Effects of a Temperature-Oxygen Squeeze on Distribution, Feeding, Growth, and Survival of Kokanee (*Oncorhynchus nerka*) in Lake Sammamish, Washington

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This is to certify that I have examined this copy of a master’s thesis by

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and have found that it is complete and satisfactory in all respects,
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Abstract

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I examined the seasonal and diel distribution of salmonids in response to changing dissolved oxygen and temperature profiles in Lake Sammamish, Washington by combining concurrent limnological measurements with gill netting and hydroacoustic surveys. Thermal stratification intensified through summer and fall with increasing temperatures in a deepening epilimnion. As the summer progressed, low hypolimnetic dissolved oxygen encroached into the metalimnion, creating a temperature-dissolved oxygen squeeze that reduced the amount of favorable (<17° C and > 4 mg/L) habitat available for salmonids by as much as 90%. Kokanee *Oncorhynchus nerka* and cutthroat trout *O. clarki,* responded to these limnological changes by moving to the metalimnion during peak stratification. The consequent overlap among zooplankton, juvenile kokanee, and piscivorous cutthroat trout influenced growth efficiency, condition, and spatial-temporal patterns of predation risk for kokanee. Climate change model projections suggest more protracted thermal stratification in future years, creating an uncertain future for kokanee in Lake Sammamish.

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Chapter I: The Effect of Temperature and Dissolved Oxygen on the Vertical Distribution of Kokanee and Cutthroat Trout in Lake Sammamish, Washington

INTRODUCTION

Movement and distribution of fishes are strongly influenced by environmental conditions, ecological constraints, and physical habitat characteristics. The niche concept in ecology provides insight into the organization and specialization of species that interact within an ecosystem (Hutchinson 1957). The fundamental niche describes the entire range of environmental attributes that are possible for an organism to survive, whereas the realized niche describes the specific conditions that a species occupies, taking into consideration biological relationships such as competition and predation. By definition, the realized niche is within the bounds determined by the fundamental niche. Building upon the niche concept, Fry (1971) documented that different species have specific tolerances to environmental attributes, including temperature, dissolved oxygen, pH, and salinity. This approach has been used to describe the realized niche of many fish species, and described how the distribution of fish is affected by species specific physiology (Coutant 1977, Magnuson et al. 1979).

In some instances, species have evolved internal processes to adjust for changes in environmental attributes, such as salinity and temperature (Neill and Magnuson 1974; Coutant 1987). Diadromous fishes, for example, are able to adjust to changes in salinity during their migration between freshwater and marine habitats (McDowall 1988). Albacore tuna (*Thunnus alalunga*) regulate internal temperature through a complex system of heat-exchanging retia (Graham 1983). In the absence of the physiological ability to adjust to changes in the environment, most species move to areas that are more conducive to growth. In many instances fish will select specific temperatures that maximize the energy available for a specific activity (Fry 1971; Kelsch and Neill 1990). For example, the diel vertical migrations of fishes in stratified lakes in part serve to facilitate efficient digestion (Brett 1971; Wurtsbaugh and Neverman 1988).

However, in many cases, habitat selection is a compromise between temperature requirements and other important factors such as dissolved oxygen, salinity, food, avoidance of predators, competition, or other constraints (Coutant 1987; Sellers et al. 1998). Generally, fish distribute themselves vertically or laterally across gradients in lakes (Ryder 1977; Brett 1971; Rowe and Chisnall 1995; Baldwin et al. 2002), rivers (Vincent and Miller 1969; Paul and Post 2001), estuaries (Brandt et al. 1992; Coutant 1985), and marine (Quinn et al. 1989; Cayre and Marsac 1993; Brill et al. 2002) environments. Like many organisms, fish respond to subtle changes in factors like temperature, dissolved oxygen, salinity, pH, turbidity, and light. Differences in physiological tolerances among species and life stages within species enable some fish to thrive under a given set of conditions while others are marginalized or even excluded (Fry 1971; Coutant 1977; Magnuson et al. 1979). In most cases, fish respond to environmental changes by moving to habitats more suitable for growth (Brett 1971; Fry 1971, Kelsch and Neill 1990; Garrett and Bennett 1995).

Temperature and dissolved oxygen are two of the most important factors that affect the distribution of fish (Birge 1906; Davis 1975; Coutant 1985; Bevelhimer and Adams 1993; Luecke and Teuscher 1994; Rowe and Chisnall 1995; Aku et al. 1997; Dillon et al. 2003). Temperature controls the metabolic rate in fishes and influences disease transmission, predation, feeding ability, activity, behavior, and fecundity (Fry 1947; Brett 1971; Crowder and Magnuson 1982; Clark and Levy 1988; Materna 2001; Crossin et al. 2004; Portz et al. 2006). High water temperatures and corresponding reductions in oxygen solubility can compound stresses to fish related to increased metabolic demand and reduced DO levels (Brett 1971; Kramer 1987). Concurrent thermal stratification and hypoxic conditions can create a habitat squeeze, reducing the amount of available habitat for fish with specific thermal or oxygen tolerances (Coutant 1987; Brandt et al. 1992; Nestler et al. 2002). This phenomenon affects many fish species, including striped bass (*Morone saxatilis,* Coutant 1985, Zale et al. 1990), gizzard shad (*Dorosoma cepedianum*, Gebhart and Summerfelt 1978), white crappie (*Pomoxis annularis*, Gebhart and Summerfelt 1978; Hale 1999), freshwater drum

(*Aplodinotus grunniens*, Gebhart and Summerfelt 1978), northern pike (*Esox lucius*, Headrick and Carline 1993), blueback herring (*Alosa aestivalis*; Nestler et al. 2002) rainbow trout (*Oncorhynchus. mykiss*, Fast 1973; Rowe and Chisnall 1995), lake trout (*Salvelinus namaycush*, Dillon et al. 2003) and cutthroat trout (*O. clarki*, Baldwin et al. 2002).

For coldwater species like salmonids with narrow temperature or oxygen tolerances, trends in climate change towards warmer conditions may create intolerable conditions in parts of their range (Rowe and Scott 1989, Magnuson et al. 1990, Rieman et al. 1997, Winder and Schindler 2004). For example, trout exhibit maximum temperature limits around 21° C (May and Gloss 1979, Stables and Thomas 1992) and oxygen constraints at values less than 6 mg/L, and acute responses at values less than 3 mg/L (Davis 1975; Ayles et al. 1976, Jones 1982; Baldwin et al. 2002). The accepted minimum dissolved oxygen level for extended salmonid use is 5.0 mg/L (U.S. EPA 1986; Bell 1991). For sockeye salmon (*O. nerka*), Brett (1971) found that the optimum temperature for juveniles was 15° C, and that conversion efficiency of food rapidly decreased at temperature greater than 17° C. Narver (1970) reported that sockeye salmon avoided surface waters in lakes where epilimnetic temperature exceeded 20° C. Growth and thermal tolerances are restricted even further if the quality and quantity of food resources decline (Eggers 1978; Beauchamp et al. 2007). In some lakes, sockeye salmon adapt to a thermal restriction in foraging efficiency through a complex pattern of diel vertical migration (DVM) (Narver 1970; Eggers 1978; Levy 1990). In DVM, sockeye salmon presumably migrate into warmer shallow water in lakes to take advantage of available prey, and then migrate into cooler waters to take advantage of better food conversion efficiency and reducing predation risk (Clark and Levy 1988; Levy 1990; Bevelhimer and Adams 1993; Scheuerell and Schindler 2003).

In the case of salmonids, habitat degradation and consequent elevated water temperatures are considered partially responsible for the precipitous decline or extinction of native trout, salmon, and char in parts of their native range (Shuter and Post 1990, Nehlsen et al. 1991, Rieman et al. 1997). In the Pacific Northwest, losses of native salmonids led to the listing of many populations as *threatened* or *endangered* under the authority of the federal Endangered Species Act (ESA; Nehlsen et al. 1991). As a result, more emphasis has been placed on the status of listed species, with a focus on restoring freshwater habitats to aid in their recovery.

After a petition was filed for listing of Lake Sammamish kokanee (the non-anadromous form of *O. nerka*) under the ESA in 1999, emphasis was placed on the importance of protecting this species from further decline. In 2003, the early-run kokanee in Lake Sammamish were considered extinct, and a new emphasis was placed on protecting the endemic late-run population (Berge and Higgins 2003; Young et al. 2004; Jackson 2006). Very little information is available on the abundance and causes for decline of these species, and most existing information was collected on the spawning grounds (Jackson 2006). Little attention has been directed toward understanding the relationship between limnological conditions and biotic interactions in the lake. Since kokanee migrate to the lake as newly emerged fry and reside in the lake until they are ready to spawn (at ages 3, 4, or 5), they are subject to various environmental stressors and ecological pressures in the lake that might influence population trends.

Lake Sammamish becomes thermally stratified during the summer, with peak epilimnetic temperatures in July-September coinciding with hypoxic conditions in the hypolimnion (Figure 1). As the summer progresses, hypoxic waters encroach into the metalimnion, reducing the amount of cold, oxygenated habitat that is available for temperature sensitive species, such as salmonids, creating a habitat “squeeze” (Figure 1). The goal of this paper was to describe the temporal and spatial relationship between temperature and dissolved oxygen on the vertical distribution of salmonids in Lake Sammamish.

STUDY AREA

Lake Sammamish is a monomictic, mesotrophic lake located in King County, Washington approximately 32 km east of Seattle (142° 05’W 46° 36’N; Figure 2). The shorelines are within the boundaries of unincorporated King County and the cities of

Redmond, Sammamish, Issaquah, and Bellevue. Eastern and western shorelines of the lake consist of relatively steep slopes composed of gravel and cobble substrate, while the northern and southern shorelines are shallower and consist of silt and sand substrate with dense aquatic macrophytes (Pflug 1981). Lake Sammamish is 12 m above mean sea level, with a mean depth of 17.7 m, and a maximum depth of 32 m. Lake Sammamish extends approximately 12.9 km north to south with a maximum width of approximately 2.4 km. Secchi depths range from a minimum of 2 m during February to a maximum of 7 m during May. Thermal stratification begins in June and continues until October. The surface area of Lake Sammamish is 19.8 km^2, with a volume of 3.5×10^8 m^3, making it the sixth largest lake in Washington. The largest tributary of Lake Sammamish, Issaquah Creek, contributes a mean annual discharge of 3.77 m^3/s (Garland and Olson 2004). Issaquah Creek is the site of a salmon hatchery operated by the WDFW (Washington Department of Fish and Wildlife) that annually releases approximately 0.5 million coho salmon *O. kisutch* smolts (age 1) in April and 2.1 million fall Chinook salmon *O. tshawytscha* pre-smolts (age 0) in May. All waters entering Lake Sammamish drain via the Sammamish River to the north end of Lake Washington, and then to Puget Sound via the Hiram M. Chittenden Locks.

Fish Community

Over 20 fish species are found in Lake Sammamish, including nonnative and native resident, adfluvial, and anadromous species (Table 1). Important sport fish include trout, salmon, bass, and perch. Little is known about the relative population sizes of any of these species; however, kokanee have been identified as a species of concern by the WDFW and their population is considered to be severely depressed from historical levels (Pfeifer 1995; Jackson 2006). Lake Sammamish kokanee were petitioned for listing in 1999 and again in 2007, and their status is under review by the U.S. Fish and Wildlife Service (USFWS 2007). Chinook salmon and steelhead trout *O. mykiss* in Lake Sammamish are part of the Puget Sound ESUs (Evolutionarily

Significant Units) that have been listed as *threatened* under the authority of the ESA (U.S. Endangered Species Act).

Thousands of adult Chinook, sockeye, and coho salmon spawn in Issaquah Creek, and occasional spawning of anadromous salmonids occurs in Laughing Jacobs, Ebright, Tibbets, and Lewis creeks. Current kokanee spawning locations include Lewis, Laughing Jacobs, Ebright, Pine Lake, and Vasa Creeks, although historic use was much more extensive (Berge and Higgins 2003). Historically, steelhead spawned in Issaquah Creek but since 1996 no steelhead spawning activity has been observed in any Lake Sammamish tributaries (Scott and Gill 2008). Cutthroat trout are found in every tributary of Lake Sammamish and their populations are believed to be stable or increasing but there is no quantitative assessment of their abundance.

METHODS

Limnological measurements, hydroacoustic surveys, and fish collection methods were combined to understand how salmonid distributions changed over seasonal and diel periods, and between the littoral and limnetic zones within Lake Sammamish. In addition, monthly zooplankton samples gave insight into the spatial and temporal overlap between zooplanktivorous fishes (such as kokanee) and their prey.

Physical Limnology and Zooplankton Sampling

Temperature and dissolved oxygen (DO) data were collected from two remote underwater sampling stations (RUSS) buoys in Lake Sammamish (Figure 2). Real-time data were collected and stored by YSI Model 6600 (YSI, Yellow Springs, OH) multi-meter sondes mounted on each buoy. Vertical profiles were recorded at 1 m depth intervals, up to six times per day during the study period. Individual sondes were calibrated as necessary according to the manufacturer's specifications, typically once every two weeks.

Transparency was measured with a Secchi disk (Smith 2001) at weekly intervals at five stations in Lake Sammamish from May through December. Surface light data were collected on the RUSS buoys using a LiCor Li-250A (LiCor Biosciences, Lincoln, NE) light meter every 15 minutes. In addition, underwater light profiles were collected at five stations during the stratified period using a Self Contained Autonomous MicroProfiler™ (SCAMP; Precision Measurement Engineering, Carlsbad, CA) with a Li-Cor 192SA sensor, measuring daytime photosynthetically active radiation (PAR) at 1 cm depth increments throughout the entire water column. Conversions from PAR units to Lx were accomplished with the following formula from Wetzel (2001):

$$X_{lux} = (0.01953)^{-1} \cdot X_{PAR}$$

where X_{lux} is the value in Lx and X_{PAR} is the value measured by the SCAMP in units of PAR.

Zooplankton samples were collected monthly in two regions of Lake Sammamish (Figure 2) using a 12.5 cm diameter Clarke-Bumpus sampler with 153 μm mesh. Samples were taken at three depth intervals of the lake, 0-10 m and 10-20 m, and 20-35 m that roughly corresponded to the epilimnion, metalimnion, and hypolimnion. Samples were analyzed and summarized by species, size frequency, depth-specific density, and biomass (Shepherd et al. 2002, King County unpublished data).

Hydroacoustic surveys

Hydroacoustic surveys were conducted several times each season to examine temporal trends in limnetic fish distribution (Table 2) associated with limnological changes across Lake Sammamish, and to evaluate ontogenetic differences within and between species at specific depths. Hydroacoustics are particularly effective in detecting and describing the behavior of suspended limnetic species (such as kokanee) when surveyed with a vertically oriented transducer (Brandt 1996). I used Biosonics DE 6000 high-frequency (430 kHz), split-beam transducer, mounted on a tow fin and pulled through the water column by a 6.7 m vessel at a depth of 0.75 m, and an average velocity of 6 km/h. The transducer was fast multiplexed at a rate of 3 pings per second and the full beam angle of the vertical transducer was 6°. Targets were collected using a pulse width of 0.4 ms and a target threshold of -65 dB. Data collected at each transect were recorded by an onboard computer and post-processed using SonarData Echoview™ (version 3.45). Data from each transect were echo counted for individual target strengths, and divided by the acoustic volume sampled within each 1-m depth interval (from Z m to Z + 1 m below the transducer) to calculate target density for each transect in 1 m intervals. The volume of each 1 m interval was based on the volume of the frustum:

$$V = \frac{\pi h}{3} \cdot (R^2 + Rr + r^2),$$

where h is the 1-m height of each depth interval, r is the radius of the circular top of the frustum nearest the transducer and R is the radius of the base of the frustum, calculated by:

$$r = Z \cdot \tan(4°) \text{ and } R = (Z + 1) \cdot \tan(4°).$$

Targets and density estimates from the 6° beam were restricted to 4° (< 2° off axis) to reduce reliance on beam angle compensation and increase confidence in target strength estimates. Targets identified within 1 m of the lake bottom were excluded to avoid potential contamination from bottom structure, and targets identified within 5 m from the boat were excluded from target density analysis due to the extremely small sampling volume. Love's (1971) equation was used to transform target strengths (TS in dB) into total lengths (TL_m in m) using the following formula for 430 kHz and assuming an average speed of sound through water of 1440 m/s:

$$TS = 19.1 \cdot \log_{10}(TL_m) - 23.43.$$

A zigzag survey pattern (Brandt 1996) was used to maximize sampling efficiency. During each survey, nine transects were sampled across the lake, covering depths from 2-32 m (Figure 2). Additionally, one long north-south transect was surveyed at night to investigate the possibility of a longitudinal gradient in the distribution of limnetic fishes in Lake Sammamish. The majority of hydroacoustic surveys were conducted at night, when limnetic fishes were most susceptible to detection in the water column (Northcote et al. 1964; Duncan and Kubecka 1993;

Luecke and Wurtsbaugh 1993; Appenzeller and Leggett 1995). In addition, selected areas of the lake (transects 3 and 4) were sampled during daylight and crepuscular periods to investigate diel variation in vertical distribution for specific dates (Figure 2; Table 2).

Fish Collection

Sinking and suspended horizontal gill nets were the primary methods for identifying the fishes detected in the hydroacoustic surveys and comparing littoral and limnetic species assemblages. During each hydroacoustic survey, at least six monofilament, variable-mesh gill nets were deployed in the lake: three sinking horizontal gill nets in epilimnetic, metalimnetic, and hypolimnetic depths of the littoral and slope zones and three suspended horizontal gill nets in epilimnetic, metalimnetic, and hypolimnetic depths of the limnetic zone (Table 3). Since hydroacoustic surveys were conducted at night, gill nets were set at dusk and retrieved at dawn on the following day to provide concurrent target identification. All gill nets were 60 m long by 2 m deep with panels of 25, 31, 38, 50, 63, and 75 mm stretch mesh. Age-0 salmonids in Lake Sammamish were not vulnerable to gill nets until early autumn since the modal size of a salmonid captured in a 25-mm stretch mesh (13 mm bar mesh) gill net is approximately 125 mm total length, or approximately 112 mm fork length (Beauchamp et al. *in press*).

Beach seines were used during May-June 2003 to capture fish in the littoral areas prior to, during, and following releases of Chinook salmon from the Issaquah Hatchery (Table 3). The goal of this effort was to sample the acute response of piscivorous fishes, to the release of potential prey and to gather additional biological data from fishes in the littoral zone of Lake Sammamish. Beach seines were set during the evening near Issaquah Creek, Lewis Creek, Vasa Creek, one eastern shoreline site, Ebright Creek, and Idylwood Park in May and June 2003 (Figure 2). Sampling occurred three days prior, the day of, and three days following the release of Chinook salmon from the Issaquah Creek hatchery at each site. The seine used was 37 m x 1.5 m, and set from a boat in a depth of approximately 2 m. The seine was set perpendicular to the shoreline, and pulled in a sweeping arc toward shore. Once both ends of the seine were on the beach, wings were pulled in simultaneously, bringing fish into shallow water along the shoreline.

Collected fish from beach seines and gill net sets were placed on dry ice immediately upon capture to halt further digestion of stomach contents except juvenile Chinook salmon caught in beach seines, which were immediately released. In the lab, all fish were weighed to the nearest gram, and FL (fork length) and TL (total length) was measured to the nearest millimeter prior to dissection. Whole stomachs were removed from each target species and from a representative sub-sample of non-target species and preserved in a 10 % buffered bicarbonate-formalin solution. Stomach contents were examined in the lab under a dissecting microscope. Prey fishes were identified to species, zooplankton were identified to genus, and other invertebrates were identified to order or family. All prey items were weighed (blotted wet weight) to the nearest 0.001 g. Standard, total, and/or fork lengths were measured for relatively intact fish prey to the nearest mm. In some cases, diagnostic bones were used to identify and estimate lengths of prey using metrics from Hansel et al. (1988). Diet composition was reported as the proportional contribution of each prey category to the total weight of food in individual stomachs. The individual weight proportions for each prey category were averaged across all non-empty stomachs for fish within the same species, size class, and time interval.

Catch per unit effort for species and size classes of limnetic gill net sets were used to identify the acoustic targets of similar size recorded during hydroacoustic transects for the same period and depth stratum (epi-, meta-, and hypolimnion). Species proportions and size frequency data were multiplied together with target densities to assign species identification to hydroacoustic targets determined to be fish during the same sampling period and pooled across transects. In the case of small fishes that were not susceptible to the smallest mesh (<110 mm), I used measured prey items from piscivores collected at the same time and depth interval to assign species identification from the hydroacoustics data.

RESULTS

The onset of thermal stratification in Lake Sammamish began in May and continued through November during the study period (Figure 3). The temperature and DO habitat "squeeze" peaked in September, with only the depths between 10 and 14 m falling below 17° C and greater than 4 mg/L. Thermal stratification began to relax in October, and by the end of November, Lake Sammamish had completely destratified (Figure 3).

The most common species in the limnetic zone were cutthroat trout, kokanee, and yellow perch (Figure 4), whereas the littoral and slope zones were dominated by yellow perch, northern pikeminnow, and peamouth (Figure 5). These patterns remained consistent between thermally stratified and destratified conditions (Figure 4 and 5).

Hydroacoustic transects 3-7 represented the limnetic community species assemblages, whereas the shallower northern and southern ends of the lake (transects 1, 2, 8, and 9; Figure 2) more closely resembled the littoral assemblage (Pflug 1981). In July, high densities of age-1 yellow perch and other juvenile non-salmonids dominated the shallow epilimnion, with moderate densities of kokanee and cutthroat trout centered around the thermocline. As thermal stratification intensified during summer and early autumn, the highest densities of fish in the limnetic zone shifted into the metalimnion where temperatures were less than 17˚C and DO concentrations exceeded 4 mg/L in depths between 10 and 15 m. In contrast, the distribution of fish during the unstratified period appeared to be unrelated to light, *Daphnia* density, DO, or temperature, although the highest nighttime densities occurred in the lower 10 m of the lake. During the stratified period (June through November), fish < 100 mm were distributed throughout the water column, while fish > 100 mm (primarily salmonids) were more common in cooler (<17˚C) areas of the lake with DO concentrations > 4 mg/L (Figure 6).

During stratified conditions, the distribution of acoustic targets > 100 mm did not differ between day, crepuscular, and nighttime periods in the epilimnion (Figure 6).

The distribution of smaller targets (<100 mm) varied among diel periods, with the nocturnal density significantly greater than both day and crepuscular periods (Figure 6; Kruskal Wallace, $p < 0.001$). The difference between day and crepuscular periods was not statistically significant (Figure 6; Mann Whitney, $p < 0.718$).

Smaller salmonids were more common in warmer water (Kruskal Wallace test, $p<0.004$) and lower DO (Kruskal Wallace test, $p < 0.003$) than larger salmonids. This pattern was consistent with multiple size classes of salmonids, but was not significant for non-salmonids. During moderate and peak thermal stratification, non-salmonids were found in significantly warmer water than salmonids (Figure 7; Mann Whitney, $p<0.001$), and lower DO concentrations (Figure 7; Mann Whitney, $p < 0.007$). During unstratified conditions, salmonids occupied regions of lower DO (Figure 7; Mann Whitney, $p < 0.005$) and warmer temperatures (Figure 7; Mann Whitney, $p < 0.018$) than non salmonids, reflective of preferences for deeper water. However, neither temperature nor DO concentrations were limiting the available habitat optimal for growth during the unstratified period (Figure 7; Bell 1991).

The temperature-DO "squeeze" that developed in Lake Sammamish reduced the amount of habitat available to salmonids by as much as 84% (Issac et al. 1966; Figure 8). For example, in August, only 20% of Lake Sammamish's volume met both the temperature and DO criteria of 17˚C and 4 mg/L (Figure 8). By the end of September, this volume was reduced to depths between 8.5 m and 12 m, corresponding to approximately 16%. Not only was the physical volume of habitat limited by species specific physiological response to temperature and dissolved oxygen, but access to prey was reduced. Kokanee are zooplanktivores and prefer *Daphnia spp*. (Foerster 1968; Beauchamp et al. 1989). In Lake Sammamish, *Daphnia* density was highest during June, July, and August in the epilimnion (Table 2). The warm epilimnion in July through September reduced access for kokanee to a smaller fraction of the available *Daphnia* in Lake Sammamish. As the summer progressed and the "squeeze" intensified, kokanee access to *Daphnia* in the epilimnion and hypolimnion was even more restricted. For example, during July, *Daphnia* densities in the 10-20 m zone (approximately the metalimnion) were as much as eight times lower than the epilimnion (Table 2), reducing the access of individual kokanee to their preferred prey.

DISCUSSION

The temporal distribution of salmonids in the limnetic zone in Lake Sammamish varied seasonally with changes in temperature and DO, and over the diel cycle. During peak thermal stratification, the realized niche of kokanee and cutthroat trout appeared to occur in the metalimnion, corresponding to near optimal temperature for growth between 15˚C and 17˚C (Brett and Higgs 1970), although optimal growth temperatures might decrease under limited prey availability (Brett 1971). With temperatures in the epilimnion exceeding 20˚C during the summer months, kokanee were restricted to depths within and below the thermocline. Concurrent low DO concentrations in the hypolimnion restricted the accessibility of kokanee to *Daphnia* below 17 m. With the densities of *Daphnia* in the epilimnion as much as eight times higher than that of the metalimnion in July, the foraging efficiency of kokanee during the temperature-DO squeeze was likely much lower than without such a condition. As expected, depth intervals with corresponding low DO concentrations were avoided by salmonids, despite the availability of prey and cooler water temperature in the hypolimnion. In some cases, salmonids were captured in water that was warmer than optimum (>17˚C) in order to avoid DO concentrations < 4 mg/L. This phenomenon has been observed in other systems (Matthews et al. 1985; Douglas and Jahn 1987; Baldwin et al. 2002). Baldwin et al. (2002) reported that cutthroat trout in Strawberry Reservoir exhibited DVM into warmer surface waters to feed, while avoiding acute DO concentrations. Our results suggest that the same phenomenon does not occur in Lake Sammamish, since the densities of larger fish at night are highest in the metalimnion, and the catches of cutthroat trout used for target identification are much higher in cooler waters of the meta- and hypolimnion. The major difference between Lake Sammamish and Lake Washington may be related to the overlap in cutthroat trout and salmonid prey as a result of the temperature-DO squeeze, and much lower occurrence of prey sized fishes in the epilimnion of Lake Sammamish (Overman et al. 2006).

Diel variation in the depth of fish > 100 mm did not change significantly on a given date, although the distribution and density of fish < 100 mm did change, suggesting the occurrence of DVM. While there is much discussion in the literature related to the mechanisms of DVM (Brett 1971; Eggers 1978; Clark and Levy 1988; Beauchamp et al. 1997; Scheuerell and Schindler 2003), temperature plays an important role, especially in determining the night-time depth occupied when the lake is stratified. The occurrence of DVM may be a consequence of increased prey capture efficiency (*sensu* Eggers 1978; Nowak and Quinn 2002), reduced predation (Clark and Levy 1988; Stockwell and Johnson 1999; Scheuerell and Schindler 2003; Hardiman et al. 2004), avoidance of low DO levels (Douglas and Jahn 1987; Baldwin et al. 2002), metabolic optimization (Wurtsbaugh and Neverman 1988; Beauchamp et al. 1997; or some combination thereof (Bevelhimer and Adams 1993; Stockwell and Johnson 1999). With *Daphnia* densities in July, October, and November being much higher in the warmer epilimnetic waters, DVM would be advantageous for planktivorous fishes such as kokanee, as well as predatory fishes such as cutthroat trout since the crepuscular and nocturnal densities of fish < 100 mm are higher than in the metalimnion. The lack of strong DVM signal in Lake Sammamish may be explained by work of Bevelhimer and Adams (1993), who concluded that DVM is optimal in systems where kokanee are thermally separated from their predators. In Lake Sammamish, the dominant limnetic predators of kokanee are cutthroat trout and residualized Chinook salmon, both having similar temperature preferences as kokanee.

Ontogenetic differences in temperature tolerance were observed in this study. Smaller size classes of fishes appear to be able to adapt to warmer water and lower DO concentrations (Brett 1971; Coutant 1985; Rosland and Giske 1994). The differences in the realized thermal niche of juvenile kokanee (and sockeye) in Lake Sammamish may have evolutionary significance by reducing the extent of spatial overlap with the dominant limnetic piscivore, cutthroat trout. Once kokanee reach age-2 (>150 mm), their risk of predation by cutthroat trout in Lake Sammamish would be greatly reduced (Keeley and Grant 2001).

The density of limnetic fishes was greater during the night than day or crepuscular periods. With a few exceptions, most of the limnetic targets in Lake Sammamish were salmonids, although gill nets used in this study were not very effective at capturing fish smaller than 90 mm (Beauchamp et al. *in press*). Using a combination of tow nets and suspended gill nets, Berggren (1974) found that the predominant pelagic fishes in Lake Sammamish were salmonids, with some pelagic cottids, peamouth, and yellow perch observed near the bottom. The limnetic fish assemblage in Lake Sammamish could have changed dramatically since Berggren's work in the 1970s but results from hydroacoustic surveys and gillnetting in Lake Sammamish in this study support the overall observations that 1) densities of kokanee were greater at night (Berggren 1974; Eggers 1977; 1978; Clark and Levy 1988; Beauchamp 1994; Beauchamp et al. 1997; Scheuerell and Schindler 2003), 2) salmonids were the dominant fishes in the limnetic zone, and 3) salmonids in Lake Sammamish were typically found in the thermocline during thermally stratified conditions (Berggren 1974). Target densities during each sampling event were highest during the night time period, and lowest during daylight. Because I was unable to account for the same number of limnetic targets between day, crepuscular, and night periods, it is likely that fish were either distributed in the near-surface or bottom layer, in schools that were not sampled effectively, or moved offshore nocturnally. Small fish <100 mm TL) were consistently detected within the uppermost 5 m during daylight hydroacoustic surveys, suggesting they may have separated from the near-surface layer during crepuscular and night time periods. For larger fish observed in the limnetic zone at night, it is more likely that they moved from the littoral or slope zone to the limnetic zone during crepuscular and nighttime periods. Nowak and Quinn (2002) observed a similar pattern in cutthroat trout movements from the littoral zone into the limnetic zone of Lake Washington during daylight and nighttime periods, respectively. With the narrow beam angles of the transducers used in this study, this pattern is difficult to resolve due to the extrapolation error associated with small sample volumes (Brandt 1996). However, consecutive, repeated surveys from day through night within of the same transect did not detect any offshore movements, or near-surface or bottom layer separation. In addition, species assemblages were remarkably different between littoral and limnetic areas of Lake Sammamish, suggesting that fish were moving within the limnetic zone rather than offshore.

Global temperatures have increased in the past 30 years, and forecasts indicate that they will probably continue to increase in the future (Hansen et al. 2006). In the Pacific Northwest, air temperatures rose by approximately 0.8˚C during the 20th century, and models suggest further warming of between 0.5 and 2.5˚C by 2030 (Mote et al. 2003). Thermal stratification in lakes is driven by climatic factors such as ambient air temperature, and the period of thermal stratification and decreased hypolimnetic oxygen is expected to increase as a result of climate change, worsening temperature-DO squeezes (Coutant 1990; DeStasio et al. 1996). In response to changes in temperature, Beauchamp et al. (2007) used bioenergetic models to predict how climate change may influence the distribution, feeding, diet, growth, and predation rates of juvenile pacific salmon. With increases in temperature as a result of climate change, coldwater species such as salmonids will likely lose habitat in the southern end of their range (Schindler et al. 1990; Mantua et al. 1997). For kokanee and sockeye salmon, Melack et al. (1997) predicted that freshwater growth rates will be reduced in response to increases in temperature and reduced zooplankton in lakes. Such changes appear to be occurring already. For instance, in nearby Lake Washington, Winder and Schindler (2004) documented a decline in *Daphnia* density over a 26 year history, a situation that could have cascading effects on the food web of that lake, and similar implications for Lake Sammamish. In combination, these studies suggest an uncertain future for kokanee in Lake Sammamish.

In an effort to restore native kokanee throughout the Lake Sammamish watershed, millions of dollars are being spent on best management practices for construction related impacts, mitigation for habitat blockages, stormwater and sewage treatment, and spawning habitat restoration. While such efforts are important for multiple purposes, they may not be enough in the face of climate change to protect kokanee from extermination if conditions within Lake Sammamish become unsuitable. Understanding current bottlenecks in the population may be more critical if kokanee are to offer adequate resilience to persist in the face of large scale forcing factors such as climate change.

FIGURES

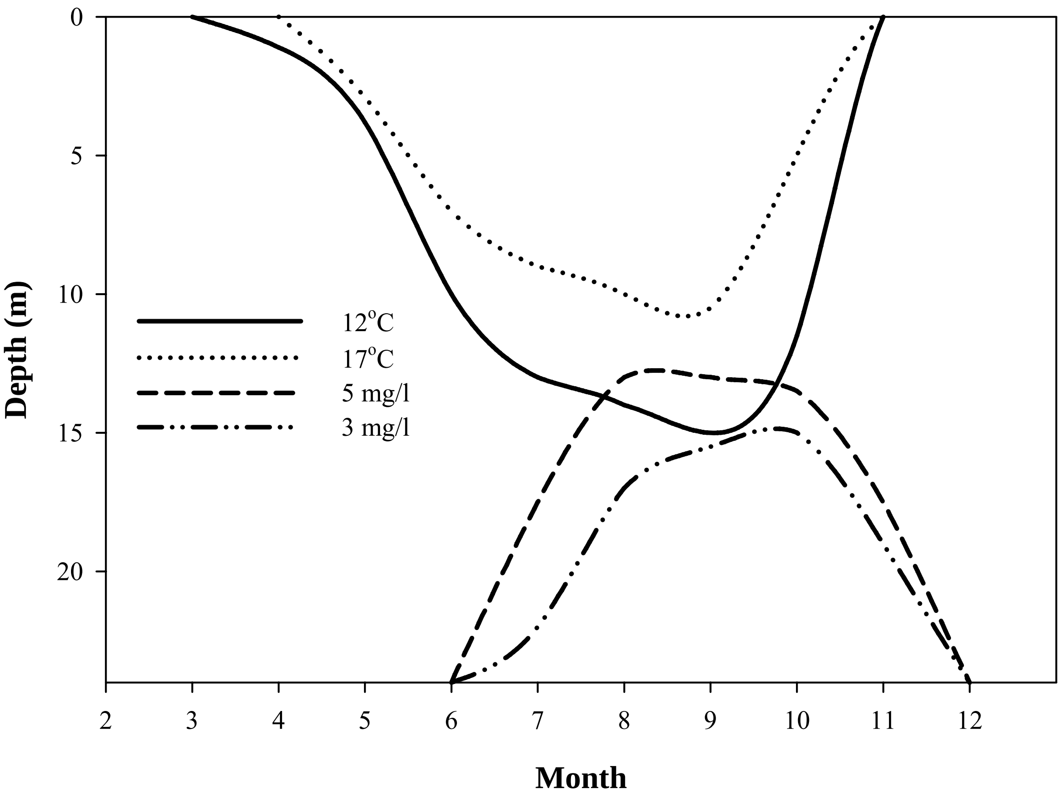

Figure 1. Annual temperature and dissolved oxygen isopleths in Lake Sammamish (2002 - 2003).

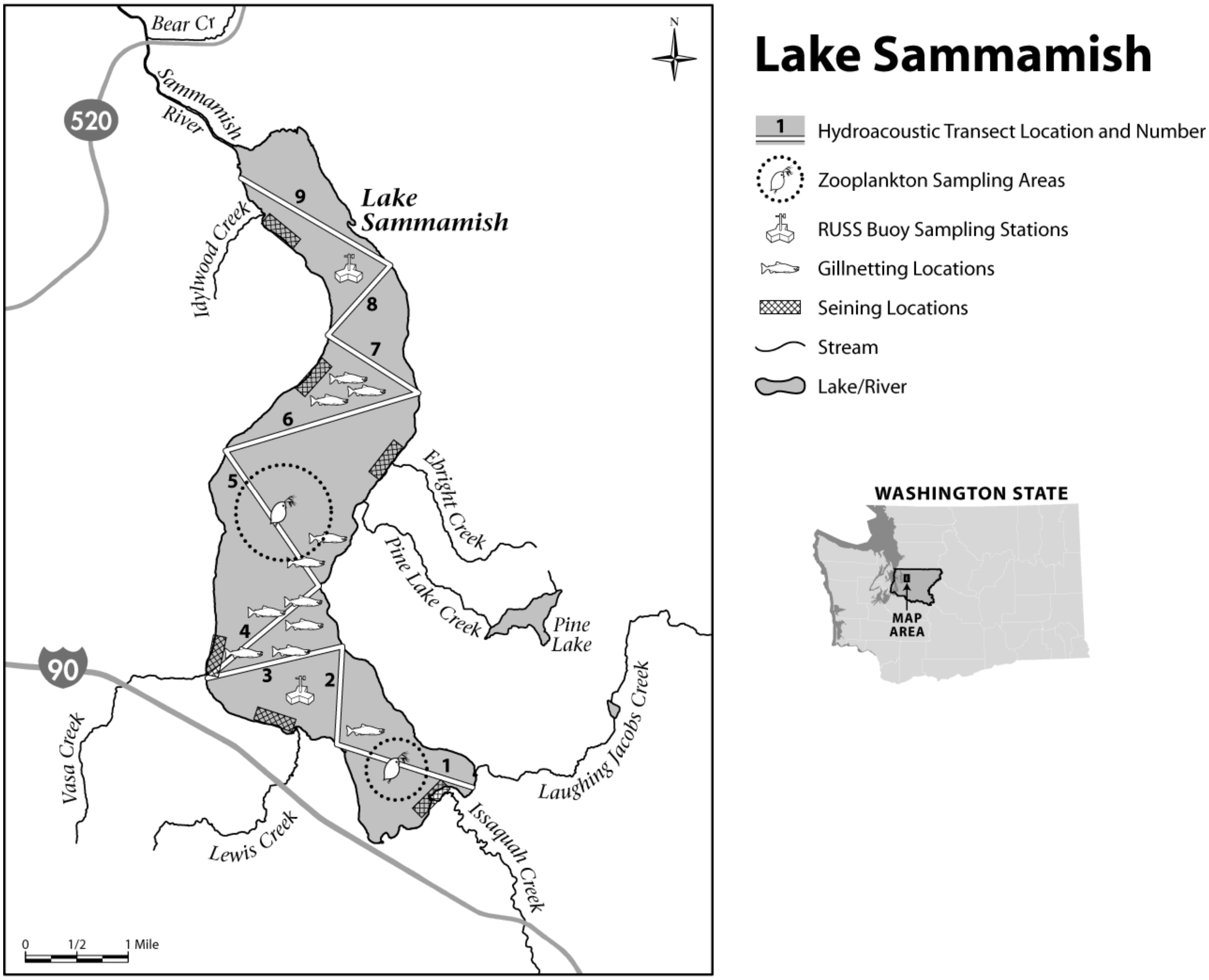

Figure 2. Map of Lake Sammamish with hydroacoustic transects, fish and zooplankton sampling locations, RUSS buoys, and tributaries where kokanee spawning currently occurs.

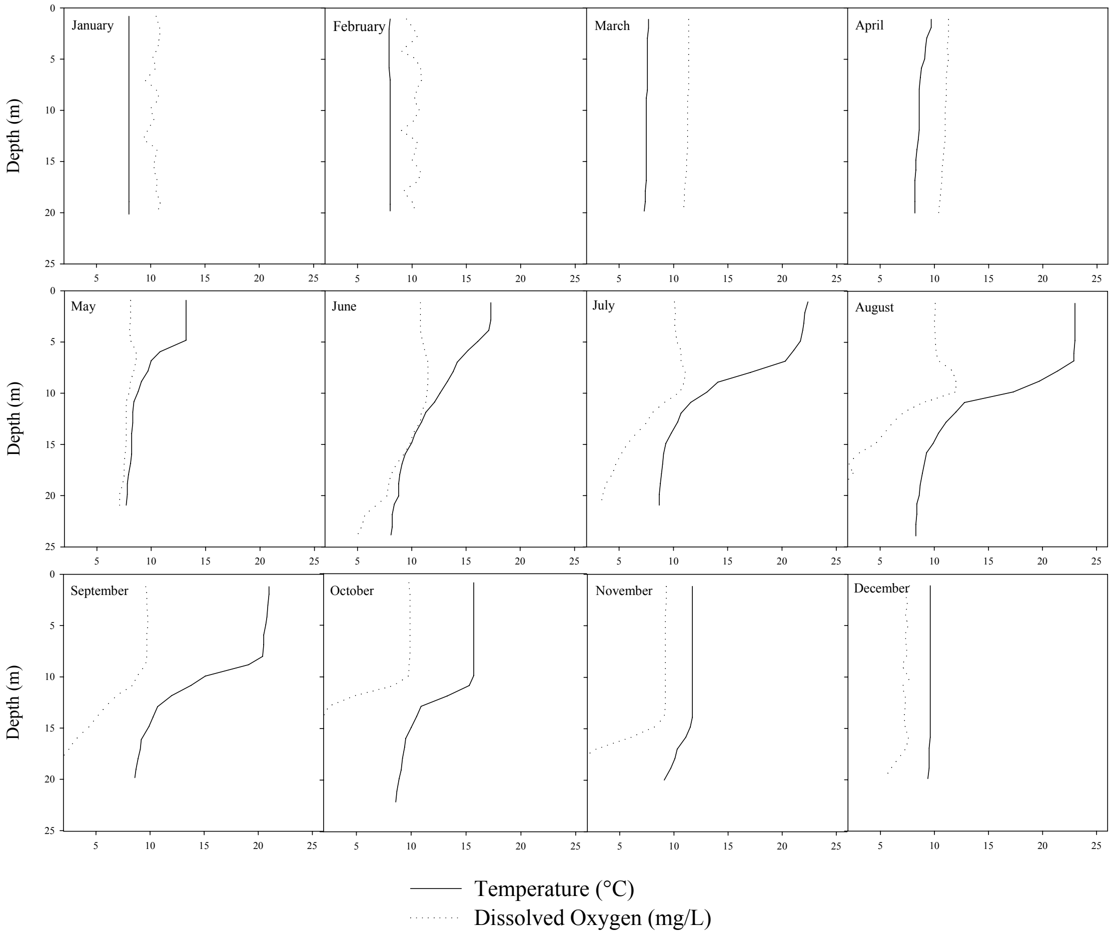

Figure 3. Monthly temperature and oxygen profiles of Lake Sammamish (2002-2003). Note the onset of thermal stratification in May, and the relaxation of thermal stratification in November, leading to complete turnover in December.

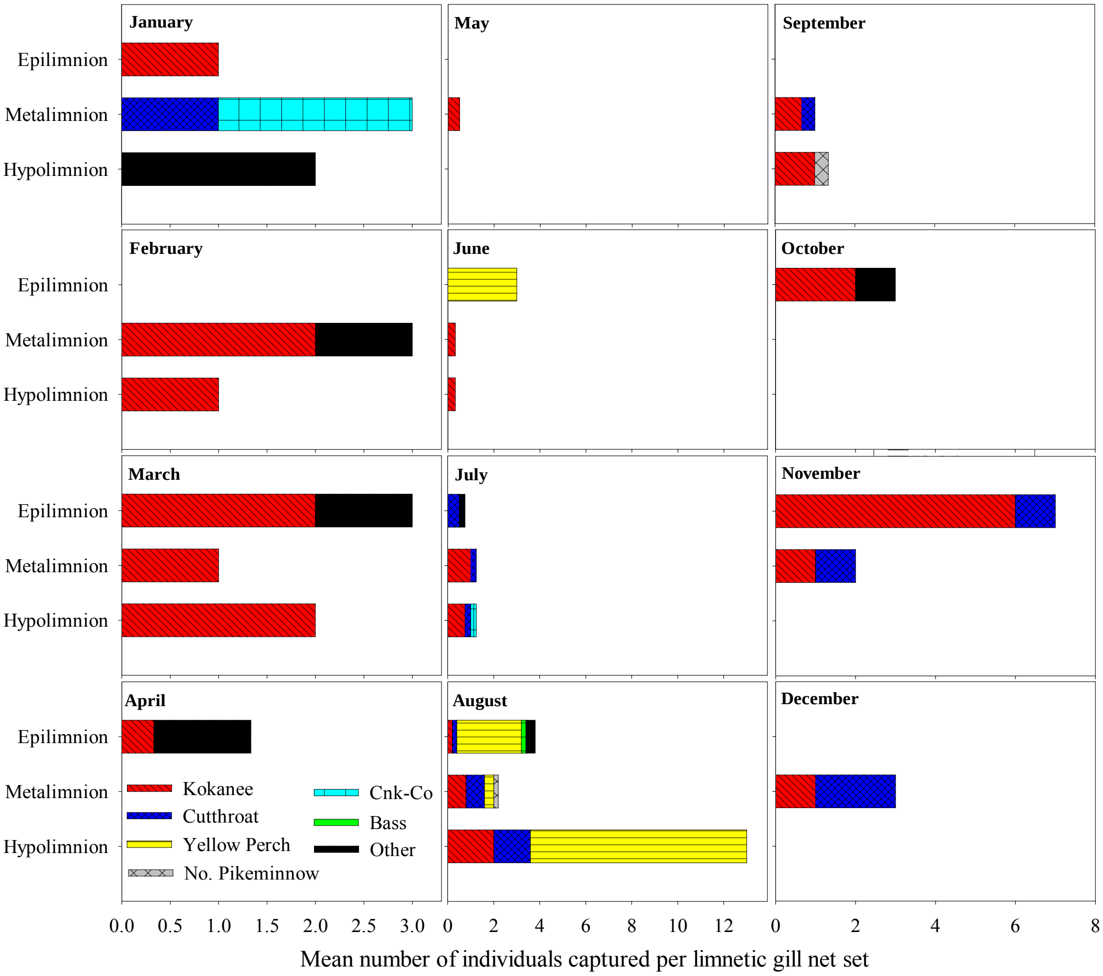

Figure 4. Catch per unit effort of the most abundant species captured in suspended gill net sets within the limnetic zone of Lake Sammamish (2002-2003). The other category represents a mixture of peamouth chubs, and large scale suckers.

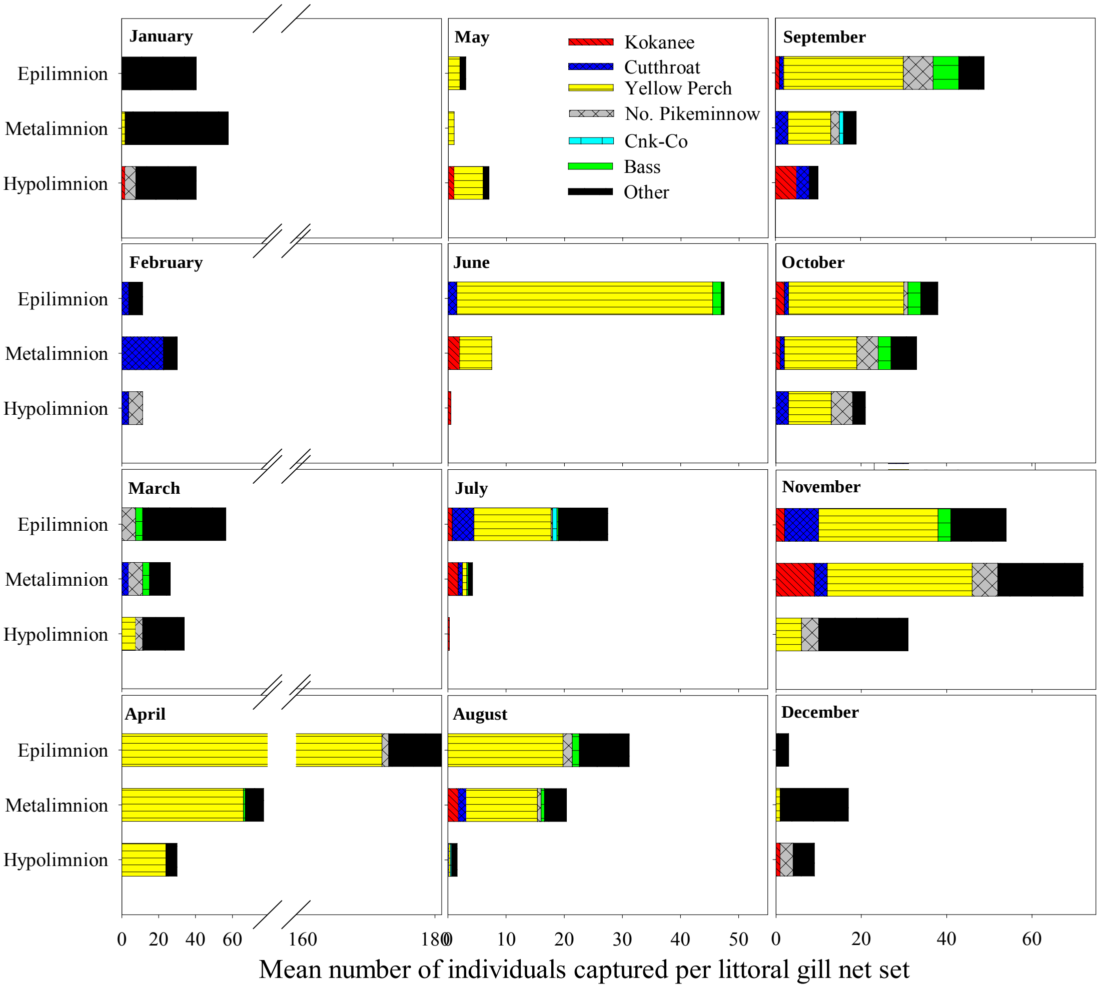

Figure 5. Catch per unit effort of the most abundant species captured in sinking gill net sets within the littoral zone of Lake Sammamish (2002-2003). The other category represents a mixture of black crappie, bluegill, brown bullhead, pacific lamprey, large scale suckers, mountain whitefish, peamouth chub, prickly sculpin, and pumpkinseed.

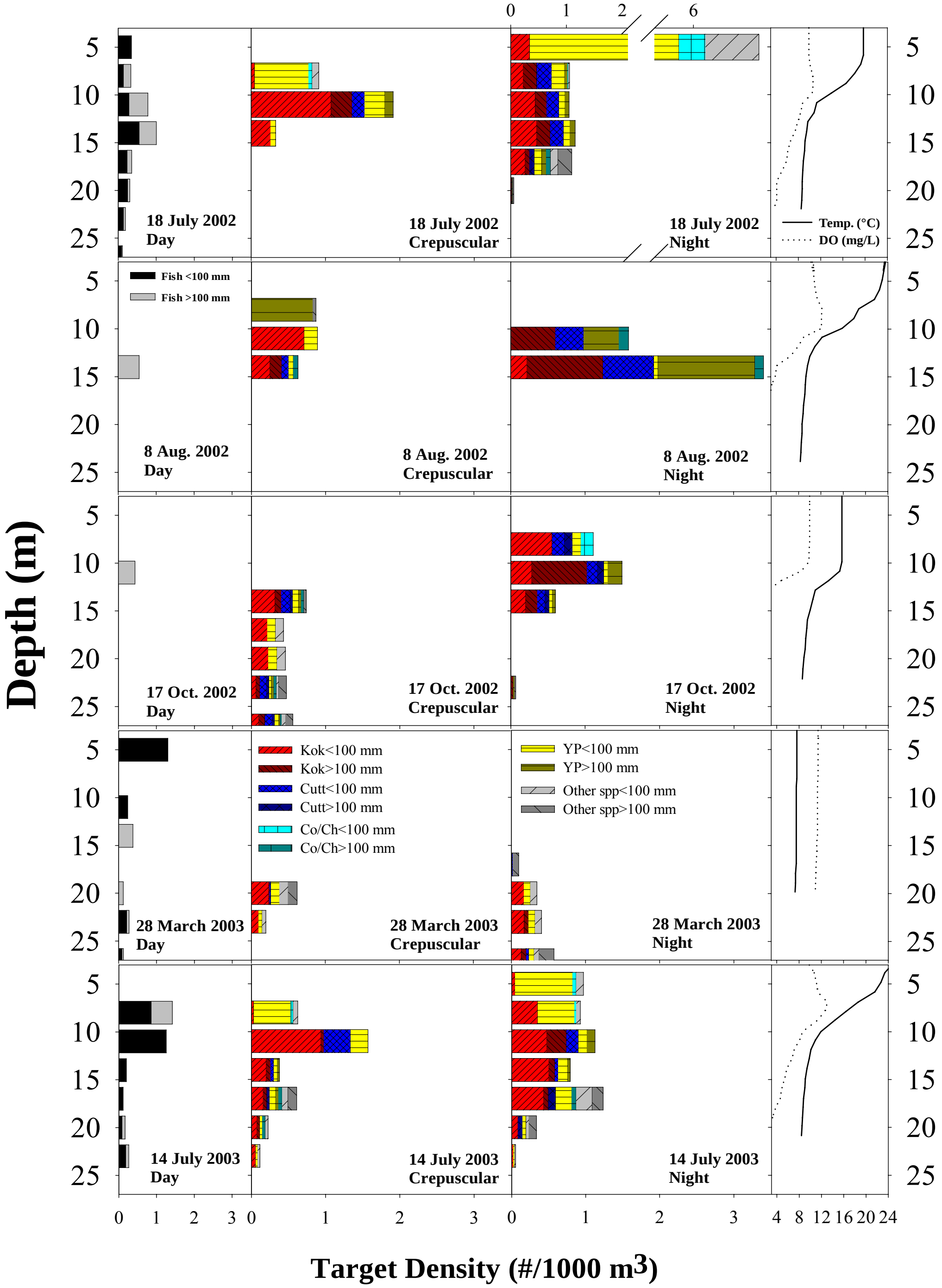

Figure 6. Seasonal and diel patterns in the distribution of fish species in Lake Sammamish during 2002 and 2003. Vertical profiles of temperature (°C) and dissolved oxygen (mg/L) are displayed in the far right panels.

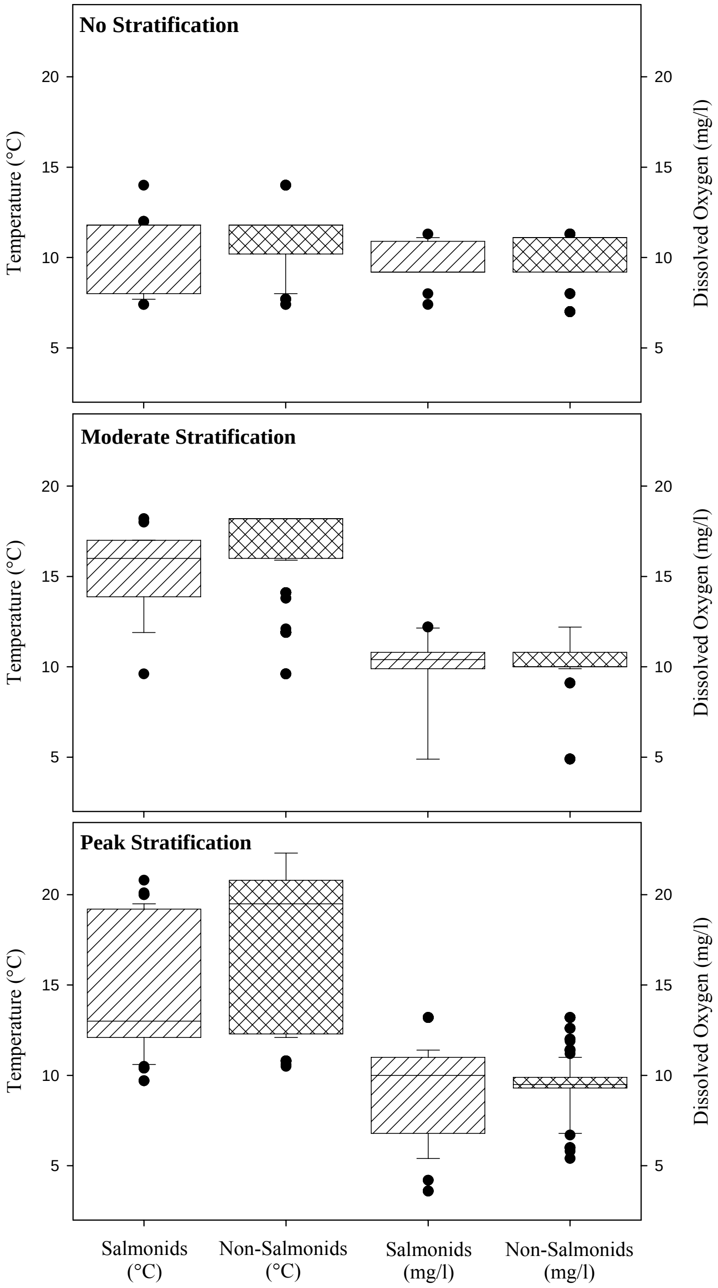

Figure 7. Box plots of the temperature and dissolved oxygen concentrations of locations in the limnetic zone of Lake Sammamish where salmonids and non-salmonids were captured in conditions of no stratification (top panel), moderate stratification (middle panel) and peak stratification conditions (bottom panel). No stratification represents the months of November through April; moderate stratification includes May, June, and October; and peak stratification includes the months of July through September.

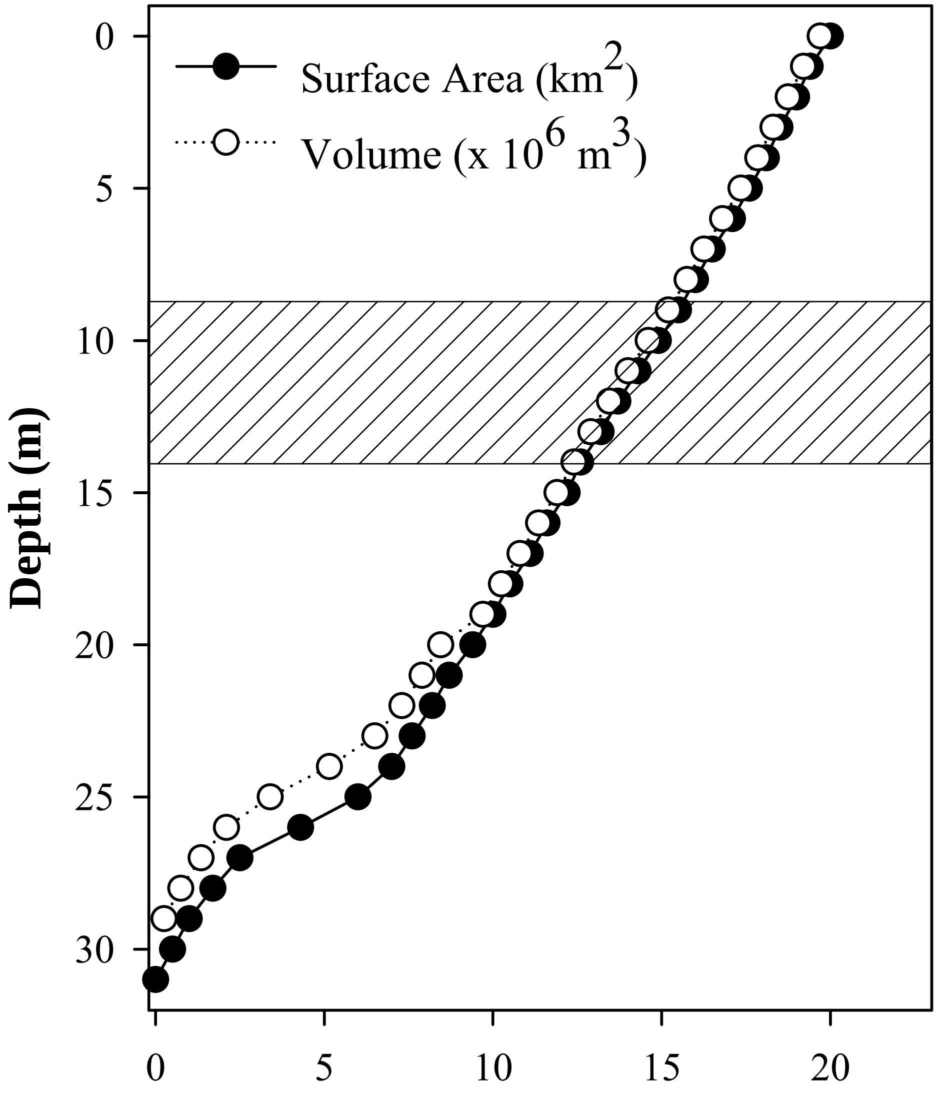

Figure 8. Hypsographic and volumetric curves for Lake Sammamish (Isaac et al. 1966). The shaded region represents the zone in which temperature is less than 17˚C (9 m), and dissolved oxygen is greater than 4 mg/L (13.8 m) during the middle of August, corresponding to approximately twenty percent of the volume of Lake Sammamish.

TABLES

Table 1. Fish species collected in horizontal gill nets and beach seines in Lake Sammamish (2002-2004).

Species	Scientific Name	Population Status	ESA Status
Black crappie (Blc)	*Pomoxis nigromaculatus*	Healthy	
Bluegill (Blg)	*Lepomis macrochirus*	Healthy	
Brown bullhead (Bb)	*Ameiurus nebulosus*	Unknown	
Common carp (Carp)	*Cyprinus carpio*	Healthy	
Chinook salmon (Chin)	*Oncorhynchus tshawytscha*	Unknown	*Threatened*
Coastrange sculpin (Cs)	*Cottus aleuticus*	Unknown	
Coho salmon (Co)	*Oncorhynchus kisutch*	Unknown	
Cutthroat trout (Ctt)	*Oncorhynchus clarki*	Unknown	
Green sunfish (Gs)	*Lepomis cyanellus*	Unknown	
Kokanee (Kok)/sockeye salmon (So)	*Oncorhynchus nerka*	Depressed	*Petition in review*
Largescale sucker (Lss)	*Catostomus macrocheilus*	Healthy	
Largemouth bass (LMB)	*Micropterus salmoides*	Healthy	
Mountain whitefish (MW)	*Prosopium williamsoni*	Unknown	
Northern pikeminnow (NP)	*Ptychocheilus oregonensis*	Healthy	
Pacific Lamprey (Lam)	*Lampetra tridentata*	Unknown	
Peamouth chub (PC)	*Mylocheilus caurinus*	Healthy	
Prickly sculpin (PS)	*Cottus asper*	Healthy	
Pumpkinseed (Pum)	*L. gibbosus*	Unknown	
Rainbow/Steelhead trout (RBT)	*Oncorhynchus mykiss*	Depressed	*Threatened*
Smallmouth bass (SMB)	*Micropterus dolomieu*	Healthy	
Three-Spine Stickleback (TSS)	*Gasterosteus aculeatus aculeatus*	Healthy	
Yellow perch (YP)	*Perca flavescens*	Healthy	

Table 2. Number of day, crepuscular, and night hydroacoustic transects collected by month in Lake Sammamish 2002 and 2003. Monthly Secchi depths and densities of *Daphnia* by depth strata are also included.

Month	***Day Transects***	***Crepuscular Transects***	***Night Transects***	***Mean Secchi Depth (m)***	***Daphnia Density (L^{-1}) 0-10 m***	***Daphnia Density (L^{-1}) 10-20 m***
January	2	1	10	5.6	0.50351	0.03053
February	0	0	10	5.2	0.01634	0.01157
March	2	1	10	3.5	0.00249	0.00254
April	2	1	10	6.8	0.02290	0.00398
May	5	4	20	7.0	0.00647	0.02470
June	8	6	20	6.4	7.57945	12.42677
July	13	10	40	5.1	9.13421	1.13090
August	14	6	30	5.1	5.41291	5.30896
September	1	2	10	5.5	1.96187	2.89234
October	9	6	20	4.7	3.37685	0.53353
November	0	2	10	6.3	2.37579	0.28439
December	0	0	0	6.0	5.48514	0.78833

Table 3. Summary of horizontal gill net sets and beach seine hauls by region and depth zone for each month in Lake Sammamish.

	Gill nets set in the Littoral Zone			***Gill nets set in the Limnetic Zone***			
Month	Epilimnion	Metalimnion	Hypolimnion	Epilimnion	Metalimnion	Hypolimnion	**Beach Seine Hauls**
January	1	1	1	1	1	1	0
February	1	1	1	1	1	1	0
March	1	1	1	1	1	1	0
April	1	1	1	3	1	1	0
May	1	1	1	2	2	2	17
June	2	2	2	3	3	3	18
July	4	4	4	4	4	4	0
August	5	5	5	5	5	5	0
September	2	2	2	2	2	2	0
October	1	1	1	1	1	1	0
November	1	1	1	1	1	1	0
December	1	1	1	1	1	1	0
TOTAL	***21***	***21***	***21***	***25***	***23***	***23***	***35***

Chapter II: The Effect of Thermal Stratification on the Condition, Growth Efficiency, and Predation Risk of Kokanee Salmon in Lake Sammamish, Washington

INTRODUCTION

The movement and spatial distribution of fishes are strongly influenced by environmental conditions, ecological constraints, and physical habitat characteristics. Individual species exhibit specific behavioral and physiological responses to changes in their environment. For example, diadromous fishes physiologically adjust to changes in salinity during migration between freshwater and marine habitats (McDowall 1988), whereas other species migrate to different habitats within or among days or seasons in order to moderate the effects of site-specific environmental change. Differences in physiological tolerances among species and life stages within species enable some fish to thrive under a given set of conditions while others are marginalized or even excluded (Fry 1971; Coutant 1977; Magnuson et al. 1979). Richter and Kolmes (2005) hypothesized that evolutionary history is tied to thermal experience and exposure. In most cases, fish respond to these environmental changes by moving to habitats more suitable for growth (Brett 1971; Fry 1971, Kelsch and Neill 1990; Garrett and Bennett 1995), but habitat choice might be constrained by predation risk or competition (Werner and Gilliam 1984; Werner and Hall 1988; Clark and Levy 1988; Scheuerell and Schindler 2003; Hardiman et al. 2004).

Habitat selection is a compromise between important physical factors such as temperature, dissolved oxygen, and salinity, and biotic factors such as food availability, predation risk, competition, or other constraints (Coutant 1987; Sellers et al. 1998). Generally, fish distribute vertically or laterally across gradients in lakes (Ryder 1977; Brett 1971; Rowe and Chisnall 1995; Baldwin et al. 2002), rivers (Vincent and Miller 1969; Paul and Post 2001), estuaries (Brandt et al. 1992; Coutant 1985), and marine (Quinn et al. 1989; Cayre and Marsac 1993; Brill et al. 2002) environments. These patterns of distribution and movement often coincide with environmental changes operating at varying temporal scales and may have important consequences to fitness. For instance, sockeye salmon (*Oncorhynchus nerka*) respond to subtle changes in factors like temperature, prey availability, presence of predators, dissolved oxygen, salinity, turbidity, or light (Clark and Levy 1988; Beauchamp et al. 1997, 1999; Stockwell and Johnson 1999; Scheuerell and Schindler 2003; Hardiman et al. 2004; Mazur and Beauchamp 2006).

Thermal stratification can greatly influence lake food webs. Temperature controls the metabolic rate in fishes and influences other important processes such as prey production and accessibility, predator feeding rate, feeding ability, activity, behavior, fecundity , and disease transmission, (Fry 1947; Brett 1971; Crowder and Magnuson 1982; Materna 2001; Crossin et al. 2004; Portz et al. 2006), so thermal stratification could influence the ability of fishes to inhabit particular habitats and thus affect growth and survival. Coldwater species such as salmonids may be particularly vulnerable and might employ complex behaviors in order to adapt to the effects of thermal stratification. For example, Brett (1971) found that the optimum temperature for juvenile sockeye salmon (*O. nerka*) to convert food into growth was 15° C, whereas Narver (1970) reported that sockeye salmon avoided surface waters in lakes where epilimnetic temperature exceeded 20° C. Unfortunately, warmer surface waters often have the highest densities of zooplankton, but could be too warm for efficient food conversion into growth. During intense thermal stratification, epilimnetic habitats might not be tolerable. In some lakes, sockeye salmon and kokanee (the landlocked form) exhibit diel vertical migration (DVM) patterns believed to be related to prey availability, predator avoidance, and growth efficiency (Brett 1971; Eggers 1978; Levy 1990; Beauchamp et al. 1997; Stockwell and Johnson 1999). With DVM, sockeye salmon presumably migrate into warmer shallow water in lakes during crepuscular or night periods to take advantage of higher prey densities while minimizing exposure to visually feeding predators, and then migrate into cooler, darker waters during daylight to take advantage of better food conversion efficiency and reduced predation risk (Clark and Levy 1988; Levy 1990; Bevelhimer and Adams 1993; Scheuerell and

Schindler 2003). Despite the potential for DVM to mitigate the effects of a warming epilimnion, annual patterns of thermal stratification may play a significant role in growth efficiency and predator avoidance for sockeye salmon and kokanee in nursery lakes (Stockwell and Johnson 1997, 1999; Hardiman et al. 2004). Hypoxia might confine sockeye salmon or kokanee to higher light levels within the metalimnion during the day, and increase exposure to predators.

The goal of this paper is to describe the effect of thermal stratification on growth and predation risk of kokanee salmon in Lake Sammamish, Washington. Specifically, the objectives are to: 1) describe how kokanee diet, condition and growth efficiency is influenced by stratification, 2) determine if thermal stratification increases predation on kokanee, and 3) examine how thermal stratification influences growth and consumption of cutthroat trout, the most important pelagic piscivore in the lake.

STUDY AREA

Lake Sammamish is a monomictic, mesotrophic lake located in King County, Washington approximately 32 km east of Seattle (142° 05'W 46° 36'N; Figure 1). The shorelines are within the boundaries of unincorporated King County and the cities of Redmond, Sammamish, Issaquah, and Bellevue. Eastern and western shorelines of the lake consist of relatively steep slopes composed of gravel and cobble substrate, while the northern and southern shorelines are shallower and consist of silt and sand substrate with dense aquatic macrophytes (Pflug 1981). Lake Sammamish is 12 m above mean sea level, with mean depth of 17.7 m, and maximum depth of 32 m. The basin extends approximately 12.9 km north to south with a maximum width of approximately 2.4 km. The surface area of Lake Sammamish is 19.8 km^2, with a volume of 3.5×10^8 m^3, making it the sixth largest lake in Washington. The largest tributary of Lake Sammamish, Issaquah Creek, contributes a mean annual discharge of 3.77 $m^3 \cdot s^{-1}$ (Garland and Olson 2004). A salmon hatchery on lower Issaquah Creek has been operated by WDFW (Washington Department of Fish and Wildlife) since the late 1930s, and annually releases approximately 0.5 million coho salmon *O. kisutch* smolts (age 1) in April and 2.1 million fall Chinook salmon *O. tshawytscha* pre-smolts (age 0) in May. All waters entering Lake Sammamish drain via the Sammamish River into the north end of Lake Washington, and then to Puget Sound via the Hiram M. Chittenden Locks.

Lake Sammamish becomes thermally stratified during the summer, with peak epilimnetic temperatures ranging 21-24°C in July-September coinciding with hypoxic conditions in the hypolimnion (Figure 2). As the summer progresses, hypoxic waters encroach into the metalimnion, reducing the amount of cold, oxygenated habitat available for temperature sensitive species, such as salmonids, creating a habitat "squeeze" beginning in mid-July and persisting through September (Figure 2). Secchi depths range from a minimum of 2 m during February to a maximum of 7 m during May.

Fish Community

Over 20 fish species are found in Lake Sammamish, including nonnative and native resident, adfluvial, and anadromous species. Important sport fishes include cutthroat trout (*O. clarki*), sockeye (*O. nerka*), kokanee (*O. nerka*), coho (*O. kisutch*), and Chinook (*O. tshawytscha*) salmon, smallmouth (*Micropterus dolomieu*) and largemouth (*M. salmoides*) bass, and yellow perch (*Perca flavescens*). Unlike salmon, little is known about the relative population sizes of cutthroat trout, smallmouth and largemouth bass, and yellow perch. Kokanee have been identified as a species of concern by the WDFW (Washington Department of Fish and Wildlife), and the population is considered severely depressed from historical levels (Pfeifer 1995; Jackson 2006). Chinook salmon and steelhead trout (anadromous *O. mykiss*) in Lake Sammamish are part of the Puget Sound ESUs (Evolutionarily Significant Units) that have been listed as *threatened* under the authority of the ESA (U.S. Endangered Species Act). Low escapement estimates of kokanee in the late 1990s (Table 4) prompted a petition for listing in 1999 and again in 2007, and currently their status is under review by the U.S. Fish and Wildlife Service (USFWS 2007).

Thousands of adult Chinook, sockeye, and coho salmon spawn in Issaquah Creek, and occasionally in Laughing Jacobs, Ebright, Tibbets, and Lewis creeks (Figure 1). Kokanee spawn in November through January in Lewis, Laughing Jacobs, Ebright, Pine Lake, and Vasa Creeks, although historic use was much more extensive (Berge and Higgins 2003). Kokanee fry emerge and migrate immediately to the lake during months of April and May. Steelhead spawned in Issaquah Creek historically, but since 1996 they have not been observed in any Lake Sammamish tributaries (Scott and Gill 2008). Coastal cutthroat trout (*O. clarki*) are found in every tributary of Lake Sammamish and their populations are believed to be stable or increasing, but there is no quantitative assessment of their abundance. Cutthroat trout typically rear in tributaries of Lake Sammamish for two years before migrating to the lake at approximately 150-200 mm FL (D. Seiler, WDFW, personal communication). Once in the lake environment, cutthroat trout initially feed on zooplankton and insects, but become increasingly piscivorous with size (Luecke 1986; Nowak et al. 2004). In the limnetic zone they are particularly piscivorous, and exert predation pressure on other juvenile salmonids, particularly sockeye and kokanee (Beauchamp 1994; Cartwright et al. 1998; Baldwin et al. 2000; Mazur and Beauchamp 2006).

METHODS

From July 2002 through January 2004, limnological measurements, hydroacoustic surveys, and fish collection methods were combined to examine how salmonid distributions changed over seasonal and diel periods, and between the littoral and limnetic zones within Lake Sammamish. In addition, monthly zooplankton samples were collected to estimate spatial and temporal patterns in the density of exploitable zooplankton (i.e., *Daphnia* and adult copepods) and their overlap with zooplanktivorous fishes such as kokanee and juvenile yellow perch. Diet and distribution information provided an opportunity to understand how foraging conditions and predation risk varied seasonally. Bioenergetic modeling offered insight into how feeding rate and growth efficiency changed during the summer as a result of thermal stratification and diet.

Physical Limnology

Temperature and dissolved oxygen (DO) data were collected from two remote underwater sampling stations (RUSS) buoys in Lake Sammamish (Figure 1). Real-time data were collected and stored by YSI Model 6600 (YSI, Yellow Springs, OH) multi-meter sondes mounted on each buoy. Vertical profiles were recorded at 1 m depth intervals, up to six times per day during the study period. Individual sondes were calibrated as necessary according to the manufacturer's specifications, typically once every two weeks. Transparency was measured with a Secchi disk (Smith 2001) at weekly intervals at five stations in Lake Sammamish from May through December (Table 2), and turbidity samples were collected monthly at 5, 10, 15, 20, and 25 m depths by and recorded in values of NTU (Nephelometric Turbidity Units) and averaged for the 0-10, 10-15, and 20-30 m depths (Table 5). Surface light data were collected on the RUSS buoys using a LiCor Li-250A (LiCor Biosciences, Lincoln, NE) light meter every 15 minutes. In addition, underwater light profiles were collected at five stations monthly during the stratified period using a Self Contained Autonomous MicroProfiler™ (SCAMP; Precision Measurement Engineering, Carlsbad, CA) with a Li-Cor 192SA sensor, measuring daytime photosynthetically active radiation (PAR; in microeinsteins·m^{-2}·s^{-1}) at 1 cm depth increments throughout the entire water column. PAR units were converted to lx using the following formula from Wetzel (2001),

$$X_{lux} = (0.01953)^{-1} \cdot X_{PAR},$$

where X_{lux} is the value in Lx and X_{PAR} is the value measured by the SCAMP in units of PAR. The light extinction coefficient (η) for Lake Sammamish was derived from a equation from Wetzel (1983),

$$\eta = \frac{\ln I_0 - \ln I_z}{\mathrm{z}}$$

where I_o is the light intensity value at the surface (lx) and (I_z) is the light intensity at depth *z* in the lake. A light dependent functional response model for kokanee (Koski and Johnson 2002) was applied to evaluate the effect of thermal stratification on the consumption rate of *Daphnia* by kokanee in Lake Sammamish. The low light model was used to predict the consumption rate of *Daphnia* by kokanee at depths below 10 m during daylight and at most shallower depths during crepuscular and night periods in Lake Sammamish since ambient light of the surface of Lake Sammamish at night (moon illuminance) ranged between 0.001 and 3.4 lx (Hardiman et al. 2004). The low light model is described as,

$$N = 1.74 \cdot P,$$

where N is consumption rate (*Daphnia* consumed $\cdot$ min^{-1}) and P is prey density (*Daphnia* $\cdot$ L^{-1}). During the day, ambient light within the upper 10 m of the lake exceeded 3.4 lx, supporting the use of Koski and Johnson's (2002) high light model, where consumption rate (N) is defined by,

$$N = \frac{(\beta_0 \cdot P)}{(\beta_1 + P)}$$

where β_0 is the maximum consumption rate (163.6 *Daphnia* $\cdot$ min^{-1}), and β_1 is the prey density at which consumption reaches half its maximum (42.2 *Daphnia* $\cdot$ L^{-1}).

Zooplankton Sampling

Zooplankton samples were collected monthly in two regions of Lake Sammamish (Figure 1) using a 12.5 cm diameter Clarke-Bumpus sampler with 153 μm mesh. Samples were taken at three depth intervals of the lake: 0-10 m epilimnion, 10-20 m metalimnion, and >20 m hypolimnion. Organisms were preserved in 95 percent ethanol and identified by species, lifestage, and length, and were enumerated for each sampling event (Shepherd et al. 2002; King County unpublished data). Density was calculated by summing the number of individual zooplankton within a given taxa collected on a given date and depth interval (0-10 or 10-20 m) and dividing by the volume of water sampled by the Clarke-Bumpus sampler. Biomass (C) was calculated by converting the length of zooplankton in the sample to dry weight per Liter (McCauley 1984; Manca and Comoli 2000), using the general formula,

$$\ln C = \ln a + b \ln L$$

where *a* and *b* are life stage species specific constants zooplankton, *L* is body length in mm, and *C* is the weight (Carbon in µg). Species specific parameters for each organism and life stage were needed for values of *a* and *b* (Table 6). For wet weight comparisons I used a dry to wet weight ratio of 10% (Dumont et al. 1975).

Hydroacoustic surveys

Hydroacoustic surveys were conducted several times each season to examine temporal trends in limnetic fish distribution (Table 2) associated with limnological changes across Lake Sammamish, and to evaluate ontogenetic differences within and among species at specific depths. Hydroacoustics are particularly effective in detecting and describing the behavior of suspended limnetic species (such as kokanee) when surveyed with a vertically oriented transducer (Brandt 1996; Beauchamp et al. 1997; Baldwin and McLellan 2008). A Biosonics DE 6000 high-frequency (430 kHz), split-beam transducer, mounted on a tow fin was pulled through the water column by a 6.7 m vessel at a depth of 0.75 m, and an average velocity of 6 $\text{km}\cdot\text{h}^{-1}$. The transducer transmitted at a rate of 3 pings per second and the full beam angle of the vertical transducer was 6°. Targets were collected using a pulse width of 0.4 ms and a target threshold of -65 dB. Data collected at each transect were recorded by an onboard computer and post-processed using SonarData Echoview™ (version 3.45). Data from each transect were echo counted for individual target strengths, and divided by the acoustic volume sampled within each 1-m depth interval (from *Z* m to *Z* + 1 m below the transducer) to calculate target density for each transect in 1 m intervals. The volume of each 1 m interval was based on the volume of the frustum,

$$V = \frac{\pi h}{3} \cdot (R^2 + Rr + r^2),$$

where *h* is the 1-m height of each depth interval, *r* is the radius of the circular top of the frustum nearest the transducer and *R* is the radius of the base of the frustum, calculated by,

$$r = Z \cdot \tan(4°) \text{ and } R = (Z + 1) \cdot \tan(4°).$$

Targets and density estimates from the 6° beam were restricted to 4° (< 2° off axis) to reduce reliance on beam angle compensation and increase confidence in target strength estimates. Targets identified within 1 m of the lake bottom were excluded to avoid potential contamination from bottom structure, and targets identified within 5 m from the boat were excluded from target density analysis due to the extremely small sampling volume. For target densities in water less than 5 m, I used the average densities of targets from the 5-10 m interval. Love's (1971) equation was used to transform target strengths (TS in dB) into total lengths (TL_m in m) using the following formula for 430 kHz and assuming an average speed of sound through water of 1440 $\mathrm{m \cdot s^{-1}}$,

$$TS = 19.1 \cdot \log_{10}(TL_m) - 23.43.$$

A zigzag survey pattern (Brandt 1996) was used to maximize sampling efficiency. During each survey, nine transects were sampled across the lake, covering depth range of 2-32 m (Figure 1). Additionally, one long north-south transect was surveyed at night to investigate the possibility of a longitudinal gradient in the distribution of limnetic fishes in Lake Sammamish. The majority of hydroacoustic surveys were conducted at night, when limnetic fishes were most susceptible to detection in the water column (Northcote et al. 1964; Duncan and Kubecka 1993; Luecke and Wurtsbaugh 1993; Appenzeller and Leggett 1995). In addition, selected areas of the lake (transects 3 and 4) were sampled during daylight and crepuscular periods to investigate diel variation in vertical distribution for specific dates (Figure 1; Table 2). Densities of prey sized fishes (30-100 mm, -57 to -47 dB) from the hydroacoustics were summed across all night time hydroacoustic transects for a given sampling date and converted into a pelagic prey population for that date by simply multiplying the number of targets per sample volume (m^3) by the volume of the corresponding depth interval from a hypsographic curve developed for Lake Sammamish (Issac et al. 1966).

Fish Collection

Sinking and suspended horizontal gill nets were the primary methods for identifying the fishes detected in the hydroacoustic surveys and comparing littoral and limnetic species assemblages. During each hydroacoustic survey, at least six monofilament, variable-mesh gill nets were deployed in the lake: a single sinking horizontal gill net was set in each of the epilimnetic, metalimnetic, and hypolimnetic depths of the littoral and slope zones, and three suspended horizontal gill nets were set: one each in epilimnetic, metalimnetic, and hypolimnetic depths of the limnetic zone (Table 3). Since hydroacoustic surveys were conducted at night, gill nets were set at dusk and retrieved at dawn on the following day to provide concurrent target identification. All gill nets were 60 m long by 2 m deep with panels of 25, 31, 38, 50, 63, and 75 mm stretch mesh. Age-0 salmonids in Lake Sammamish were not vulnerable to gill nets until early autumn since the modal size of a salmonid captured in a 25-mm stretch mesh (13 mm bar mesh) gill net was approximately 125 mm total length, or approximately 112 mm fork length (Beauchamp et al. *in press*).

Beach seines were used during May-June 2003 to capture fish in the littoral areas prior to, during, and following releases of Chinook salmon from the Issaquah Hatchery (Table 3). Beach seines were set during the evening near Issaquah Creek, Lewis Creek, Vasa Creek, one eastern shoreline site, Ebright Creek, and Idylwood Park in May and June 2003 (Figure 1). Sampling occurred three days prior, the day of, and three days following the release of Chinook salmon from the Issaquah Creek hatchery at each site. The beach seine was 37 m x 1.5 m, and was set from a boat in approximately 2-m deep water. The seine was set perpendicular to the shoreline, and pulled in a sweeping arc toward shore. Once both ends of the seine were on the beach, wings were pulled in simultaneously, bringing fish into shallow water along the shoreline.

Fish collected from beach seines and gill nets were placed on dry ice immediately after retrieval to halt further digestion of stomach contents, except that ESA-listed juvenile Chinook salmon caught in beach seines were immediately released. In the lab, all fish were weighed to the nearest gram, and FL (fork length) and TL (total length) was measured to the nearest millimeter prior to dissection. Otoliths and scales were removed from all target species and a subset of non-target species. Aging procedures followed those described in Devries and Frie (1996). Whole stomachs were removed from each target species (kokanee, cutthroat trout, coho and Chinook salmon, smallmouth and largemouth bass, yellow perch, and northern pikeminnow) and from a representative sub-sample of non-target species (large scale suckers and peamouth chub). The stomach samples were preserved in a 10 % buffered bicarbonate-formalin solution. Stomach contents were examined in the lab under a dissecting microscope. Prey fishes were identified to species, zooplankton were identified to genus, and other invertebrates were identified to order or family. All prey items were weighed (blotted wet weight) to the nearest 0.001 g. Standard, total, and/or fork lengths were measured for relatively intact fish prey to the nearest mm. In some cases, diagnostic bones were used to identify and estimate lengths of prey using metrics from Hansel et al. (1988). Diet composition was reported as the proportional contribution of each prey category to the total weight of food in individual stomachs. The individual weight proportions for each prey category were averaged across all non-empty stomachs for fish within the same species, age, size class, and time interval (Chipps and Garvey 2007) to provide diet inputs for bioenergetics model simulations of kokanee and cutthroat trout feeding.

Catch per unit effort for species and size classes of limnetic gill net sets were used to identify the acoustic targets of similar size recorded during hydroacoustic transects for the corresponding period and depth stratum (epi-, meta-, and hypolimnion). Species proportions and size frequency data were multiplied together with target densities to assign species identification to hydroacoustic targets during the same sampling period and were pooled across transects. In the case of small fishes that were not susceptible to the smallest mesh (<110 mm), I used a combination of measured prey items from piscivore diets collected at the same time and depth interval to assign species identification from the hydroacoustics data, and in a very few instances used species composition and size distribution from beach seining for littoral zone targets.

Bioenergetics modeling

Bioenergetics modeling was used to estimate consumption rates, provide an index of predation risk by cutthroat trout on kokanee, estimate consumption and growth by kokanee, and evaluate bioenergetic growth trade-offs associated with feeding in the epilmnion or metalimnion, based on food availability and thermal regime. The Fish Bioenergetics v3.0 software (Hanson et al. 1997) was used and age-specific model inputs were estimated from the data collections described above for seasonal simulations during 2002. Published physiological parameters were used for kokanee (Beauchamp et al. 1989) and cutthroat trout (Beauchamp et al. 1995). The model inputs included: initial and final weights and diet proportions for cutthroat trout (Table 7) and kokanee (Table 8), thermal experience for both species (Table 9), and prey energy density. Prey energy density inputs for the model were 3,559 $J \cdot g^{-1}$ for *Daphnia* (Luecke and Brandt 1993), 3,348 $J \cdot g^{-1}$ for benthic invertebrates (Beauchamp et al. 1995), 4,435 $J \cdot g^{-1}$ for mysids and 3,064 $J \cdot g^{-1}$ for chironomid pupae (J. McIntyre, University of Washington, unpublished data), 5,050 $J \cdot g^{-1}$ for juvenile Chinook salmon (Madenjian et al. 2004), 5,338 $J \cdot g^{-1}$ for kokanee (Hanson et al. 1997), 5,442 $J \cdot g^{-1}$ for coho salmon (Trudel et al. 2002) 2,512 $J \cdot g^{-1}$ for larval yellow perch (Post 1990), and 4,186 $J \cdot g^{-1}$ for other fish (Hanson et al. 1997). Thermal experience was determined by combining monthly vertical temperature profiles with modal capture depths in gill nets, hydroacoustic results.

Growth inputs for the model were derived from the mean weights for specific age classes and seasons for cutthroat trout (Table 7) and kokanee (Table 8). Simulation days for cutthroat began on 1 January (day 1) and ended on 31 December (day 365). Spawning losses for cutthroat trout were taken into account on February 15th (day 46) with an estimated loss in body mass of 14% for Age-3, and 20% for age-4 and older cutthroat (Jonsson et al. 1984). Initial and final weights for each season and cohort were used to fit consumption to observed growth for cutthroat (Table 7) and kokanee

(Table 8). For kokanee bioenergetics simulations, day 1 began on April 1st, approximating the date when age-0 kokanee emigrated from tributaries into Lake Sammamish, and ended on 31 March (day 365). For consumers that exhibited diel vertical migrations, thermal experience was derived from time- and depth-weighted daily averages based on diel depth distributions from hydroacoustic data and concurrent vertical temperature profiles obtained from the RUSS buoys (Table 9).

Estimates of consumption from the bioenergetics model for kokanee and cutthroat trout were used to determine how feeding rate, growth efficiency, and consumption of key prey items differed seasonally. Since age-0 kokanee were not collected in this study, they were excluded from the bioenergetics analysis. The relative growth consequences for kokanee that either resided exclusively in the epilimnion or metalimnion, or exhibited diel vertical migrations during July-September were explored by estimating consumption rates from light-dependent functional response curves and corresponding *Daphnia* densities in the epilimnion and hypolimnion. Growth rates and growth efficiencies were simulated with the bioenergetics model using the consumption rates and thermal experiences that resulted from epilimnetic, metalimnetic, and DVM scenarios. Predation risk for kokanee was estimated from seasonal consumption estimates for cutthroat trout from the bioenergetics model simulations.

Annual age specific mortality (Z) was calculated for kokanee and cutthroat trout. For kokanee, the equation used was

$$\frac{\ln(N_f / N_o)}{3.67} = -Z$$

where N_f is the number of females on the spawning grounds, N_o is the number of outmigrants produced per female spawner. Kokanee are semelparous, and the modal spawning age was 3.67 years for kokanee in Lake Sammamish, with an average fecundity of 656 eggs per female (H. B. Berge, King County, unpublished data). Egg-fry survival for kokanee in Lewis Creek was estimated at 11% in 2007 and 2% in 2008 (M. Taylor, Trout Unlimited, unpublished data). I used a mean value of 6.5% to calculate average productivity, and estimated 50% of the fish on the spawning grounds were females, and used the average of the escapement estimates from 1999-2002 as brood years for kokanee in Lake Sammamish during 2002 and 2003 (Table 4). Using these inputs, I estimated an age based population estimate for Lake Sammamish kokanee in 2002-2003 of 21,000 age-0, 8,200 age-1, 3,100 age-2, 1,158 age-3, 434 age-4, and 162 age-5 kokanee. The annual mortality rate used for cutthroat trout was 33%, based on data from nearby Lake Washington (D. A. Beauchamp, University of Washington, personal communication). Therefore, the annual instantaneous mortality rate (Z) for cutthroat trout was $\ln(0.33) = -Z = 1.10866$ or daily instantaneous mortality of $Z_d = 1.10866/365 = 3.03742 \times 10^{-3}$. To calculate an age-structured population of 1000 cutthroat trout in Lake Sammamish, I applied the equation,

$$N_{yt} = N_y \cdot e^{(-Zt)}$$

where Ny_t was the abundance of age-y cutthroat trout at time t, and N_y was the initial number of age-y cutthroat trout. Using this equation, I calculated an age-structured population of 1,000 age 2-7 cutthroat trout in Lake Sammamish to combine with per capita estimates of consumption from the bioenergetics model, resulting in initial age-specific abundances of approximately 671 age-2, 221 age-3, 73 age-4, 24 age-5, 8 age-6, and 3 age-7 cutthroat trout.

Visual Foraging Modeling

A visual foraging model for cutthroat trout (Mazur and Beauchamp 2006) was applied to assess risks associated with alternative movement strategies during thermal stratification for kokanee residing in either exclusively in the epilimnion or metalimnion, or for kokanee that employed DVM between the metalimnion and epilimnion daily. Hypoxia precluded access to the hypolimnion during thermal stratification. Predation risk was evaluated by calculating a depth-specific prey encounter rate from Beauchamp et al. (1999) and refined for cutthroat trout by Mazur and Beauchamp (2006), using the formula,

$$E_{z,t} = V_{z,t} \cdot D_{z,t}$$

where $E_{z,t}$ is the prey encounter rate at depth z and time t, $V_{z,t}$ is the search volume, and $D_{z,t}$ is the prey density at depth z and diel period t. Search volume takes the general shape of a cylinder and is defined by,

$$V_{z,t} = \pi R^2_{z,t} \cdot Ss_t \cdot T_t$$

where $R_{z,t}$ represents the reaction distance of the predator at depth z and diel period t, and $V_{z,t}$ represented the volume searched by a piscivores (cutthroat in this case) swimming at an average speed of $Ss_t = 30$ cm·s^{-1} during the day, 22.5 cm·s^{-1} for crepuscular periods, and 14 cm·s^{-1} at night (Baldwin et al. 2002), and T_t was the duration of the diel period (h). The reaction distance under low light (<17 lx at depth z) and low turbidity (<1.0 NTUs), *Rz,t*, (cm) was defined by the equation,

$$R_{z,t} = 33.7 \cdot I_{z,t}^{0.194}$$

where $I_{z,t}$ is the ambient light intensity at depth z (defined previously) and diel period t (Mazur and Beauchamp 2006). A threshold value of $R_{z,t} = 58.4$ cm was used for cutthroat trout at light levels >17 lx and turbidity <1.0 NTUs (Mazur and Beauchamp 2003, 2006). For turbidity >1.5 NTUs, and light <21.4 lx, Mazur and Beauchamp (2003) calculated *Rz,t* (cm) as

$$Rz,t = 36.99 \cdot I_{z,t}^{0.118}.$$

The maximum $R_{z,t}$ in conditions with higher turbidity (>1.5 NTUs), was 53.16 cm, where ambient light intensity at depth was also >21.4 lx (Mazur and Beauchamp 2003). The probability of capture (P_c) for a visual predator varied with light and turbidity. Mazur and Beauchamp (2006) applied a P_c for cutthroat trout based on experimental predation trials of lake trout (*Salvelinus namaycush*) feeding on juvenile salmonids at differing light levels. For $I_{z,t} \leq 0.75$ lx, P_c was assumed to be 1.0, and for $I_{z,t} > 0.75$ lx, P_c was 0.49 (Mazur and Beauchamp 2006).

Condition Index

Relative weight (W_r) was used as a condition index (Wege and Anderson 1978) to determine the effects of thermal stratification on kokanee. Relative weights of kokanee were compared across seasons and size classes. The equation for relative weight is described by,

$$W_r = (W/W'),$$

where *W* is the observed weight of an individual (g) and *W'* is the standardized weight determined by a weight-length regression for kokanee (Hyatt and Hubert 2000). The *W'* equation for kokanee is,

$$\log_{10}(W') = -5.062 + 3.033 \log_{10}(TL),$$

where *TL* is total length (mm). Values of W_r less than 1.0 indicate lower than normal weight for a fish of a given length and suggest diminished feeding conditions. Values greater than 1.0 suggest more favorable recent growing conditions. Seasonal changes in relative weight were combined with consumption estimates generated from bioenergetics simulations to explore how feeding and growth were influenced by thermal stratification.

RESULTS

Thermal stratification initiated in May and continued through November during the study period (Figure 9). The peak of the temperature and DO "squeeze" occurred in September, when only 10-14 m depths remained below 17° C and DO > 3 mg $\cdot L^{-1}$. This squeeze resulted in an estimated loss of 84% of useable habitat in Lake Sammamish. The depth at which light levels were <3.4 lx varied around 9-11 m during the day, and 2.0- 2.8 m during crepuscular periods throughout the year (Figure 9). Similarly, light levels >17 lx during summer stratification occurred at 8-9 m during the day, and 1-2 m during crepuscular periods (Figure 9; Table 10). Nocturnal light levels remained less than 1 lx for each survey date, and turbidity was less than 1.5 NTU on all dates, except 1 March 2003 (Table 10). The higher turbidity on 1 March 2003 was due to a diatom bloom, a common occurrence in Lake Sammamish for that time of the year.

Access to prey was also influenced by thermal stratification. The highest densities of fish in the limnetic zone shifted into the metalimnion where temperatures were less than 17°C and DO concentrations exceeded 3 mg$\cdot L^{-1}$ at depths between 10 and 15 m. The density and biomass of *Daphnia* and adult copepods changed seasonally, and by depth (Figure 10). During the winter, the dominant biomass of adult zooplankton at all depths was copepods (both cyclopoid and calanoid). *Daphnia* increased dramatically in June and dominated the biomass of crustacean zooplankton during June through December. During thermal stratification, the density of *Daphnia* in the epilimnion (0-10 m) was 1.5-8.0 times higher than in the metalimnion (10-20 m; Figure 10). The high and low light level functional response models from Koski and Johnson (2002) predicted that during thermal stratification, the consumption of *Daphnia* would be much greater in the epilimnion than in the metalimnion, and as expected, the predicted consumption of *Daphnia* would be much greater during daylight (high light) than crepuscular or nocturnal periods (low light; Figure 11). Peak consumption rate of *Daphnia* during thermal stratification occurred in July at almost 60 *Daphnia* min^{-1}. In fact, based on the functional response curves, *Daphnia* consumption by kokanee was much higher in the epilimnion than the metalimnion during every month of the year except February (Figure 11).

Daphnia was the most important prey item for kokanee in Lake Sammamish during spring through autumn across size classes and generally accounted for at least 50% of the diet by weight (Figure 12). Chironomids (during winter), copepods (during spring), and mysids (during summer and autumn) were seasonally important (Figure 12). Larval and post-larval yellow perch (September through autumn), Chinook salmon, and aquatic insects all contributed to the diets of certain size classes of kokanee. Kokanee < 200 mm FL primarily consumed *Daphnia*, during spring-summer, along with copepods during spring, mysids and chironomid pupae during summer, and chironomid pupae during winter (Figure 12). *Daphnia* were the primary prey throughout the year for kokanee 200-300 mm FL, but diets also included copepods in spring, juvenile Chinook salmon and chironomids in August, mysids during September through autumn. Some kokanee > 200 mm FL became piscivorous, consuming both larval and post-larval yellow perch and Chinook salmon (<58 mm FL). Larger kokanee were more piscivorous during June (feeding on Chinook salmon) and during peak stratification in August through autumn, consuming yellow perch (Figure 12).

Bioenergetics simulations indicated that across all age classes kokanee consumed and estimated 6,058 kg of *Daphnia*, 599 kg of copepods, 1,424 kg of invertebrates (mostly chironomids), 489 kg of mysids, 315 kg of yellow perch, and 213 kg of Chinook salmon (Figure 13). Kokanee consumed more than 50% of the estimated monthly standing crop of *Daphnia* during February, March, and through December (Table 11). Although not a major component in the diet of kokanee, fish flesh was consumed by kokanee more during thermal stratification than the rest of the year. Growth efficiency was greatest for kokanee during the spring, and lowest during summer and autumn for all size classes during thermal stratification (Figure 14). Although *Daphnia* production is greatest during the summer overall, the growth efficiency of kokanee was reduced, and access to the most productive zone (the epilimnion) was limited by thermal conditions.

The consequences of seasonally-differing growth efficiency and consumption were measured by changes in condition indices such as relative weight. In Lake Sammamish, the mean relative weight (W_r) of kokanee was significantly lower (two-sample t-test; $P < 0.001$) during the stratified period $W_r = 0.897$ (SD = 0.0833; n=74) than during the rest of the year $W_r = 0.982$ (SD = 0.1505; n=15), thus supporting the hypothesis that growth was limited during the thermally stratified period.

Predation

The most significant kokanee predator was cutthroat trout (Kruskal-Wallace $p<0.01$), although kokanee were found in the diets of four different species in Lake Sammamish including cutthroat trout, northern pikeminnow, yellow perch, and Chinook salmon. A similar trend of increasing piscivory with increasing body size was common to all piscivores in Lake Sammamish (Figure 15). Cutthroat trout > 300 mm FL were the primary limnetic piscivores with kokanee representing 5-20% of the diet by weight during spring and summer, while juvenile yellow perch contributed 15-70% of the diet over the same seasons. In Lake Sammamish, cutthroat trout consumed kokanee during spring, summer, and autumn (Figure 16). For a given population size of 1,000 cutthroat trout (671 age-2, 221 age-3, 73 age-4, 24 age-5, 8 age-6, and 3 age-

7) approximately 2,021 age-0 and age-1 kokanee were consumed per year, distributed across all seasons with 1 eaten in the winter, 865 eaten during the spring, 537 eaten in the summer, and 619 individuals consumed during the autumn. Of the kokanee observed in the diet of cutthroat trout, 45% of the kokanee consumed were age-0, and 55% were age-1 across all seasons. With estimates of 21,000 age-0 and 8,200 age-1 kokanee in the lake, the estimated loss due to predation by cutthroat trout was 4.6% age-0 and 12.2% age-1 kokanee per 1,000 cutthroat trout.

The growth efficiency of cutthroat trout was greatest during the winter and lowest during autumn (Figure 17). In contrast to kokanee, mean W_r for cutthroat trout was significantly higher (t-test, $p<0.002$) during the stratified period 0.954 (SD = 0.1166; n=63) than during unstratified conditions (W_r = 0.773, SD = 0.1315; n=78). These apparent differences in W_r supported the hypothesis that predators benefited from more overlap with prey fishes during stratified periods.

The density of prey fishes (30-100 mm TL) varied by diel period and season (Figure 18). During the winter, prey-sized fishes were distributed randomly throughout the water column during day and crepuscular periods, but were found at higher densities below 20 m at night (Figure 18). During spring, relatively high densities of prey fish were located in the upper 10 m throughout all diel periods with a second density mode around 15-20m during crepuscular and night periods. During the summer months, prey fish density was highest in the epilimnion (<10 m) increasing from day through the crepuscular and night periods, while a second mode appeared in the metalimnion at night (Figure 18). When temperature and oxygen concentrations were not limiting during autumn, prey fishes occupied all depths with peak density near 5 m during daylight, a strong peak at 11-13 m during crepuscular periods, and a relatively even distribution across all depths at (Figure 18).

The prey encounter rates of cutthroat trout during each diel period were greatest during the summer and lowest during the winter (Figure 19). The encounter rate during the day was generally greater than crepuscular and night, and greatest near the surface for all seasons, but still relatively high in the upper metalimnion between 10 and 12-14 m, depending on the season (Figure 19). With increased light and thermal stratification during summer and autumn, prey encounter rates during the crepuscular and night periods would have also been higher near the surface of Lake Sammamish (Figure 19). Strategies such as DVM during the summer and autumn would be risky with increased prey encounter rates due to surface light and low turbidity (Figure 19). Cutthroat trout foraging during daylight hours at depths less than 12 m have much higher prey encounter rates than those residing at deeper depths (Figure 19).

DISCUSSION

The vertical distribution of salmonids in Lake Sammamish varied seasonally and by diel period in response to thermal stratification and hypoxia patterns, and these patterns appeared to influence seasonal growth of planktivorous kokanee and piscivorous cutthroat trout differently. During peak thermal stratification, kokanee and cutthroat trout selected depths corresponding to near optimal temperature for growth between 15˚C and 17˚C (Brett and Higgs 1970), although optimal growth temperatures decrease under limited prey availability (Brett 1971) or reduced accessibility to the more productive environments. During unstratified conditions in winter and spring, salmonids were found throughout the water column in each diel period.

Ontogenetic differences in temperature tolerance of salmonids were observed in this study (previous chapter). Smaller size classes of fishes appear to be able to adapt to warmer water and lower DO concentrations (Brett 1971; Coutant 1985; Rosland and Giske 1994). The differences in the realized thermal niche of juvenile kokanee (and sockeye) in Lake Sammamish may have evolutionary significance by reducing the extent of spatial overlap with the dominant limnetic piscivore, cutthroat trout, while maximizing the opportunity to consume *Daphnia* in the epilimnion.

During thermal stratification the distribution of smaller targets (<100 mm) varied among diel periods, with the nocturnal density significantly greater than both day and crepuscular periods. This finding would support the hypothesis that prey sized fishes foraged during darkness to avoid predation by visual predators such as cutthroat trout, although cutthroat trout predation in the epilimnion during stratification may not be a major factor. For example, Nowak and Quinn (2002) found that cutthroat trout in Lake Washington occupied the metalimnion during thermal stratification with only brief forays into the epilimnion at dawn, independent of ambient light levels. In Lake Sammamish, I did not observe a strong signal of DVM, consistent with previous findings of Berggren (1974). The occurrence of DVM by juvenile sockeye salmon and kokanee in other systems may be a consequence of increased prey capture efficiency (*sensu* Eggers 1978; Nowak and Quinn 2002), reduced predation (Clark and Levy 1988; Stockwell and Johnson 1999; Scheuerell and Schindler 2003; Hardiman et al. 2004), avoidance of low DO levels (Douglas and Jahn 1987; Baldwin et al. 2002), metabolic optimization (Wurtsbaugh and Neverman 1988) or some combination thereof (Clark and Levy 1988; Bevelhimer and Adams 1993; Beauchamp et al. 1997; Stockwell and Johnson 1999; Scheuerell and Schindler 2003; Hardiman et al. 2004). Beauchamp et al. (1997) found that kokanee foraging behavior is focused on predator avoidance primarily and then changes to optimizing metabolic efficiency within specific depth intervals of lakes in central Idaho. Predation in Lake Sammamish occurs during all diel periods at shallow depths reducing the effectiveness of DVM as a predator avoidance strategy. With *Daphnia* densities in the metalimnion greater than the 0.4 ind L^{-1} threshold observed by Scheuerell et al. (2005), perhaps the energetic consequence of staying in the metalimnion with lower *Daphnia* density (Figure 10) and consumption rate (Figure 11) is not as important as other lake systems. A more precise hypothesis for the apparent lack of DVM in Lake Sammamish may be explained by work of Bevelhimer and Adams (1993), who concluded that DVM is optimal in systems where kokanee are thermally separated from their predators. In Lake Sammamish, the dominant limnetic predators of kokanee are cutthroat trout and residualized Chinook salmon, both having similar temperature preferences as kokanee making the spatial and temporal overlap between limnetic predators and kokanee more extensive during stratification . Stockwell and Johnson (1999) found that when temperature is not a constraint for kokanee, the foraging behavior of kokanee is focused on avoiding predators. During thermal stratification in Lake Sammamish, temperature is a constraint to growth, making kokanee balance thermal stressors with predation risk.

Kokanee are zooplanktivores and prefer to prey on *Daphnia* across their range (Foerster 1968; Stockwell and Johnson 1999; Baldwin et al. 2000), including Lake Sammamish. *Daphnia* are the most important prey item of kokanee in Lake Sammamish across all size classes and seasons. During thermal stratification the density of *Daphnia* in the epilimnion is much greater than in the metalimnion, although densities of *Daphnia* in the metalimnion are high enough (>0.4 ind L^{-1}) that kokanee will still selectively feed on them (Scheuerell et al. 2003). Model results for consumption of *Daphnia* during the summer suggest that prey density, water transparency, and light would favor kokanee consumption of *Daphnia* in the epilimnion, although warm epilimnetic water and greater predator encounter rates would limit the overall success of such a strategy. Despite the opportunity for kokanee to adapt to thermal stratification, the relative weight of kokanee in Lake Sammamish was significantly lower during stratified than during unstratified conditions. This phenomenon is not restricted to kokanee and has been reported for northern pike (*Esox lucius*, Headrick and Carline 1993) and striped bass (*Morone saxatilis*, Moss 1985). Despite high densities of *Daphnia*, growth efficiency of kokanee was much lower during the summer than the spring when *Daphnia* densities are almost undetectable, and predictions from Koski and Johnson’s (2002) model suggest very high consumption rates during June through December for both the high and low light periods. It is apparent that kokanee in Lake Sammamish were not able to maximize growth during the thermally stratified period.

Kokanee diet was more diverse during thermal stratification and included such prey as zooplankton, insects, mysids, and fish. Although piscivory was rare for kokanee (Collins 1971; Miller et al. 2007), the spatial and temporal overlap during the stratified period between larger kokanee and larval yellow perch and 2.1 million Chinook pre-smolts created a unique situation in Lake Sammamish for kokanee to exploit. The absolute contribution of fish flesh to the growth of kokanee is very small.

Black bass were rarely encountered in the limnetic zone of Lake Sammamish and were unlikely to consume many kokanee after the fry migrate offshore, consistent with the work of others (e.g., Pflug 1981; Tabor et al. 2007). Although not observed in this study, kokanee could be susceptible to bass predation in the littoral zone during fry outmigration in April and May. Chinook and coho salmon outmigrants in April and May were found in the diets of bass and yellow perch, and it is likely that kokanee fry would be susceptible at the same time. Yellow perch in Lake Sammamish were very abundant, piscivorous, and cannibalistic at a relatively small size, and may be an important predator of kokanee at a population level.

The consumption of kokanee during thermal stratification by cutthroat trout was much greater than during other seasons. Without known abundances of predators, it is difficult to understand the absolute extent of predation on kokanee in Lake Sammamish (Beauchamp et al. 1995; Baldwin et al. 2000). With depressed numbers of spawners in Lake Sammamish tributaries, any predation that occurs on juvenile kokanee is significant. For every 1000 cutthroat trout in the lake, an estimated 12.2% of age-1 kokanee were consumed. It is important to note that I was not able to differentiate between age 0-1 kokanee and sockeye salmon in Lake Sammamish, and a large escapement of sockeye salmon in Lake Sammamish tributaries would likely buffer predation on kokanee by limnetic piscivores such as cutthroat trout. Baldwin et al. (2000) found cutthroat trout in Strawberry Reservoir, consumed kokanee up to 39% of their length. Although the largest kokanee observed in a cutthroat trout stomach sample in Lake Sammamish was a 120 mm FL age-1 kokanee, but applying the 39% criteria, kokanee up to 150 mm (age-2) were vulnerable to cutthroat trout predation. The relative weight of cutthroat trout during thermal stratification was significantly greater than during the unstratified period, suggesting cutthroat trout are able to take advantage of increased light, and spatial overlap with prey fishes in the metalimnion during day, crepuscular, and night diel periods. Prey encounter rates in Lake Sammamish were greater than those observed in Strawberry Reservoir, Lake Tahoe, and Lake Washington during peak thermal stratification (Beauchamp et al. 1999;

Mazur and Beauchamp 2006). Although limnetic prey fishes include yellow perch and sticklebacks, the temporal and spatial overlap between predatory cutthroat and prey sized kokanee lead to greater predation risk for kokanee during thermal stratification than conditions where thermal constraints do not exist in Lake Sammamish.

Global temperatures have increased in the past 30 years, and forecasts indicate that they will probably continue to increase in the future (Hansen et al. 2006). In the Pacific Northwest, air temperatures rose by approximately 0.8˚C during the 20th century, and models suggest further warming of between 0.5 and 2.5˚C by 2030 (Mote et al. 2003). Thermal stratification in lakes is driven by climatic factors such as ambient air temperature, and the period of thermal stratification and decreased hypolimnetic oxygen is expected to increase as a result of climate change, thus exacerbating the temperature-DO squeezes (Coutant 1990; DeStasio et al. 1996). With increases in temperature as a result of climate change, coldwater species such as salmonids will likely lose habitat in the southern end of their range (Schindler et al. 1990; Mantua et al. 1997). For kokanee and sockeye salmon, Melack et al. (1997) predicted that freshwater growth rates will be reduced in response to increases in temperature and reduced zooplankton in lakes. Such changes appear to be occurring already. For instance, in nearby Lake Washington, Winder and Schindler (2004) documented a decline in *Daphnia* density over a 26 year history, a situation that could have devastating cascading effects on the food web of that lake, and similar implications for Lake Sammamish. With reduced growth of kokanee during the summer and autumn in the future, fecundity and age of maturity may be altered resulting in an increased annual mortality rate and a decline in the abundance of kokanee in Lake Sammamish. In addition, a protracted squeeze in Lake Sammamish could reduce the access of kokanee and cutthroat trout to important hypoxia-tolerant benthic invertebrates for longer periods while zooplankton were less abundant. In combination, local studies of climate in the Pacific Northwest and this study of kokanee in Lake Sammamish suggest an uncertain future for kokanee in the context of climate change.

The future of kokanee in Lake Sammamish is uncertain. In an effort to restore native kokanee throughout the Lake Sammamish watershed, millions of dollars are being spent on best management practices for construction-related impacts, mitigation for habitat blockages, stormwater and sewage treatment, and spawning habitat restoration. While such efforts are important for multiple purposes, they may not be enough in the face of climate change to protect kokanee from extermination if conditions within Lake Sammamish become unsuitable. Understanding current bottlenecks in the population and monitoring the interactions with predators and prey in Lake Sammamish may be more critical to create an environment that offers resilience for kokanee to persist in the face of large scale forcing factors such as climate change.

FIGURES

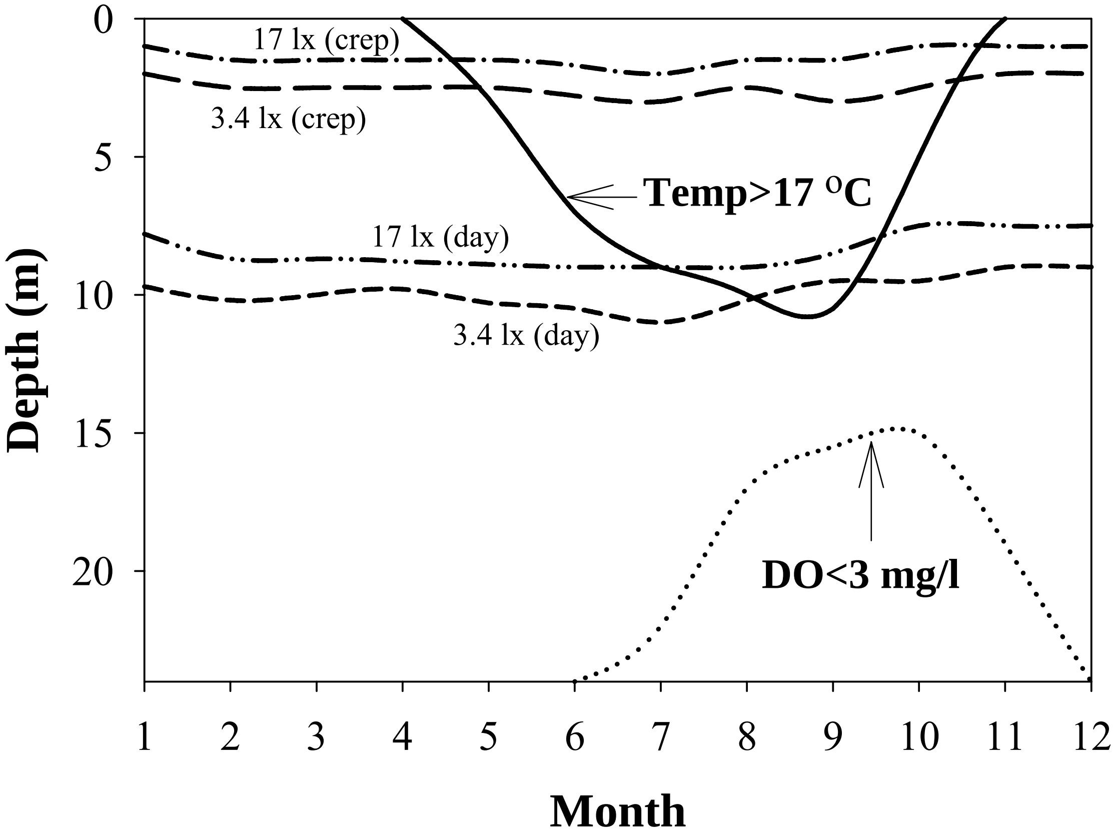

Figure 9. Annual temperature and dissolved oxygen isopleths and isolumes for Lake Sammamish (2002 - 2003). Isolumes include values of 3.4 and 17 lx for diel periods representing day and crepuscular (crep) periods.

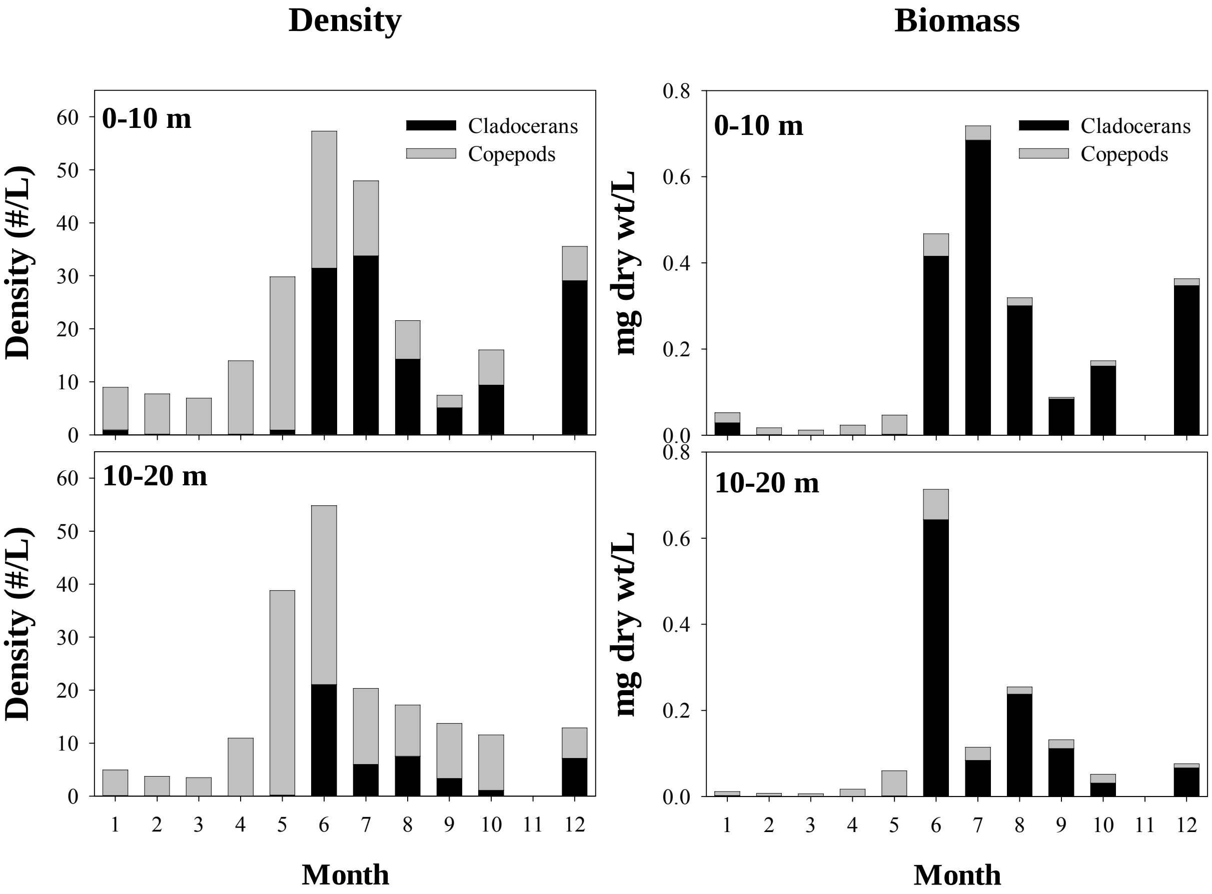

Figure 10. Monthly density and biomass of adult cladocerans and copepods in Lake Sammamish during 2002. Samples were collected using a 12.5 cm diameter Clarke-Bumpus sampler with 153 µm mesh, and composited from 0 to 10 m and from 10 to 20 m depths.

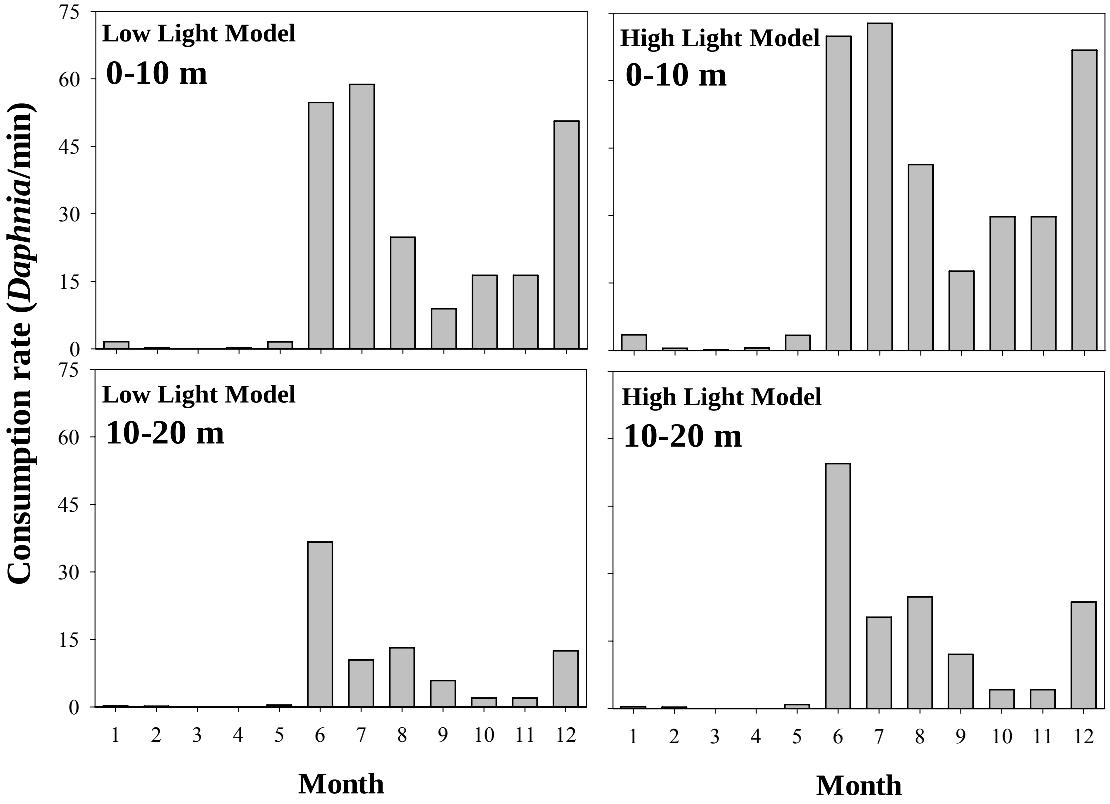

Figure 11. Monthly estimates of consumption rates of *Daphnia* by kokanee in Lake Sammamish in the epilimnion (0-10 m) and metalimnion (10-20 m) for low (<3.4 lx) and high (>3.4 lx) light conditions (Koski and Johnson 2002).

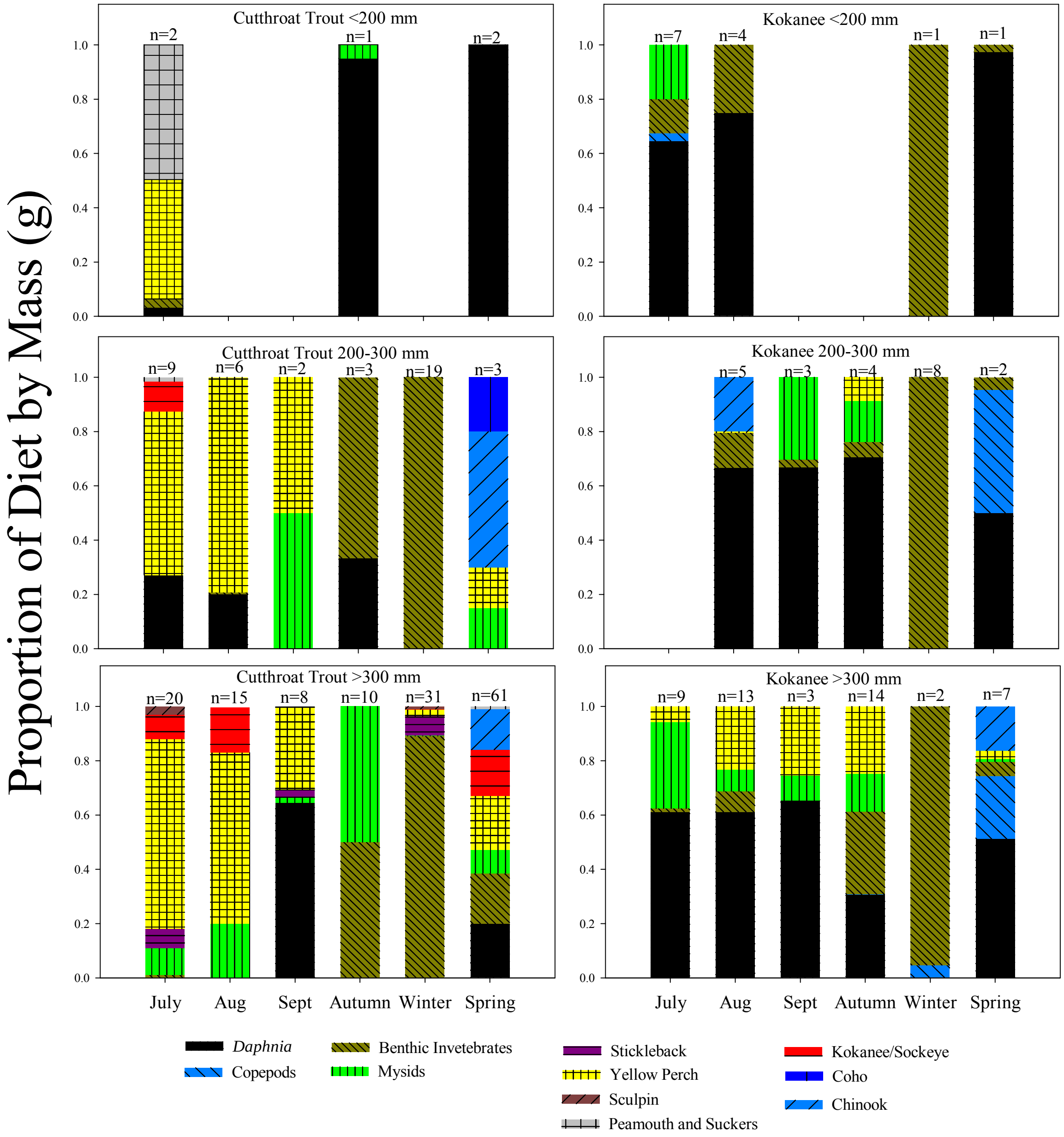

Figure 12. Ontogenetic changes in the diet of kokanee and cutthroat trout in Lake Sammamish for each season. Summer months are broken out individually.

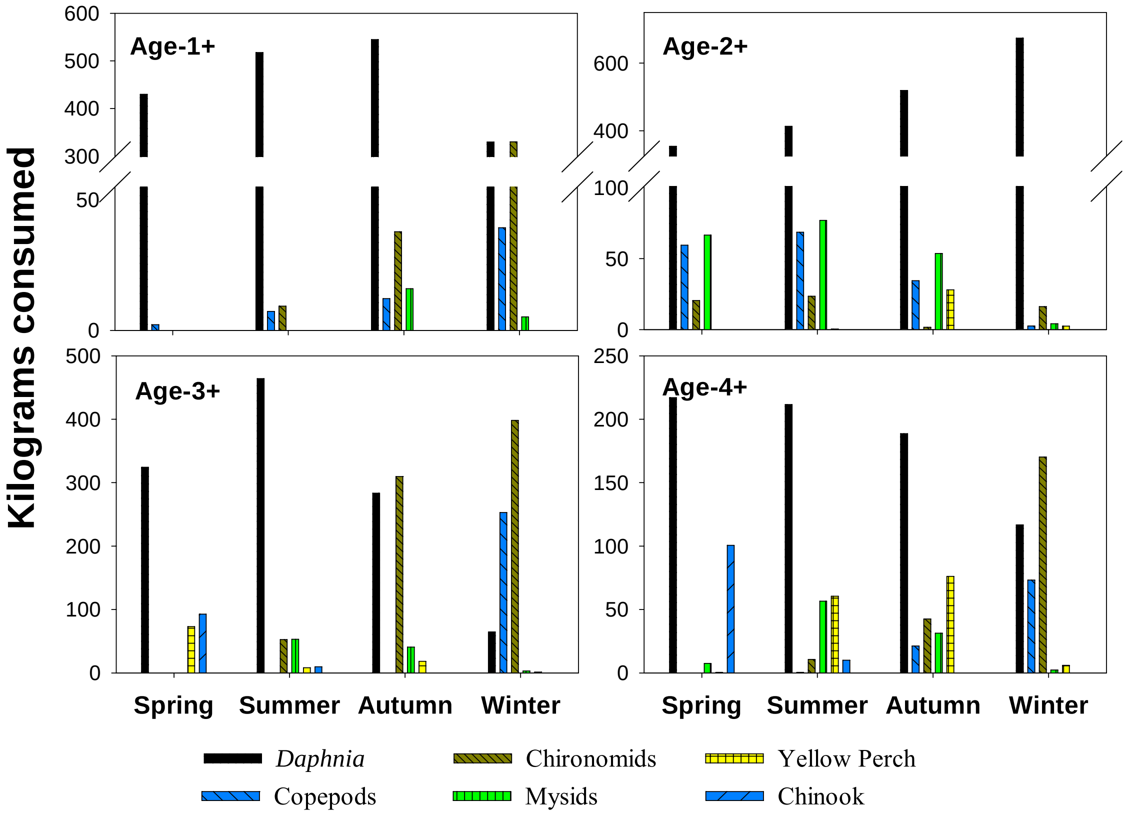

Figure 13. Population level seasonal consumption estimates of major prey items (in kg) by all age classes of kokanee in Lake Sammamish. Population estimates were 8,200 age-1, 3,100 age-2, 1158 age-3, 434 age-4, and 162 age-5 kokanee.

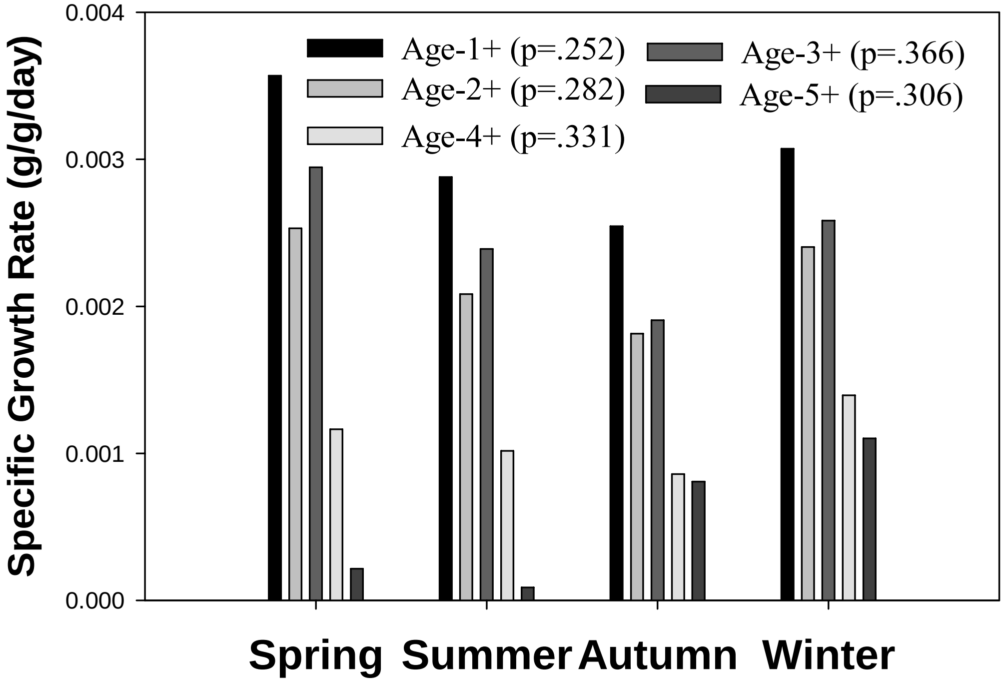

Figure 14. Specific growth rate of individual kokanee in Lake Sammamish for spring (April through June), summer (July through September), autumn (October through December) and winter (January through March). Thermal stratification begins in July and continues until mixing occurs in November. Specific growth rate is used as a measure of efficiency and is simply the average number of grams of prey consumed that is allocated to growth per gram of predator mass for a particular day. P values (proportion of maximum consumption) generated for each age class are annual estimates.

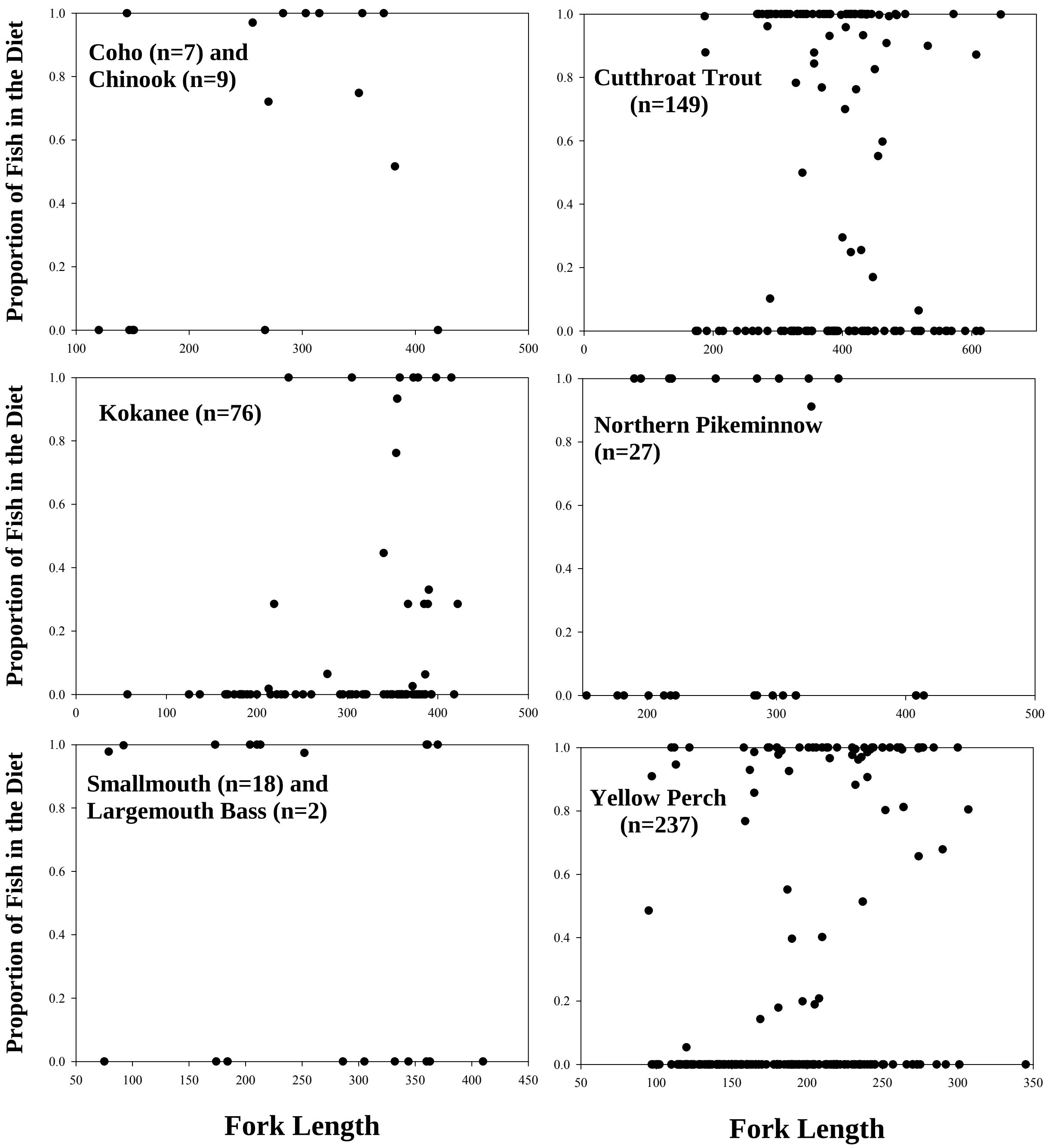

Figure 15. Proportion of fish in the diets of piscivores as a function of fork length in Lake Sammamish.

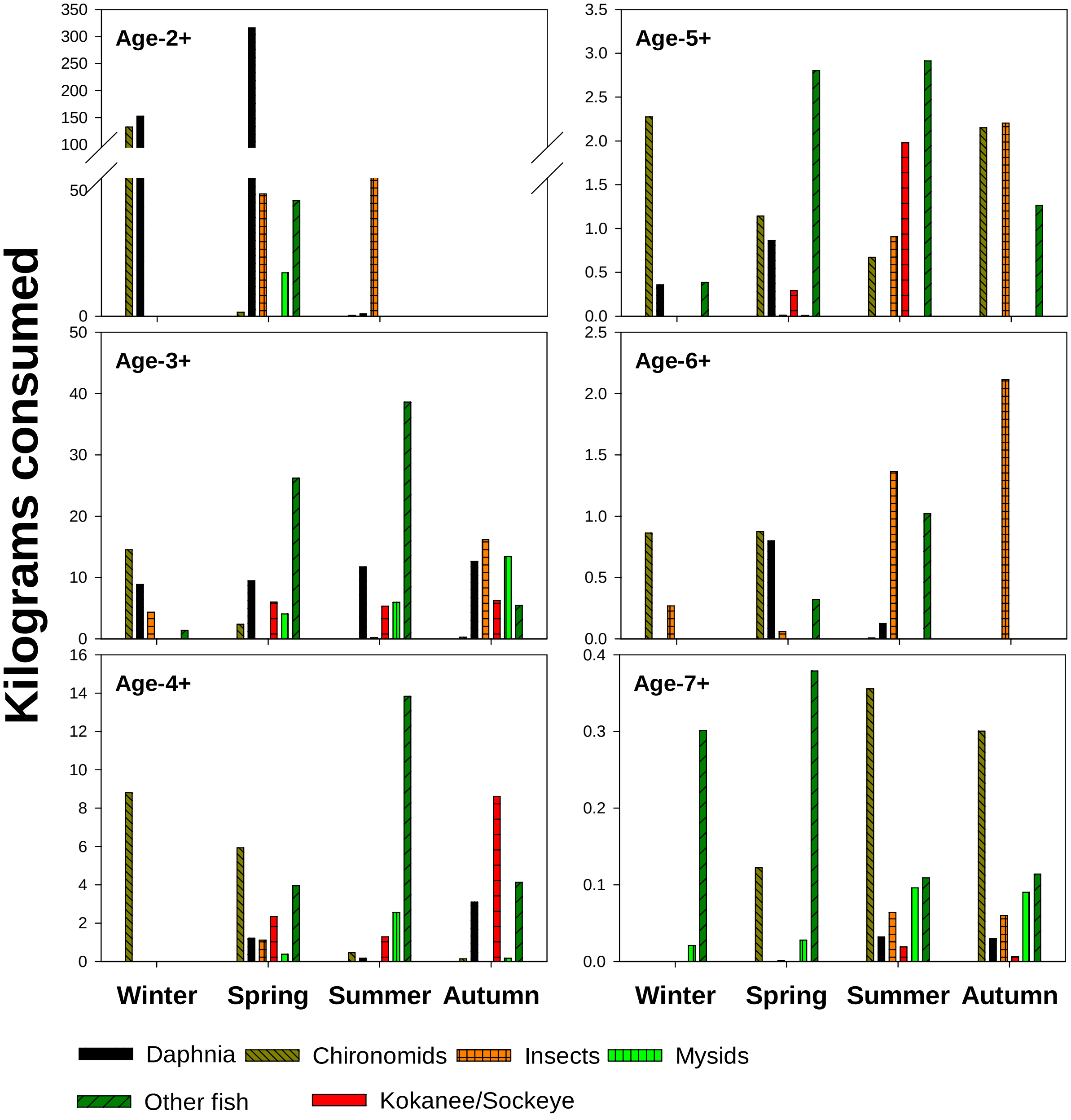

Figure 16. Seasonal consumption estimates by cutthroat trout of major prey items for an estimated population size of 1000 individuals, distributed across age classes from 2 to 7, with 671 age-2, 221 age-3, 73 age-4, 24 age-5, 8 age-6, and 3 age-7 cutthroat trout.

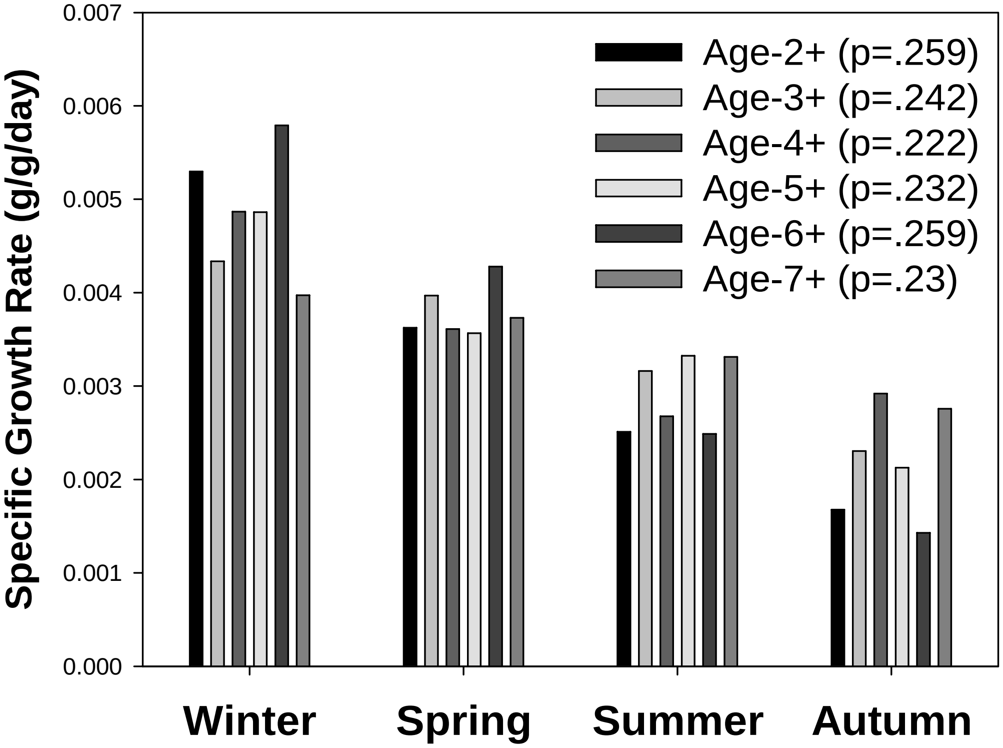

Figure 17. Specific growth rate of individual cutthroat trout of each age class in Lake Sammamish for spring (April through June), summer (July through September), autumn (October through December) and winter (January through March). Thermal stratification begins in July and continues until mixing occurs in November. Specific growth rate is used as a measure of efficiency and is simply the average number of grams of prey consumed that is allocated to growth per gram of predator mass for a particular day. P values (proportion of maximum consumption) generated for each age class are annual estimates.

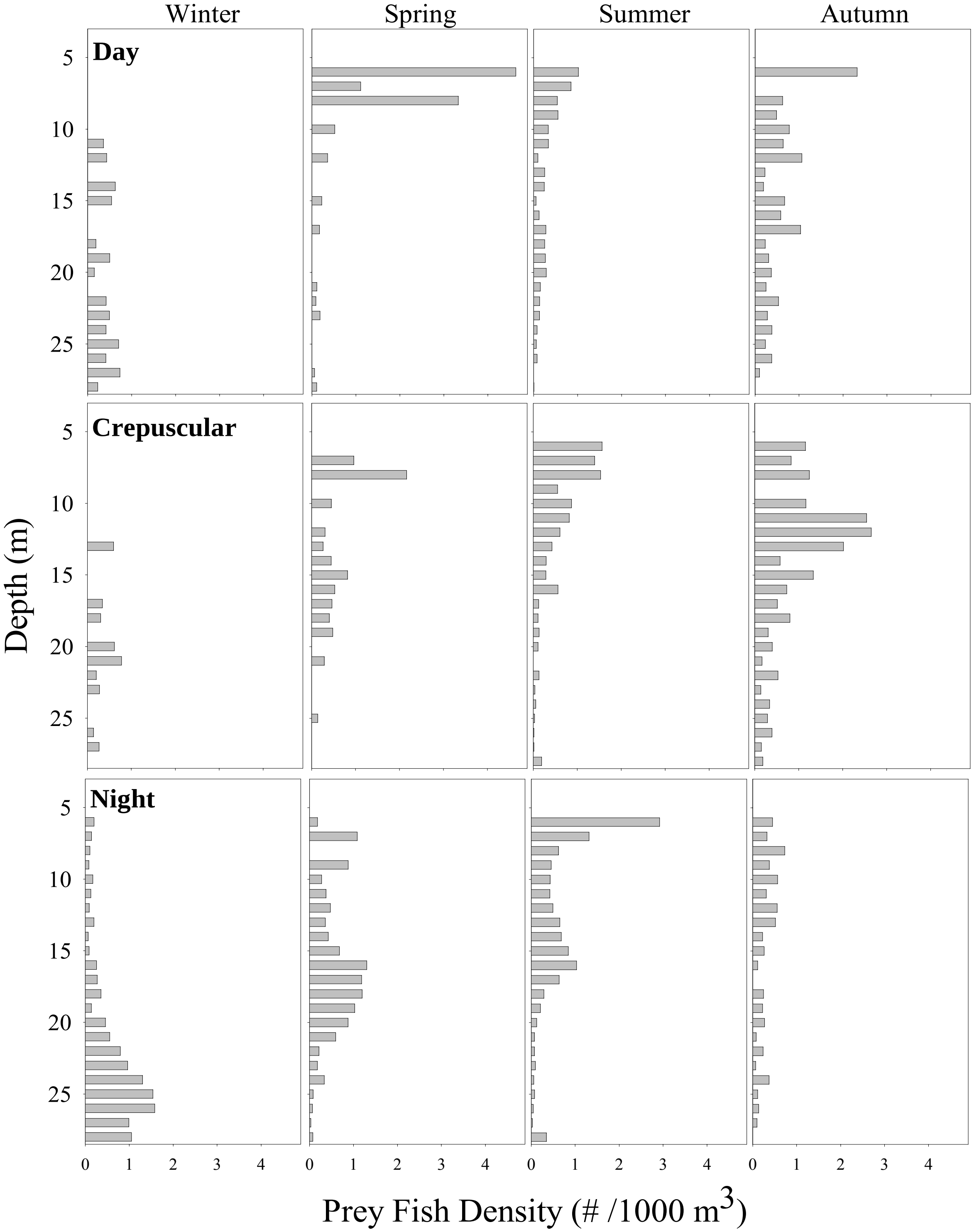

Figure 18. Vertical distribution of prey sized fishes (30-100 mm) from hydroacoustics for each season during day, crepuscular, and night periods in Lake Sammamish.

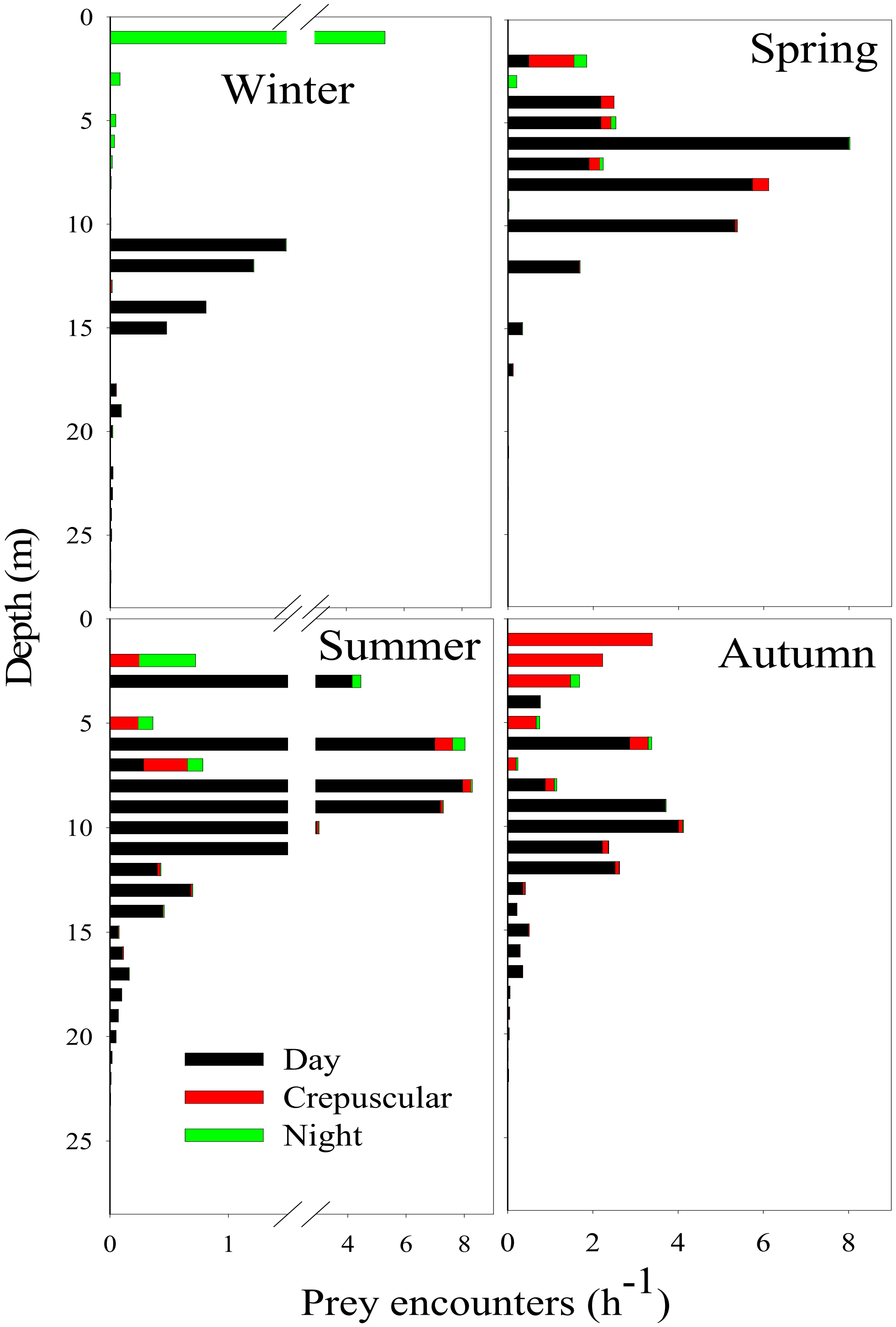

Figure 19. Depth specific predicted prey encounter rates for cutthroat trout in Lake Sammamish for each season and diel period.

TABLES

Table 4. Annual spawning ground escapements using the area-under-the-curve methodology for kokanee and sockeye in tributaries of Lake Sammamish. Kokanee spawn timing begins in November and continues into January, while sockeye spawning initiates in September and finishes in November in Issaquah Creek.

Brood Year	Lewis Creek Kokanee	Laughing Jacobs Creek Kokanee	Ebright Creek Kokanee	Pine Lake Creek Kokanee	Issaquah Creek Sockeye
1996	219	170	70	16	2580
1997	10	29	15	11	580
1998	43	0	40	0	1330
1999	247	27	134	8	200
2000	143	92	362	7	1000
2001	722	2	110	3	500
2002	1002	384	319	4	1500
2003	3296	232	1063	111	500
2004	442	18	134	1	500
2005	217	44	135	1	270
2006	330	65	292	26	500
2007	111	15	21	0	300

Table 5. Mean monthly turbidity (NTUs) measured at depth in Lake Sammamish.

	Depth (m)		
Month	<10	10-15	20-30
1	0.98	0.98	0.93
2	1.90	1.97	1.60
3	1.25	1.25	1.20
4	0.83	1.40	1.25
5	0.55	0.61	0.90
6	0.60	0.78	1.48
7	0.69	0.78	1.39
8	0.59	0.88	0.76
9	0.53	0.75	0.84
10	0.52	0.63	0.82
11	0.81	0.84	1.77
12	1.60	1.75	1.90

Table 6. Species specific parameters for zooplankton collected in Lake Sammamish used to calculate biomass in dry weight (mg dry weight per liter) from length measurements.

Zooplankton Species	Lifestage	lna	B	Source
Bosmina longirostris	Females (mature + immature)	2.7116	2.5294	Bottrell et al. 1976
Cyclops bicuspidatus thomasi	Males + females + immature copepodids	1.51	2.56	Persson and Ekbohm 1980
Daphnia galeata	Immature females	1.51	2.56	Dumont et al. 1975
Daphnia galeata	Total males (mature + immature)	1.51	2.56	Dumont et al. 1975
Daphnia pulicaria	Females (Adult)	1.9445	2.72	O'brien and deNoyelles 1974
Daphnia pulicaria	Immature females	1.9445	2.72	O'brien and deNoyelles 1974
Daphnia pulicaria	Total males (mature + immature)	1.9445	2.72	O'brien and deNoyelles 1974
Daphnia thorata	Females (Adult)	1.51	2.56	Dumont et al. 1975
Daphnia thorata	Immature females	1.51	2.56	Dumont et al. 1975
Daphnia thorata	Total males (mature + immature)	1.51	2.56	Dumont et al. 1975
Diaphanosoma birgei	Total females (mature + immature)	1.2894	3.039	Rosen 1981
Diaphanosoma birgei	Total males (mature + immature)	1.2894	3.039	Rosen 1981
Diaptomus ashlandi	Females (Adult)	1.05	2.46	Pace and Orcutt 1981
Diaptomus ashlandi	Males (Adult)	1.05	2.46	Pace and Orcutt 1981
Epischura nevadensis	Females (Adult)	1.05	2.46	Pace and Orcutt 1981
Epischura nevadensis	Males (Adult)	1.05	2.46	Pace and Orcutt 1981
Leptodora kindtii	Total females (mature + immature)	-0.822	2.67	Rosen 1981

Table 7. Bioenergetics model inputs and diet composition of age-2 through age-7 cutthroat trout (percent wet weight). Prey categories: Dap = *Daphnia*; Inv = benthic invertebrates; Mys = mysids; Stck = 3-spine sticklebacks; YP = yellow perch; Kok = kokanee/sockeye; Ck = Chinook; Co = coho; Cott = cottids; Chb = peamouth chub. Day 1 of the simulation corresponds to 1 January and day 365 represents 31 December. Win = Jan - Mar, Spr = Apr - June; Sum = July - Sept, and Aut = Oct - Dec.

			Mean	Mean	Prey Categories (%)										
Season	Day of Sim	*N*	Fl *(mm)*	Mass *(g)*	*Dap*	Chi	Inv	Mys	Stck	YP	Kok	Ck	Co	Cott.	Chb
Age-2+															
Win	1-91	3	176	54	100	0	0	0	0	0	0	0	0	0	0
Spr	92-182	4	189	69	50.3	2.1	0.8	0	0	22	0	0	0	0	24.8
Sum	183-274	4	220	123	16.5	17	0	66.5	0	0	0	0	0	0	0
Aut	275-365	1	261	202	100	0	0	0	0	0	0	0	0	0	0
Age-3+															
Win	1-91	11	270	208	10	11.1	9.6	0	0	60.7	3.3	3.2	1	0	1.1
Spr	92-182	13	311	356	25.7	14.9	0	0.2	0	59.2	0	0	0	0	0
Sum	183-274	25	349	467	11	28.5	4.1	1.9	8.3	32.4	10.4	0	0	0.4	3
Aut	275-365	6	366	544	0	30	0.7	3.8	12.5	42	11	0	0	0	0
Age-4+															
Win	1-91	2	365	578	0	0	0	0	0	100	0	0	0	0	0
Spr	92-182	20	385	600	5	34.7	6.2	0	0	30.6	17.9	5.6	0	0	0
Sum	183-274	15	437	784	5.6	10.2	0	8.8	0	8.9	21	31.5	8.5	5.5	0
Aut	275-365	4	444	814	20	16.9	5	12.4	8.3	33.3	0	0	0	0	4.1
Age-5+															
Win	1-91	5	459	834	51.7	1.7	0	0	0	29.9	0	16.7	0	0	0
Spr	92-182	16	462	1063	8.1	11.3	0.2	8.8	0	56.7	12.1	2.8	0	0	0
Sum	183-274	1	532	1188	9.2	0.1	0	0.7	0	90	0	0	0	0	0
Aut	275-365	1	550	1200	33	17	1	12	0	33	0	0	0	0	4
Age-6+															
Win	1-91	2	542	1220	49	50.8	0.2	0	0	0	0	0	0	0	0
Spr	92-182	4	561	1399	48.2	17.6	0.8	0	0	33.4	0	0	0	0	0
Sum	183-274	1	607	1480	0	0	0	12.8	0	87.2	0	0	0	0	0
Aut	275-365	0													
Age-7+															
Win	1-91	2	630	1512	0	50	0	0.1	0	0	0	49.9	0	0	0
Spr	92-182	1	590	1631	0	100	0	0	0	0	0	0	0	0	0
Sum	183-274	1	620	1688	4.6	0.1	0	6.8	0	88.5	0	0	0	0	0
Aut	275-365	0													

Table 8. Bioenergetics model inputs and seasonal diet composition (percent wet weight) for kokanee in Lake Sammamish. Prey categories: Dap = *Daphnia*; Copepod = cyclopoid copepods; Inv = benthic invertebrates; Mys = mysids; YP = yellow perch; Ck = Chinook. Day 1 of the simulation corresponds to 1 April and day 365 represents 30 March. Winter = January through March, Spring = April through June; Summer = July through September, and Autumn = October through December.

Season	Day of Simulation	*N*	Mean Fl *(mm)*	Mean Mass *(g)*	Prey Categories (%)					
					Dap	Copepod	Inv	Mys	YP	Ck
							Age-1+			
Winter	1-91	1	125	16	0.0	0	100.0	0	0	0
Spring	92-182									
Summer	183-274	2	147	37	99.5	0.5	0	0	0	0
Autumn	275-365	1	157	48	100.0	0	0	0	0	0
							Age-2+			
Winter	1-91	1	176	68	97.5	0	2.5	0	0	0
Spring	92-182	0								
Summer	183-274	12	222	132	70.7	11.9	4.1	13.3	0	0
Autumn	275-365	4	231	152	82.2	5.0	0	8.1	4.7	0
							Age-3+			
Winter	1-91	4	235	174	6.4	37.9	55.7	0	0	0
Spring	92-182	2	258	241	66.0	0	0	0	15.2	18.8
Summer	183-274	7	267	267	80.9	0	8.8	10.3	0	0
Autumn	275-365	2	313	433	41.3	0	50.0	5.5	3.2	0
							Age-4+			
Winter	1-91	2	320	482	30.0	21.0	49.0	0	0	0
Spring	92-182	3	341	544	66.7	0	0	2.2	0	31.1
Summer	183-274	24	366	624	60.0	0	3.2	17.8	19.0	0
Autumn	275-365	13	392	774	51.9	6.3	12.4	8.1	21.3	0
							Age-5+			
Winter	1-91	0								
Spring	92-182	1	364	640	97.2	0	0	2.8	0	0
Summer	183-274	1	386	744	100.0	0	0	0	0	0
Autumn	275-365	1	389	698	22.8	0	0	48.7	28.5	0

Table 9. Simulation day and corresponding thermal experience used for inputs to the bioenergetics model for kokanee and cutthroat trout in Lake Sammamish.

	Thermal Experience (°C)	
	Kokanee	Cutthroat
Simulation day	Day 1 = 1 April	Day 1 = 1 January
1	11.8	8
31	9.6	7.55
62	12.5	8.6
92	12.7	11.8
123	10.4	9.6
154	10.1	14.1
184	16	12.1
215	11.8	15.1
245	9.35	10.7
274	8	16
305	7.4	11.8
334	8.6	9.35

Table 10. Measurements of surface light for each diel period, light extinction coefficient (μ), mean monthly turbidity (NTU) for the water column (0-20 m), and length of diel period (h) used in the visual foraging model. The crepuscular period corresponds to 1.5 hours after sundown and 1.5 prior to sunrise.

	Surface Light (lx)					Length of Diel Period (h)		
Survey Date	Day	Crepuscular	Night	μ	Turbidity (NTU)	Day	Crepuscular	Night
2-Jul-02	134473	68	<1	0.615	0.795	14	3	7
18-Jul-02	135269	18	<1	0.615	0.795	14	3	7
25-Jul-02	90427	36	<1	0.615	0.795	14.25	3	6.75
6-Aug-02	81303	55	<1	0.628	0.695	13.75	3	7.25
8-Aug-02	87335	45	<1	0.628	0.695	14.1	3	6.9
20-Aug-02	83841	56	<1	0.628	0.695	13.5	3	7.5
29-Aug-02	75552	54	<1	0.628	0.695	13.5	3	7.5
26-Sep-02	62130	55	<1	0.662	0.61	12	3	9
17-Oct-02	44843	41	<1	0.498	0.525	11	3	10
14-Nov-02	29102	41	<1	0.617	0.89	9.5	3	11.5
27-Jan-03	38224	45	<1	0.621	0.98	9	3	12
1-Mar-03	72364	56	<1	0.626	1.75	11.5	3	9.5
28-Mar-03	66878	45	<1	0.659	1.25	12	3	9
29-Apr-03	60707	45	<1	0.547	1.1	13.75	3	7.25
29-May-03	111776	41	<1	0.502	0.55	15.5	3	5.5
9-Jun-03	123461	55	<1	0.604	0.795	15.5	3	5.5
17-Jul-03	120647	56	<1	0.615	0.795	15.3	3	5.7
4-Aug-03	101747	60	<1	0.628	0.695	14.3	3	6.7
28-Aug-03	104251	50	<1	0.628	0.695	13.7	3	7.3
3-Oct-03	43602	45	<1	0.498	0.525	11.6	3	9.4

Table 11. Estimate of *Daphnia* consumption by month for all age classes of kokanee from bioenergetics modeling. Wet weight standing stock was estimated for each month by using biomass dry weight estimates and converting those to wet weights using a ratio of 10% (Dumont et al. 1975). Percent consumed is the total consumption for each age of kokanee divided by the wet weight standing stock. Population size estimates are 8,200 age-1, 3,100 age-2, 1,158 age-3, 434 age-4, and 162 age-5 kokanee.

	Kokanee consumption of *Daphnia* by age class (kg)						
Month	Age-1	Age-2	Age-3	Age-4	Age-5	Wet weight Standing Stock (kg)	Percent Consumed
1	57.58	207.69	37.90	44.01	28.52	998.83	37.6
2	91.32	211.89	14.31	34.41	34.17	680.76	56.7
3	190.77	265.75	18.03	42.22	41.63	536.48	104.1
4	131.96	111.25	101.02	70.52	43.37	1180.48	38.8
5	151.69	124.57	113.68	76.34	45.93	3131.06	16.4
6	162.72	130.82	122.36	77.55	45.94	3733.59	14.4
7	173.73	137.44	152.36	73.28	47.00	1941.88	30.1
8	178.02	142.37	164.74	72.29	46.62	1072.14	56.3
9	194.70	158.86	166.14	75.22	42.67	737.58	86.4
10	411.72	332.64	364.71	163.10	98.78	1006.41	136.2
12	172.30	179.46	91.81	62.72	10.35	771.25	67.0

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