutthroat trout spends actively foraging should improve foraging model estimates.

The current form of the model simplifies several possible influences on prey encounter and consumption rates for cruising cutthroat trout, such as individual predator distributions, heterogeneous prey distributions (Grunbaum 1998) within an acoustic transect, predator and prey learned behavior (Hughes et al. 1992), and capture success (Juanes 1994; Christensen 1996; Lundvall et al. 1999; Scharf et al. 2003). The model did not discriminate between prey fish species or the differences associated with the three major prey species found in the limnetic areas of Lake Washington. Three-spine stickleback are found in the diet of cutthroat trout in the summer while they are still less than 50 mm TL, but grow to relatively invulnerable sizes by fall and have been found in great numbers during daytime trawl samples in October high in the water column (Beauchamp et al. 2003). Three-spine sticklebacks remain distributed high in the water column through winter (Figure 3.3) until they aggregate to spawn during spring and complete their lifecycle. Similarly, differences in body pigmentation between longfin smelt and sockeye salmon probably influence detectability for both species by foraging cutthroat trout and may explain the differences in depth specific prey selection (Figure 3.11). Differences in detectability may account for why longfin smelt generally ascend sooner at dusk than sockeye parr and are found higher in the water column at night during all seasons (Chigbu et al. 1998); Beauchamp et al. 2003).

Prey vulnerability to a predator in general is a function of prey distribution, size, morphology, and coloration (Savitz and Bardygula 1989; Christensen 1996; Lundvall et al. 1999). However, mechanistically the ability for a visual predator to encounter, decide to attack, and be successful in its attack is mediated more directly by its ability to perceive its environment, which is influenced by ambient light levels and turbidity (Mazur and Beauchamp 2003; De Robertis et al. 2003). The depth specific selectivity observed in this study suggests that a predator's ability to distinguish between prey types and decide to attack depends on ambient light levels as would be predicted by current theory (Breck 1993; Christensen 1996). The selectivity of three-spine stickleback consistently decreased with increasing ambient light (Figure 3.11), theoretically resulting from the increased ability of a predatory cutthroat trout to identify its prey and choose not to attack (e.g. pre-capture constraint; Christensen 1996). Alternatively, ambient light may be influencing the stickleback's ability to recognize an attack and be able to position its spines to decrease the probability of attack or retention by the predator given an attack. Under either scenario ambient light levels mediates the predator-prey interaction.

The consistent overestimation of cutthroat trout consumption by the foraging model compared to independent estimates from the bioenergetics model was expected and results from the estimation of near surface prey densities in the top

5 m of water, disproportionate prey vulnerability, and the interaction of ambient light and capture success. Estimating near surface prey densities with hydroacoustics has been a consistent problem in pelagic research (Yule 2000). The sample volumes are reduced and fish densities are biased higher near the surface of the water as a result of the conical geometry of the vertically positioned hydroacoustic beam. The near surface bias in prey density was reduced during summer when the lake was strongly stratified and both prey and predator were rarely in the surface water resulting in more consistent estimates of consumption between models (Figure 3.9). However, as three-spine stickleback increased in size through the fall and became less vulnerable to predation and thermal stratification became less pronounced, prey fish and predator densities increased in the surface water and surface estimates of prey density influenced foraging model estimates. Similarly, differences in prey fish vulnerability affected model estimates because we were unable to discount consumption of less vulnerable prey types, such as stickleback, in well lighted depths occupied by cutthroat trout. The capture success of a predator is primarily a size mediated event (Christensen 1996), but light also influences the success of an attack (Mazur and Beauchamp 2003; De Robertis et al. 2003) in ways we have not currently quantified.

Attempts to predict predator performance and behavior within a habitat through the use of mechanistically based foraging models is worthwhile. The ability to transform general prey abundances into a quantifiable characteristic of the environment increases our understanding and ability to manage predator and prey systems. Our results suggest that this modeling approach has merit, both as a predictor of cutthroat trout performance in a given habitat and as a tool to investigate how cutthroat trout influence the habitat where they reside. Further refinement and testing of this modeling approach is critical to its utility.

Table 3.1. Values used to model the probability of capture (PC) as a step function of light under two capture success scenarios (see Figure 3.9).

	$I_{z,t}$ (lux)	PC
Conservative capture success	≤ 0.75 lux	1.00
	> 0.75 lux	0.49
Sablefish capture success (De Robertis et al. 2003)	≤ 0.75 lux	0.40
	> 0.75 lux	0.20

Table 3.2. Estimated surface light for day and crepuscular periods and mean measured light for night periods along with seasonal light extinction coefficient (k), monthly mean turbidity (NTU), and number of hours applied in a diel cycle for cutthroat trout in a visual foraging model for Lake Washington. Missing values indicate when day and crepuscular hydroacoustic surveys were not available to perform foraging model runs.

	Surface light (lux)					Number of hours		
Survey date	Day*	Crepuscular*	Night	NTU**	k	Day	Crepuscular	Night
2/26/2002			3.0	0.96	0.32			10.0
3/6/2002			3.0	0.95	0.32			9.5
4/18/2002			3.5	1.22	0.35			7.0
5/15/2002			3.5	1.14	0.40			5.5
5/21/2002	94564		3.5	1.14	0.40	15.5		5.5
6/24/2002	97524	50	3.5	0.76	0.31	16.0	3	5.0
7/24/2002	93577	50	2.1	0.75	0.31	15.0	3	6.0
8/20/2002	84527	50	2.1	0.93	0.35	14.0	3	7.0
10/15/2002	51485	50	3.2	0.84	0.35	11.0	3	10.0
12/2/2002		50	3.2	0.94	0.35		3	12.0
1/22/2003	32511	50	3.0	1.13	0.32	9.0	3	12.0
2/4/2003	38754	50	3.0	0.96	0.32	11.0	3	10.0
2/26/2003	52273	50	3.0	0.96	0.32	11.0	3	10.0
3/18/2003			3.0	0.95	0.32			7.5
3/25/2003	76427	50	3.0	0.95	0.32	13.5	3	7.5
4/23/2003			3.5	1.22	0.35			7.0
5/21/2003	94564	50	3.5	1.14	0.40	15.5	3	5.5
6/24/2003	97524	50	3.5	0.76	0.31	16.0	3	5.0
8/7/2003	84527	50	2.1	0.93	0.35	14.0	3	7.0
10/15/2003	57337	50	3.2	0.84	0.35	11.5	3	9.5
11/5/2003	38701	50	3.2	0.99	0.35	10.0	3	11.0

* Estimates beyond 10/15/2002 generated from Janiczek and De Young (1987)
** Mean turbidity recorded by King County Metro, 1993-2000.

Table 3.3. Mean weight at age of cutthroat trout and proportional size structure from purse seines and gill net catches used in bioenergetics model simulations.

Age	N	Weight	December 1998	March 1999	April 1999	October 1999	2002-2003
1	1	47	0.00	0.00	0.00	0.00	0.00
2	9	120	0.00	0.00	0.00	0.00	0.00
3	15	420	0.12	0.17	0.16	0.17	0.00
4	21	570	0.29	0.34	0.47	0.34	0.25
5	7	722	0.24	0.14	0.09	0.20	0.59
6	4	1137	0.29	0.31	0.25	0.20	0.15
7	1	1629	0.06	0.03	0.03	0.09	0.01

Table 3.4. Diet data collected in 2003 for cutthroat trout > 350 mm FL used in bioenergetics modeling.

Date	Model day	Chironomid pupae	larvae	Neomysis	3 - spine Stickleback	Yellow Perch	Sockeye
1/1	1	0.48	0.25	0.00	0.25	0.00	0.00
3/16	76	0.01	0.00	0.00	0.00	0.00	0.59
3/23	83	0.01	0.00	0.00	0.41	0.00	0.45
4/6	97	0.00	0.00	0.06	0.06	0.07	0.04
6/22	174	0.00	0.00	0.08	0.08	0.09	0.00
8/4	217	0.00	0.00	0.00	0.45	0.00	0.00
8/18	231	0.00	0.00	0.00	0.75	0.00	0.00
8/25	238	0.00	0.00	0.00	0.00	0.00	0.00
10/1	275	0.00	0.00	0.00	0.64	0.00	0.00
12/30	365	0.48	0.25	0.00	0.25	0.00	0.00

Date	Model day	Cottid	Longfin Smelt	Coho	salmonid	unidentified fish	Aquatic insect
1/1	1	0.00	0.00	0.00	0.00	0.02	0.00
3/16	76	0.00	0.20	0.00	0.00	0.00	0.20
3/23	83	0.00	0.00	0.00	0.00	0.13	0.00
4/6	97	0.13	0.41	0.05	0.12	0.00	0.06
6/22	174	0.15	0.38	0.06	0.15	0.00	0.00
8/4	217	0.00	0.55	0.00	0.00	0.00	0.00
8/18	231	0.00	0.25	0.00	0.00	0.00	0.00
8/25	238	0.00	1.00	0.00	0.00	0.00	0.00
10/1	275	0.00	0.00	0.00	0.36	0.00	0.00
12/30	365	0.00	0.00	0.00	0.00	0.02	0.00

Table 3.5. Mean and standard deviation values used to produce a normal distribution of random input values use in the Monte Carlo simulations.

Input variable	Mean	Standard deviation
Prey density (n/1000 m^3)		
6-m	0.019	0.027
7-m	0.022	0.030
8-m	0.018	0.025
9-m	0.009	0.007
10-m	0.005	0.004
11-m	0.005	0.003
12-m	0.005	0.007
13-m	0.005	0.010
14-m	0.006	0.013
15-m	0.007	0.019
Swimming speed * (m/sec)	0.14	0.06
Capture success ** (0-1)		
lux $\leq$ 0.75	1	0.087
lux > 0.75	0.49	0.087

* (Baldwin et al. 2002)
** Standard deviation derived from De Robertis et al. (2004)

Table 3.6. Visual foraging model estimates of a) daily average prey fish encounter rates (prey/predator/period) and b) consumption rates (prey/predator/period) for cutthroat trout in each season and diel period. Estimates were weighted by the seasonal vertical distribution patterns of cutthroat trout as in Figure 3.5.

a) Average encounter rate weighted for a 24 hour diel cycle

Season	Day	Crepuscular	Night	24 hour total
Winter	1.7	2.8	13.9	18.4
Spring	4.2	4.9	11.0	20.1
Summer	1.8	2.8	6.7	11.3
Fall	6.0	5.7	9.9	21.7

b) Average consumption rate weighted for a 24 hour diel cycle

Season	Day	Crepuscular	Night	24 hour total
Winter	0.8	1.5	6.7	9.0
Spring	2.1	2.5	6.5	11.1
Summer	0.9	1.8	6.7	9.3
Fall	2.9	2.9	6.6	12.3

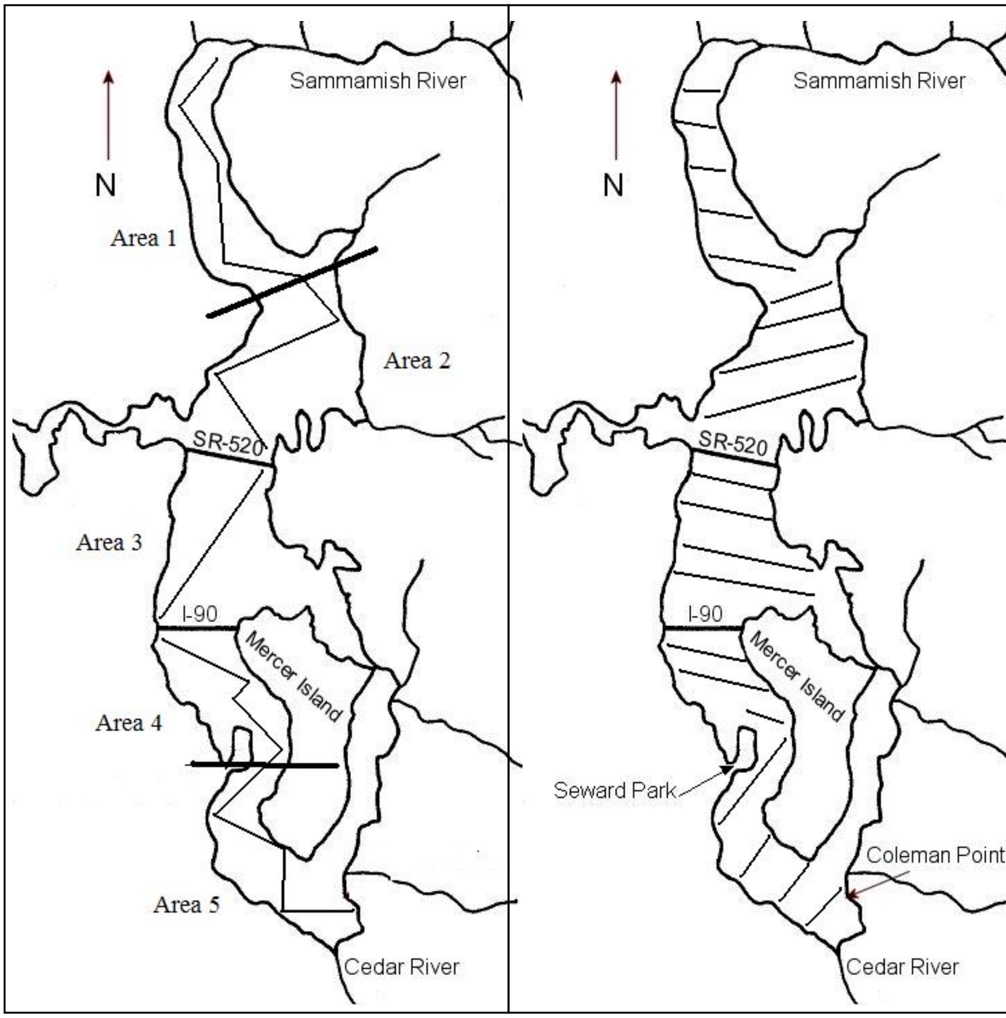


Figure 3.1. Map of Lake Washington showing the two survey designs for hydroacoustic transects used in this study and the five sampling areas used for trawl surveys (left panel). The left map depicts a zigzag survey used on a monthly interval and the map on the right depicts a survey design used in February, March, August, and October for spatially explicit growth model estimates. Visual foraging model estimates were made on individual transects using both surveys and results were expressed as monthly means for each diel period.

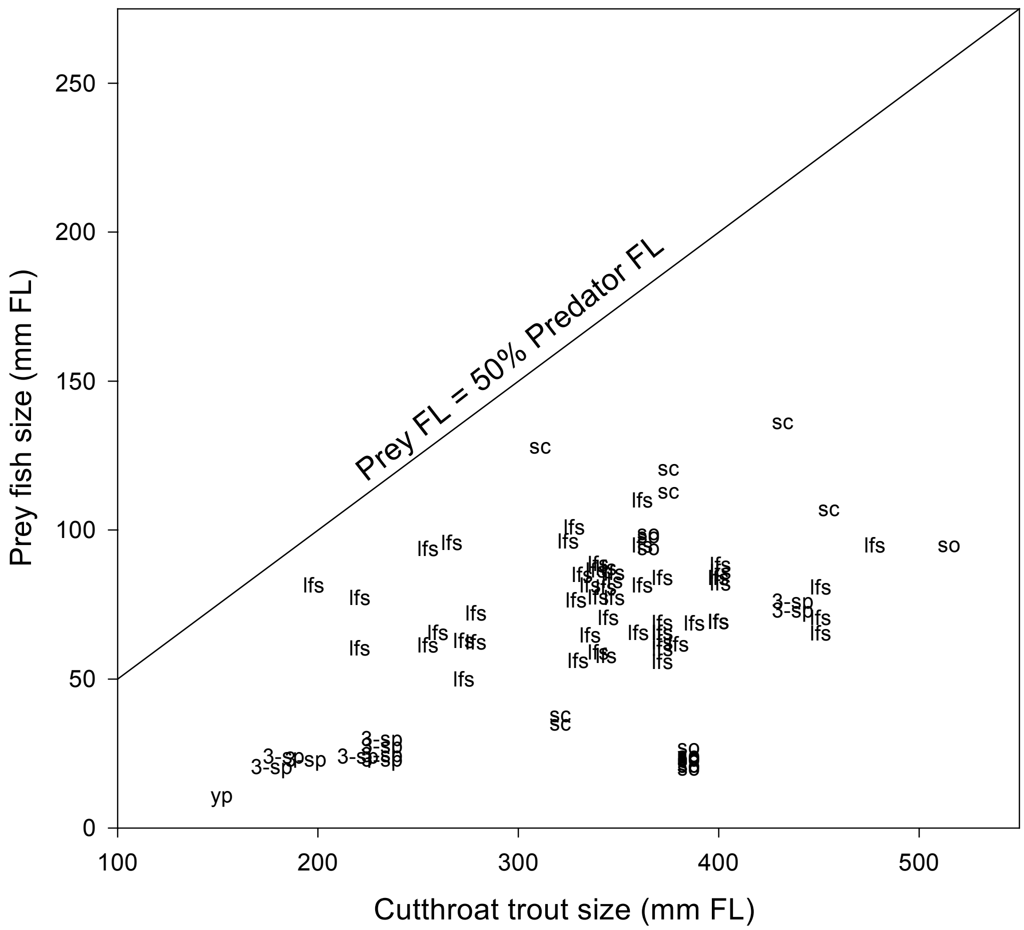


Figure 3.2. The relationship of predator size (mm FL) to prey fish size (mm FL) observed in cutthroat trout stomachs during 2002-2003. Line represents 50% prey length to predator length. Individual prey species are yellow perch (yp), three-spine stickleback (3-sp), longfin smelt (lfs), prickly sculpin (sc), and sockeye salmon (so).

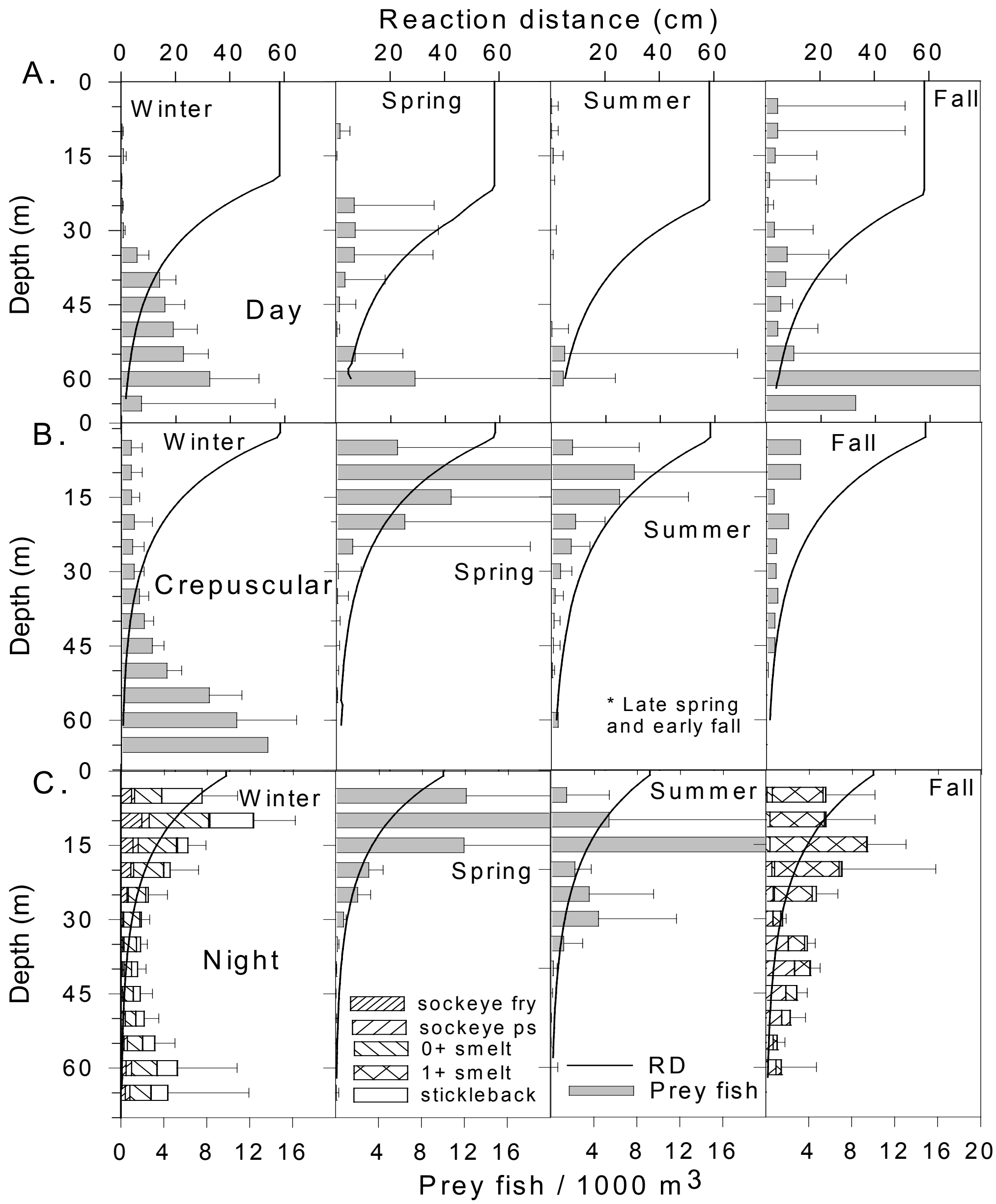


Figure 3.3. Hydroacoustic estimates of vertical prey fish (40-150 mm fork length) distributions in Lake Washington during day (A) upper panels, crepuscular (B) middle panels, and night (C) lower panels, measured during winter, spring, summer, and fall of 2003. Gray bars represent prey fish density (prey fish/1000 m3; lower x-axis) and lines represent the modeled decline in cutthroat trout reaction distance (upper x-axis) to prey fish by depth and diel period. Prey fish densities are species specific for winter and fall nights (prey species/1000 m3) when midwater trawling was available to identify hydroacoustic targets. Error bars represent 95% CI.

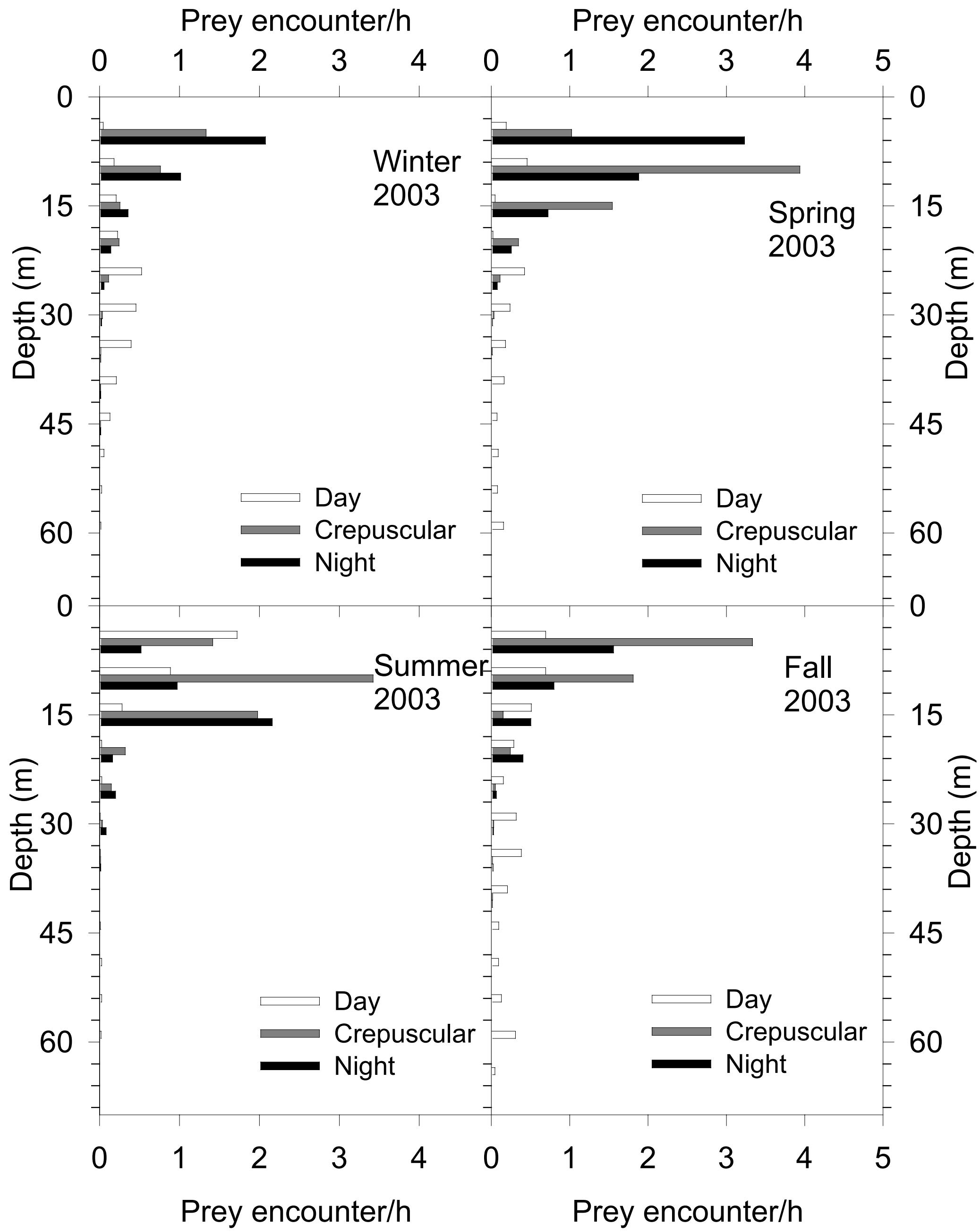


Figure 3.4. Seasonal, depth specific prey fish encounter rates (prey fish/hour) predicted for the visual foraging model during day (white bars), crepuscular (dark gray bars), and night (black bars) periods for predators if they were distributed uniformly across all depths.

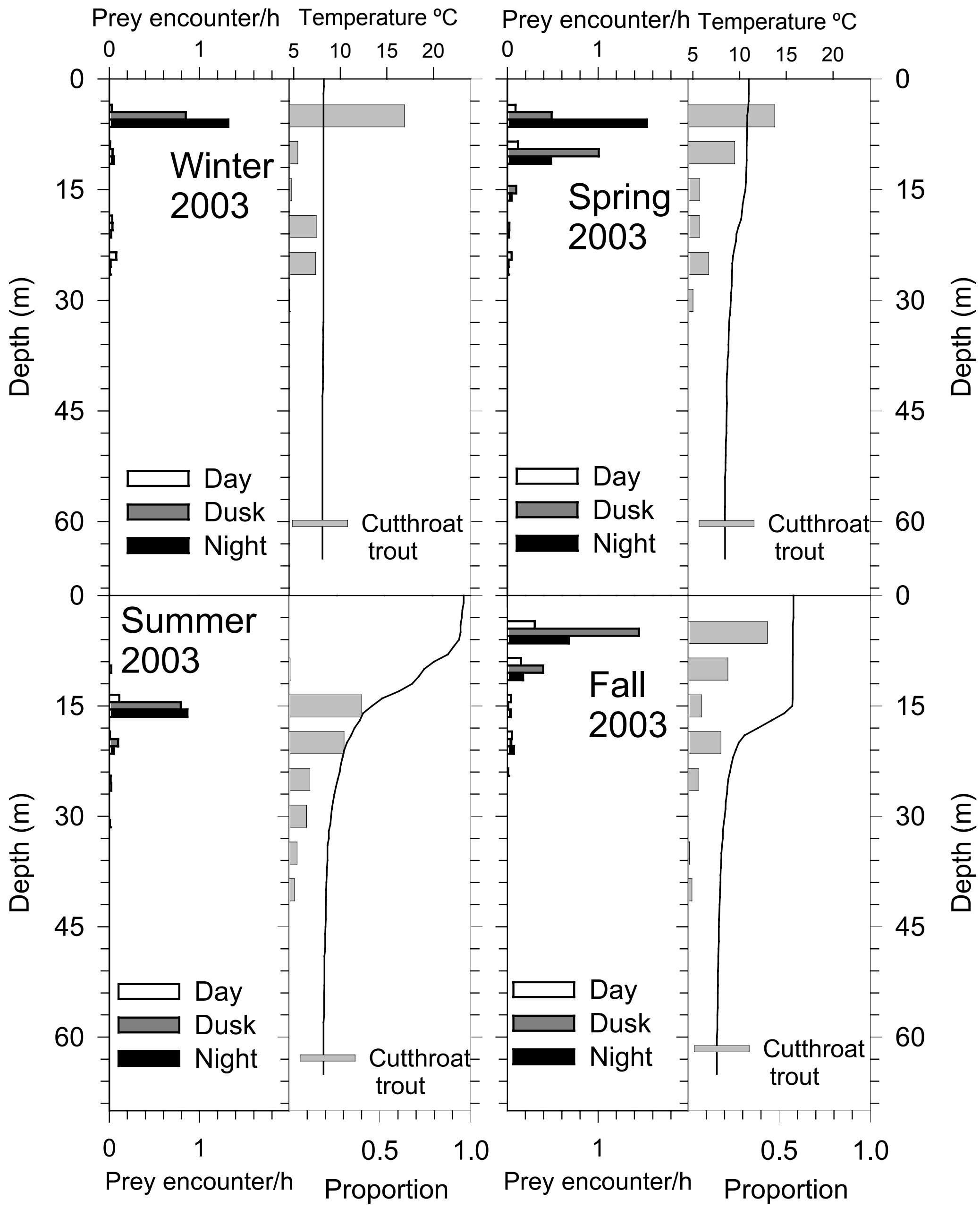


Figure 3.5. Predicted encounter rates (left panels) weighted by the proportional depth distribution of cutthroat trout (right panels) observed in 1998 and 1999 during a ultrasonic tag tracking study (Nowak and Quinn, 2002) in winter, spring, summer, and fall of 2003. Prey fish encounters were estimated during day (white bars), dusk (dark gray bars), and night (black bars). The vertical depth specific cutthroat trout distributions (gray bars) represented the observed proportion of time spent at depth and lines represent average temperature profiles corresponding to each season collected in 2003 (unpublished data, King County Dept. of Natural Resources).

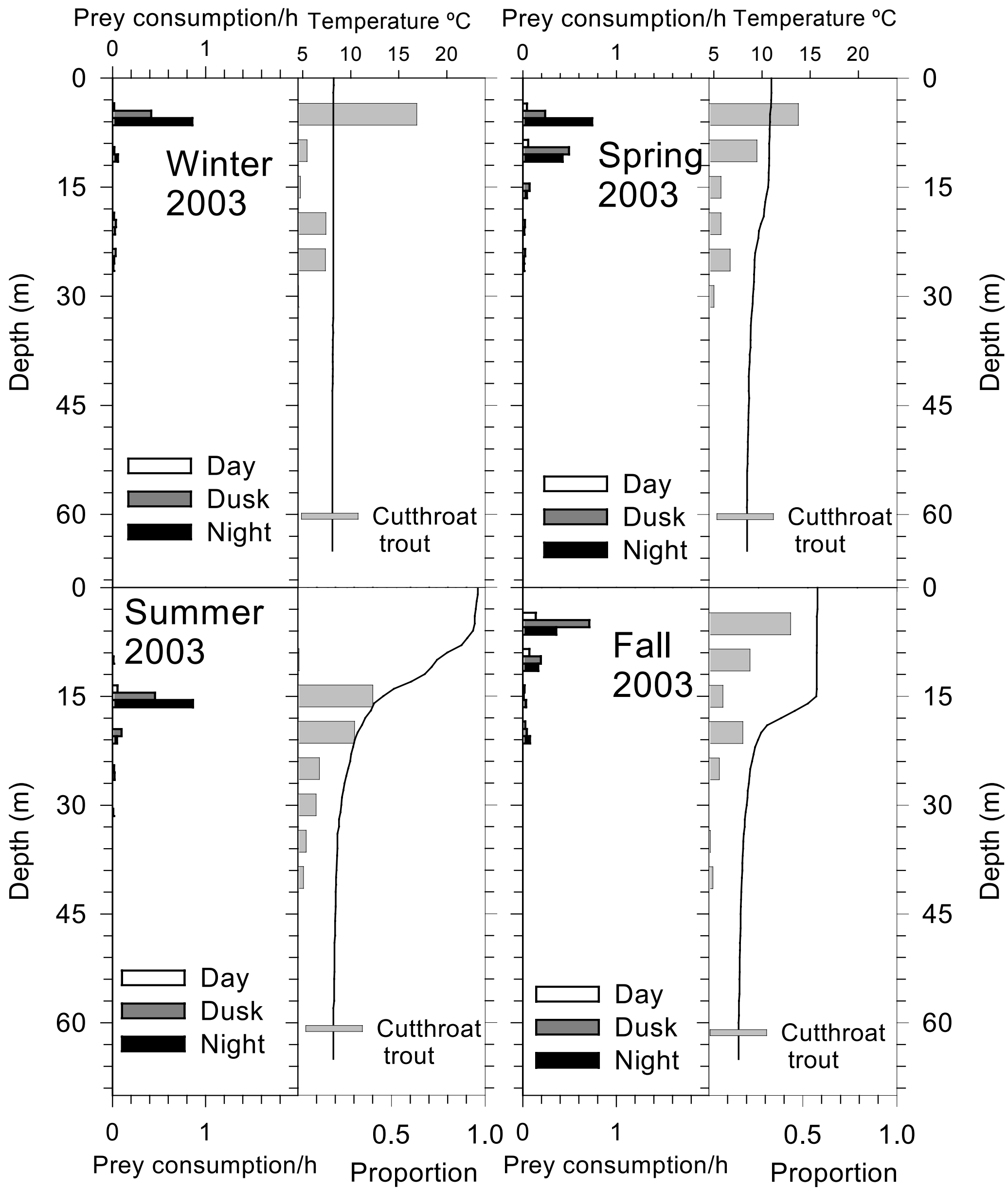


Figure 3.6. Predicted diel and depth specific consumption rates (left panels) for cutthroat trout weighted by light-dependent capture success and by the depth specific cutthroat trout distributions (right panels) observed in 1998 and 1999 (Nowak and Quinn 2002) for winter, spring, summer, and fall of 2003. Cutthroat trout consumption rates (prey fish/hour) were estimated for day (white bars), crepuscular (dark gray bars), and night (black bars). The vertical depth specific cutthroat trout distributions (gray bars) represent observed proportion of time spent at depth and lines represent average temperature profiles corresponding to each season collected in 2003 (unpublished data, King County Dept. of Natural Resources).

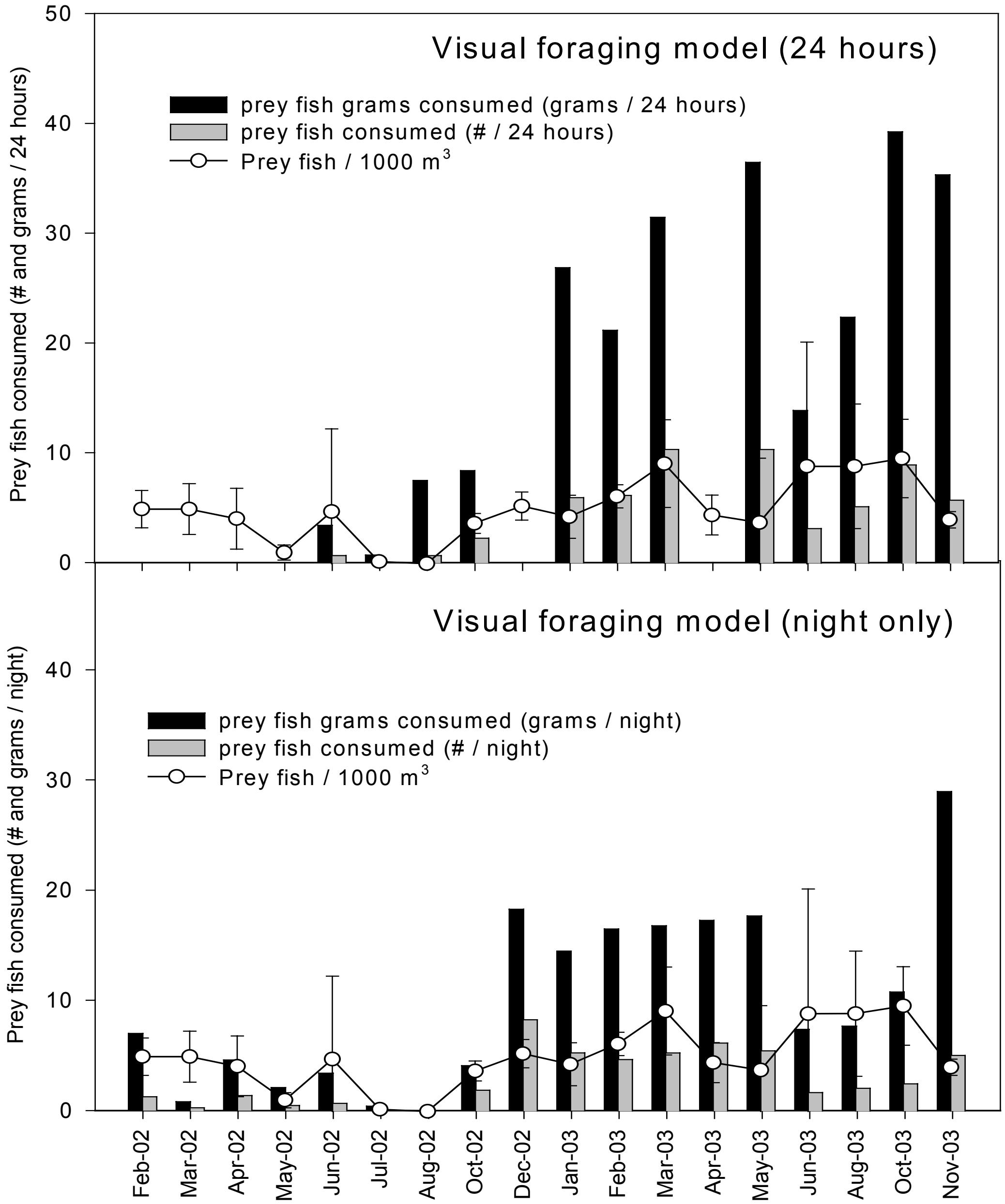


Figure 3.7. Model predictions of the number and weight (grams) of prey fish consumed by cutthroat trout for an average 24 hour period (Top panel) and one night period (Bottom panel) for each month in Lake Washington and corresponding mean prey fish densities (prey fish/1000 m^3).

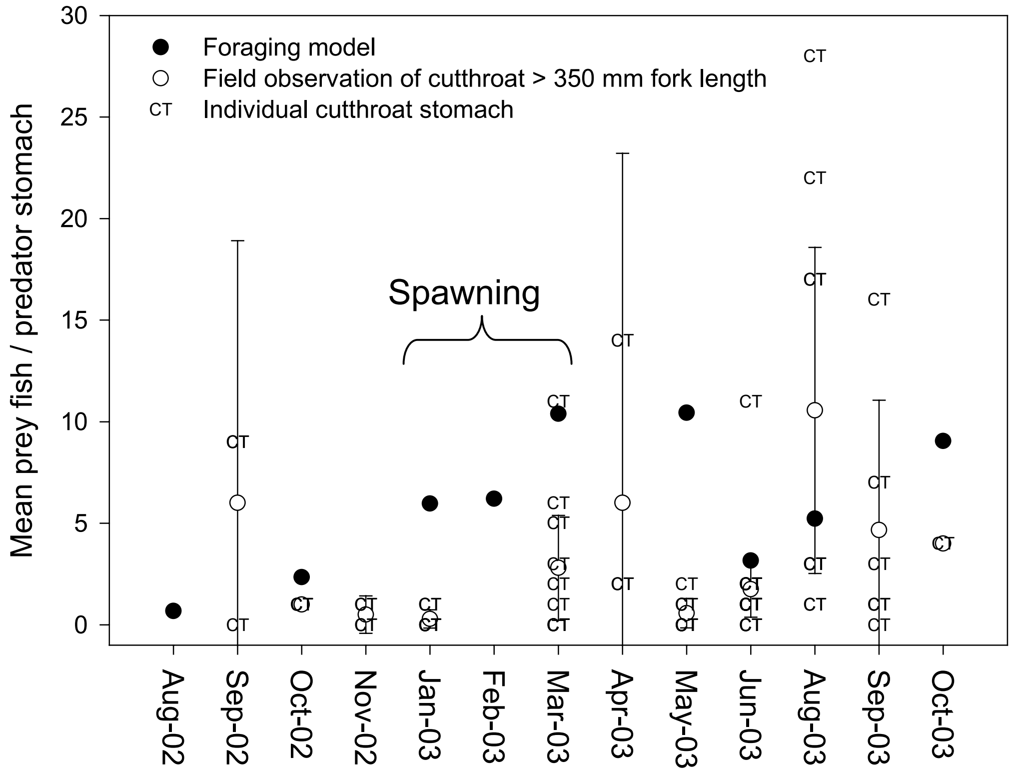
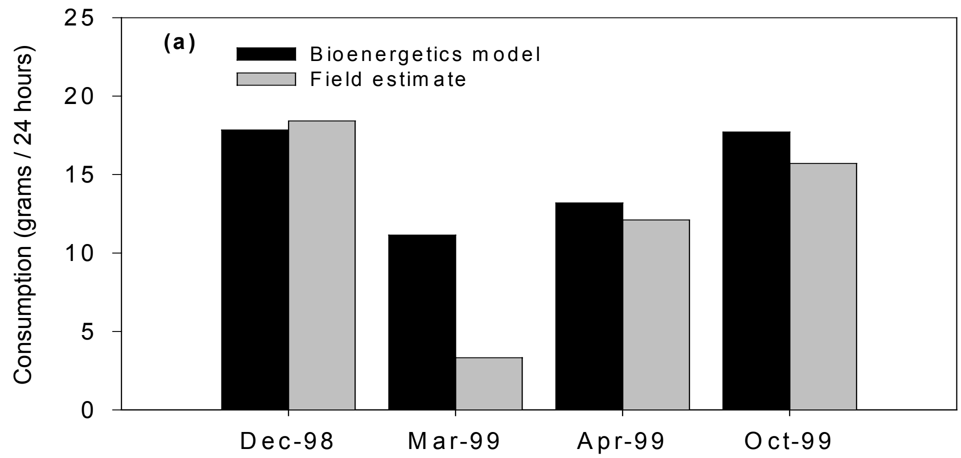


Figure 3.8. Mean predicted number of prey fish consumed by large cutthroat trout using the visual foraging model (black circles) and mean observed prey fish (white circles) in gill net captured cutthroat trout stomachs. The number of prey fish observed in individual cutthroat trout (ct) is shown and the general timing of cutthroat trout spawning is represented by the area inside the bracket. Error bars represent 95% CI.



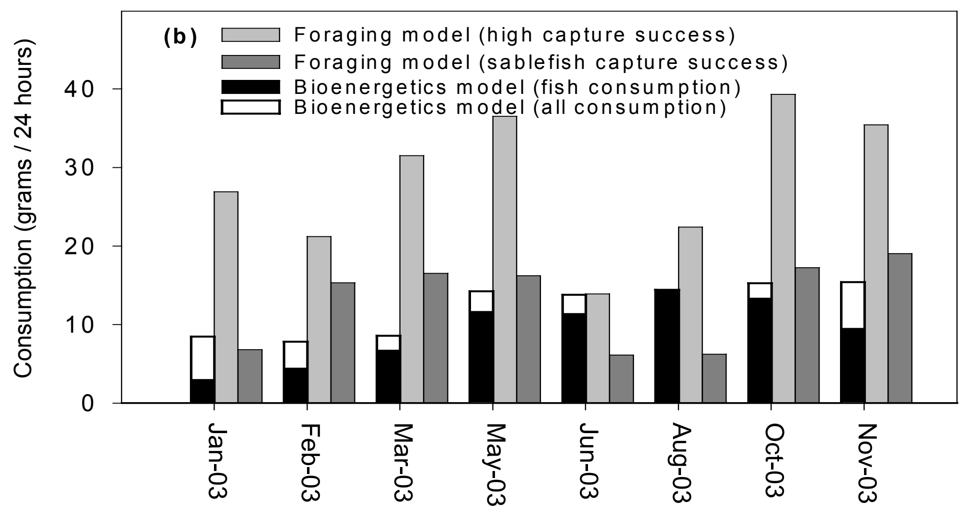


Figure 3.9. Comparison between piscivorous cutthroat trout estimates of consumption during a 24 hour period produced from (a) a gastric evacuation technique “field estimate” (gray bars) and bioenergetics model (black bars) and (b) a foraging model run using a high capture success (light gray diagonal hatched bars), a foraging model run using the capture success observed for piscivorous sablefish (dark gray diagonal hatched bars) and a bioenergetics model of total (black bars) and only prey fish consumption (cross hatched bars). Estimates of consumption in the top panel (a) were made using diet and annual growth collected in 1998 and 1999 (Nowak 2000) while the bottom panel (b) were made in 2002 and 2003. Capture success was modeled both at a high level (1 at light levels ≤ 0.75 lux and 0.49 > 0.75) and low level observed for sablefish feeding on chum salmon (0.2 > 0.75 lux and scaled to 0.4 ≤ 0.75 lux; De Robertis et al. 2004).

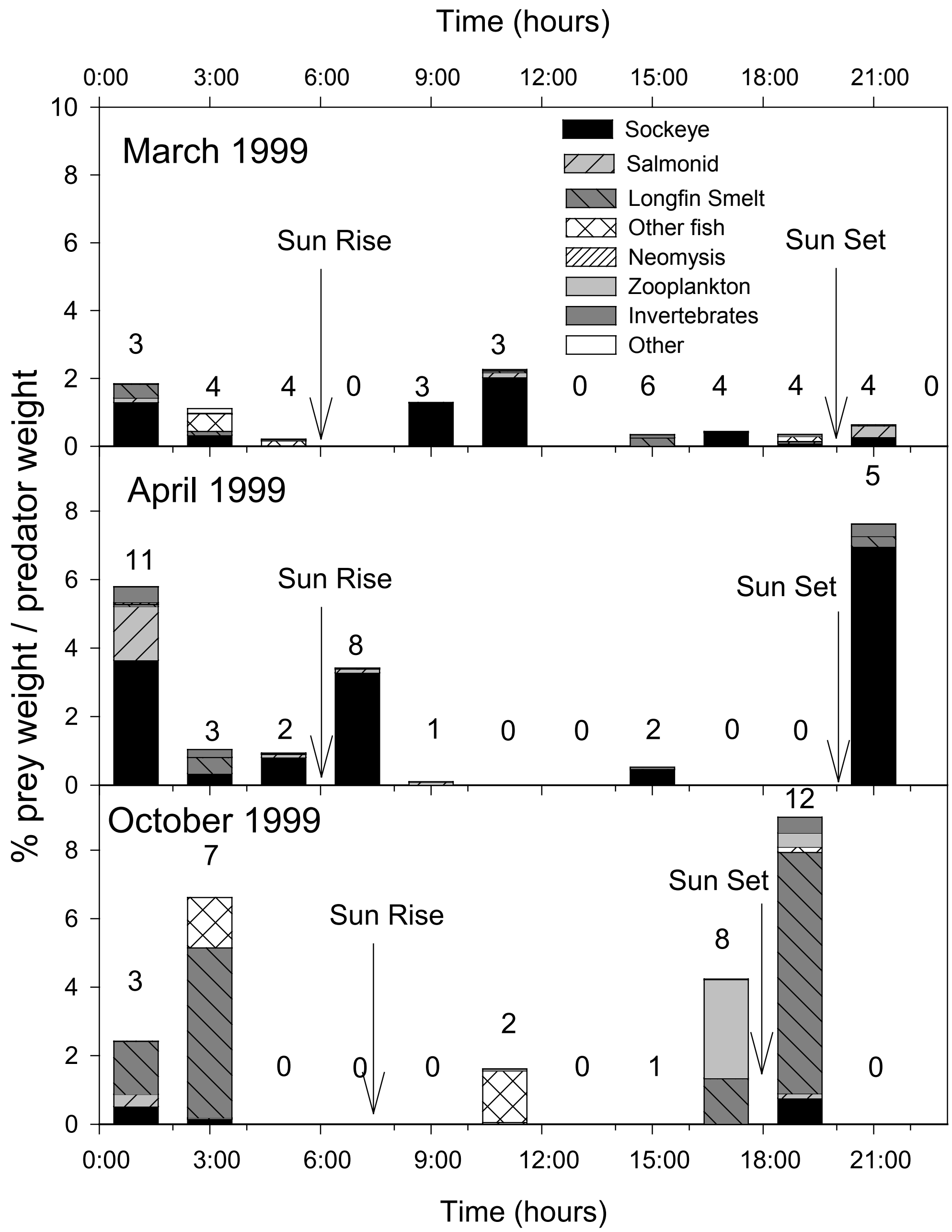


Figure 3.10. Diel gut fullness of cutthroat trout larger than 350 mm fork length captured in purse seine hauls in 1999 in limnetic regions of Lake Washington (Nowak et al 2004, unpublished data). Diets were pooled into 2 hour intervals and corrected for the difference in predator size by dividing the percent weight of prey by the individual predator weight. Arrow indicate times of sunrise and sunset and numbers represent sample sizes.

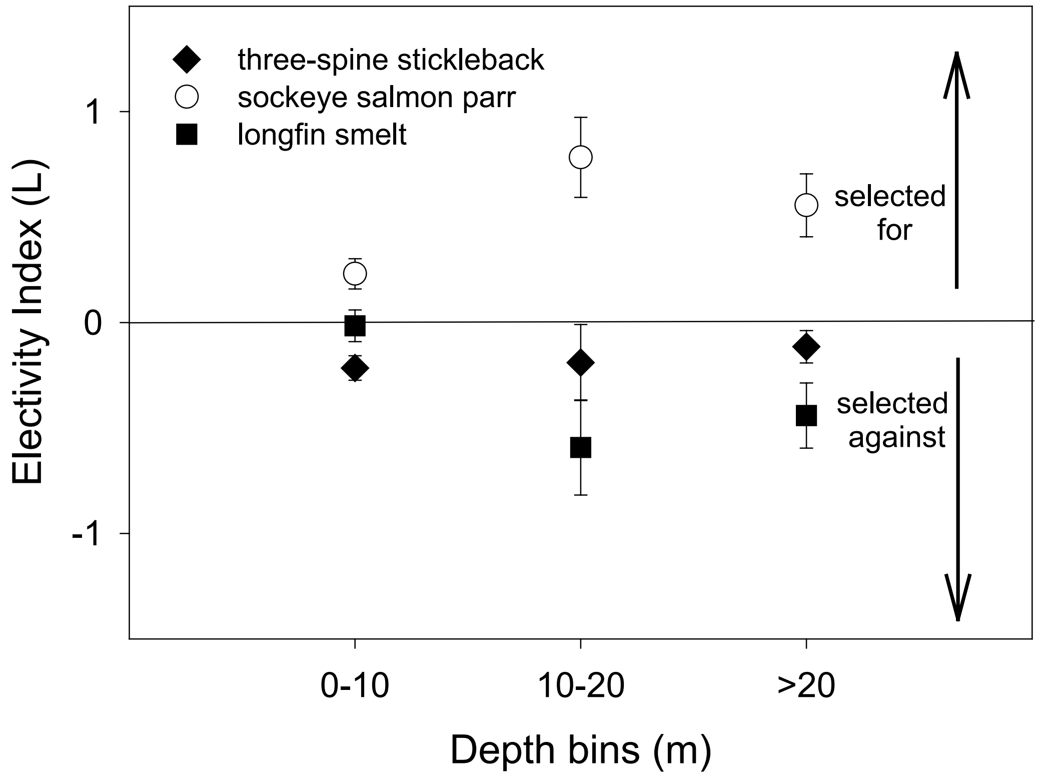


Figure 3.11. Prey selectivity by piscivorous cutthroat trout preying on three-spine stickleback (black diamond), sockeye salmon parr (white circle), and longfin smelt (black square) by depth (0-10, 10-20, >20 m) during March 2003. The Strauss electivity index (Strauss 1979) was used and error bars represent 95% CI.

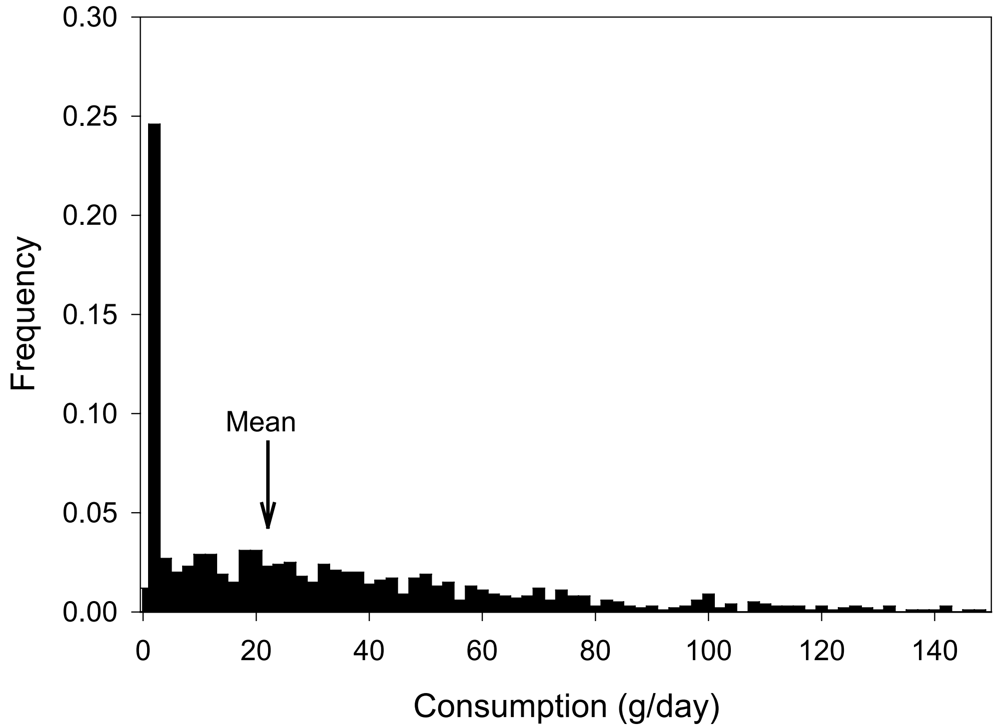


Figure 3.12. Distribution of cutthroat trout prey fish consumption (g/day) for a night period in May 2003 based on 1000 Monte Carlo replicates. Simulated variables were near surface prey density (1-15 m), predator swimming speeds, and light dependent capture success. Mean consumption equaled 24.8 grams with a standard deviation of 16.7.

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CHAPTER 4

Integration of a visual foraging model into a spatial-temporal model of predation and growth rate potential

Synopsis

A light-dependent foraging model for piscivorous cutthroat trout was integrated within a spatially explicit growth potential model to assess how cutthroat trout predatory impact on pelagic planktivores and their growing conditions changed across seasons in Lake Washington. The visual foraging model was applied to time and depth-dependent light intensities, temperature, and prey-fish densities within discrete spatial cells and was linked to a bioenergetics model to estimate spatially-explicit predation rates. The quality of pelagic habitat in terms of potential growth available to a piscivore was quantified. The spatial model was applied to day, crepuscular, and night hydroacoustic transects distributed across the lake for each season from spring 2002 to fall 2003. Comparison between the light-dependent foraging module and a constant reaction distance foraging module indicated that the quality of deep water habitat to the growth of visual feeding cutthroat trout was overestimated when light was not incorporated into the foraging module. Positive growth cells were more abundant below 15, 20, 40 m during the night, crepuscular, and day periods using the constant reaction distance model. Despite regional differences in prey fish densities within the lake, predation rates and growth by cutthroat trout were more dependent on the diel vertical distribution of prey. Simulations indicated that the volume of positive growth habitat was limited to less than 3% of the lake volume and were located in the north and south ends of the lake during spring and summer of 2002. During fall 2002, recruitment of an abundant year class of longfin smelt to a vulnerable size increased the availability of positive growth habitat to 15% of the lake volume,

and this increased availability persisted through fall 2003. Changes in growth potential for cutthroat trout were consistent with annual changes in growth estimated from scale analysis of captured fish and seasonal changes in condition factor. These results emphasize the importance of integrating optical conditions into models of growth for visual feeding fishes and further support the utility of these models for assessing the availability of growth habitat.

Introduction

Applications of spatially explicit models have increased markedly over the last decade with increasing scope and complexity (Werner et al. 2001). These modeling approaches share the common trait of attempting to account for spatial variability within systems at scales relevant to organisms of interest. Spatially explicit growth potential models (here after referred to as growth potential models) attempt to break aquatic habitats into homogeneous cells that account for the growing conditions for fish (Brandt et al. 1992). Errors associated with homogeneous groping of the environment are reduced by growth potential models (Brandt and Kirsch 1993). Estimates of predator demand generally derived from a foraging model, convert prey supply at smaller spatial scales into potential predation rates (Hondorp and Brandt 1996). Prey consumption estimates are then converted into potential growth for individual predators via a species-specific bioenergetics module (Brandt et al. 1992; Hondorp and Brandt 1996; Luecke et al. 1999). Both the foraging model and bioenergetics model are repeated within each cell at the selected level of spatial resolution to produce a landscape of cells offering potentially different growth potentials (Brandt et al. 1992). By dividing the habitat into discrete blocks with homogeneous characteristics, it becomes possible to account for the inherent spatial variability of aquatic habitats among cells. Accounting for variable prey distributions and thermal structure through space and time enables estimates of foraging and growth at a scale relevant to the predator.

Despite the complex nature of growth potential models they have correlated with annual changes in lake trout condition (Luecke et al. 1999). Similarly, results from a spatially explicit model of Lake Ontario were correlated with the results from an individual-based model of fish growth (Tyler and Brandt 2001). Convergence in model results does not validate or corroborate either modeling approach (Gurney et al. 1995), but suggests that consistency exists in more than one estimating tool.

Models of growth rate potential depend heavily on how the foraging module converts prey distribution and abundance into consumption and ultimately into growth rates for the predator (Mittelbach and Osenberg 1994, Mason et al. 1995). For cruising predators, prey encounter rates are derived from prey densities and search volumes as determined by the swimming speed of the predator and its reaction distance to prey. Encounter rates are sensitive to reaction distance estimates because search volume is generally modeled as a cylinder with reaction distance representing the radius, a squared term (Beauchamp et al. 1999).

Most applications of growth potential models have used constant reaction distances over time and through all depths of the water column (Brandt et al. 1992; Brandt and Kirsch 1993; Mason et al. 1995; Luecke et al. 1999). However, pelagic salmonids are visual feeders (Ali 1959), and incident light levels greatly influence their foraging capability (Eggers 1977; Henderson and Northcote 1985; Vogel and Beauchamp 1999; Koski and Johnson 2002; Mazur and Beauchamp 2003). Similarly, a difference in light-dependent reaction distances exists among genera of salmoninae reacting to both zooplankton (Henderson and Northcote 1985) and fish prey (Mazur and Beauchamp 2003) suggesting that reaction distance equations should vary among genera and possibly species. Ambient light can affect prey encounter rates the probability of attack, and capture success (De Robertis et al. 2003; Mazur and Beauchamp 2003).

Prey encounters for visual feeding piscivores are affected by light and predator and prey distributions (Beauchamp et al. 1999), while the capture success of each encounter is further influenced by predator and prey sizes (Brooks and Dobson 1965) and ambient light (De Robertis et al. 2003; Mazur and Beauchamp et al. 2003). The relative sizes of predator and prey can reduce the size fraction of the prey population that is vulnerable to predation (Juanes 1994; Christensen 1996). Because of this, much of ecological research has focused on size selective processes in relating diet contents to available prey in the environment (Brooks and Dodson 1965; Persson et al. 1996; Lundvall et al. 1999). However, size-selective processes only occur if visual predators and prey overlap in time and space during periods when optical conditions enable prey detection. The subset of vulnerable prey in deep aquatic environments is often limited by ambient light levels (Fiksen et al. 1998; Aksnes et al. 2004) resulting from the influence of light on the ability of predators to detect (Eggers 1977) and capture prey (De Robertis et al. 2003; Mazur and Beauchamp 2003). The influence of light on the availability of refuge space structures food webs in many fjord systems through its influence on the prey detection and capture capabilities of predators (Aksnes et al. 2004).

Growth potential models need to account for the spatial and temporal availability of detectable prey that are vulnerable to capture. Most growth potential models for pelagic salmonids utilize hydroacoustics to measure available prey at night when pelagic prey fishes are most detectable by this method (Brandt et al. 1992; Brandt and Kirsch 1993; Mason et al. 1995; Luecke et al. 1999); however nocturnal estimates of prey density might be inappropriate measures of the foraging opportunities for piscivores. Considerable piscivory can occur during crepuscular or daylight periods (Beauchamp et al. 1992) when light regimes and prey distributions differ markedly from nocturnal patterns (Clark and Levy 1988; Beauchamp et al. 1999). Diel differences in foraging opportunity are influenced primarily by changes in light and prey distributions, and should therefore be integrated into growth potential models for pelagic piscivores.

Cutthroat trout are an important pelagic picivore in the Lake Washington system (Beauchamp 1994; Nowak et al. in press) and current management concerns focus on their predation on juvenile salmon and other pelagic planktivores in the lake. Piscivorous cutthroat trout are cruising foragers that are active throughout a 24 hour day (Nowak and Quinn 2002) consuming prey fish during the day, night, and crepuscular time periods (Beauchamp et al. 1992). The high spatial variability in abundance of different prey fishes among seasons and years (Chigbu and Sibley 1994; Chigbu et al. 1998) has made it difficult to accurately account for the predatory demand of cutthroat trout, thus hampering management.

In this paper we apply a visual foraging model for cutthroat trout in a spatially explicit modeling framework to Lake Washington. Because prey fish abundances were highly variable in Lake Washington (Beauchamp 1994; Chigbu and Sibley 1994) and cutthroat trout are largely opportunistic foragers, we estimated the predator influence and growth potential of cutthroat trout through 24 hour periods and across seasons. Growth potentials were compared among different regions of the lake to assess the relative contribution of each area to the growth potential for cutthroat trout. We then compared the predictions of growth potential with observed seasonal changes in length-weight conditions and growth rates of cutthroat trout to determine if seasonal shifts in growth potential influenced actual growth. Growth rate predictions from this model were compared to those generated from using nocturnal prey density distributions and a fixed reaction distance model as in earlier spatially-explicit growth models (e.g. Brandt et al. 1992).

Methods

Spatially explicit model development

A spatially-explicit model was developed to assess the growing environment in Lake Washington for piscivorous cutthroat trout. This model was structured following the general procedure outlined in Brandt et al. (1992). The model divided the lake into discrete cells of uniform size where physical measures of temperature and light were combined with prey fish densities in a foraging model to estimate predation which was then used in a bioenergetics model to estimate the potential for growth (Figure 4.1). The foraging model uses a light-dependent reaction distance and swimming speeds to determine the search volumes accomplished in each cell. The search volumes and prey densities estimated for each cell varied by depth, time, and season, and prey fish densities also varied by lake area. Prey densities were multiplied by search volumes to estimate encounter rates in each cell and encounters were converted into prey consumptions by multiplying by a light-dependent probability of capture success. Prey consumption in each cell was not allowed to exceed the theoretical maximum daily consumption (C-max) as determined by the bioenergetics model. Consumptions estimates were input into a bioenergetics model that uses predator and prey energy content (J/g) and temperature to estimate growth in each cell for each diel period and season. This modeling framework was applied to day, night, and crepuscular periods within each season from spring 2002 through fall 2003 using hydroacoustic surveys conducted May 21, August 15, October 15, 2002, and February 4, May 21, August 7, November 4, 2003.

The appropriate cell size for the model was selected based on an analysis of the variability in prey consumption rates in the foraging model between cells. The vertical dimension was selected priori at 1 m to capture the influence of light at a fine scale. Because prey fish consumption is the metric most associated with the amount of vulnerable prey in the environment (Chapter 3), the variability in consumption rate associated with cell size was measured across model runs of varying horizontal cell sizes. For simplicity and because we were comparing the growth potential output among areas and diel periods based on the proportion of positive growth cells (Luecke et al. 1999), we used a fixed cell size for all model runs rather than varying the cell size based on the variability associated with each hydroacoustic transect (Mason and Brandt 1996). A crepuscular transect (3 km long) conducted during May 2003 in the middle of the lake was used to determine the horizontal cell size by visually identifying the point where the variability in prey consumption associated with cell size began to asymptote (Figure 4.2). The number of cells was then converted into a horizontal distance (26 m) to create a standardized cell size (1 m x 26 m) for use in each model transect.

Visual foraging model

A visual encounter rate modeling approach (Chapter 3; Beauchamp et al. 1999) was used to estimate consumption of prey fish in each cell of the growth potential model. An experimentally derived reaction distance equation for cutthroat trout (chapter 2; Mazur and Beauchamp 2003) was applied to seasonal diel hydroacoustic measurements of cell-specific prey fish densities from May 2002 through November 2003 in Lake Washington. The amount of prey fish that a large cutthroat trout could consume during each diel period was estimated for each cell based on light dependent prey encounters and capture success. Consumption estimates were limited to the hypothetical maximum consumption, for the average sized age 3-4 cutthroat trout weighting 900 g, as determined from the bioenergetics model (Beauchamp et al. 1995). Maximum consumption in that cell (g/day) was divided by the mean weight (g) of the average prey fish to obtain a maximum number of consumable prey fish. Average prey fish sizes were estimated by converting the mean target strength of prey size targets (-52 to -42 dB; Chapter 3) to total length (TL) using Love's equation (Love 1971). The total length was then converted into fork length (FL) using a generalized prey fish equation generated from March and October 2001-2003 trawl catches of longfin smelt (*Spirinchus thaleichthys*) and sockeye salmon (*Oncorhynchus nerka*) in Lake Washington.

$$FL\ (mm) = 0.91 \cdot TL\ (mm) + 0.55,\ r^2 = 0.995,\ n = 39$$

Average prey fish weights (W) in grams were then estimated using a generalized length-weight equation generated for sockeye salmon, longfin smelt, and three-spine stickleback (*Gasterosteus aculeatus*) captured throughout the year during 2001-2003.

$$W\ (g) = 2.00 \cdot 10^{-5} \cdot FL\ (mm)^{2.94},\ r^2 = 0.85,\ n = 201$$

Prey encounter rates were modeled using Beauchamp et al. (1999) equation 1 for temporally and depth-explicit search volumes and prey densities:

$$ER_{z,t} = SV_{z,t}\, PD_{z,t}$$

Where $ER_{z,t}$ is the prey encounter rates for that diel period at depth *z* and diel time *t* estimated by multiplying the diel search volume SV by the prey density PD in each cell obtained from hydroacoustic surveys. Search volume was modeled as a cylinder:

$$SV_{z,t} = \pi RD^2_{z,t} SS_t\, T_t$$

with radius $RD_{z,t}$ representing reaction distance of the piscivore at depth *z* and time *t*, and *SS* a cylinder length of the swimming speed of the piscivore within diel period *t*, multiplied by T_t, the duration in hours of each diel period. Reaction distance $RD_{z,t}$ (cm) was a light-dependent function (Mazur and Beauchamp 2003):

$$RD = 33.70\ I^{0.194}\ cm \qquad \text{for I 0.00-17.00 lux}$$

$$RD = RD_{max} = 58.38\ cm \qquad \text{for I > 17.00 lux}$$

Where I is the ambient light condition (lux) determined from incident light levels and seasonal-specific light extinction coefficients. Field estimates of *in* *situ* diel swimming speeds for large cutthroat trout were borrowed from an ultrasonic telemetry study conducted on Strawberry Reservoir, Utah (Baldwin et al. 2002) and were very similar (21 $cm \cdot s^{-1}$) to average swimming speeds (22 $cm \cdot s^{-1}$) from Lake Washington measured during 1998-1999 (Nowak and Quinn 2002). Swimming speeds of 14 ± 6 $cm \cdot s^{-1}$ for night, 22.5 ± 12 $cm \cdot s^{-1}$ for crepuscular, and 30 ± 9 $cm \cdot s^{-1}$ for day periods were used.

A light-dependent capture probability developed in Mazur et al, (Chapter 3) was used to convert diel encounter rates into estimates of consumption:

$$C_{z,t} = ER_{z,t}\, PC(I_{z,t})$$

The probability of a successful capture was modeled as a step function of light (Table 3.1; Chapter 3) where consumption $C_{z,t}$ at depth *z*(m) and time *t* was equal to the encounter rate $ER_{z,t}$ multiplied by the light-dependent probability of capture given an encounter $PC(\ I_{z,t})$ at that depth and time.

Surface light intensities used in the foraging model were recorded for Lake Washington ($I_{0,t}$) in 2001- 2002 using a LI-COR radiation sensor (terrestrial type photometric sensor) and were used to estimate night specific seasonal profiles. The sensor malfunctioned in October of 2002 and subsequent estimates of day and crepuscular surface light intensities were generated by a computer program (Janiczek and De Young 1987) to coincide with the dates and times of hydroacoustic surveys (Table 3.2; Chapter 3). Spring, summer, and fall light extinction coefficients were estimated from depth specific light recordings acquired between 1000 and 1400 hours. The winter extinction coefficient was generated using light profile data from January 2003 (J. Scheuerell and Schindler unpublished data). Surface light intensities from each diel period were used to estimate ambient light at each depth interval in the lake.

$$I_{z,t} = I_{0,t}e^{zk}$$

The light level (I) at depth *z*(m), and time *t* was calculated using the surface light ($I_{0,t}$) multiplied by the exponential decline of light with depth *z*(m), based on the light extinction coefficient K (Table 3.2).

Prey supply

Seasonal prey fish distributions were collected from May 2002 thru November 2003 using diel hydroacoustic surveys (Figure 4.3). Transects were positioned to capture the north to south variability in prey fish density. Equal lengths of hydroacoustic transects based on the proportion of surface area were assigned to 5 north to south areas of the lake to facilitate comparison among areas. Day and night surveys followed the same design with 20 transects each while crepuscular transects varied in number depending on conditions and were located in the middle section (Area 3) of the lake. Surveys were conducted over consecutive day and night periods when possible. Hydroacoustic surveys were conducted with a BioSonics split beam echosounder (DE6000) with a 430-kHz transducer mounted on a tow fin. The tow fin was deployed from the side of a 7 m boat and suspended at a depth of 0.5-1 m. The transducer was operated at 1.5-3 pings per second with a vertically positioned 6º full-angle beam. Samples were collected using a TVG of 40 Log R, minimum target threshold of -65 dB, and a pulse width of 0.4 ms. The boat speed ranged between 6 and 8.5 km/h. Transects were recorded to the hard drive and post processed using SonarData Echoview ® 3.10.129 software.

Transects were echo counted for individual targets and individual target strengths were collected for each spatial cell in the model. Target strengths were converted to total length using Love's equation (Love 1971). Targets between -52 and -42 dB (roughly 4–15 cm), which corresponded to the most frequently observed prey fish sizes in cutthroat trout stomachs (Figure 3.2; Chapter 3), were considered prey fish and depth specific densities for each cell were calculated by dividing the total count of returned targets in that cell by the total volume sampled for that depth in that cell. The sample volume within each 1 m depth interval was calculated for each transect by multiplying the total number of pings sampled at each depth interval by the volume of a 1 m high frustrum at each depth. Targets and density estimates from the 6º beam were restricted to a

4º beam (< 2º off axis) to increase confidence in target strength estimates and decrease reliance on beam angle compensations. Targets closer than 1 m to the bottom and within 2 m of the transducer were excluded from the analysis.

Bioenergetics model

The Wisconsin bioenergetics model, version 3.0 (Hanson et al. 1997) was used to estimate growth potential for large piscivorous cutthroat trout in each cell from the weight of prey fish consumed estimated by the foraging model. The bioenergetics model, parameterized for cutthroat trout (Beauchamp et al. 1995; Cartwright et al. 1998) was used to estimate growth potential within each cell from a balanced energy budget where energy available for growth equals the total energy consumed minus the energy lost to waste, activity, and respiration (Hanson et al. 1997). A prey fish energy content of 6181 J/g wet weight was estimated by taking the average energy content of Lake Washington prey fish measured seasonally using bomb calorimetry (McIntyre et al. unpublished data). Cutthroat trout energy content was estimated at 6651 J/g wet weight using the relationship generated for coho and chinook salmon (Stewart and Ibarra 1991) and assuming a 900 g body weight. Thermal inputs to the bioenergetics model were taken at 500 m intervals, along hydro-acoustic transects when possible. Thermal profiles were supplemented with data from King County R.U.S.S. buoys located in the north and central basins of the lake (unpublished, King County Dept. of Natural Resources).

Cutthroat trout growth and condition

Cutthroat trout growth was estimated based on scale samples collected during 2001-2003 (Chapter 1). Measurements from the center of the scale to each annuli and to the outer scale margin were recorded using Image-Pro plus® software (version 4.1; Media Cybernetics). Measurements in millimeters were taken from the scale focus to the outer edge of the posterior field along the longest axis. A linear relationship between scale radius and fish length was established by regressing the distance (R) between focus to posterior scale margin and the fork length (FL in mm) for each fish.

$$FL\ (mm) = 45.1 + 229.6\ R,\ r^2 = 0.72,\ p < 0.001,\ n = 58$$

This regression was then used to back-calculate FL at each age and year for each cutthroat trout. Estimated fork lengths were transformed into body weight at age using an annual length weight regression determined from all cutthroat trout captured during 2002 thru 2003.

$$W(g) = 5 \times 10^{-6}\ FL\ (mm)^{3.14},\ r^2 = 0.99,\ n = 258$$

The condition factor of cutthroat trout for each season was estimated using the slope of the log transformed FL and log transformed W linear regression relationship from cutthroat trout captured within each season (Cone 1989; Luecke et al. 1999). Overnight vertical and horizontal gill net sets were deployed monthly (Chapter 1) from September 2002 –February 2004 and a purse seine (600m x 40 m deep; 25 m effective capture depth) was deployed in afternoon, dusk and night sets during June of 2003. Vertical gill nets were 60 meters long x 2.3 meters wide and were suspended on floating aluminum rollers. Each vertical net consisted of one monofilament panel of a single mesh size. The available vertical mesh sizes were 25, 38, 50, 63, 75, 83, 95, 108 mm stretch mesh and nets were adjusted to match the bottom depth where they were deployed. Horizontal nets (3 x 60 m with variable mesh sizes of 25, 31, 38, 50, 63, and 75 mm stretch mesh) were suspended in the water column, at depths of 10, 15, 20, and 25 m by surface floats spaced every 7 m.

The proportion of spatial cells that resulted in positive growth was used as the metric to compare lake-wide growth among seasons and diel periods. This metric standardized the available growth potentials in each discrete lake area for differences in spatial and temporal scales. Similarly, we used the proportion of positive cells for comparisons to both the back-calculated growth estimate and seasonal condition index (Luecke et al. 1999).

To explore the influence of a light-dependent foraging model on predictions made by a growth potential model, we compared growth potential predictions from a fixed reaction distance module to those generated using a light dependent reaction distance module. A diel survey during May 2003 was processed with a fixed reaction distance of 0.5 m, as assumed by Brandt et al. (1992), throughout the water column and re-processed with the light dependent reaction distance equation (Mazur and Beauchamp 2003; Chapter 2). Reaction distance was the only modeling constraint altered in this analysis.

Results

Prey fish distribution

In general prey fish were distributed in higher densities below 30 m during the day and above 30 m at night in all seasons and regions of the lake (Figure 4.4). The summer of 2002 was an exception, with overall low system wide densities of 4-15 cm prey fish, but higher daytime densities were more frequently above 30 m. Prey fish densities in individual cells ranged between 0–0.72 prey fish/m^3 during day periods and 0-0.85 prey fish/m^3 during night for all seasons (Figure 4.4). Thermal stratification (Figure 4.5) during fall 2002 resulted in a general deeper distribution of prey fish during nocturnal period than observed during the spring or winter seasons. Prey fish were predominantly found in the top 10 m of the water column at night during the summer of 2002 despite temperatures in excess of 20 ºC (Figure 4.4).

Spatially explicit growth potential

Growth potential for cutthroat trout varied in the position and frequency of positive growth cells across both diel and seasonal time frames (Figure 4.6). Thermal stratification in summer and fall resulted in a deeper distribution of positive growth cells during nocturnal periods. The frequency of positive growth cells peaked at 30 m during the night in the fall compared to 10-20 m during the thermally mixed winter and spring seasons. Daytime positive growth cells were relatively unaffected by thermal stratification with peak frequencies between 30-40 m during all seasons. Positive growth cells were more frequent during the day in spring and summer 2002, when relatively low densities of 4-15 cm prey fish were found throughout the lake. Conversely, positive growth cells were more frequent at night during fall 2002, winter 2003, and spring 2003 when system-wide densities of prey fish were relatively high. Overall, positive growth potentials were more frequent during the fall of 2002, winter and spring of 2003 representing 15-16% of all cells compared to spring and summer of 2002 when positive cells only represented 1-4 % of all cells. The difference between seasons in growth potential is associated with the increase in availability of the abundant even year class of longfin smelt reaching vulnerable sizes (> 40 mm FL) in the fall of 2002.

General differences within areas of the lake were less variable than those observed between seasons and diel periods. No consistent pattern in the frequency of positive growth cells emerged among areas during the night (Figure 4.7). The proportion of positive growth cells during the day was consistently higher in area 4 (Figure 4.7) reflecting a consistent prey fish presence in an area with increased bathymetric complexity.

Cutthroat trout growth and condition

Back calculated growth of cutthroat trout captured in 2003 indicated that age 3 fish gained an average of 199 g, 44 g more weight than age 3 fish gained during 2002 (Figure 4.8). Similarly, the slope of the log-transformed lengths and weights indicated that cutthroat trout condition increased from a low of 2.89 in fall 2002 to a high of 3.49 in fall 2003 (Figure 4.8). The length-weight regressions during all seasons were significant with r^2 ranging between 0.967 and 0.998 ($p < 0.05$).

The proportion of spatial cells offering positive growth increased more than 3-fold from spring-summer 2002 to fall 2002 through summer 2003, then increased further during fall 2003 (Figure 4.8). The improved proportion of positive cells preceded the increase in condition factor by two seasons (fall and winter) and preceded the increased annual growth increments by one season (winter). The time lag between increases in growth potential and condition as reflected by the slope of the length-weight regression may have been accentuated by the spawning period and reduced scope for growth during winter.

Reaction distance comparison

When compared to predictions made by the light dependent reaction distance model a fixed reaction distance of 0.5 m for cutthroat trout both increased the amount of cells offering positive growth potentials in the lake and broadened the vertical extent of positive growth habitat (Figure 4.9). The proportion of positive growth cells increased for all diel periods when the constant reaction distance model was used in contrast to the light-dependent model runs (Figure 4.10). The constant reaction distance model increased the proportion of positive growth cells below 40 m during the day, below 20 m during crepuscular periods, and below 15 m at night. The constant reaction distance model run also influenced the growth potential of cells horizontally through its disproportionate increase in growth potential in different areas of the lake (Figure 4.11). Area 1 in the north end of the lake was least influenced by the constant reaction distance, only increasing the proportion of positive cells by 15% while area 5, the south end of the lake had the largest increase with 47% more positive cells. Areas 2-4 showed increases in the proportion of positive growth cells that ranged between 25% and 36%.

Discussion

The comparison between growth potential models using a constant piscivore reaction distance versus a light-dependent reaction distance illustrated the importance of accounting for the spatial and temporal variability of these relevant attributes when determining the value of dynamic 3-dimensional habitat in terms of growth to the organism of interest. Similarly, spatial-temporal heterogeneity was an important influence on the timing and location of predation potential imposed by piscivores on the pelagic planktivore community. Our analysis indicated that foraging models that did not account for variability in the visual environment overestimated the value of dark, deep water habitat to the growth of these fish. Mobile prey in deep pelagic systems often vertically migrate to reduce their vulnerability to predators (Eggers 1978; Clark and Levy 1988; Scheuerell and Schindler 2003). The visual foraging model enabled us to convert the abundance of prey across all habitats into the spatial-temporal fraction available for encounter by piscivores, based on the ambient light environment. How prey availability and temperature changed across space and time dictated the quality of that habitat cell for growth of a predator.

The growth potential model predicted an increase in positive growth habitat between 2002 and 2003 that was reflected by a measured growth increase by cutthroat trout (Figure 4.8). Similar consistency between growth potential model predictions and annual predator growth patterns were also observed over a longer time interval for lake trout in Flaming Gorge reservoir in Wyoming and Utah (Luecke et al. 1999). However, growth potential models are finite predictors of the growing environment and annual growth estimates are a relatively coarse integration of predator growth. Growth potential for cutthroat trout varied seasonally in Lake Washington as did growth potentials of lake trout in Lake Michigan (Goyke and Brandt 1993) and monthly for striped bass in Chesapeake Bay (Brandt and Kirsch 1993). Therefore the agreement between our growth potential estimates on a seasonal time scale and the observed seasonal increases in cutthroat trout condition offers finer scale evidence for the value of growth potential models as predictors of piscivore growth. The observed time lag between seasonal increases in modeled growth potential and cutthroat trout conditions were expected, because condition reflected an integration of growth history and required time for weight to accrue following improvements in growing conditions. However, the three to six month lag observed was broader than expected suggesting that an increase in cutthroat trout condition may have been delayed due to the temporal overlap with spawning in February and temperature limits on growth during winter.

Seasonal shifts in prey availability and thermal regimes resulted in estimates of growth potential that varied more among seasons and vertically in the water column than they did horizontally within the lake basin. The influence of variable prey fish abundances in Lake Washington (Beauchamp 1994; Chigbu and Sibley 1994) was captured in the seasonal growth rate estimates. Spring and summer of 2002 encompassed a period when vulnerable sizes (>40 mm FL) of longfin smelt were not available to piscivores in the lake (Chapter 3). Although age-0 longfin smelt were extremely abundant during spring and summer 2002, they were smaller than the size of prey fish found in stomach samples. The small size and extreme transparency of age-0 smelt potentially reduces predator detection ranges in a contrast based visual foraging system. By fall 2002 the abundant even year class of longfin smelt had reached 40 mm FL, the size that they become less transparent and enter piscivore diets (Figure 3.2; Chapter 3). The abundant even year class remained available to piscivores through the winter of 2004 (beyond the sampling period for this study) when they spawned and died. Comparisons between the spring and summer of 2002 and 2003 demonstrated the influence of the highly variable prey fish availability in Lake Washington on the seasonal growth rates of cutthroat trout between years. Cutthroat trout growth potentials for the spring and summer differed dramatically between 2002 and 2003 resulting from highly variable prey fish abundances.

Diel differences in growth potential were more associated with the vertical migrations of prey fishes and vertical changes in light regimes than in horizontal differences. The abundance and distribution of longfin smelt and juvenile sockeye salmon, two of the major limnetic prey fishes in Lake Washington varied seasonally among different regions of the lake (Chigbu et al. 1998; Beauchamp et al. 2003). Despite horizontal differences in prey fish density, the growth potential estimates suggested that cutthroat trout growth should be more sensitive to changes in vertical distribution of prey fishes than horizontal distribution.

Previous applications of growth potential models have suggested that predator distribution is associated with areas of positive growth (Goyke and Brandt 1993). In Lake Washington large cutthroat trout were tracked using ultrasonic telemetry during 1998 and 1999, and average vertical distributions of 13.1 m at night and 16.9 m during the day were observed during thermally stratified periods (Nowak and Quinn 2002). Summer and fall growth potential estimates at night had peaks in the vertical distribution of positive cells at 15 m in the summer and 13m in the fall and corresponded with the observed depths of telemetered cutthroat trout. The daytime distribution of positive growth cells was below 30 m and much deeper than observed average cutthroat trout distributions, but cutthroat trout were more likely to move vertically in the water column during the day. Winter and spring growth potentials also corresponded to nocturnal distributions of cutthroat trout if we assume nocturnal distributions of cutthroat trout were similar to observed daylight distributions when the lake was thermally mixed (Nowak and Quinn 2002). Nocturnal catches of large cutthroat trout in gill nets and daylight angler catches suggested that they were distributed in the upper 10 m during mixed periods of the year.

If cutthroat trout distribution is associated with areas of positive growth then our analysis suggests that on average cutthroat trout attempt to maximize growth during nocturnal periods and forgo some foraging opportunities during daylight. This conclusion is consistent with observations from a diel gut fullness analysis which indicated that cutthroat trout consumed most of their prey fish during crepuscular and nocturnal periods (Beauchamp et al. 1992; Chapter 3).

Additionally, the bioenergetics estimates of consumption indicated that over half of all positive cells from nocturnal estimates were capable of maximizing consumption for a full 24 hour period.

Schools of prey fish primarily occurred during the day and early crepuscular periods below 30 m, and were often associated with the bottom of the lake. Estimates of growth potential were not greatly influenced by schooling fishes because the schools were generally small and confined within a small number of cells. Prey fish schools were rarely detected during nocturnal periods and those that were encountered were small and located in the top 10 m of water near the floating bridges and other areas of high urban light pollution. The background level of urban light pollution around Lake Washington (Tabor et al. 2004) increased the access of visual feeding cutthroat trout to nocturnal foraging prey fishes (Chapter 3). The high levels of nocturnal light available on Lake Washington both increase the risk of being predated for prey fish and increase their visual foraging ability for zooplankton (Chapter 3).

Given that prey fish vertically migrate to balance the risks of potential predation against their need to feed and grow (Clark and Levy 1988; Scheuerell and Schindler 2003), and that cutthroat trout were distributed in regions that maximized their growth potential (Stephens and Krebs 1986), then most prey fish consumption should occur at depths of 5-15 m during crepuscular and night periods. Cutthroat trout might alter their horizontal distribution in the lake to take advantage of seasonal shifts in prey fish abundance, but our analysis suggests that their vertical distribution will have a stronger influence on growth. Estimates of growth potential in the vertical dimension were heavily influenced by diel shifts in prey fish distributions and the light and thermal environment. Alterations to the environment that affect the foraging capability of visual feeding fishes have the potential to alter the current predator-prey relationship between cutthroat trout and prey fish in Lake Washington.

Our analysis suggests that integration of a light-dependent foraging model will improve the predictive capability of spatially explicit growth potential models. Accounting for the influence of light on visual foraging fishes enables us to incorporate prey vulnerability into model estimates of prey fish availability (Mittelbach and Osenberg 1994) and will increase our capability to predict growing conditions within systems for piscivores. Our growth potential model was able to reflect annual changes in cutthroat trout growth as well as seasonal shifts in cutthroat trout condition. Future improvements in our understanding of how light influences all aspects of predator-prey interactions will strengthen our ability to predict how environmental changes will influence fish community structure.

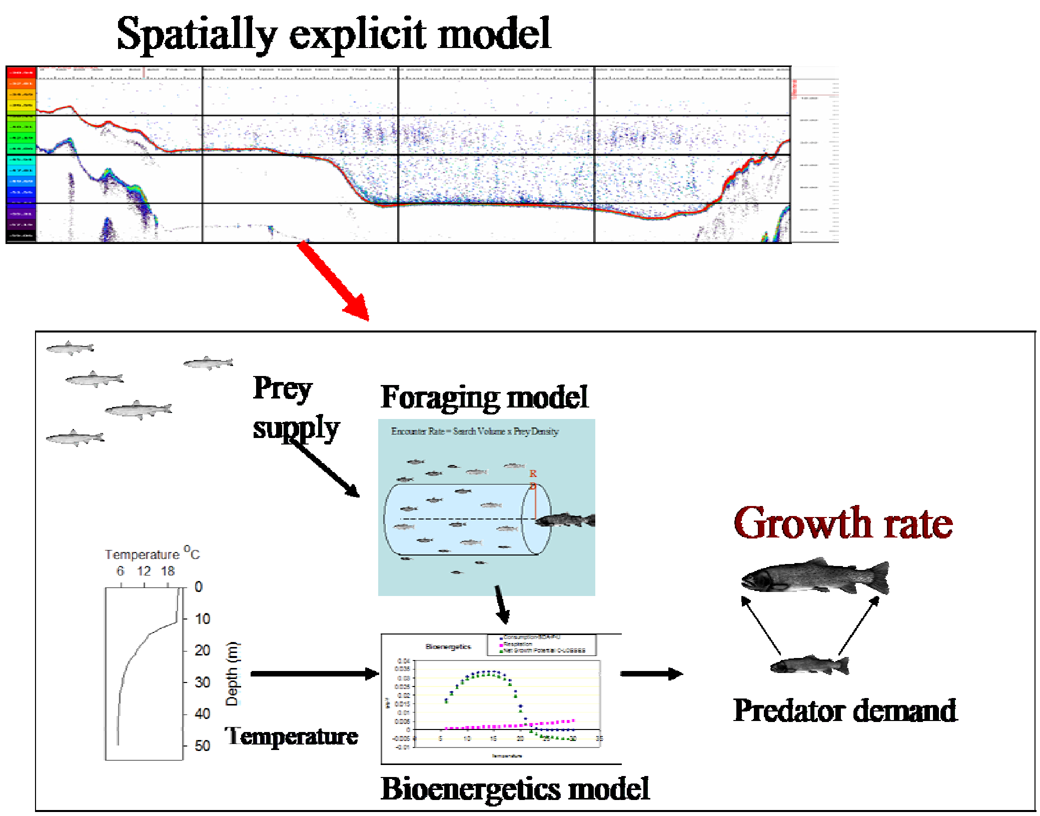

Figure 4.1. Conceptual representation of a spatially explicit model of fish growth. Prey fish distributional information is combined with temperature and a foraging model to estimate the growth of predators given predator demand and the species-specific bioenergetics constraints. Fish illustrations courtesy of Montana State University, Bozeman.

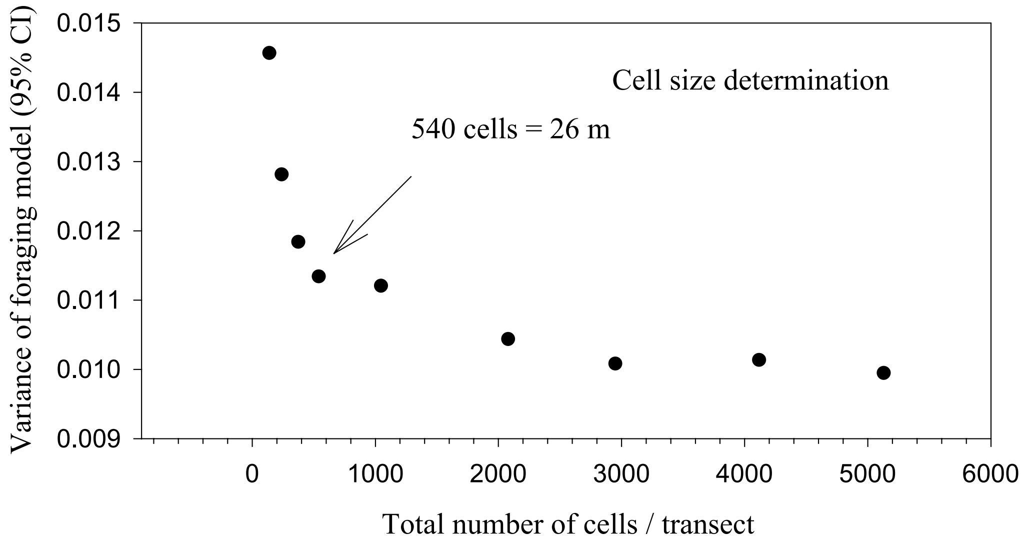

Figure 4.2. The relationship between the horizontal size of individual cells (smaller size as cell numbers increase) and the variation among cells in prey fish consumption estimated by the foraging module in the spatially explicit model. All depth intervals below 20 m were used. The horizontal cell size selected for use in the spatially explicit model is indicated by the arrow (540 cells) or 26 m.

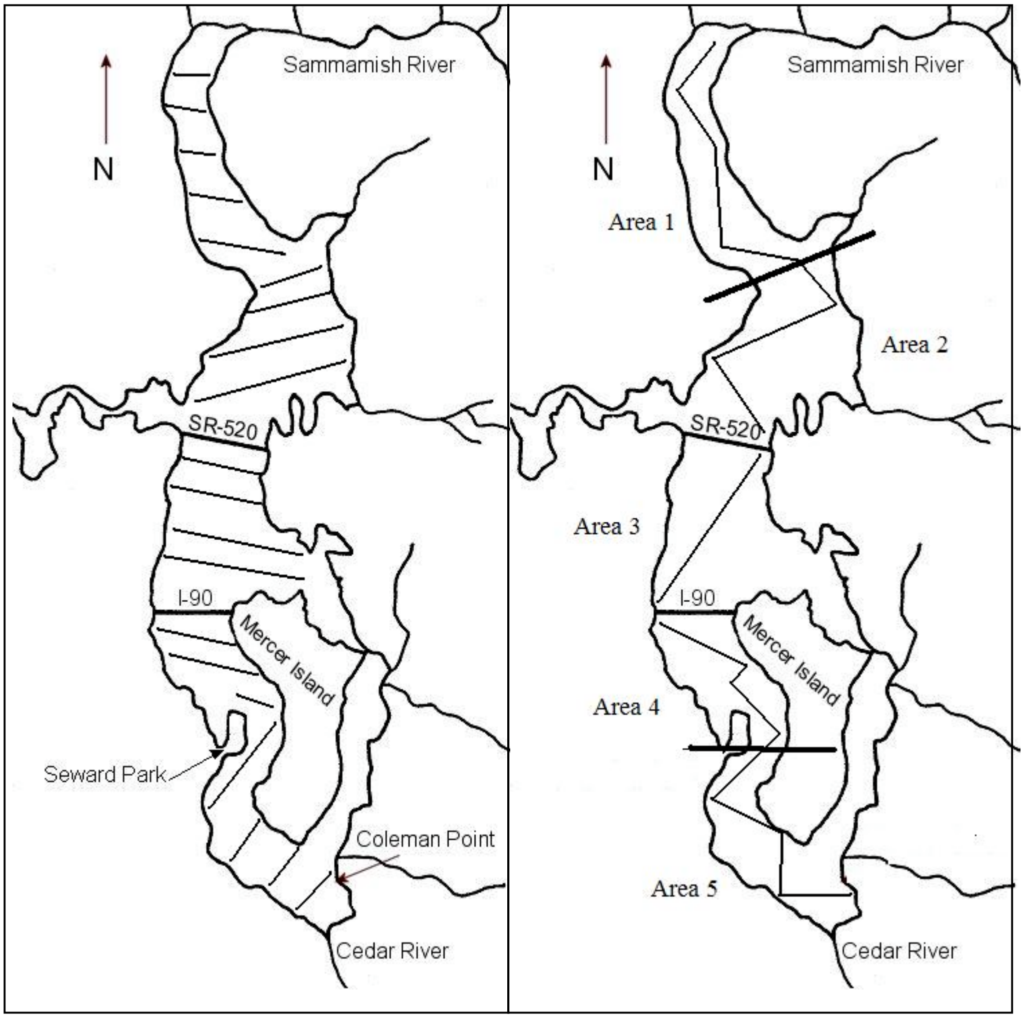

Figure 4.3. Map of Lake Washington showing the survey designs for hydroacoustic transects used in this study (left panel) and the five sampling areas (right panel). The zig-zag survey design on the right map was used to produce growth potential estimates for summer 2003.

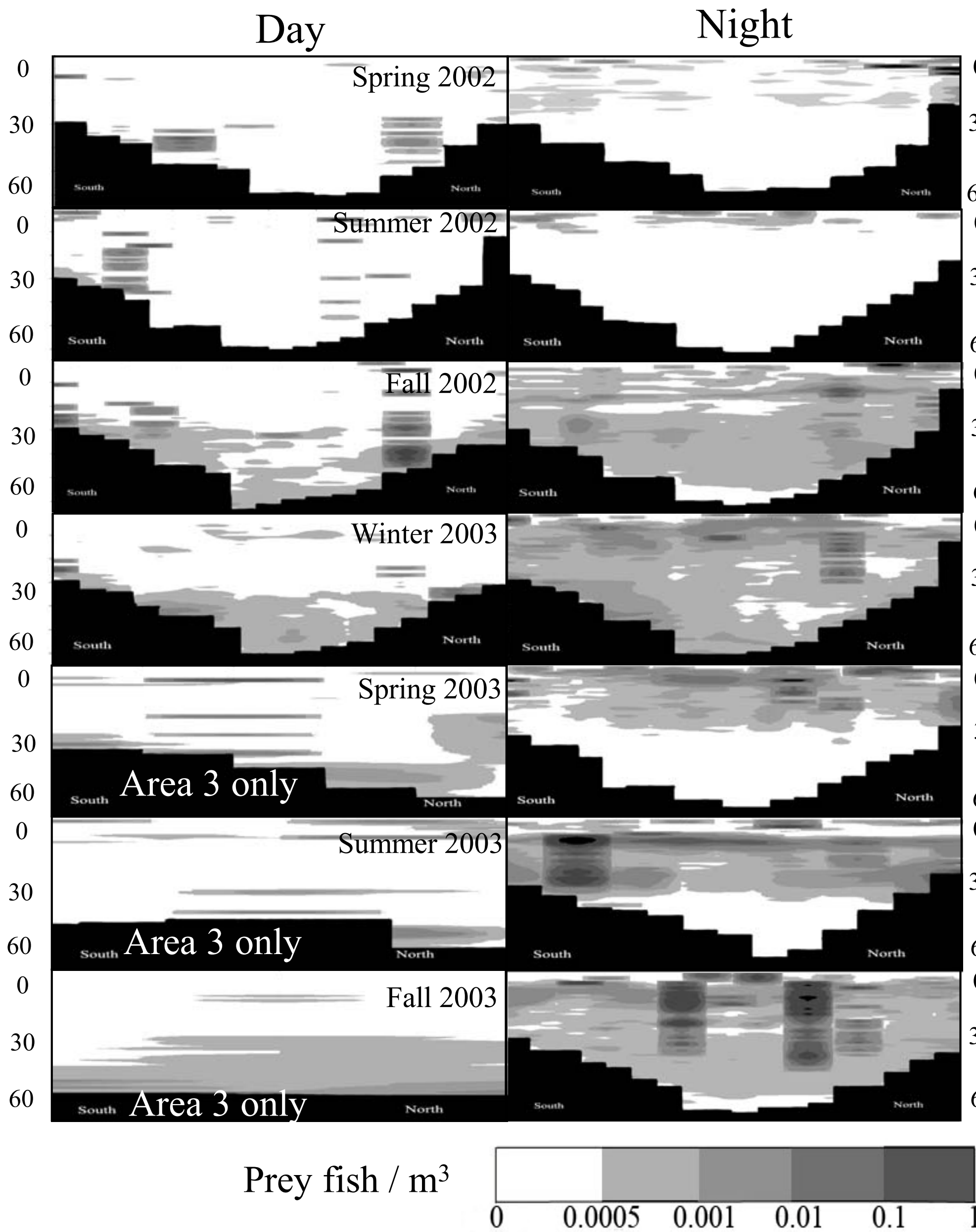

Figure 4.4. Mean prey fish densities (prey fish/m^3) for day and night periods during the spring, summer, and fall 2002 and winter, spring, summer, and fall 2003. Prey fish densities are means for each depth interval of individual hydroacoustic transects from the south (left side of each panel) to the north (right side of each panel) end of Lake Washington. Darker areas represent areas of higher prey fish density and black areas represent the bottom of the lake. Depth is represented on the vertical axis.

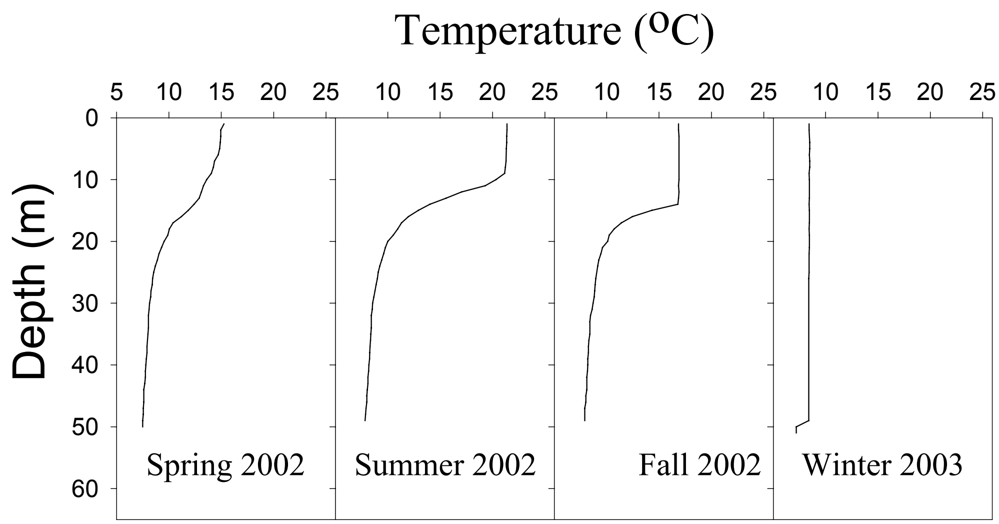

Figure 4.5. Monthly mean temperature profiles (ºC) from King County R.U.S.S. buoys acquired during spring 2002-winter 2003 (unpublished, King County Dept. of Natural Resources).

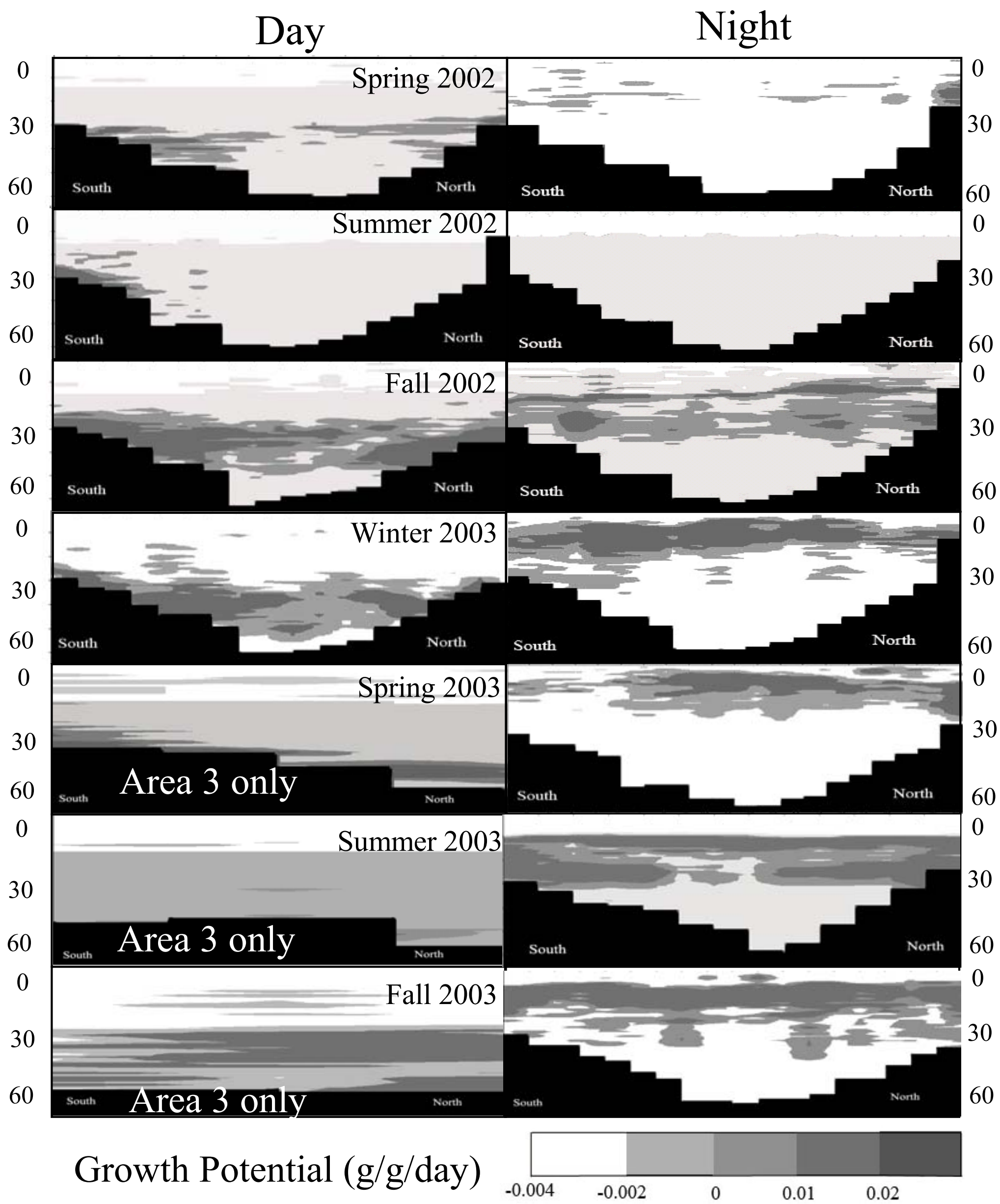

Figure 4.6. Spatial distribution of cutthroat trout growth potential ($g \cdot g^{-1} \cdot day^{-1}$) for day and night periods during spring, summer, and fall 2002 and winter, spring, summer, and fall 2003. Darker areas represent areas of higher growth potential and black represents the bottom of the lake. Growth potentials are means for each depth interval of individual transects from the south to north end of the lake. Depth is represented on the vertical axis.

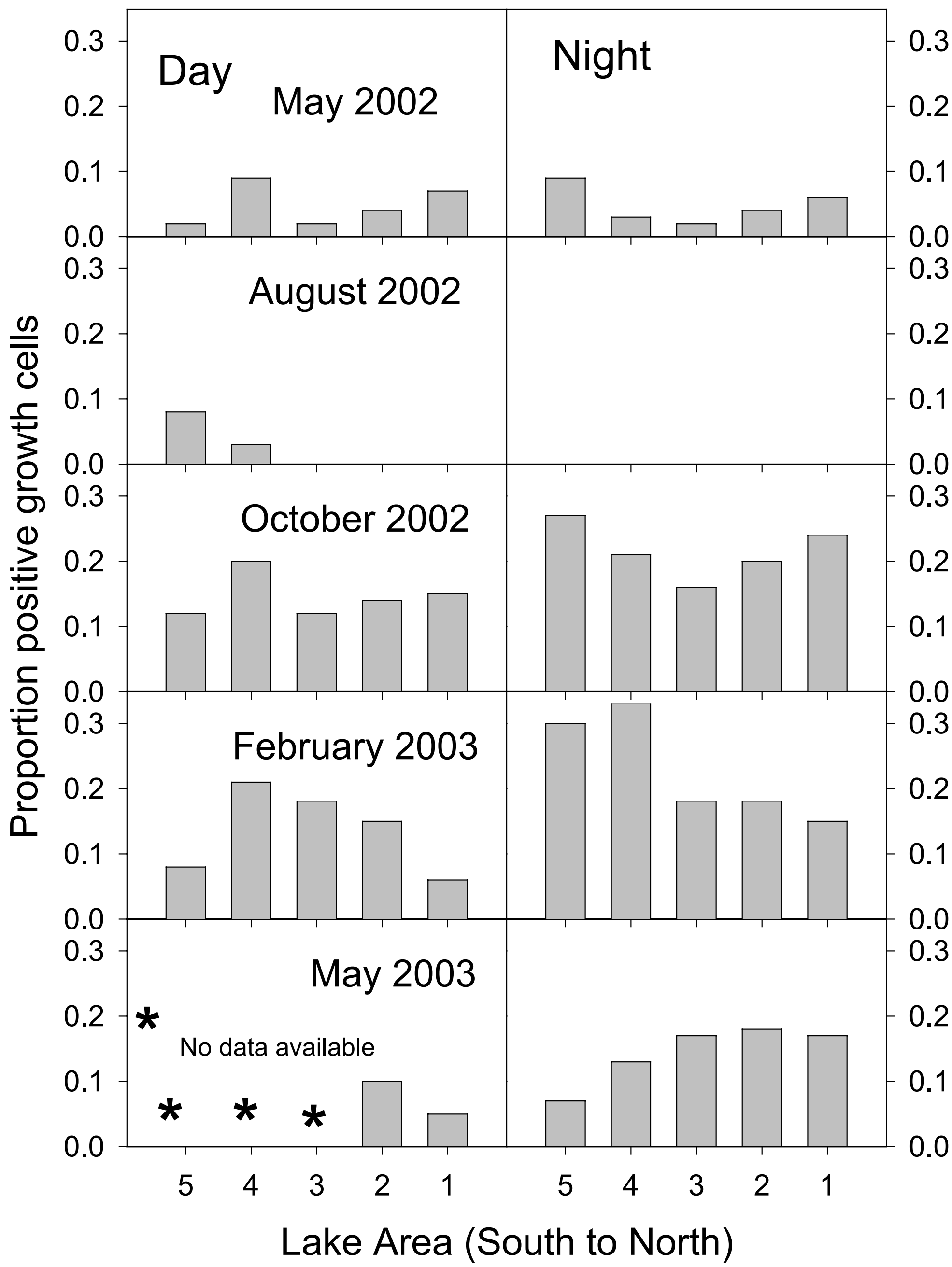

Figure 4.7. Comparison between the seasonal proportion of positive growth cells in each sampling area of the lake for day and night periods spring 2002-spring 2003. The horizontal axis represents lake areas (5-1) from the south to north ends of the lake. Asterisks indicate areas of the lake where no hydroacoustic transects were available.

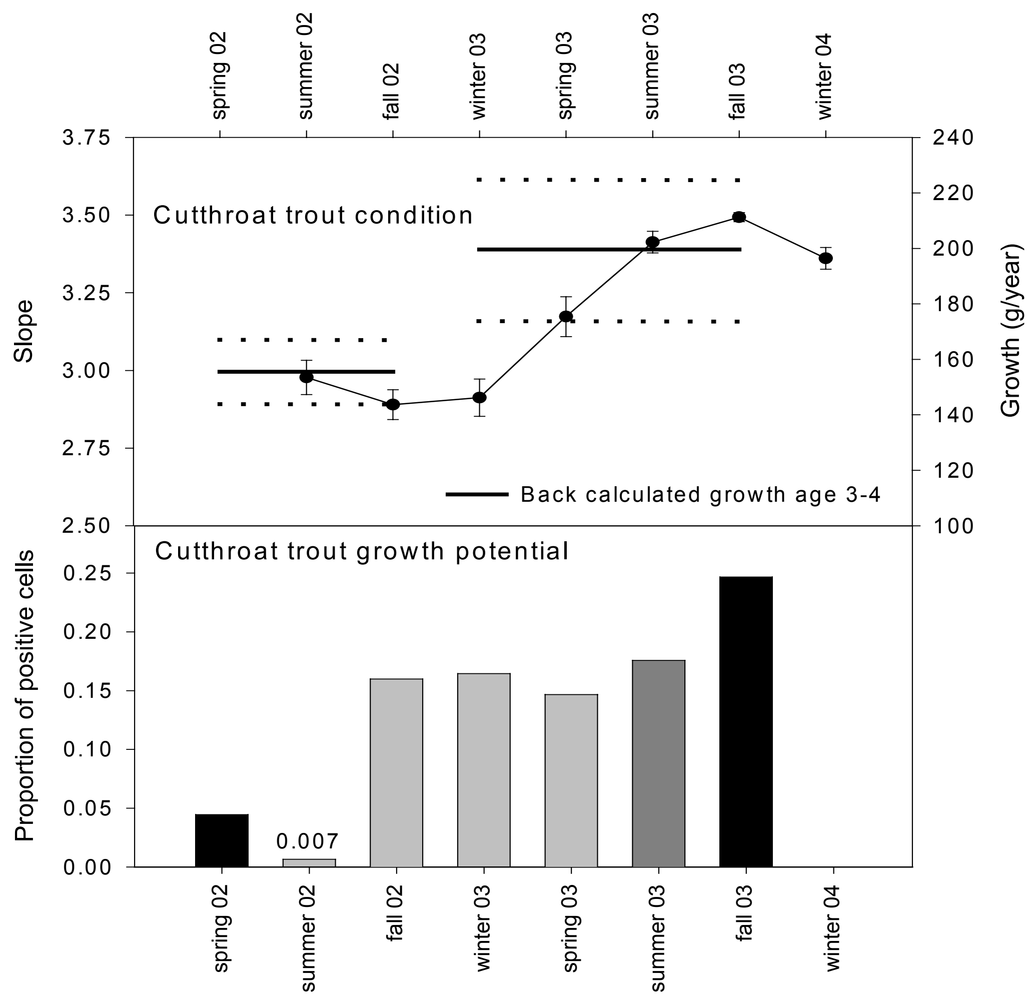

Figure 4.8. The slope of seasonal length-weight regressions for cutthroat trout captured in gill net sets from spring 2002-winter 2004 (black circles; top panel) and back-calculated annual growth estimates (g/year) from age 3 to age 4 for cutthroat trout (solid black line; top panel). Error bars represent ±1 SE for slopes and dotted black lines represent ±1 SE for back calculated growth estimates. The comparison of the seasonal proportion of positive growth cells available in the environment from a full diel sequence during each season between spring 2002-fall 2003 (bottom panel). Black bars indicate surveys where no crepuscular transects are available, and dark gray bars indicate the use of a zig-zag survey design (Figure 4.3). Weight loss from spawning occurs during winter.

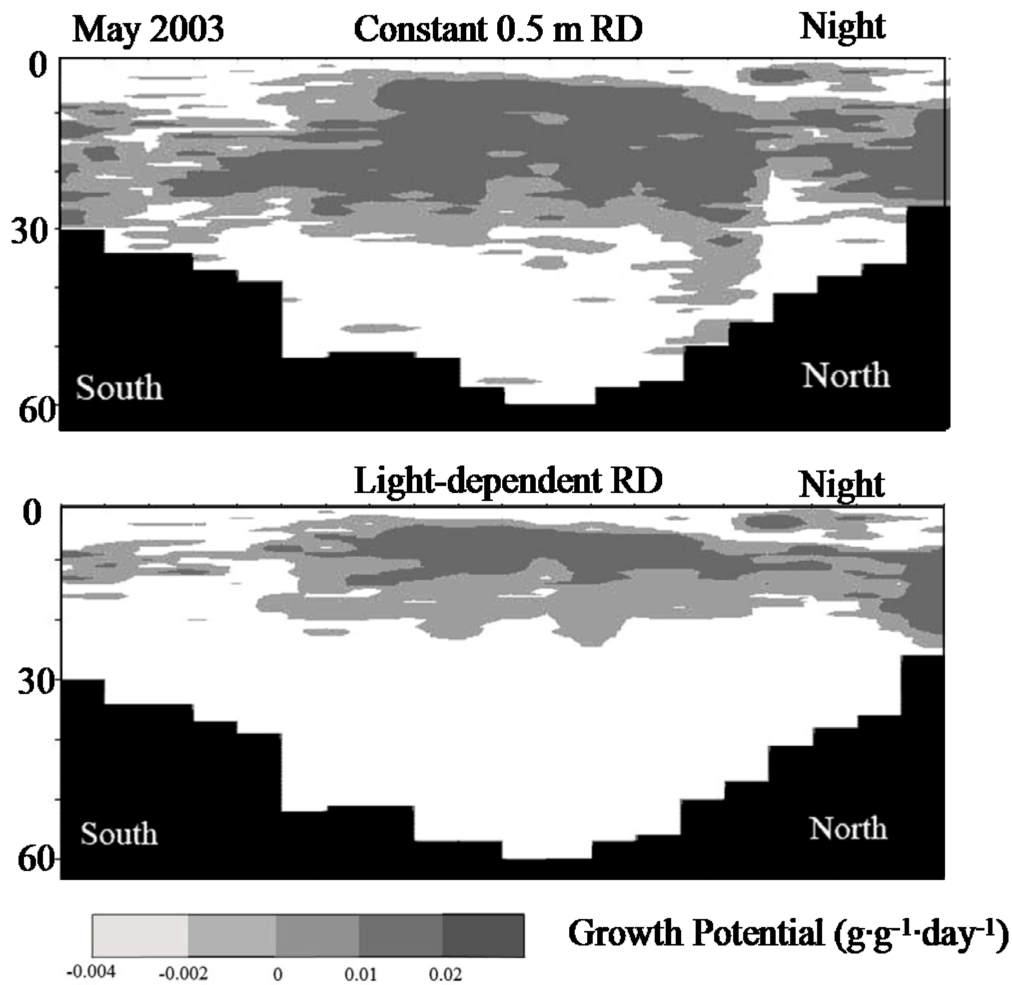

Figure 4.9. Comparison of the spatial distribution of cutthroat trout growth potential ($g \cdot g^{-1} \cdot day^{-1}$) for a night period during May 2003 estimated using a 50 cm fixed reaction distance (top panel) and a light-dependent reaction distance (bottom panel) in the foraging module. Darker areas represent areas of higher growth potential and black represents the bottom of the lake. Growth potentials are means for each depth interval of individual transects from the south to the north end of the lake. Depth is represented on the vertical axis.

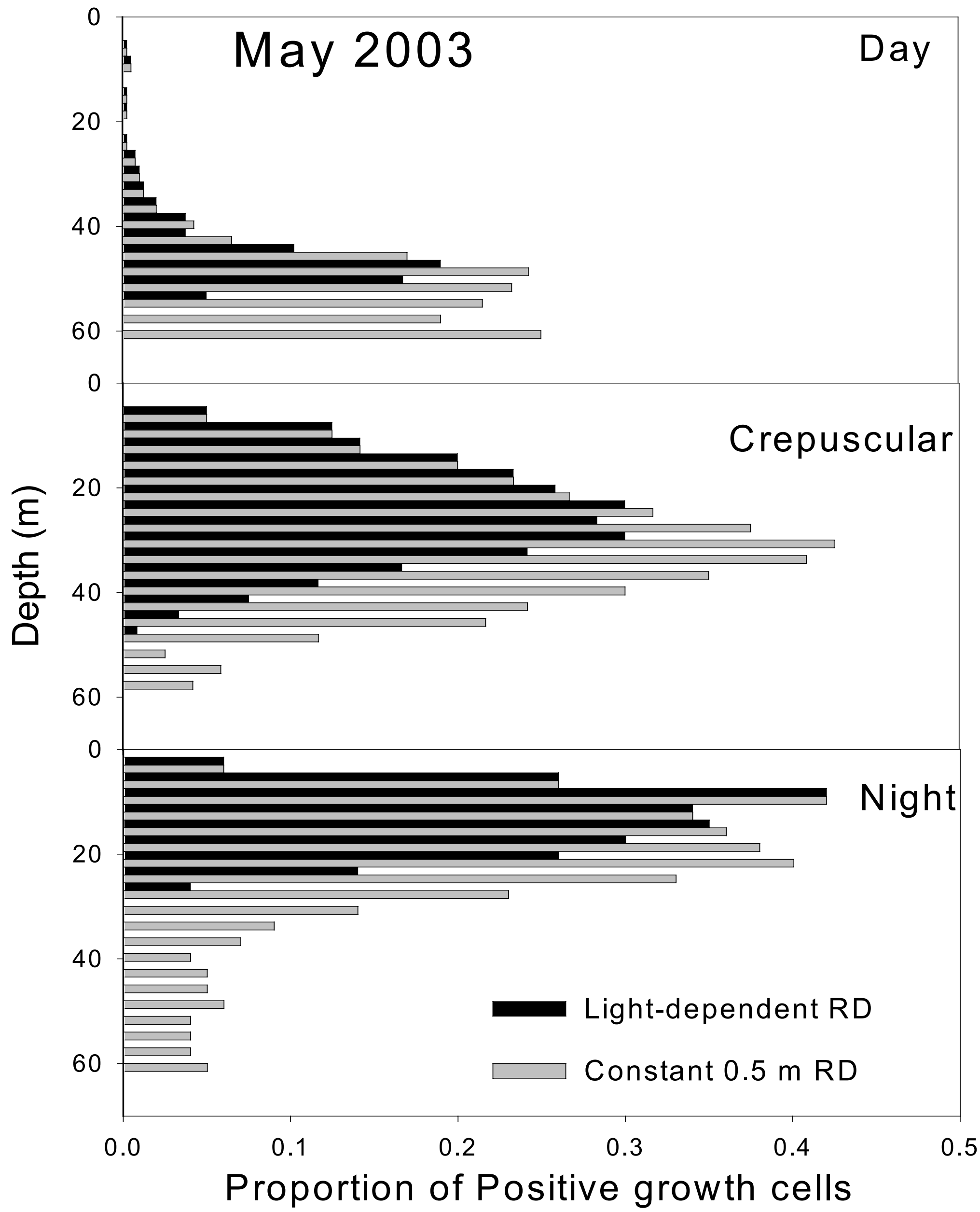

Figure 4.10. The vertical distribution of the proportion of positive growth cells for a day, crepuscular, and night period during May 2003 estimated using a 0.5 m fixed reaction distance (gray bars) and a light-dependent reaction distance (black bars) in the foraging module. Depth is represented on the vertical axis.

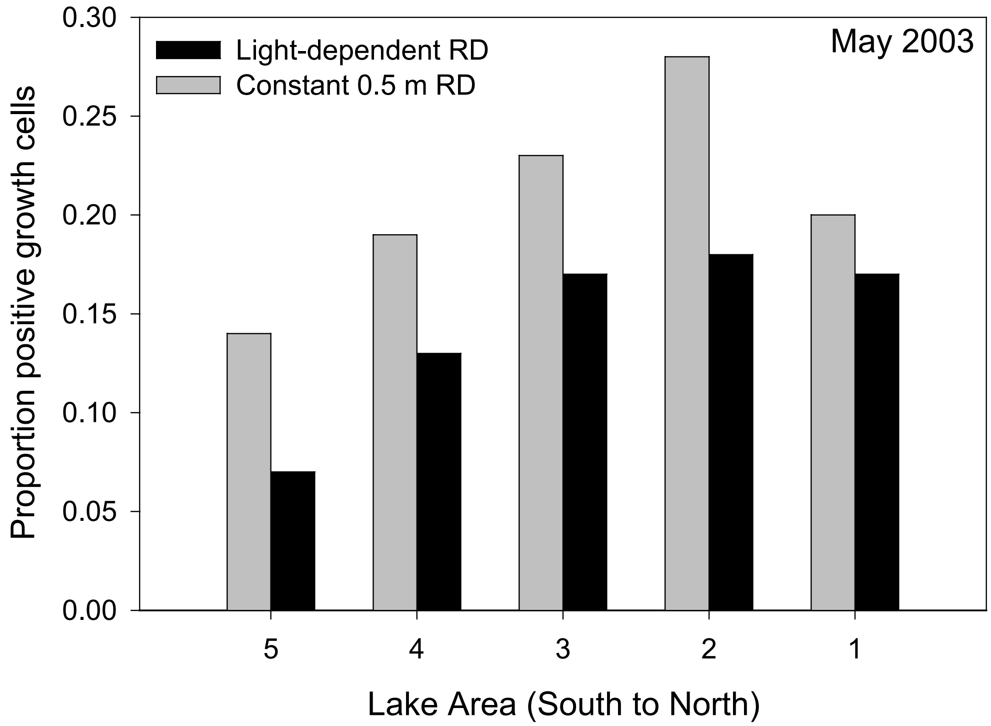

Figure 4.11. Comparison of the proportion of positive growth cells in each sampling area of the lake for a night period in May 2003 estimated using a 0.5 m fixed reaction distance (gray bars) and a light-dependent reaction distance (black bars) in the foraging module. The horizontal axis represents lake areas (5-1) from the south to north ends of the lake.

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VITA

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