DISSERTATION

PREDICTING THE EFFECTS OF ENVIRONMENTAL CHANGE ON THE BEHAVIOR, GROWTH, AND PREDATION RISK OF JUVENILE KOKANEE SALMON

Submitted by

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In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

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Fort Collins, Colorado

Fall 2004

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August 18, 2004

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ABSTRACT OF DISSERTATION

PREDICTING THE EFFECTS OF ENVIRONMENTAL CHANGE ON THE BEHAVIOR, GROWTH, AND PREDATION RISK OF JUVENILE KOKANEE SALMON

Kokanee (*Oncorhynchus nerka*) have shown great variation in diel vertical migration (DVM) patterns throughout their geographic range. I utilized a bioenergetics-based foraging model to characterize DVM patterns exhibited by juvenile kokanee in Blue Mesa Reservoir (BMR), Colorado, and to address how environmental change (e.g., eutrophication, climate warming, drought, and dam operations) could affect kokanee growth and predation risk. I enhanced an existing bioenergetics-based foraging model by incorporating a light-dependent functional response that utilizes light availability and prey density to better predict feeding rates. By executing a series of simulations that considered either bioenergetic efficiency or predator avoidance, I determined that kokanee DVMs in BMR are controlled more by predator avoidance in early summer. Diel vertical migrations become more bioenergetically efficient in August, when warmer temperatures and thermal stratification provide some protection from cold-water predators such as lake trout (*Salvelinus namaycush*). I also investigated the effects of drought and dam operations (specifically, the installation of a temperature control device (TCD)) on kokanee growth and predation risk from lake trout in BMR. Predation risk was characterized by lake trout reaction distance (a function of turbidity and light level) and probability of occurrence (a function of temperature). I found that predation risk was lowest under full reservoir conditions and highest in drought conditions. Because drought is characterized by high water clarity, and both drought and TCD conditions had cooler metalimnetic temperatures, the volume of foraging habitat available to lake trout was increased. Additionally, environmental changes like climate warming and eutrophication have the potential to alter the degree and timing of DVMs. Increased eutrophication lowered water clarity and decreased visibility at greater depths, so kokanee needed to inhabit shallower water to see zooplankton prey. Consequently, spending more time in warmer surface waters increased bioenergetic expenses which were further amplified by climate warming. In general, I found that neither eutrophication nor climate warming alone affected kokanee growth, but their interactive effects reduced kokanee growth to a great degree. My results suggest that kokanee behavior must be plastic in response to resource availability and predation risk, which will vary with environmental conditions.

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ACKNOWLEDGEMENTS

Funding for this work was provided through a U.S.D.A. National Needs Fellowship in Water Sciences, with additional resources supplied by the U.S. Bureau of Reclamation, Upper Colorado Region, Salt Lake City Office.

I could not have completed this project without the help of many people. Sathish Kumar Chittibabu was integral to the programming aspects of this project; I am extremely grateful for all the time he generously invested in ensuring that the model was the best it could possibly be. I'm also thankful for my committee (Jim Loftis, Jill Baron, Will Clements, and Ken Wilson) who thoughtfully reviewed my work and manuscripts. My advisor, Brett Johnson, survived six years of my shenanigans and deserves accolades for this feat. He patiently helped me accomplish more than I thought I was capable of, and I will surely use much of what he has taught me about writing, presenting, and science in general, long into the future.

Without my friends and family, my sanity surely would have suffered a great deal more than it already has. Steve Del Grosso, Brenda Moraska-LaFrancois, Nicole Vieira, Jill Hardiman, Cecily Mui, and Harold Fraleigh provided endless encouragement. And finally, I could not have completed this project without the support of my mother, Catherine Grant, who helped me survive the most challenging time of my life.

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INTRODUCTION

Research Background and Questions

Aquatic organisms have developed complex behaviors to survive in a heterogeneous environment. Animals living in lakes and reservoirs must cope with gradients in light, temperature, and food availability seasonally, during the course of a day, and at different depths in the water column. Kokanee and sockeye salmon (*Oncorhynchus nerka*) perform diel vertical migrations (DVMs) but the particular patterns of these DVMs vary greatly throughout their geographic range. Diel vertical migrations in kokanee and sockeye are thought to be driven by three main mechanisms: tracking zooplankton prey that vertically migrate, maximizing bioenergetic efficiency, and predator avoidance (Levy 1987; Clark and Levy 1988). Scheuerell and Schindler (2003) found that in northern latitudes, sockeye DVMs are driven largely by predator avoidance and that DVMs are triggered by light level. However, DVMs of kokanee and sockeye in warmer environments may be affected by bioenergetic considerations (Brett 1971; Bevelhimer and Adams 1993). Kokanee and sockeye forage on zooplankton, which are usually most abundant in warmer surface waters. Conversely, higher temperatures increase respiration costs for fish, so it may be beneficial to spend non-feeding periods at greater depths where temperatures are lower. In addition, light at greater depths is also decreased, so kokanee and sockeye may be able to use DVMs to avoid visually foraging predators during the day.

A bioenergetics-based foraging model developed by Stockwell and Johnson (1997; 1999) has been utilized to study the behavior of older fish in Blue Mesa Reservoir (BMR), Colorado, but the vertical migration behavior of juvenile kokanee was, until recently, unknown. Juvenile kokanee in BMR perform DVMs partly in response to predaceous lake trout (Hardiman et al. in press). However, the extent to which bioenergetic considerations affect DVMs was not understood. The Stockwell and Johnson (1997, 1999) bioenergetics model required a better functional response to link feeding rates with environmental conditions, and was recently enhanced with a light-dependent functional response developed by Koski and Johnson (2002). Feeding rates are now calculated as a function of prey density and light, which varies with depth, time of day, and season. This improvement greatly increased the ability of the model to predict kokanee feeding rates and energy acquisition throughout a range of environmental conditions and DVM scenarios.

In addition to simply determining what drives juvenile kokanee DVMs in BMR, the model can be used to assess the effects of environmental change on kokanee growth and behavior. Water resource management and dam operations have the potential to change the thermal structure of reservoirs. Temperature control devices (TCDs) have been installed on several dams to regulate downstream temperatures and flow rates to benefit endangered native fishes. Temperature control devices can take warm water from the epilimnion, removing heat from the reservoir and cooling the meta- and hypolimnion (Boyer and Cutler in review). Dam operations can also be affected by inter-annual climate variability that can result in either full-pool or drought conditions in the reservoir. In addition to directly changing energetic demands of vertically migrating fish and affecting its food resources, interactions with predators may be influenced as well. In BMR, lake trout are cold water predators that prey heavily on kokanee (Johnson and Martinez 2000). If metalimnetic temperatures in the reservoir cool from either TCD effects or drought, the amount of kokanee-lake trout habitat overlap may increase, escalating the potential for lake trout to more easily find kokanee prey. To effectively manage kokanee populations in BMR, it is necessary to determine how dam operations and inter-annual climate variability affect not only growth, but predation risk to lake trout as well.

Long-term environmental change can also affect lake and reservoir ecosystems. Eutrophication has plagued some aquatic ecosystems for decades and is a threat to both freshwater resources for humans and the organisms inhabiting these systems (Carpenter et al. 1998). Moderate levels of eutrophication may stimulate zooplankton production and increase food resources for kokanee, which are nearly 100% planktivorous throughout their entire lives (Finnell and Reed 1969; Stockwell et al. 1999). However, increased algal abundance can greatly reduce water clarity, (Canfield and Bachmann 1981; Portielje and Van der Molen 1999), and increase production of toxic cyanobacteria that restrict zooplankton abundance (Kotak et al. 1996; Watson et al. 1997; Carpenter et al. 1998). Climate warming is another agent of environmental change, the effects of which are not yet so apparent. Global circulation models predict that average global surface temperatures will increase by up to 6 °C in the next century (Houghton et al. 2001). In addition to directly increasing the energetic demands of fish in warmer water (Brett 1971), increased temperatures can affect zooplankton productivity by decreasing egg development time (Gabriel et al. 1987) and bolstering reproductive rates. However, climate warming can trigger other environmental changes, including eutrophication, and while much work has focused on the effects of one aspect of environmental change, very little work has been done to predict the interactive effects of two or more factors.

In light of the several issues that can potentially influence kokanee growth and mortality, I have focused my research on several questions regarding the behavior and growth of juvenile kokanee in BMR. First, is there a bioenergetic advantage to juvenile kokanee that perform DVMs, and why do DVM patterns change seasonally? Second, how does short-term environmental variability, such as the effects induced by drought or a TCD, affect kokanee growth and predation risk to lake trout in BMR? And last, what are the potential interactive effects of climate warming and eutrophication on juvenile kokanee growth? The Stockwell and Johnson (1997, 1999) bioenergetics-based foraging model is well-suited to approach questions such as these, particularly after the incorporation of the light-dependent functional response (Koski and Johnson 2002).

Overview of Research Findings

In Chapter 1, I utilized the bioenergetics-based foraging model to demonstrate the bioenergetic advantages of DVMs performed by juvenile kokanee during the summer of 2002 in BMR. Daily growth was computed for three sampling dates in June, July, and August using various DVM patterns as defined by either predator avoidance (DVMs triggered by light level) or bioenergetic efficiency (DVMs triggered by stomach fullness). In general, predator avoidance scenarios underestimated growth by 0.03 g, 0.14 g, and 0.26 g in June, July and August, whereas the bioenergetic efficiency scenarios overestimated growth by 0.10 g in June and July, and 0.06 g in August. This suggests that both predator avoidance and bioenergetic efficiency drive kokanee behavior but that the relative importance of each changes over the summer. Later in the summer, kokanee may be able to concentrate more on growth than predator avoidance because warmer temperatures create a thermal barrier to cold-water predators such as lake trout. While this doesn't completely eliminate all possibility of predation, the amount of time that cold-water predators spend above the hypolimnion can be greatly reduced by warmer temperatures in late summer, enabling kokanee to perform DVMs that further minimize predation risk while maximizing energy consumption.

In Chapter 2, I compared kokanee growth and predation risk across a range of conditions resulting from dam operations (the installation of a TCD) and short-term inter-annual climate variability (either full-pool or drought conditions). If kokanee performed the same DVMs in June that were observed in the drought year (DVMs in other conditions were unknown), kokanee in full-pool and TCD scenarios lost weight compared to kokanee in drought conditions (-0.01 vs. 0.02 $g \cdot g^{-1} \cdot d^{-1}$). In July and August, daily growth in full-pool and TCD conditions was approximately equal (~0.01 $g \cdot g^{-1} \cdot d^{-1}$ for July and August) but was less than the observed growth in drought conditions (0.02 $g \cdot g^{-1} \cdot d^{-1}$). Predation risk from lake trout was estimated as a function of depth, light level and turbidity, predator reaction distance, and temperature. Predation risk profiles generated across depths and time of day indicate that predation risk throughout the summer was highest under drought conditions and lowest under full-pool conditions, with TCD conditions being intermediate. For kokanee performing drought year DVMs, the predation risk to foraging gain ratio (μ/g) in July and August was lowest for full-pool conditions, and highest in TCD conditions. However, it is unlikely that kokanee would perform these same DVMs in a full-pool year or under the effects of a TCD; predation risk is lower overall and kokanee could take advantage of high food resources in shallower waters while avoiding predators due to lower water clarity (thus, reducing μ/g). Because predation risk can change dramatically between different thermal scenarios, kokanee DVM patterns should be plastic. When predation risk is low, kokanee should perform DVMs that result in greater bioenergetic efficiency and when predation risk is high bioenergetic efficiency should decline.

Finally, Chapter 3 concentrates on evaluating the potential effects of climate warming and eutrophication on growth of juvenile kokanee. Daily growth was calculated for different sized kokanee (1, 5, 10, and 15 g) in June, July, and August under nine scenarios consisting of three trophic states (mesotrophic, eutrophic, and hypereutrophic) and three climate scenarios (current temperatures, and increased surface temperatures of 3 and 6 °C). Model inputs (temperatures, Secchi depths and zooplankton densities) for the different trophic states were derived from measurements at representative systems, using BMR as the mesotrophic system, Lake Mendota as the eutrophic system, and Lake Washington in the early 1960's as the hypereutrophic system. Climate warming and eutrophication alone did not significantly affect daily growth for any sized fish during any month, and in fact increased daily growth slightly (up to 0.5% body weight) in some cases. However, the interaction of these two factors greatly reduced kokanee growth, especially for larger (10 and 15 g) fish, which lost weight (up to 3% of their body weight per day in June and July). Eutrophication reduced water clarity, requiring kokanee to move to shallower, warmer water to find their prey, resulting in decreased growth. As a result, kokanee may be constricted to narrow depth ranges where they are bounded by potentially lethal temperatures above and insufficient light to find prey below. In addition, predation risk may also be affected by changes in temperature and light availability. These simulations demonstrate the need to examine interactive effects of ecosystem perturbations; by studying the effects of one factor alone, potential effects of environmental change on aquatic ecosystems may be greatly underestimated. Plasticity in kokanee behavior is a necessary adaptation to changing environmental conditions, whether they are from inter-annual or seasonal variability in climate (e.g., wet vs. drought years) or anthropogenic in origin (e.g., global warming, eutrophication, or dam operations).

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CHAPTER 1

TRADEOFFS BETWEEN BIOENERGETIC EFFICIENCY AND PREDATOR AVOIDANCE DRIVE BEHAVIOR OF AGE 0 KOKANEE

Abstract

I enhanced a bioenergetics-based foraging model that predicts kokanee (*Oncorhynchus nerka*) growth by incorporating a new light-dependent functional response that links feeding rate with environmental conditions such as light level and prey density, both of which vary as kokanee perform diel vertical migrations (DVMs). I used the foraging model to help ascertain the bioenergetic advantages of DVMs performed by age 0 kokanee during the summer of 2002 in Blue Mesa Reservoir, Colorado. I compared daily growth on three sampling dates by performing simulations with various DVM patterns as defined by either predator avoidance or bioenergetically efficient strategies. In June, July, and August, observed growth rate was approximately 1.8% body mass increase per day. In general, predator avoidance scenarios underestimated growth by an average of 0.03 g, 0.14 g, and 0.26 g in June, July and August. Bioenergetic efficiency scenarios overestimated growth by an average of 0.10 g in June and July, and 0.06 g in August, suggesting that juvenile kokanee integrate both mortality risk and growth efficiency in their behavior but that the relative importance of each may change over the summer. Optimal foraging theory predicts that the mortality

risk: growth maximization ratio should be minimized for animals searching for food. By incorporating a light-dependent functional response into the foraging model, the amount of time spent at differing light levels may be used as a "common currency" to quantify mortality risk (capture by visual predators) and growth maximization (energy gain by visually foraging by planktivores).

Introduction

Many mechanisms behind animal behavior remain elusive, presenting a puzzle to solve using pieces created from observations of animals in their natural habitats. One intriguing behavior is the diel vertical migrations (DVMs) of some fish, where DVM patterns are thought to be the result of tradeoffs between tracking food resources, bioenergetic efficiency, and predator avoidance (Levy 1987, 1990a, 1990b). In lakes and reservoirs, a wide range of food densities, light availability, and temperatures can be experienced during the course of a day as a fish moves up and down in the water column. Zooplankton prey are often concentrated in the epilimnion, but if zooplankton migrate in response to predators or light (Lampert 1989; Han and Straskraba 1998; Ringelberg and Van Gool 2003) planktivorous fish must be able to track their movements to exploit them as food (Levy 1990a). Additionally, depth affects the rates at which food is consumed and assimilated. Incident light changes as a function of time of day, season, and geographic location; it also attenuates with depth, and is a major factor in determining the ability of a fish to locate and capture prey, affecting its functional response (Ali 1959; Townsend and Risebrow 1982; Vogel and Beauchamp 1999; Koski and Johnson 2002). Temperature drives rates of digestion and growth (Brett 1971a; Brett and Glass 1973) and is vertically heterogeneous in many lentic environments. Additionally, planktivorous fish must avoid predation and some use DVMs to evade predators by seeking low-light environments (Eggers 1978; Clark and Levy 1988; Scheuerell and Schindler 2003).

The relative effects of each of these factors probably vary across systems, and it can be difficult to assess the degree to which predation risk and bioenergetic demands drive the DVM patterns of fishes. The extent to which DVMs provide a bioenergetic advantage continues to be debated, and scientific literature has provided conflicting explanations for the reasons that fish perform DVMs (e.g., Johnston (1990) and Scheuerell and Schindler (2003) vs. Bevelhimer and Adams (1993), Brett (1971a), and Stockwell and Johnson (1997, 1999)). Bioenergetics-based foraging models have been utilized to explain movements in terms of energetic efficiency (Beauchamp et al. 1989; Bevelhimer and Adams 1993; Stockwell and Johnson 1997, 1999). In this case, vertically migrating fish may forage in an environment with high energetic costs (due to higher temperatures in the epilimnion where prey might be found), but rest and digest in deeper water with lower energetic costs; DVMs are thought to balance energetic tradeoffs between these two environments (Brett 1971a). On the other hand, recent work (Scheuerell and Schindler 2003; Hardiman et al. in press) has focused on assessing predation risk as a function of light level and exposure to predators, and examining to what extent planktivores exploit low-risk "anti-predation" windows (Clark and Levy 1988) while foraging. Results suggest that movements of fish in some systems can be largely driven by predator avoidance instead of bioenergetic efficiency.

One of the most prominent examples of a fish that makes DVMs is sockeye salmon (*Oncorhynchus nerka*) and its landlocked variety, kokanee. Sockeye and kokanee have been extensively studied in northern climates and their growth and behavior are well documented (Rogers 1973; Hyatt and Stockner 1985; Brett 1986; Levy 1990a, 1990b; Adkison et al. 1996; Luecke et al. 1996; Edmundson and Mazumder 2001; Mazumder and Edmundson 2002; Scheuerell and Schindler 2003). Scheuerell and Schindler (2003) have proposed that in northern latitudes the predominant reason for juvenile sockeye DVMs is predator avoidance. However, the behavior of kokanee introduced to warmer regions differs, and so might the importance of predator avoidance in comparison to bioenergetic efficiency. Predators in warmer regions can be different from those in their native systems, and thermal stratification during summer months presents novel conditions that affect energetic requirements. So for kokanee in warmer climates, there is still much uncertainty surrounding the reasons for observed DVMs – is there a bioenergetic advantage to performing DVMs, are DVMs driven more by predator avoidance, or are DVMs the result of a combination of these factors.

Bioenergetics models have served as unique and helpful tools in analyzing the behavior of fish that make DVMs (Beauchamp et al. 1989; Hanson et al. 1997). These models work on the premise that the amount of energy consumed through feeding must balance energetic outputs in the form of waste products, metabolism, and growth (Hanson et al. 1997). Because kokanee are nearly 100% planktivorous throughout their lives (Finnell and Reed 1969; Beauchamp et al. 1989; Stockwell et al. 1999) and their physiology has been studied intensively (Brett and Groot 1963; Brett 1971b, 1971a; Brett and Glass 1973; Brett and Shelbourn 1975) they are ideal for use with bioenergetics models. A significant shortcoming of these models, however, is the inability to predict energetic inputs. Predicting how much energy a fish actually consumes is vital to predicting how much a fish will grow. In this paper, I have incorporated an enhanced functional response submodel for small kokanee (Koski and Johnson 2002) into an existing bioenergetics-based foraging model (Stockwell and Johnson 1999). The functional response submodel integrates light level as a driver for determining which functional response a fish will utilize (e.g., Type I, Type II, or no feeding) based on its depth and time of day. The generality of the model is improved by linking the functional response to light conditions by calculating incident light level as a function of geographic location, date, and time of day (Janiczek and DeYoung 1987). The capability to simulate the effects of food density and light conditions on kokanee feeding represents a significant improvement in the ability of the model to predict how the environment affects kokanee growth.

Recent work by Hardiman et al. (in press) examined the behavior of age 0 kokanee in Blue Mesa Reservoir (BMR), Colorado, but to fully explain DVM patterns in warmer climates a bioenergetic assessment of how age 0 kokanee are procuring and expending energy is required. In this paper I use field data collected by Hardiman et al. (in press) in conjunction with the improved bioenergetics-based foraging model to predict kokanee growth rates under various DVM patterns. I varied fish depth, which affects the amount of food consumed by kokanee and the temperatures at which the food is processed. I compared these simulations to observed DVMs of age 0 kokanee in BMR to determine whether or not their movements were bioenergetically favorable strategies or if other factors such as predator avoidance were operating.

Methods

Model Inputs

I used a bioenergetics-based foraging model to simulate daily growth of age 0 kokanee using inputs from field data measured at BMR during the 2002 growing season. Similar to previous versions of the model (Stockwell and Johnson 1997, 1999), this model operates on 30 minute time steps to simulate a 24 hour day, and the amount of energy consumed by the fish, the amount of energy expended through excretion, egestion, and respiration, and the amount of energy remaining for growth is calculated for each time step. The user provides temperature and zooplankton density profiles by depth, as well as the size of the fish and its vertical migration strategy for a 24 hour time period. Additionally, the user provides zooplankton length and secchi depth.

Blue Mesa Reservoir is a 3,700 ha mesotrophic reservoir with a maximum depth of 101 m, and is located in southwestern Colorado. Large-bodied zooplankton are abundant; *Daphnia pulex* compose up to 97% of the kokanee diet in this system (Stockwell and Johnson 1999). Kokanee growth is well above the average for the species (Stockwell and Johnson 1999). The kokanee's main predator in BMR is the lake trout (*Salvelinus namaycush*). Other fish present are rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), and white and longnose sucker (*Catostomus commersoni* and *C. catostomus*). All simulations used data collected during June, July, and August 2002 by Hardiman et al. (in press). Hydroacoustic surveys and gill nets were used to obtain information on DVM patterns and fish growth. To obtain estimates of kokanee growth rates I fit an exponential growth function to observed weights. I calculated W_t (fish mass at time zero for each day) and daily growth increment for June 5, July 10, and August 6 and used these data to calibrate baseline simulations (described below). These three baseline simulations represent the observed movements of age 0 kokanee in BMR and their growth for each date; these are the simulations to which all other simulations were compared. Additional data collected for model inputs included secchi depths, temperature profiles, and zooplankton densities, which were collected in 0-5, 5-10, 10-15, and 15-30 m depth strata. Because zooplankton were not collected below 30 m, I used a negative exponential for each of June, July, and August to calculate *Daphnia* densities below 30 m (Appendix III) using average monthly *Daphnia* densities collected from BMR in 1994-1997 and 2002 (Johnson et al. 1995; Johnson et al. 1997; Johnson and Stockwell 1998). The assumption that *Daphnia* density decreased exponentially with depth below 30 m is supported by work elsewhere (Wissel and Ramacharan 2003). Data collection and sampling methods are further detailed in Hardiman et al. (in press).

Functional Response

New to this version of the model is a light-dependent functional response that was modeled after laboratory feeding experiments using age 0 kokanee (Koski and Johnson 2002). In addition to the above information, the user must also provide a geographic location, time zone, and date so that a sub-model (Janiczek and DeYoung 1987) can calculate incident light levels. Using secchi depth, a light extinction coefficient (Idso and Gilbert 1974) is calculated (Equation 1.1). This enables the model to calculate light level at any depth (Equation 1.2), using the relationship described by Horne and Goldman (1994):

$$\eta = 1.7 \cdot z_{sd}^{-1} \tag{1.1}$$

(1.2) $$I_z = I_0 \cdot e^{-\eta z}$$

where η is the light extinction coefficient, z_{sd} is secchi depth in meters, I_0 is incident light level (lx), z is fish depth (m), and I_z is the light level at depth z. If light level experienced by the fish was below 0.001 lx I assumed it was too dark for the fish to feed (Ali 1959). If light level was between 0.001 and 3.4 lx the model selected the Type I functional response (Equation 1.3) for food consumption rate, and if light level was above 3.4 lx the fish utilized a Type II functional response (Equation 1.4) and the model calculated feeding rate as a function of prey density at that depth:

(1.3) $$N = X \cdot V$$

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

where N is feeding rate (*Daphnia* consumed/min), X is the slope of the Type I functional response (mean value = 1.74), V is prey density (*Daphnia*/L), β_0 is maximum feeding rate (mean value = 163.3 *Daphnia*/min), and β_1 is the prey density at which feeding rate is equal to half its maximum value (mean value = 42.2 *Daphnia*/L) (Koski and Johnson 2002). The amount of food that the fish could eat during the course of a 24 h simulation was limited by maximum daily consumption, C_{max}, which is a function of the fish's mass in grams (Beauchamp et al. 1989):

(1.5) $$C_{max} = 0.303 \cdot \text{mass}^{-0.275}$$

I performed a sensitivity analysis on the parameters in the two functional response equations, X, β_0, and β_1, by calculating 10% upper and lower bounds for each parameter

(Appendix IV). The resulting equations approximated the 90% confidence intervals for the functional response equations that were obtained in laboratory studies (Koski and Johnson 2002). Sensitivity analyses for the other parameters in the bioenergetics model have been addressed in Bartell et al. (1986), Kitchell et al. (1977), and Stockwell and Johnson (1997).

Model Calibration

I calibrated the new model with the light-dependent functional response to the conditions of BMR. I found that average *D. pulex* densities measured with a Clark-Bumpus sampler underestimated kokanee growth. This probably occurred because zooplankton are very patchily distributed in the environment (Pinel-Alloul 1995; Folt and Burns 1999), and kokanee likely seek patches of zooplankton in which to forage. Therefore, the average zooplankton density measured by a Clarke-Bumpus sampler is probably very different from the zooplankton density that is experienced by foraging kokanee. Koski and Johnson (2002) conducted their functional response experiments in well-mixed vessels in the laboratory, which probably reflected a situation more representative of kokanee foraging in a patch of zooplankton. Therefore, average pelagic zooplankton densities are not appropriate for use with this model. Because densities of *Daphnia* within patches can be several orders of magnitude greater than the average environmental zooplankton density (e.g. Davies (1985), Jürgens et al. (1994), and Kvam and Klieven (1995)), I corrected for patchiness by multiplying average *Daphnia* density by a calibration factor so that simulated kokanee growth in the three baseline simulations matched observed daily growth on each sampling date.

Model Simulations

I used the observed diel vertical migrations and age 0 kokanee growth rates from Hardiman et al. (in press) to estimate zooplankton patch density and calibrate the model for June 5, July 10, and August 6, 2002. I used the median monthly depth of age 0 kokanee determined by hydroacoustics to create generalized DVM patterns which were used for baseline simulations. To calibrate the model, I adjusted the *Daphnia* calibration factor for the baseline simulations until simulated kokanee growth matched the daily incremental growth for each sampling date.

After I calibrated the model using the three baseline simulations, I ran three suites of simulations that utilized varying DVM behaviors (Table 1.1). For each suite of simulations on a given date, fish position was the only variable that changed among simulations. Fish depth was adjusted by 5 m increments down to 60 m so that fish could be positioned at depths of 0-5 m (or 2.5 m), 5-10 m (or 7.5 m), and so on down to 55-60 m (or 57.5 m). For the first suite of simulations (the "Fixed Depth" scenarios), the fish was kept at a constant depth for the entire 24 hour simulation. I performed one simulation for each depth zone at 5 m increments down to 57.5 m, for a total of twelve scenarios.

For the second suite of simulations (the "Bioenergetic Efficiency" scenarios) I predicted fish growth as a function of food availability and temperatures at which the fish was feeding and digesting. Vertical migrations were triggered by stomach fullness, where fish initially located at a "feeding depth" stopped feeding when its stomach became full, moved to a deeper "non-feeding" depth during the day, and did not move up in the water column again to feed until its stomach was 90% empty. Brett (1971b) suggested that appetite in young sockeye reached its maximum rate of change when the stomach had been 90% evacuated; therefore, I assumed that this change in appetite caused the fish to resume feeding. For the first of these scenarios, I started with a feeding depth of 2.5 m and let the fish feed until it reached stomach fullness. At this time the fish stopped feeding and I kept the fish at a 2.5 m non-feeding depth until the fish's stomach was 90% emptied; I then let the fish feed again until C_{max} was reached. This particular simulation is the same as the first simulation in the "Fixed Depth" scenarios. For the next eleven scenarios, while I kept the feeding depth at 2.5 m, the fish's location for the non-feeding depth was moved downward (7.5 m to 57.5 m) for subsequent simulations. I then repeated this process but changed feeding depth so that I had a set of simulations where the feeding depth was 7.5 m, and the non-feeding depths were 7.5 m, 12.5 m, and so on down to 57.5 m. This pattern was repeated until I reached feeding depth / non-feeding depth combinations where the fish's stomach didn't completely fill, so that there was no trigger to initiate a downward migration.

The final suite of simulations was the "Predator Avoidance" scenarios, where kokanee avoided depths that would put them in areas where light level exceeded 0.5 lux, making them more vulnerable to predators (Hardiman et al. in press; Mazur and Beauchamp in press). The general pattern for these simulations was the same for the Bioenergetic Efficiency scenarios; that is, kokanee stayed at a shallower depth during the night, early morning, and evening (the "safe upper depth"), but then retreated to greater depths during the day (the "midday hiding depth"). For the first scenario in this suite, I positioned the fish at 2.5 m at midnight, and then waited until light level reached 0.5 lux, at which time I moved the fish down to its midday hiding depth, the shallowest depth at which light level was less than 0.5 lux at noon. When the light level at 2.5 m again dropped below 0.5 lux I returned the fish to its original position. For subsequent simulations, I kept the safe upper depth at 2.5 m, but moved the fish's midday hiding depth further down by 5 m increments to a maximum depth of 57.5 m. I then repeated this process using a safe upper depth of 7.5 m, 12.5 m, and so on. For these scenarios, light level was used as the trigger for initiating a DVM instead of stomach fullness, which played little part in these simulations. Additionally, if the fish was initially located at a depth where light level never exceeded 0.5 lux during the day, no DVM occurred. For these scenarios, there were no discreet feeding and non-feeding periods; if there was food and adequate light, fish could feed no matter the depth.

Results

Model Inputs

Temperature and *Daphnia* density profiles and secchi depths for June, July, and August 2002 are detailed in Hardiman et al. (in press), and *Daphnia* densities below 30 m were calculated (Table 1.2). For each month the R^2 value for the *Daphnia* vs. depth regression was high (>0.89). Zooplankton length was 1.84 mm, the average length of *D. pulex* in BMR (Stockwell et al. 1999), with a handling time of 0.36 seconds (Koski and Johnson 2002).

Detailed results of the sensitivity analysis can be found in Appendix IV. In general, calculated daily growth increments for kokanee in the baseline simulations are much more sensitive to changes in the Type II functional response parameters than to changes in the Type I functional response. A ±10% change in the Type II parameters changed growth by ±15-30%, but a ±10% change in the Type I parameter resulted in a ±1-6% change in growth. Fish utilize the Type I functional response during periods of low light levels, which occur when light level changes as a result of the sun rising or setting, or from a vertical migration. These times are fleeting though, as light level changes rapidly during crepuscular periods or with a DVM, and the fish spends more time feeding under Type II conditions than Type I conditions in our baseline simulations.

Model Calibration

I fit a growth curve for age 0 kokanee using estimated weights on June 5, July 10, and August 6, 2002 (mass = $0.2634 \cdot e^{(0.018 \cdot t)}$). Methods for obtaining these weight estimates are described in Johnson et al. (2002) and Hardiman (2003). Computed daily growth increments were approximately 1.8% body mass increase per day or 0.078 g, 0.157 g, and 0.238 g for June 5, July 10, and August 6 respectively. *Daphnia* calibration factors for June 5, July 10, and August 6 were 2.1, 2.4, and 12.4 respectively.

Model Simulations

Hydroacoustic data indicated that in June and July, kokanee made one round-trip migration over a 24 hour period, whereas in August kokanee were more concentrated in the metalimnion (12.5 m – 27.5 m) and stayed at approximately the same depth throughout the day (Figure 1.1). Generally, early in the summer kokanee came to minimum depths only under the cover of darkness, but as the temperature in the epilimnion increased in later months kokanee spent more time above the hypolimnion (i.e., remained there into daylight hours) and didn't migrate to such deep depths during the middle of the day.

On June 5, if fish did not vertically migrate (Fixed Depth), they could grow at least two times the observed amount at depths above 30 m, with a maximum growth increment of approximately 0.2 g at 17.5 m (Figure 1.2). Below 30 m, fish did not reach observed growth and even lost weight at depths below 50 m. The results of the Bioenergetic Efficiency simulations suggest that fish could grow more than observed under all depth scenarios where the fish filled its stomach at least once (Figure 1.3). Maximum daily growth increments were obtained at feeding depths of 17.5 m or less; however, at 17.5 m growth declined with decreasing non-feeding depths. At feeding depths less than 17.5 m, the difference in growth was negligible between different non-feeding depths; therefore, results from simulations using non-feeding depths of 27.5 – 57.5 m were averaged. The coefficient of variation for these averages ranged from 0.2% to 2.7% for all dates. The June 5 Bioenergetic Efficiency scenario that produced the highest daily growth increment (0.2 g, a 4.6% increase in body mass) occurred when feeding depth and non-feeding depth were 17.5 m, which was the same simulation as in the Fixed Depth scenarios. Bioenergetic Efficiency simulations were not performed for feeding depths below 30 m because fish could not fill their stomach completely during the 24 hour simulation period; if the fish's stomach didn't fill, there would be no prompt for a DVM to occur.

Predator Avoidance simulations for June 5 indicate that observed growth was achieved or exceeded only when the safe upper depth was 15 m or less (Figure 1.4). Even at a safe upper depth of 7.5 m, fish did not reach observed growth when the midday hiding depth was below 47.5 m. The maximum daily growth increment (approximately 0.14 g, a 3.2% body mass increase) occurred when fish were at a 2.5 m safe upper depth and went down to a 37.5 m midday hiding depth. Simulated growth was below observed growth in all cases where the safe upper depth was below 15 m, and fish lost weight when they descended to a midday hiding depth of 57.5 m. The movements of the fish in the June 5 baseline scenario most resembled the Predator Avoidance scenario in which the fish was at a safe upper depth of 17.5 m but then went down to 57.5 m for its midday hiding depth; however, this simulation resulted in almost no growth at all (0.003 g) because the timing of this migration was significantly different than the generalized baseline DVM. In June, light level at noon was below 0.5 lux at depths of 37.5 m and greater. If the safe upper depth of the fish was at 37.5 m or below, no DVM occurred because the higher light levels that trigger a DVM were absent.

On July 10, if fish did not vertically migrate (Fixed Depth) they had the opportunity to surpass observed growth, with a maximum growth increment of approximately 0.27 g (a 3.1% increase in body mass) at a fixed depth of 12.5 m (Figure 1.2). Simulated growth was very close to observed growth at fixed depths of 2.5 m, 17.5 m, 22.5 m, and 27.5 m. Below 30 m, fish did not reach observed growth and lost weight at depths below 45 m. The Bioenergetic Efficiency simulations suggest that fish could grow more than observed under all depth scenarios (Figure 1.3). Maximum daily growth increments were obtained when feeding depth was 12.5 m. Daily growth increment increased with non-feeding depth, with maximum growth occurring at non-feeding depths at or below 27.5 m. The scenario that produced the highest daily growth increment (nearly 0.3 g, or a 3.4% increase in body mass) had a feeding depth of 12.5 m and non-feeding depths anywhere between 27.5 m and 57.5 m. Bioenergetic Efficiency simulations were not performed for feeding depths below 12.5 m because fish could not fill their stomach completely during the 24 hour simulation period.

Predator Avoidance simulations for July 6 predicted growth increments below observed growth except in scenarios where the safe upper depth was 2.5 m and the midday hiding depth was at 52.5 or 57.5 m, when the observed growth was barely reached (Figure 1.4). Fish lost weight in every simulation when they were at a safe upper depth of 12.5 m or greater. There were only two midday hiding depths (52.5 m and 57.5 m) because high water clarity allowed for high light penetration and noon light level was less than 0.5 lux only at depths greater than 50 m. In the baseline simulation, fish resided at an upper depth of 17.5 m – 22.5 m and went down to 42.5 m during the day, which did not match any simulations in either the Bioenergetic Efficiency or Predator Avoidance suites. In July, light level at noon was below 0.5 lux at depths of 52.5 m and greater; therefore, if the safe upper depth of the fish was 52.5 m or below, no DVM occurred because higher light levels that could prompt a DVM were absent.

On August 6, if fish did not vertically migrate (Fixed Depth), they could achieve approximate observed growth at depths of 27.5 m and above, with a maximum growth increment of approximately 0.26 g at a fixed depth of 12.5 m (Figure 1.2). Below 30 m, fish lost weight, up to -0.06 g (a decrease of about 0.5% mass) at a fixed depth of 57.5 m. The results of the Bioenergetic Efficiency simulations are similar to those of July 10 in that the highest daily growth increment was reached at a feeding depth of 12.5 m (0.35 g, or a 2.6% increase in mass), and that growth increased with greater non-feeding depths regardless of feeding depth (Figure 1.3). With warm temperatures in the epilimnion, observed growth was not reached when feeding depth was less than 10 m and non-feeding depth was shallower than 15 m. Bioenergetic Efficiency simulations were not performed for feeding depths below 12.5 m because fish could not fill their stomach completely during the 24 hour simulation period.

Predator Avoidance simulations for August 6 clearly show that observed growth was never reached under any scenario (Figure 1.4). The maximum daily growth increment (approximately 0.1 g) occurred when fish were at a 2.5 m safe upper depth and went down to a 42.5 m midday hiding depth, and this was less than half the observed growth increment for this date. Fish lost a significant amount of weight when they had a safe upper depth of 17.5 m or deeper, regardless of midday hiding depth, with the most weight loss occurring at a safe upper depth of 17.5 m and midday hiding depth of 57.5 m (-0.1 g). Because the August 6 observed DVM was simply a fixed depth of 22.5 m, there was no scenario in either the Bioenergetic Efficiency or Predator Avoidance simulations that closely resembled the observed DVM. In August, light level at noon was below 0.5 lux at depths of 42.5 m and greater; therefore, if the safe upper depth of the fish was 42.5 m or below, no DVM occurred because higher light levels that could prompt a DVM were absent.

In addition to calculating daily growth increments, I examined the amount of time spent feeding for each simulation (Figures 1.3 and 1.4). This is the amount of time that fish were actively consuming food, not simply the amount of time spent in a feeding location. For simulations that were averaged (where the non-feeding depth was between 27.5 and 57.5 m), the standard deviations and coefficients of variation for time spent feeding were exceedingly small and often zero. For the June Bioenergetic Efficiency scenarios, kokanee located at feeding depths above 15 m fed for approximately the same amount of time, between three and four hours. At feeding depths below 15 m the amount of time spent feeding increased; up to seven hours for fish at a constant depth of 17.5 m. The amount of time spent feeding in the Predator Avoidance scenarios varied not so much with changes in the safe upper depth, but changed greatly as the safe midday hiding depth changed within any given safe upper depth. Fish with a midday hiding depth of 37.5 m and 42.5 m spent approximately 15 hours feeding, whereas fish with a midday hiding depth of 57.5 m spent less than five hours feeding due to extremely low light levels and food availability at their midday location. In July, fish in the Bioenergetic Efficiency simulations that had a feeding depth within the upper 10 m of the water column fed for approximately three hours; this time increased to approximately 7 hours when the fish went down to a feeding depth of 12.5 m where food availability was less and it took more time to fill its stomach. In the July Predator Avoidance simulations, time spent feeding was fairly uniform for all scenarios, approximately 15 hours no matter the safe upper depth. The amount of time spent feeding in August Bioenergetic Efficiency scenarios was slightly reduced from those in July. The amount of time spent feeding in the Predator Avoidance scenarios mimicked the pattern found in June, except that the time spent feeding varied between 10 and 15 hours.

Discussion

These simulations indicate that neither predator avoidance nor bioenergetic optimization alone can explain observed behavior of age 0 kokanee in BMR. On average, the Bioenergetic Efficiency simulations overestimated growth by 0.10 g in June and July, and 0.06 g in August; and the Predator Avoidance simulations underestimated growth by 0.03 g, 0.14 g, and 0.26 g in June, July and August (Figure 1.5). This suggests that observed DVMs are a result of a combination of both predator avoidance and bioenergetic considerations. In order to grow as much as observed, fish must assume some risk, venturing into waters that are more illuminated for longer periods of time in order to consume a sufficient amount of food. However, the observed growth is not the maximum amount of growth that could occur, so at some point increased risk must stimulate fish to seek a lower risk environment in which to hide from predators.

The relative strengths of factors that influence the behavior of age 0 kokanee probably change as fish grow. Age 0 kokanee are susceptible to greater predation risk and need to adopt behaviors that specifically address pressures associated with their small size, which include not only avoiding predators but finding enough food to meet the demands of high specific physiological rates. A great advantage of incorporating the light environment explicitly in the foraging model is the ability to evaluate how environmental cues affect behavior. While high light levels may enable kokanee to find and capture food at a high rate, light also exposes them to predators that forage visually. In this sense, light can be either a boon or a bane, potentially increasing growth and mortality rates at the same time. The tradeoffs between growth opportunity and predation risk have been addressed in an aspect of optimal foraging theory (Werner and Gilliam 1984). That theory posits that habitat profitability can be evaluated by calculating the mortality risk: growth rate ratio, or μ/g, and where the ideal habitat is where this ratio is minimized (Giske et al. 1998). In their work with bluegill sunfish (*Lepomis macrochirus*), Werner et al. (1983) found that the presence of piscivorous largemouth bass (*Micropterus salmoides*) caused smaller bluegill to spend more time in suboptimal foraging habitats, which decreased growth when compared to the growth of bluegill living in an environment without bass. In the Predator Avoidance scenarios, I assumed that mortality risk was equal for all scenarios when light level was the only criterion by which lake trout captured kokanee. Clearly then, the DVMs that the kokanee should make are the ones which yield highest growth, as this will minimize μ/g for any given date. In June, these DVMs are the ones at which the safe upper depth is in the epilimnion and the midday hiding depth is at least 37.5 m (Figure 1.4). Most other DVMs underestimate growth; so in order to achieve observed growth, some risk must be taken.

Of the three sampling dates modeled, only the June simulations encompassed observed growth in the Predator Avoidance scenarios. Avoiding predators early in the summer may outweigh the benefits of growing quickly and spending more time in high-light, high-exposure environments. However, the strategy appears to change in July and August, when observed growth was achieved in only two of the July Predator Avoidance simulations. By August, observed growth more closely resembled the results of the Bioenergetic Efficiency simulations (Figure 1.3). Thus, in August, kokanee had to assume more light-dependent risk than in other months in order to obtain the amount of food necessary to grow the observed amount. However, the presence of a thermal refuge in the epilimnion from predators like cold-water lake trout may reduce actual risk. In BMR, lake trout have rarely been observed at temperatures above 10 °C, which occurs at a depth of approximately 25 m in August (Hardiman et al. in press). In the observed DVM the average kokanee remained just above this depth in the metalimnion during most of the day (Figure 1.1). If a thermal refuge "safety zone" is superimposed on the results of the Predator Avoidance simulations (Figure 1.4), fish might behave more like they did in the Bioenergetic Efficiency at depths shallower than 15 m in June, 20 m in July, and 25 m in August because high temperatures in the epilimnion may limit predation risk at all light levels.

With several DVM strategies that kokanee could adopt to grow more than the observed amount – even in June under the Predator Avoidance scenarios – why didn't they? In fact, I have shown that in many cases no vertical migration at all would still yield observed growth rates, or exceed them (Figure 1.2). Most of the DVMs that facilitate higher growth entail spending significant periods of time in the epilimnion where zooplankton density is highest. In reality, the epilimnion could be a dangerous place for small kokanee, even if there is a thermal refuge that limits lake trout predation. Kokanee, instead of taking advantage of high food abundance in the epilimnion for the majority of the day, probably choose to spend more time in the metalimnion where food is still available but where lower light levels can offer some amount of cover from any predator. It is likely that kokanee and other salmonids avoid feeding at high light levels (Petrell and Ang 2001) no matter how warm the water temperature is because not all predators are restricted to colder environments.

One could categorize risk on different scales: light-dependent risk as one scale, and temperature-dependent risk as another, and risk is compounded where they coincide (e.g., Figure 1.2). High light and low temperatures produce the greatest risk from predation by lake trout, but high light levels may only be moderately risky when temperatures are greater than 10 °C. Locations where temperatures are lower than 10 °C may present little risk when light is very low because, even though predators are present, they may not be able to see their prey. Kokanee in the Bioenergetic Efficiency scenarios often faced maximum risk but had to feed for only 3-6 hours to reach stomach fullness at least once, sometimes even reaching C_{max} (Figure 1.3). However, kokanee in the Predator Avoidance scenarios typically fed between 10-15 hours, and usually failed to fill their stomachs even once (Figure 1.4). The amount of time spent feeding is not necessarily correlated to the amount of growth experienced by the fish because fish at different locations fed at vastly different rates depending upon light level and prey density, which determined which functional response was used. Fish that utilized strategies to maintain low predation risk in July and August did not meet observed growth, even when they fed whenever they possibly could (Figure 1.4). However, fish that were willing to take some amount of risk by exposing themselves to predators for relatively short periods of time grew at least as much as observed and had the potential to grow much more (Figure 1.3).

I calibrated the model using observed DVM patterns and fish growth, and a known functional response; the only unknown was in situ zooplankton densities. While there is some uncertainty in the functional response parameters, it is the relative change in growth between environmental scenarios that is important; the parameters of the functional response should not change across scenarios. Furthermore, even though there are gaps in the hydroacoustic data, I am confident in my characterization of the generalized DVM patterns; in simulations, fish never filled their stomachs twice in reaching C_{max}, suggesting that only one round-trip DVM could occur and this is consistent with field observations. Because there was no measure of actual *Daphnia* densities experienced by foraging kokanee, I utilized a *Daphnia* calibration factor to adjust the average sampled *Daphnia* density for input to the model. Plankton ecologists widely agree that horizontal patchiness occurs in natural systems (Pinel-Alloul 1995; Folt and Burns 1999). Patchiness also probably varies vertically throughout the water column, with patches being less dense in surface waters due to the homogenizing affects of wind mixing. Measuring patch density is difficult because most sampling gear operates at spatial and temporal scales that are usually very different than those of a foraging fish. Further, fish are routinely found to have items in their guts that are not observed in sampling – they are better at sampling their environment than we are. Overestimating *Daphnia* abundances in the epilimnion would inflate growth increments for scenarios where a DVM incorporates shallower depths. However, considering that patch density can be orders of magnitude greater than the average zooplankton density (Malone and McQueen 1983; Folt and Burns 1999), increasing the average zooplankton density throughout the water column by a factor of 2 or even 12, as I did, could be an underestimate of true patch density. I used patch density as a calibration factor but obtaining direct measures of patch density need not be impossible. Stationary sampling devices such as the Schindler-Patalas sampler can provide plankton density estimates on a fine-grained spatial scale. Video cameras (e.g., Tiselius (1998)) and hydroacoustic techniques could reveal more information about within- and between-patch density. A major challenge for future fish foraging models is the need to match human observational scales and measurements to those experienced by fishes in nature.

Predicted daily growth could also be affected by our assumptions of when feeding and non-feeding periods occurred. In the Bioenergetic Efficiency scenarios, I restricted feeding to two distinct feeding periods, with no feeding during the day. This differs from the Predator Avoidance scenarios in that kokanee could feed at any time if food was available and there was sufficient light to find prey. While there is currently no field data from BMR to support these assumptions, the model can easily be configured to incorporate this information when such data become available. In general, however, the timing of food consumption did not affect growth significantly; that is, a fish that consumed all its food in the morning grew the same amount as a fish that consumed the same amount of food in the afternoon.

The results of this work have yielded new insights about factors that drive juvenile kokanee DVM patterns in BMR. When comparing DVM behavior across a latitudinal gradient, the actions of juvenile kokanee and sockeye appear to be quite plastic, with vertical migrations varying both in timing and magnitude. The main question in examining kokanee behavior in BMR was to determine whether or not there was a bioenergetic advantage to performing DVMs. Much work has focused on predator avoidance and the existence of "anti-predation windows" as being a primary driver for sockeye movements in northern climates, e.g., Clark and Levy (1988) and Scheuerell and Schindler (2003). In these habitats, juvenile sockeye seek to maintain a constant light environment that allows them to feed on zooplankton prey but minimize visual detection by predators. Kokanee in warmer climates, however, face different conditions in which to survive, grow, and reproduce. Thermal stratification and elevated temperatures in the epilimnion, where most zooplankton are found, increase metabolic costs and may necessitate the need to incorporate factors other than predator avoidance when making behavioral decisions about how to maximize growth. Levy (1987) suggested that DVMs could be explained by three competing hypotheses: foraging strategy, bioenergetic optimization, and predator avoidance. In BMR, the foraging strategy hypothesis does not appear to apply because kokanee inhabit waters that are deeper than the location of the majority of their prey; if they were to exploit surface waters, much higher growth rates could be obtained (Figures 1.3 and 1.4).

Evidence from these simulations points towards a combination of both bioenergetic efficiency and predator avoidance strategies as driving DVMs in BMR. While this hypothesis is not new, the enhanced model allowed me to explicitly compare potential growth resulting from behaviors influenced by either predator avoidance or bioenergetic efficiency. The incorporation of a light-dependent functional response enabled me to examine light as a cue that kokanee use to help them either achieve maximum growth by finding food, or avoid visual predators. In future work, the amount of time spent at different light levels may be used as a "common currency" to quantify both growth potential and predation risk to planktivores that move through gradients of food, temperature, and light in their environment.

Acknowledgements

I am grateful for the help of Sathish Kumar Chittibabu who assisted with programming. Mark Kershner generously shared program code for calculating incident light levels. The U.S. Bureau of Reclamation (Upper Colorado Region, Salt Lake City Office) provided financial support for this project, and the U.S.D.A. provided funding through a National Needs Fellowship in Water Sciences.

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Table 1.1. Assumptions for model simulations. Three types of scenarios were considered: no diel vertical migrations (Fixed Depth), Bioenergetic Efficiency scenarios where migrations were triggered by stomach fullness, and Predator Avoidance scenarios where migrations were triggered by light level (perceived predation risk).

Simulation Type	Assumptions
All Simulations	1. The *Daphnia* calibration factor is the same for all depths on a given date.
	2. In simulations where DVMs occur, kokanee make a single round-trip DVM – higher in the water column at night, and lower during the day.
	3. Kokanee can never eat more than C_{max} in the course of one 24 hour period.
Fixed Depth	1. Kokanee do not change depth during the 24-hour simulation period.
	2. Feeding stops when the stomach fills; feeding resumes when the stomach is 90% empty.
Bioenergetic Efficiency	1. Vertical migrations are triggered by stomach fullness. Fish move downward when the stomach is full.
	2. Fish do not feed again until the stomach is 90% empty. They then they return to their original depth and resume feeding.
	3. If stomach doesn't reach fullness or doesn't empty by 90% within the simulation period then no DVM occurs.
	4. Vertical migrations are not necessarily symmetrical around noon.
Predator Avoidance	1. Fish start the simulation at a "Safe Hiding" depth. When light level at that depth becomes greater than 0.5 lux they must move to a midday hiding depth where light is less than 0.5 lux.
	2. Fish return to the safe hiding depth when light level at that depth is once again below 0.5 lux.
	3. Feeding can occur at the midday depth, as DVMs are not triggered by stomach fullness. Feeding occurs if food and sufficient light are present.
	4. Vertical migrations are approximately symmetrical around noon.

Table 1.2. Model inputs for each simulation date. Fish mass on each date was 4.31, 8.65, and 13.13 g, secchi depth was 5.1, 7.0, and 5.6 m, and the zooplankton calibration factor was 2.1, 2.4, and 12.5 in June, July, and August, respectively. Temperature (°C) and *Daphnia* densities (number/L) were averaged on 5 m depth intervals.

	June 5, 2002		July 10, 2002		August 6, 2002	
Depth	Temp.	*Daphnia* Density	Temp.	*Daphnia* Density	Temp.	*Daphnia* Density
2.5	13.9	13.3	19.6	11.2	19.4	6.7
7.5	12.2	6.2	18.1	8.4	19.1	7.4
12.5	10.0	11.1	14.2	2.7	18.1	1.8
17.5	9.0	2.4	10.8	0.66	14.7	0.21
22.5	7.9	2.4	8.1	0.66	10.9	0.21
27.5	6.8	2.4	7.2	0.66	8.3	0.21
32.5	6.3	0.57	6.7	0.52	7.2	0.06
37.5	6.0	0.46	6.3	0.42	6.7	0.04
42.5	5.7	0.38	5.9	0.34	6.3	0.03
47.5	5.5	0.32	5.6	0.29	6.0	0.03
52.5	5.4	0.27	5.6	0.24	5.9	0.02
57.5	5.1	0.23	5.5	0.21	5.8	0.01

List of Figures

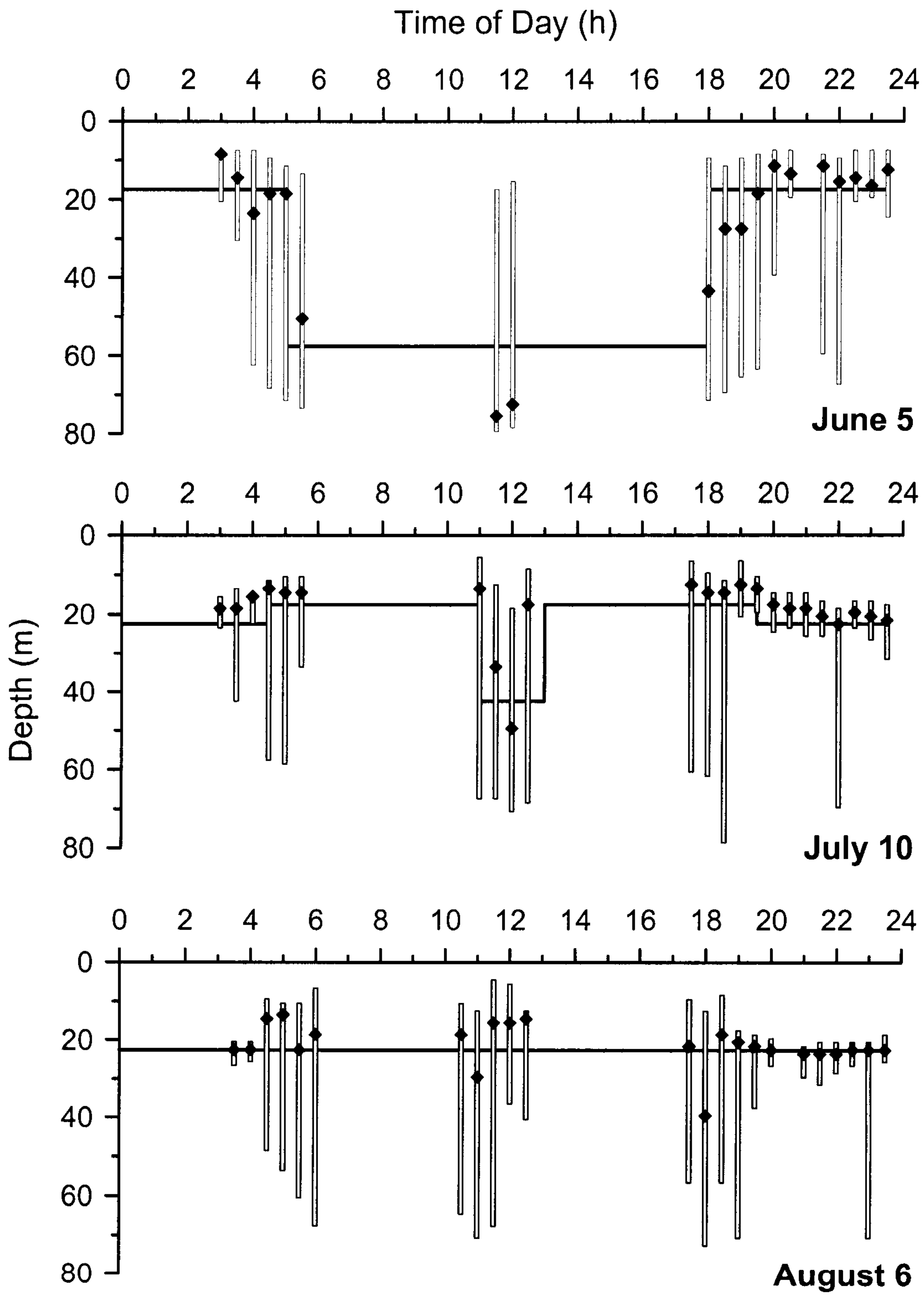
Time of Day (h)
0
2
4
6
8
10
12
14
16
18
20
22
24
Depth (m)
0
20
40
60
80
June 5
July 10
August 6

Figure 1.1

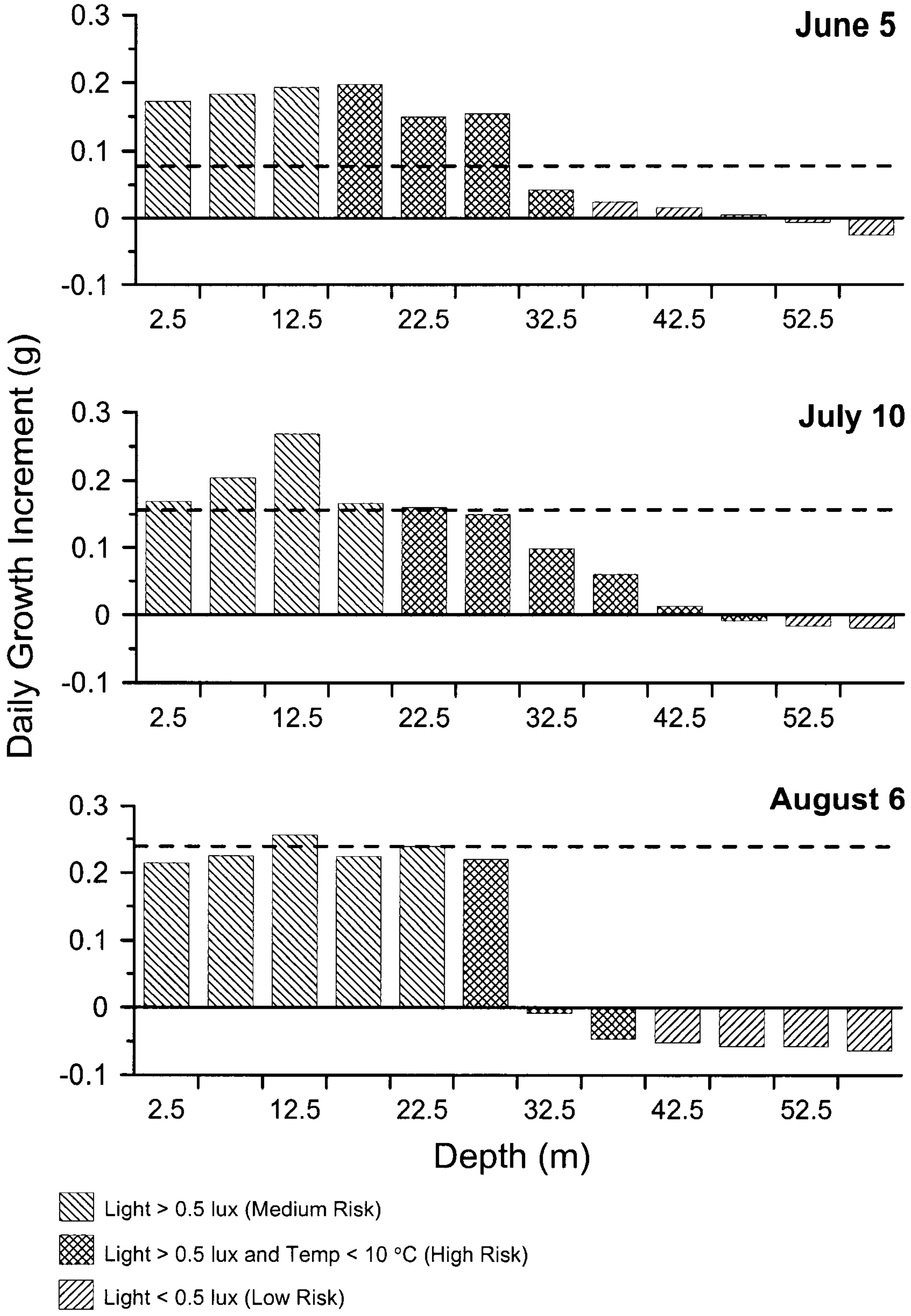
Daily Growth Increment (g)
June 5
July 10
August 6
0.3
0.2
0.1
0
-0.1
2.5
12.5
22.5
32.5
42.5
52.5
Depth (m)
Light > 0.5 lux (Medium Risk)
Light > 0.5 lux and Temp < 10 °C (High Risk)
Light < 0.5 lux (Low Risk)

Figure 1.2

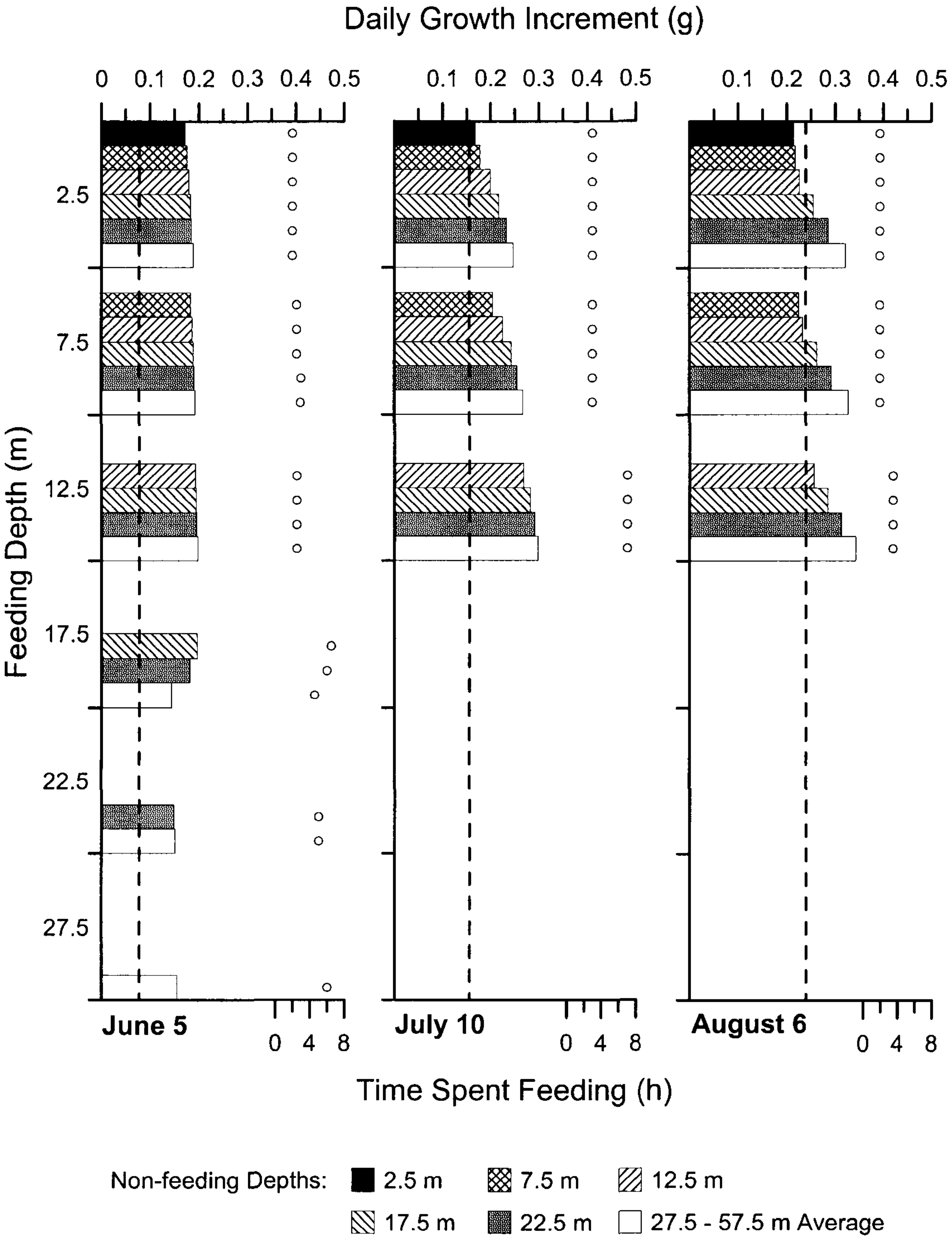
Daily Growth Increment (g)
0 0.1 0.2 0.3 0.4 0.5
0.1 0.2 0.3 0.4 0.5
0.1 0.2 0.3 0.4 0.5
Feeding Depth (m)
2.5
7.5
12.5
17.5
22.5
27.5
June 5
July 10
August 6
0 4 8
0 4 8
0 4 8
Time Spent Feeding (h)
Non-feeding Depths:
■ 2.5 m
▩ 7.5 m
▨ 12.5 m
▧ 17.5 m
▦ 22.5 m
☐ 27.5 - 57.5 m Average

Figure 1.3

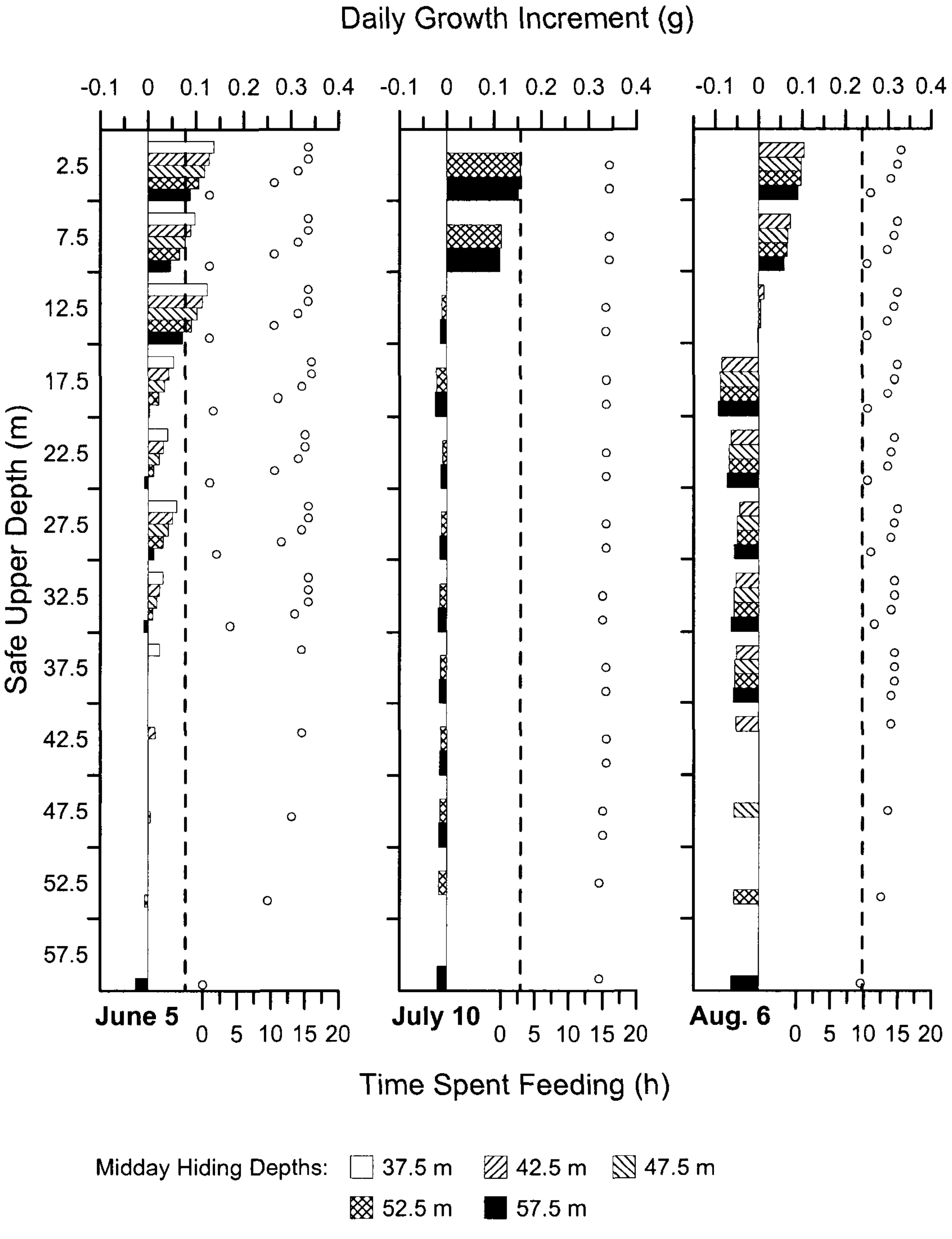
Daily Growth Increment (g)
-0.1 0 0.1 0.2 0.3 0.4
-0.1 0 0.1 0.2 0.3 0.4
-0.1 0 0.1 0.2 0.3 0.4
Safe Upper Depth (m)
2.5
7.5
12.5
17.5
22.5
27.5
32.5
37.5
42.5
47.5
52.5
57.5
June 5
July 10
Aug. 6
0 5 10 15 20
0 5 10 15 20
0 5 10 15 20
Time Spent Feeding (h)
Midday Hiding Depths:
37.5 m
42.5 m
47.5 m
52.5 m
57.5 m

Figure 1.4

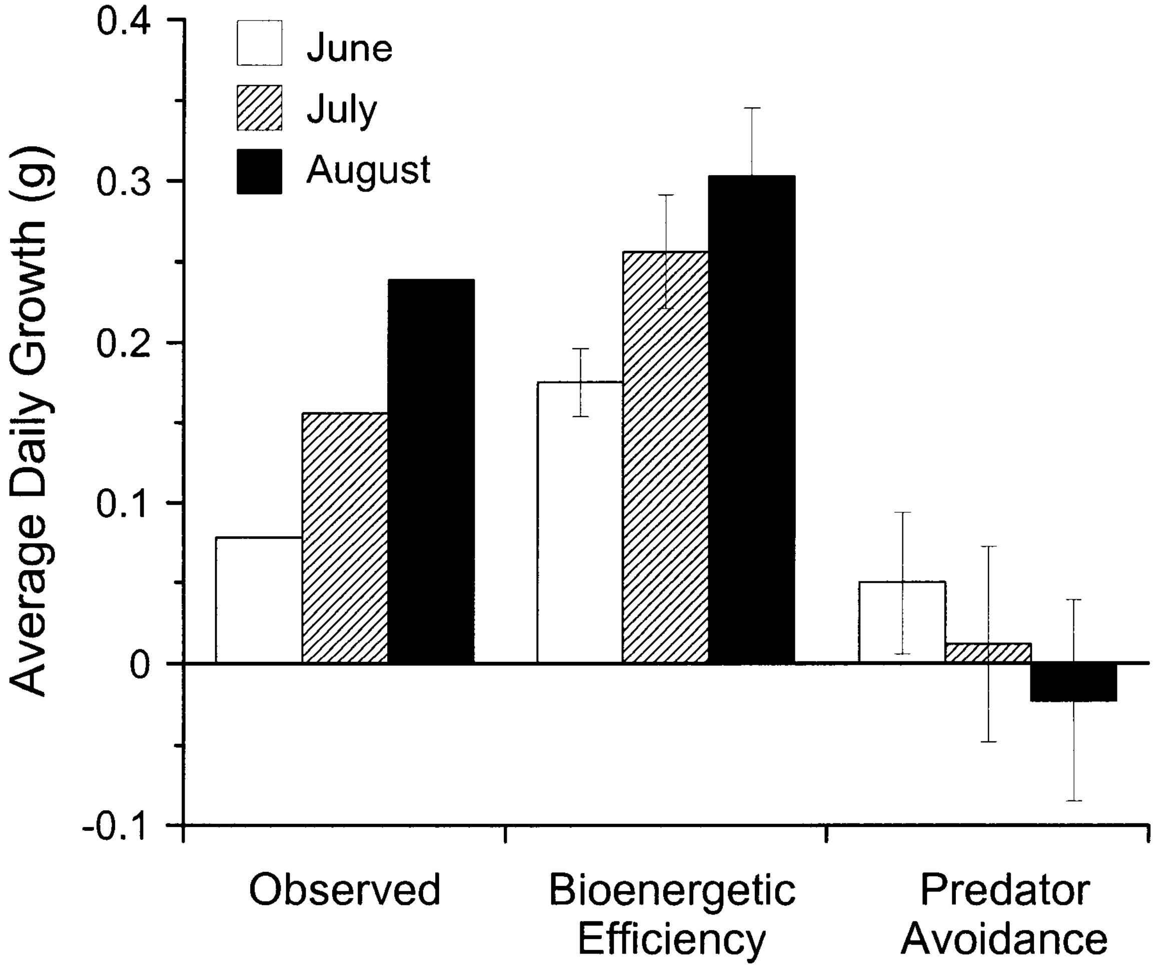
Average Daily Growth (g)
0.4
0.3
0.2
0.1
0
-0.1
June
July
August
Observed
Bioenergetic Efficiency
Predator Avoidance

Figure 1.5

CHAPTER 2

EFFECTS OF DROUGHT AND A TEMPERATURE CONTROL DEVICE ON AGE 0 KOKANEE PREDATION RISK AND GROWTH

Abstract

Juvenile kokanee in Blue Mesa Reservoir, Colorado, perform diel vertical migrations (DVMs) to avoid predators and increase bioenergetic efficiency. Daily growth and predation risk of age 0 kokanee during a drought year were compared to simulated growth and risk of kokanee under full-pool hydrologic and thermal conditions and under thermal conditions induced by a temperature control device (TCD). Growth was computed using a bioenergetics-based foraging model. If kokanee performed the same DVMs in June that were observed in the drought year (DVMs in other conditions were unknown), kokanee in full-pool and TCD scenarios lost weight compared to kokanee in drought conditions (-0.01 vs. 0.02 $g{\cdot}g^{-1}{\cdot}d^{-1}$). In July and August, daily growth in full-pool and TCD conditions was approximately equal (~0.01 $g{\cdot}g^{-1}{\cdot}d^{-1}$ for July and August) but was less than observed growth in drought conditions (0.02 $g{\cdot}g^{-1}{\cdot}d^{-1}$). Predation risk was estimated as a function of depth, light level and turbidity, predator reaction distance, and temperature. Predation risk throughout the summer was highest under drought conditions and lowest under full-pool conditions, with TCD conditions being intermediate. For kokanee performing drought year DVMs, the predation risk to

foraging gain ratio (μ/g) in July was 48 for full-pool conditions, 91 in drought conditions, and 103 in TCD conditions; in August μ/g was 16 for full-pool conditions, 38 in drought conditions, and 100 in TCD conditions. Because predation risk can change dramatically between different thermal scenarios, kokanee behavior should be plastic. When predation risk is low, kokanee should perform DVMs that result in greater bioenergetic efficiency and when predation risk is high bioenergetic efficiency should decline.

Introduction

Reservoirs can exhibit great variability in their physical characteristics as a result of both climatic and operational controls. Reservoirs may be more sensitive than natural lakes to environmental conditions because inflow patterns control limnological conditions to a large degree (Thornton et al. 1990). Climate can have pronounced effects on physical characteristics such as thermal profiles, the timing and degree of stratification, and water clarity (e.g., Bouvy et al. (2003), Johnson et al. (2004), and Nowlin et al. (2004)). Drought, in particular, may significantly increase water temperatures in the epilimnion and increase water clarity because lower inflow and outflow rates increase water residence time in the system, allowing suspended particles to settle to the bottom (Theilling et al. 1996, J. Miller, U.S. Bureau of Reclamation, personal communication). Warmer air temperatures can strengthen stratification resulting in a deepened epilimnetic layer and increased thermal resistance to mixing within the metalimnion (Wetzel 2001).

The use of selective withdrawal to manipulate outflow regimes and temperature of releases can also affect reservoir conditions. Temperature control devices (TCDs) have been implemented on some reservoirs to change downstream flow temperatures to benefit native endangered fishes (e.g., Shasta Lake, California (Bartholow et al. 2001; Lieberman et al. 2001) and Flaming Gorge, Utah) and are being considered at more reservoirs (e.g., Glen Canyon, Arizona and Blue Mesa Dam, Colorado). These TCDs facilitate greater control of downstream river temperatures and flow rates to better fulfill thermal requirements of native fishes for growth, survival, reproduction, and egg viability. While the downstream effects of TCDs are the focus of much research, TCD effects in upstream reservoir systems have not been well studied.

Reservoir ecosystems are characterized by gradients such as light and temperature. Light availability is affected by depth, water clarity (turbidity), time of day, and season. Biological gradients also exist, with primary productivity often being highest in surface waters (Wetzel 2001). The vertical distribution of zooplankton can be controlled by factors such as chlorophyll-*a*, water clarity, temperature, dissolved oxygen (Murtaugh 1985; Marcogliese and Esch 1992; Wissel and Ramacharan 2003), and predator avoidance (Gliwicz and Pijanowska 1988; Lampert 1989; Lampert et al. 2003). Consequently, many planktivorous fish have evolved complex behaviors to exploit these gradients, seeking out different zones for food consumption, maximizing bioenergetic efficiency, and predator avoidance (Werner et al. 1983; Levy 1987; Adams et al. 1994; Jacobsen and Perrow 1998). Behavioral changes may be due to shifts in food abundance and location, or from changes in predation risk, both of which can change with hydrologic and thermal properties of the reservoir. The most optimal behavioral patterns minimize predation risk (μ) and maximize energetic gain (g) (Werner and Gilliam 1984; Gilliam and Fraser 1988; Giske et al. 1998).

Blue Mesa Reservoir (BMR) is a large, deep reservoir in southwest Colorado that has three basins, Sapinero basin being the deepest and closest to the dam. Recently, a one-dimensional thermal model (CE-THERM) was used to predict the effects of various dam operations that would create a more natural downstream flow regime (i.e., high spring flows and lower summer flows) for native endangered fish (Johnson et al. 2004). However, these scenarios considered releases only from the hypolimnion and results indicated that climate was more important in determining thermal structure in BMR than dam operations using the hypolimnetic outlet. The U.S. Bureau of Reclamation is currently investigating the possibility of installing a TCD on Blue Mesa Dam, and has modeled the thermal effects of a TCD in the reservoir (Boyer and Cutler in review). Simulated metalimnetic temperatures were cooler compared to full-pool conditions (i.e., when the reservoir was filled to maximum capacity), and by August, temperatures were generally cooler down to approximately 60 m. Climate has also affected BMR; in 2002, drought in Colorado likely influenced thermal profiles and water quality in the reservoir. Sapinero basin was characterized by a very warm, deep epilimnion (especially in August) and very high water clarity during the drought (Hardiman et al. in press).

Blue Mesa Reservoir contains a number of fish species, among them two popular sport fish: kokanee (*Oncorhynchus nerka*) and lake trout (*Salvelinus namaycush*). Kokanee perform diel vertical migrations (DVMs) throughout the water column in order to both avoid predation by lake trout and gain some bioenergetic advantage (Chapter 1). Kokanee have a diet of nearly 100% zooplankton prey (Finnell and Reed 1969; Beauchamp et al. 1989; Stockwell et al. 1999) which they consume in warmer, shallower water where bioenergetic expenses are high. They move to cooler, deeper water during the day to both avoid predators and decrease energetic demands while digesting food (Chapter 1). In recent years, the kokanee population in BMR has been declining, probably as a result from high lake trout predation (Johnson and Martinez 2000). Lake trout are cold-water predators that prefer temperatures close to 10 °C (Dillon et al. 2003); subsequently, they usually reside in deeper waters of the reservoir. However, thermal shifts could change the extent of kokanee–lake trout habitat overlap, either lowering or increasing predation risk to kokanee. In cases where metalimnetic temperatures cool, lake trout may be able to exploit shallower depths that are more illuminated, enabling them to find kokanee prey more easily.

The objective of this study was to determine how predation risk and growth of age 0 kokanee change across full-pool, TCD, and drought conditions in BMR. Changes in predation risk were calculated for these three thermal scenarios over depth, time of day, and season. Diel vertical migrations of age 0 kokanee were known for the summer of 2002, a drought year (Chapter 1); growth in 2002 was compared to simulated growth under full-pool and TCD conditions from 1997 using the same DVMs observed in 2002. A bioenergetics-based foraging model was used to predict daily growth (described in Chapter 1). After determining relative predation risk for these three thermal scenarios, alternative DVMs that focused on maximizing bioenergetic efficiency were defined and predation risk and growth were calculated for each. By examining μ/g for each set of possible DVMs for each month and thermal scenario, alternative DVM strategies were proposed to predict growth in full-pool or TCD conditions.

Methods

I compared kokanee growth and predation risk under three thermal scenarios: full-pool conditions, TCD effects, and drought. Temperatures in the reservoir change during the summer so each of the three thermal scenarios were examined during June, July, and August. Temperature-depth profiles for full-pool conditions and TCD effects were predicted using CE-QUAL-W2 (A. Cutler, U.S. Bureau of Reclamation, unpublished data), a two-dimensional hydrodynamic and water quality model (Cole and Wells 2002) that provided thermal profiles in the middle of each month of summer. Full-pool and TCD temperature profiles were based on data collected during 1997, which was a full-pool year at BMR. Inputs used to model temperature-depth profiles included meteorological data (dew point temperature, air temperature, cloud cover, wind speed, and wind direction), inflow rates and temperatures from major tributaries to BMR, mass balance of the reservoir, observed temperature profiles in the reservoir, and reservoir elevation. Field measurements collected at BMR in 2002 (Chapter 1), a drought year, were used as temperature inputs for drought scenarios.

Predation risk was computed from light, water clarity, and observed depth distributions of lake trout for each month and thermal scenario. Incident light was calculated at BMR for June 6, July 10, and August 5 in 1997 and 2002 in 10 minute increments from midnight to midnight using a light model developed by Janiczek and DeYoung (1987). Secchi depths in 1997 and 2002 were used to calculate light at all depths using Equations 2.1 (Idso and Gilbert 1974) and 2.2 (Horne and Goldman 1994):

$$\eta = 1.7 \cdot z_{sd}^{-1} \qquad (2.1)$$

(2.2) $$I_z = I_0 \cdot e^{-\eta z}$$

where η is the light extinction coefficient, z_{sd} is Secchi depth (m), I_0 is incident light level (lx), z is fish depth (m), and I_z is the light level (lx) at depth z. Lake trout reaction distances were then calculated for each time/depth cell using Equation 2.3 (Vogel and Beauchamp 1999):

(2.3) $$\mathrm{RD} = 26.84 + (2.81 \cdot I_z) - (6.09 \cdot \ln \mathrm{NTU}) - (0.025 \cdot \ln \mathrm{NTU} \cdot I_z)$$

where reaction distance (RD in cm) is calculated using light level (lx) and turbidity (NTU in Nephelometric Turbidity Units). I used 2002 turbidity values for drought simulations, but turbidity was not collected in the reservoir prior to 2001 so 2001 turbidity values were used for all 1997 simulations because Secchi depths were similar to those measured in 1997. Vogel and Beauchamp (1999) found that lake trout reaction distance peaked at 17.83 lx for all turbidity values tested, and further research indicated that reaction distance neither increased nor decreased at light levels above 17.83 lx when turbidity was low (D. Beauchamp, University of Washington, personal communication). Depth (and hence temperature) distribution of lake trout in simulations was estimated from depths at which lake trout were captured in 3 m x 60 m vertical gill nets during June, July, and August 1994 – 2002 (B. Johnson, Colorado State University, unpublished data). Relative frequency of lake trout occurrence was calculated for each temperature above 10 °C in 1 °C intervals. Lake trout captured at or below 10 °C were combined to compute relative frequency of occurrence because these temperatures were within their thermal preference

(Stewart et al. 1983; Madenjian and O'Connor 1999; Dillon et al. 2003). Predation risk (μ), a function of lake trout reaction distance (RD) and probability of lake trout occurrence (P) based on temperature, was calculated for each depth (z) and time (t):

$$\mu_{z,t} = \mathrm{RD}_{z,t} \cdot P \tag{2.4}$$

Surfer 8.0 (Golden Software Inc. 2002) was used to develop predation risk profiles using a radial basis function, which interpolates between data points to create a smooth surface.

A bioenergetics-based foraging model (described in Chapter 1) was used to predict potential foraging weight gain (g) of age 0 kokanee in June, July, and August under the three thermal scenarios. The bioenergetics-based foraging model calculates the fish's energy budget (energy consumed and expended in wastes, metabolism, and growth) as a function of body size and temperature (Stockwell and Johnson 1997, 1999). In addition, it uses a light-based functional response (Koski and Johnson 2002) to predict feeding rate as a function of prey density and light level; depth-specific light was calculated from date, time of day, and water clarity (Secchi depth) using Equations 2.1 and 2.2. Other inputs to the model included temperature- and zooplankton density-depth profiles, size and energy content of prey consumed, prey handling time, fish mass, and DVM pattern. Aside from water clarity and temperature profiles, all inputs for the simulations in this study were the same as the inputs described in Chapter 1.

Drought and TCD temperature profiles were similar in June, July, and August. Extensive data existed for 2002, including limnological data (Secchi depth, turbidity, and thermal profiles) and biological data (zooplankton densities, and age 0 kokanee size and

DVM patterns). I assumed that zooplankton densities would remain constant across the two 1997 thermal scenarios and the 2002 drought scenario because average zooplankton densities have been similar over the past decade (Johnson 2004), and the effects of drought and TCDs on zooplankton abundance have not been well studied. Thus, 2002 zooplankton densities were used for all thermal scenarios (Chapter 1 and Appendix III). Water clarity, however, varied over the past decade (Johnson 2004) so 2002 Secchi depths were used for the drought scenario, and 1997 Secchi depths were used for full-pool and TCD scenarios.

The bioenergetics-based foraging model was calibrated to BMR conditions using 2002 kokanee growth, zooplankton densities and DVMs (as in Chapter 1). I first used the model to predict daily kokanee growth for each of the three thermal scenarios in June, July, and August using the observed generalized DVMs from 2002 (Chapter 1). Predation risk was averaged over all 48 thirty-minute time steps to obtain an average predation risk value for that day. Then, μ/g was calculated for each simulation by dividing average daily predation risk by daily growth increment (g/d).

Because predation risk profiles indicated that drought conditions posed the most predation risk to kokanee, I assumed that fish in the other two thermal conditions would change their DVMs to increase bioenergetic efficiency. Both predicted growth and predation risk were compared among thermal scenarios for different months by conducting a series of simulations based on alternative DVMs that would enhance bioenergetic efficiency. For each thermal scenario during each month, two fish depths were designated: a feeding depth and a non-feeding depth. The fish initially stayed at the feeding depth until its stomach became full, at which time it moved to a deeper non-feeding depth (Chapter 1). The fish remained at the non-feeding depth until its stomach became 90% empty, at which time appetite increases at its fastest rate (Brett 1971). The fish was then returned to its original feeding depth to consume food, with a limit to consumption of C_{max}, the maximum amount of food that can be consumed by a particular sized fish during a single day (Beauchamp et al. 1989). All possible combinations of feeding / non-feeding depths were simulated from 2.5 – 57.5 m, until the fish could either not fill its stomach or reach C_{max} during the day, or if it didn't have time to evacuate its stomach by 90% by the end of the 24 hour simulation period. For all simulations, fish depth was the only variable; temperature profiles, zooplankton densities, and water clarity remained consistent within each month/thermal scenario combination. Simulations within each month/thermal scenario set were then compared to determine which DVMs would yield lowest μ/g values and predict how kokanee might respond to conditions with varying degrees of predation risk.

Results

Temperature-depth profiles generated by CE-QUAL-W2 for full-pool and TCD scenarios were compared to drought condition thermal profiles that were measured in 2002 (Figure 2.1). In general, drought profiles were similar to TCD profiles, except in August. In June and July, epilimnetic temperatures in the drought scenario were up to 2.5 °C warmer than the TCD scenario; in August, the drought scenario was warmer than either of the 1997 scenarios by a maximum of approximately 6 °C at a depth of 12 m. In addition, the 10 °C isotherm in August was almost 20 m shallower in TCD and drought scenarios than in full-pool conditions. Water clarity was greatest during the drought year (Table 2.1), peaking at 7 m in July 2002, and being lowest (1.75 m) in June 1997.

There were a total of 41 lake trout caught in long vertical gill nets during June – August between the years of 1994 and 2002 (B. Johnson, unpublished data). Of the 41 lake trout netted, 51.2% were captured in temperatures ≤10 °C, 17.1% between 10.1-11 °C, 19.5% between 11.1-12 °C, 7.3% between 12.1-13 °C, and 4.9% were captured between 13.1-14 °C. No lake trout were observed at temperatures above 14 °C. Maximum lake trout reaction distances (at and above the saturating light level of 17.83 lx) varied between 73.1 and 79.8 cm.

Changes in temperatures and water clarity affected predation risk for each month, impacting not only the magnitude of predation risk, but times and depths in the reservoir where predation risk was highest. In all months, predation risk was lowest for full-pool conditions and greatest for drought conditions (Figures 2.2 – 2.4). In general, the amount of time and locations that were characterized by high predation risk increased with warmer months, and shifted to deeper depths. When DVMs observed in 2002 were superimposed on predation risk profiles computed for drought conditions it appeared that fish avoided areas of high predation risk (Figures 2.2 – 2.4), and were able to lower μ/g ratios as summer progressed (Table 2.2).

Daily growth and predation risk were compared among fish performing DVMs that were observed during the summer of 2002 (Table 2.2). In June under these DVMs, only kokanee in drought conditions grew whereas kokanee in the other two thermal scenarios lost weight because light availability at fish depths was not sufficient to see prey. In July and August, kokanee in the drought conditions grew more than kokanee in the other two thermal scenarios. In June, μ/g was negative for full-pool and TCD scenarios because fish lost weight. The μ/g ratio was used to determine the best foraging strategy, but because these fish lost weight while the fish in the drought scenario grew, it is inappropriate to compare negative μ/g values to positive ones (i.e., a high positive μ/g value is better than a low negative μ/g value). In July and August, when observed growth was highest under drought conditions, drought condition μ/g ratios fell between the full-pool conditions and TCD effects scenarios, with full-pool condition μ/g ratios being the lowest (Table 2.2). Predation risk to foraging gain ratios declined as the summer months progressed for all thermal scenarios following the 2002 observed DVMs (Table 2.2).

For the sets of simulations considering DVMs that would increase bioenergetic efficiency under reduced predation risk, fish generally grew least under drought conditions, and grew most under TCD scenarios (Figure 2.5); however, growth among the thermal scenarios was similar. In June, there was little difference in growth between the three thermal scenarios, varying on average between 4.1 and 4.3% body weight increase (Figure 2.5). Under full-pool conditions, maximum growth was achieved with a feeding depth of 17.5 m and non-feeding depth of 57.5 m (0.047 $g \cdot g^{-1} \cdot d^{-1}$); considering the effects of a TCD, maximum growth occurred with a feeding depth of 17.5 m with non-feeding depths ranging from 37.5 – 57.5 m (0.047 $g \cdot g^{-1} \cdot d^{-1}$); and under drought conditions, maximum growth occurred when feeding depth was 12.5 m and non-feeding depths ranged between 47.5 m and 57.5 m (0.046 $g \cdot g^{-1} \cdot d^{-1}$). High water clarity in June under drought conditions permitted fish to fill their stomachs completely at lower feeding depths, down to 27.5 m, as opposed to only 17.5 m for the 1997 scenarios. In July, growth varied between 2.9 and 3.3% body weight increase (Figure 2.5). Under full-pool conditions, maximum growth was achieved with a feeding depth of 12.5 m and non-feeding depth of 57.5 m (0.035 $g \cdot g^{-1} \cdot d^{-1}$). With TCD effects, maximum growth occurred with a feeding depth of 12.5 m and non-feeding depths ranging from 52.5 – 57.5 m (0.036 $g \cdot g^{-1} \cdot d^{-1}$). Under drought conditions, maximum growth occurred when feeding depth was 12.5 m and non-feeding depth was 57.5 m (0.035 $g \cdot g^{-1} \cdot d^{-1}$). In August, growth varied between 2.3 and 2.6% body weight increase (Figure 2.5). Under full-pool conditions, maximum growth was achieved with a feeding depth of 12.5 m and non-feeding depth of 52.5 m (0.029 $g \cdot g^{-1} \cdot d^{-1}$); under the effects of a TCD, maximum growth occurred with a feeding depth of 12.5 m and non-feeding depth of 32.5 m (0.031 $g \cdot g^{-1} \cdot d^{-1}$); and under drought conditions, maximum growth occurred when feeding depth was 12.5 m and non-feeding depths were between 42.5 – 47.5 m (0.026 $g \cdot g^{-1} \cdot d^{-1}$).

Predation risk to foraging gain ratios varied more than growth among bioenergetic efficiency simulations for each thermal scenario (Figure 2.6). Predation risk to foraging gain ratios were higher in June than in July and August, and were generally highest under drought conditions. In June, lowest μ/g ratios were achieved when fish spent most of their time in the upper 5 m; in drought scenarios, μ/g ratios were highest when non-feeding depths were between 20 and 30 m. In July, lowest μ/g ratios were seen in full-pool and TCD conditions when feeding depth was 7.5 m and non-feeding depth was 12.5 m. As in June, drought conditions in July produced the highest μ/g ratios when non-feeding depths varied between 20 and 35 m. In August, μ/g ratios were lower under full-pool conditions, and were lowest across thermal scenarios when non-feeding depth was in the epilimnion. Drought and TCD scenarios had highest μ/g ratios when non-feeding depths were between 25 and 35 m.

Discussion

Simulation results indicated that juvenile kokanee behavior must be flexible to achieve positive growth and minimize predation risk under variable hydrologic and thermal conditions. Overall predation risk in the reservoir was highest during the drought year due to high water clarity and reduced temperatures in the metalimnion (especially in June and July), and lowest in full-pool conditions. When kokanee utilized DVMs observed in 2002 across thermal scenarios, growth declined under full-pool and TCD conditions compared to growth during the drought year; in fact, growth in June was negative because of reduced water clarity. Because of high kokanee growth rates in BMR during the past decade (Johnson et al. 1997), it is unlikely that kokanee in full-pool conditions would perform the same DVMs as in the drought year, especially since lower overall predation risk would permit them to better exploit food-rich waters and avoid predators in the epilimnion.

Because predation risk was highest in drought conditions for all summer months examined, I assumed that predation risk would shape observed DVMs in 2002 to a greater extent than it would in both 1997 scenarios. Hence, DVMs in both 1997 scenarios were likely to be more bioenergetically efficient; by executing simulations that maximized energy intake (i.e., filling the stomach or reaching C_{max}) I was able to compare the effects of each thermal scenario on growth and μ/g. In order to either fill the stomach or reach C_{max}, kokanee needed feeding depths shallower than 30 m (and in most cases, shallower than 15 m), where the effects of the TCD and drought were prominent. Growth was not greatly affected by different feeding/non-feeding depths in the simulations that sought to increase bioenergetic efficiency under reduced predation risk.

That is, in any month and for any particular DVM, growth was not very different between full-pool, TCD, or drought conditions. Most differences in growth occurred with non-feeding depths that were in the metalimnion, owing to differences in temperatures and rates that energy was assimilated.

Unlike growth, there were notable changes in μ/g between the three thermal scenarios. First, μ/g was highest for all thermal scenarios in June. This was because thermal stratification was not strong and temperatures were lower throughout the water column; lake trout had a higher probability of occurring anywhere in the reservoir. Also, kokanee were small at this time (4.3 g) and were limited in energy acquisition by their stomach size and C_{max} in how much food they could consume and subsequently, how much they could grow. Later in the season, larger kokanee could consume more food and growth was higher relative to predation risk. Among the three thermal scenarios, μ/g was highest for drought conditions. This was because water clarity was higher during the drought year, allowing for greater light penetration and increased lake trout reaction distances at greater depths. In addition, both drought and TCD scenarios yielded cooler temperatures between 5 – 60 m. In August, the 10 °C isotherm was almost 20 m shallower in both TCD and drought scenarios compared to full-pool conditions, which could allow lake trout to exploit more of the water column under these thermal scenarios. Under full-pool conditions, warmer epilimnetic temperatures in July and August can create a thermal barrier to lake trout preying on kokanee. As temperatures warm over the summer, DVMs are driven more by bioenergetic efficiency (Chapter 1), presumably because of reduced risk from coldwater piscivores. However, under TCD and drought conditions, the depth of this thermal barrier was shallower and predation risk increases over a greater volume of the reservoir.

Estimates for predation risk in the epilimnion may be underestimated (zero in some cases) because of the observed lake trout temperature distribution. That lake trout were not observed at temperatures above 14 °C doesn't mean that they never travel into warmer waters. Lake trout have been observed occasionally in epilimnetic zones elsewhere (Snucins and Gunn 1995; Sellers et al. 1998), and considering the lag time of body temperatures warming to ambient temperatures, lake trout are energetically able to make short journeys into suboptimal thermal environments (Snucins and Gunn 1995). So, at temperatures above 14 °C, predation risk estimates may be lower than the perceived predation risk by kokanee. High light levels, regardless of temperature, may inhibit kokanee from exposing themselves to predators even if lake trout are rarely present; there may be other predators in the system that spend more time foraging in warmer waters than lake trout.

The tradeoffs between energetic gain and predation risk have been addressed in optimal foraging theory by Werner and Gilliam (1984) and Gilliam and Fraser (1988). Different habitats can be evaluated by calculating μ/g, and the ideal habitat (or combination of habitats) is one where this ratio is minimized (Giske et al. 1998). In their classic experiments, Werner et al. (1983) and Werner and Hall (1988) found that the presence of piscivorous largemouth bass (*Micropterus salmoides*) caused smaller bluegill (*Lepomis macrochirus*) to forage in suboptimal habitat. Salmonids have also been shown to incorporate predation risk in their foraging habits; in streams, juvenile coho salmon (*Oncorhynchus kisutch*) preferred pool habitats with brushy cover only in the presence of piscivorous birds (Reinhardt and Healey 1997). In another study (Magnhagen 1988), juvenile pink salmon (*Oncorhynchus gorbuscha*) were found more often in vegetated habitats having lower food resources when predators were present; in the absence of predators, the salmon were much more likely to be found in open habitats with higher food availability. Predation risk and thermal habitats are varied for kokanee and sockeye salmon throughout their range, which have resulted in different behaviors exhibited by these fish. In more northern latitudes, DVMs are driven largely by predator avoidance (Clark and Levy 1988; Scheuerell and Schindler 2003) but thermal stratification in warmer climates presents conditions that affect bioenergetic requirements and subsequently, DVM patterns (Beauchamp et al. 1989; Bevelhimer and Adams 1993; Stockwell and Johnson 1997, 1999).

It may be possible to predict which DVM strategies kokanee may employ under different environmental scenarios by comparing DVMs for which μ/g ratios are lowest. In the simulations that increased bioenergetic efficiency under reduced predation risk, DVMs that generated highest growth rates did not always produce the lowest μ/g ratio. For example, in July under full-pool conditions, a juvenile kokanee can maximize growth if it has a feeding depth of 12.5 m but goes to 57.5 m during non-feeding periods. Such fish increase their body weight by 3.5%; however, this particular DVM had the highest μ/g ratio (28) of all the possible simulations that were executed under full-pool scenarios in July. By changing its DVM to feeding at 7.5 m and going to 12.5 m during non-feeding periods, μ/g was lowered to a value of five, but fish only increase their body mass by 2.9%. Across the three thermal scenarios, to minimize μ/g kokanee may have to change to a different non-feeding depth for any given feeding depth but simulation results indicate that growth would likely not change much.

Kokanee DVMs were not measured in 1997 and must be predicted with calculations such as μ/g ratios. Comparing observed DVMs of juvenile kokanee in 2002 (Hardiman et al. in press) to times and depths of high predation risk, fish closely follow hazardous zones but do not stay long within them. In June, kokanee stayed at an upper depth just until light level exposed them to predators, but then descended to great depths during the day, returning to their original depth just after predation risk had decreased. In July, kokanee ventured further into higher risk zones, and descents were shallower. In August, kokanee didn't make any DVMs at all, but stayed just above the zone of high predation risk at a depth of 22.5 m. If kokanee were to perform the same DVMs in a full-pool year as in 2002, μ/g would be reduced by half in July and August. However, μ/g would increase for fish performing these DVMs in conditions incurred by a TCD; in August especially, a constant depth of 22.5 m would locate fish in the zone of maximum predation risk.

Even though 2002 DVM patterns resulted in lower μ/g ratios for kokanee in full-pool conditions, there are more optimal DVMs kokanee could perform. Minimum μ/g ratios resulted from feeding and non-feeding depth combinations between 0 and 15 m. The effects of the TCD appear to increase predation risk, but not to the extent of drought conditions. Under these conditions, kokanee DVMs should ideally have feeding and non-feeding depth combinations between 0 and 10 m. While epilimnetic temperatures under drought scenarios can still be very warm later in the summer, relatively lower temperatures under full-pool and TCD scenarios would decrease energetic costs and shallower depths would yield greater food resources, increasing growth while maintaining low predation risk.

Thermal and hydrologic conditions vary seasonally in reservoir ecosystems, and inter-annual variability may be amplified by anthropogenic disturbance. Whether driven by climate change or reservoir management, planktivores such as kokanee must respond to changing physical conditions in their environment to both maintain energy acquisition and avoid predation. While growth may not be greatly affected by environmental change, increased predation risk could pose a threat for kokanee under drought conditions or altered dam operations. Granted, the effects of short-term environmental change are difficult to predict, but managers may be able to mitigate some of these effects to some degree. For example, fishing regulations may be changed so that increased harvest of lake trout is encouraged while kokanee become temporarily protected from sport-fishing during drought years or when water clarity is high. More importantly, if a TCD is installed at BMR, dam operations could be changed by incorporating both hypolimnetic and epilimnetic releases in order to maintain a thermal profile that is suitable for kokanee growth and survival. Regardless of management actions, however, dynamic DVM behaviors have evolved so that fish can cope with environmental change, enabling kokanee to simultaneously maintain high growth rates and avoid coldwater predators such as lake trout.

Acknowledgements

This work could not have been completed without the assistance of Amy Cutler (U.S. Bureau of Reclamation), who conducted all CE-QUAL-W2 modeling. The U.S.

Bureau of Reclamation (Upper Colorado Region, Salt Lake City Office) provided financial support for this project, and the U.S.D.A. provided funding through a National Needs Fellowship in Water Sciences.

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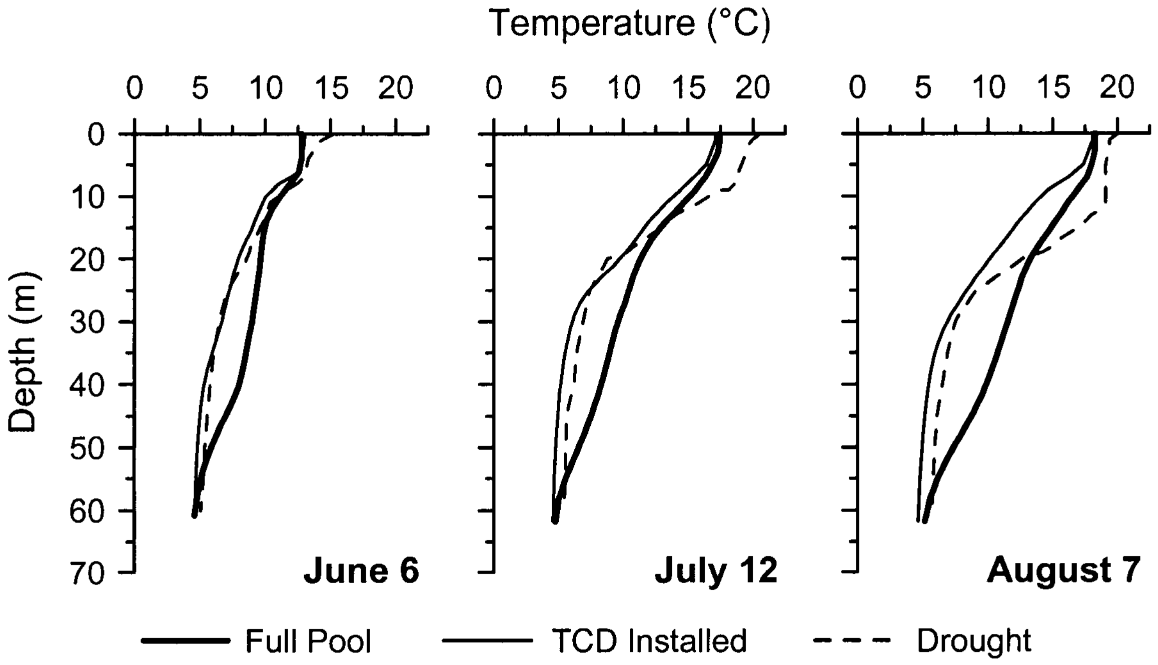
Table 2.1. Water clarity input data for the three thermal scenarios in Blue Mesa Reservoir, Colorado. Secchi depths are listed in m, and turbidity values are in NTUs (italicized). The same Secchi depths and turbidity values from full-pool conditions were used in TCD scenarios.

	June 5		July 10		August 6	
Thermal Scenario	Secchi Depth	Turbidity	Secchi Depth	Turbidity	Secchi Depth	Turbidity
Full-pool Conditions (1997)	1.75	*1.8*	4.5	*0.65*	4.0	*0.75*
Drought (2002)	5.06	*0.9*	7.0	*0.8*	5.6	*0.95*

Table 2.2. Daily growth ($g \cdot g^{-1} \cdot d^{-1}$) and μ/g (italicized) for fish performing the same DVMs that were observed during the summer of 2002 in Blue Mesa Reservoir.

	June 5		July 10		August 6	
Thermal Scenario	Growth	μ/g	Growth	μ/g	Growth	μ/g
Full-pool Conditions	-0.007	*-481*	0.014	*48*	0.013	*16*
TCD Installed	-0.007	*-521*	0.015	*103*	0.014	*100*
Drought (Observed)	0.018	*192*	0.018	*91*	0.018	*38*

List of Figures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0 5 10 15 20
0 5 10 15 20
Depth (m)
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Full Pool
TCD Installed
Drought

Figure 2.1

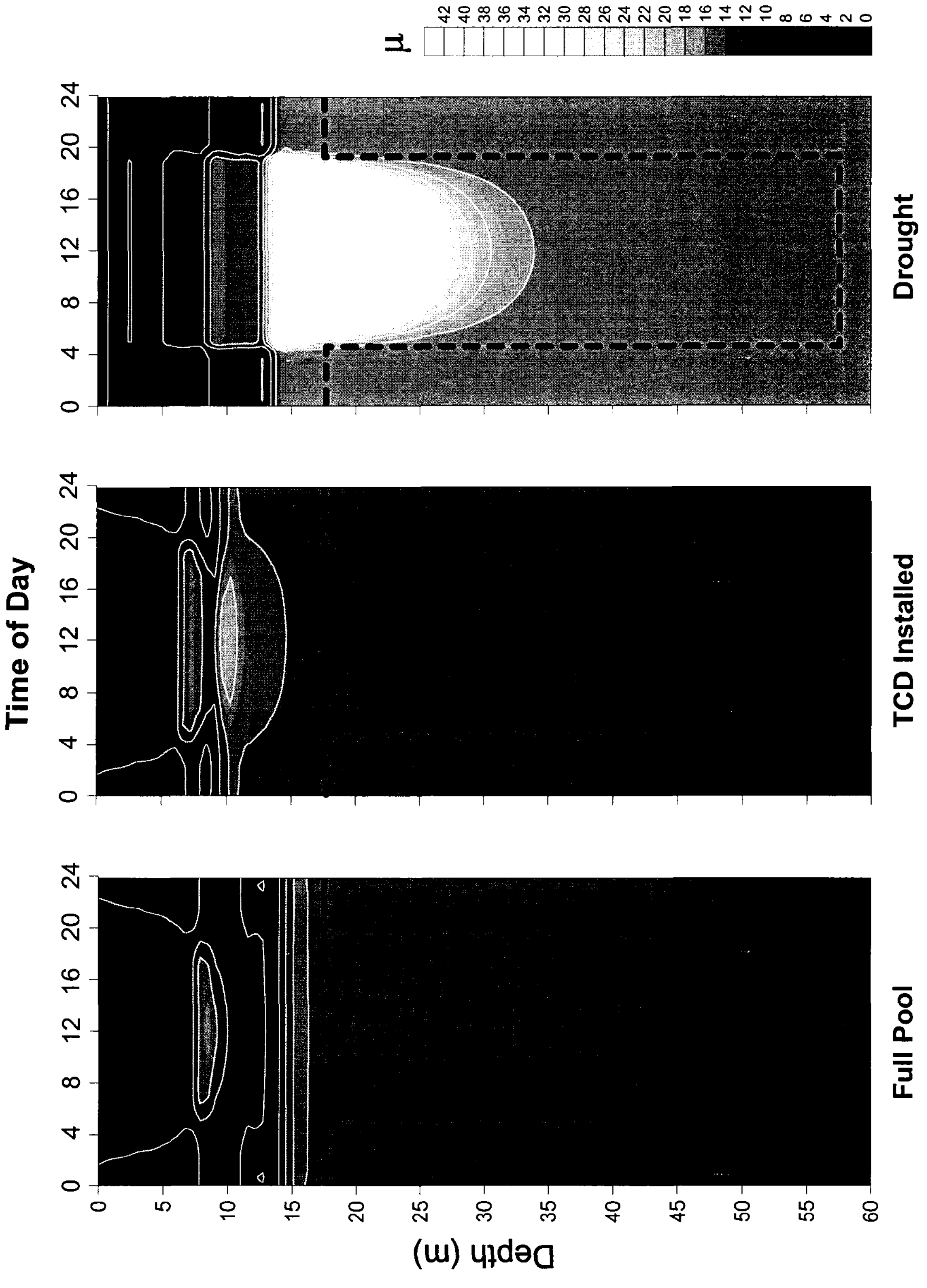
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Figure 2.2

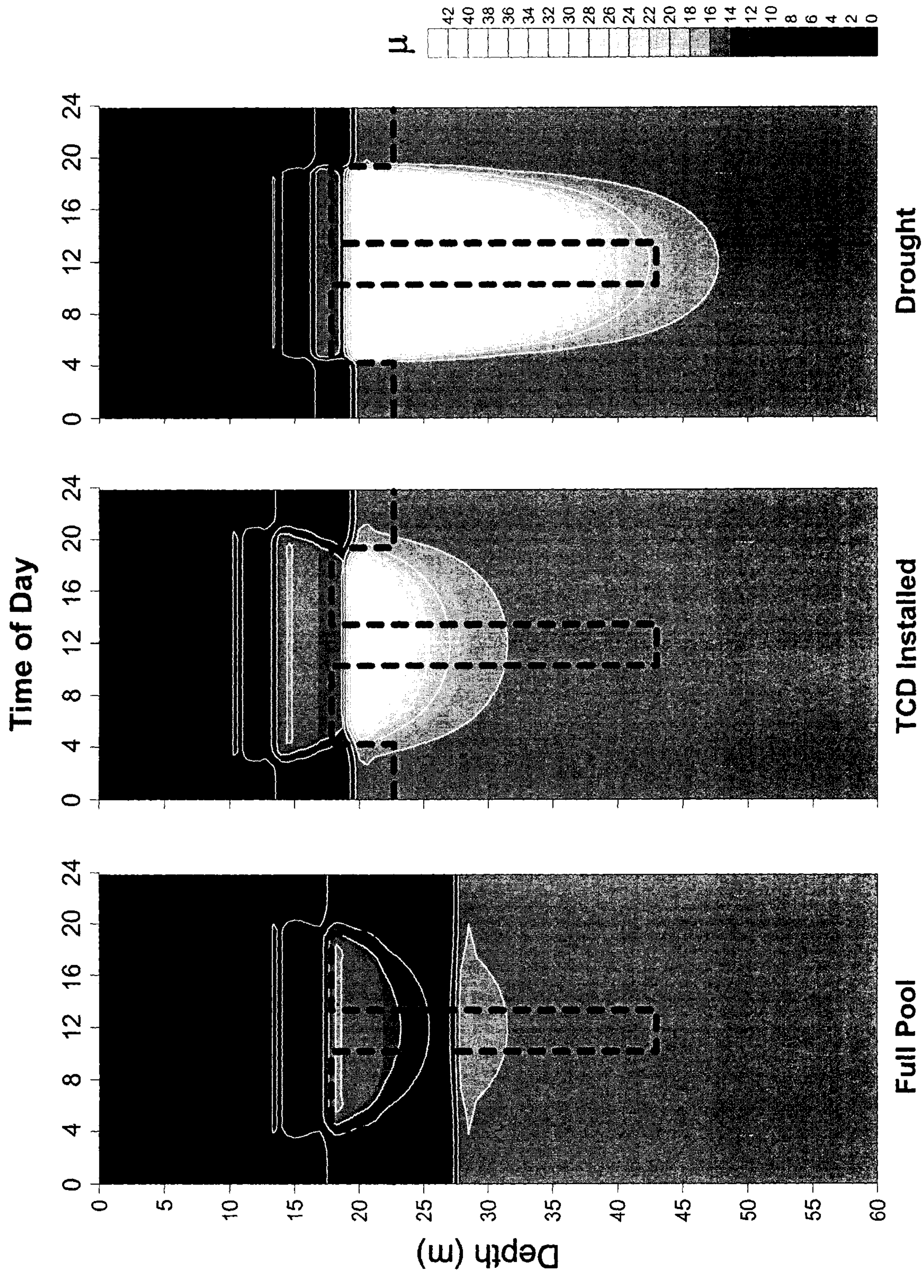
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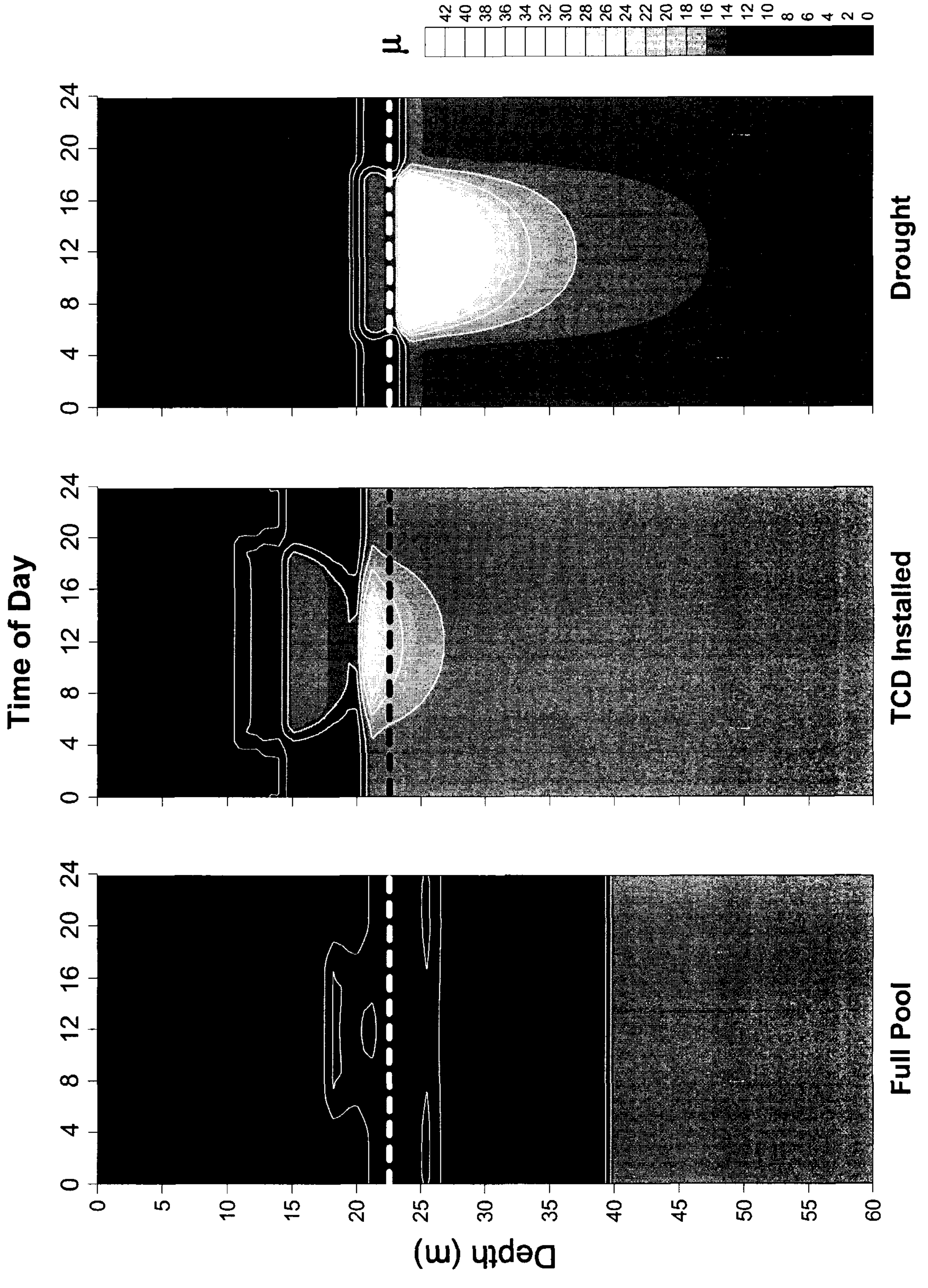
Figure 2.3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Drought
TCD Installed
Full Pool

Figure 2.4

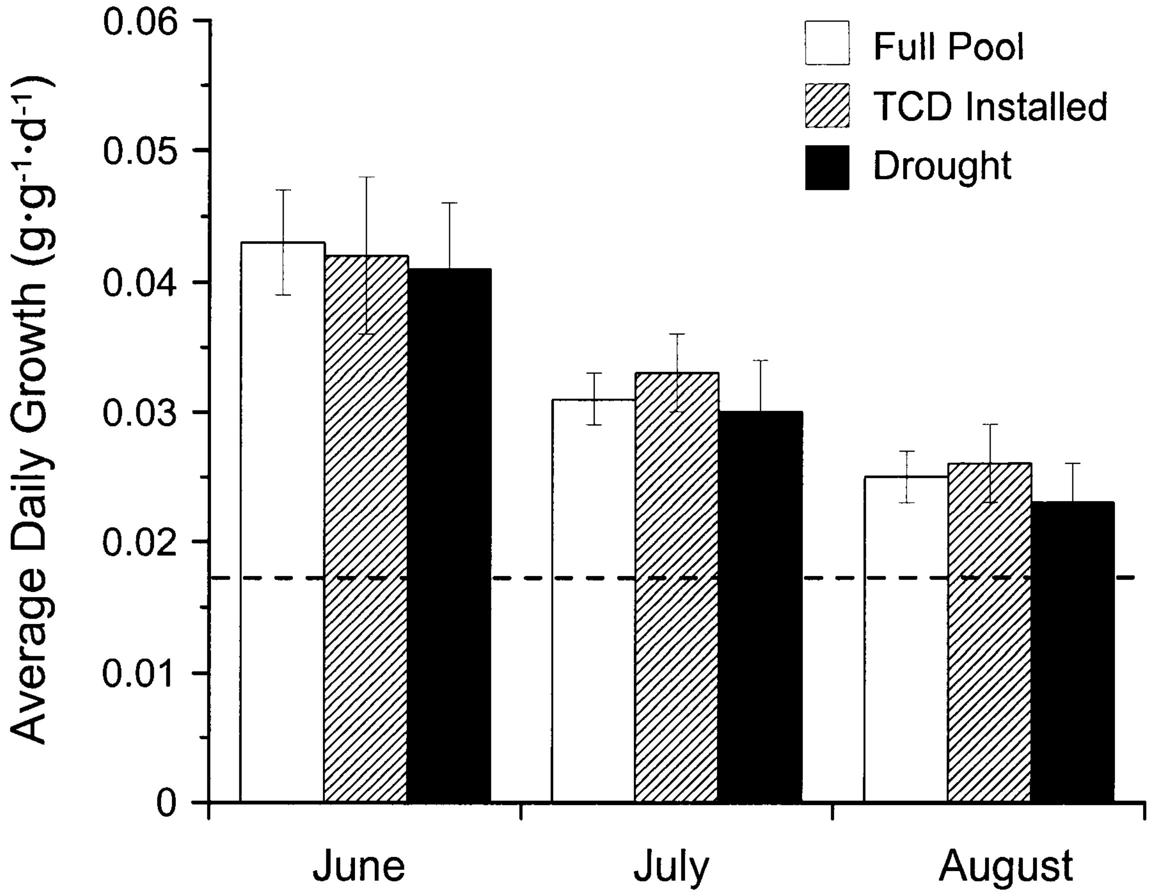
Average Daily Growth ($g \cdot g^{-1} \cdot d^{-1}$)
0.06
0.05
0.04
0.03
0.02
0.01
0
June
July
August
Full Pool
TCD Installed
Drought

Figure 2.5

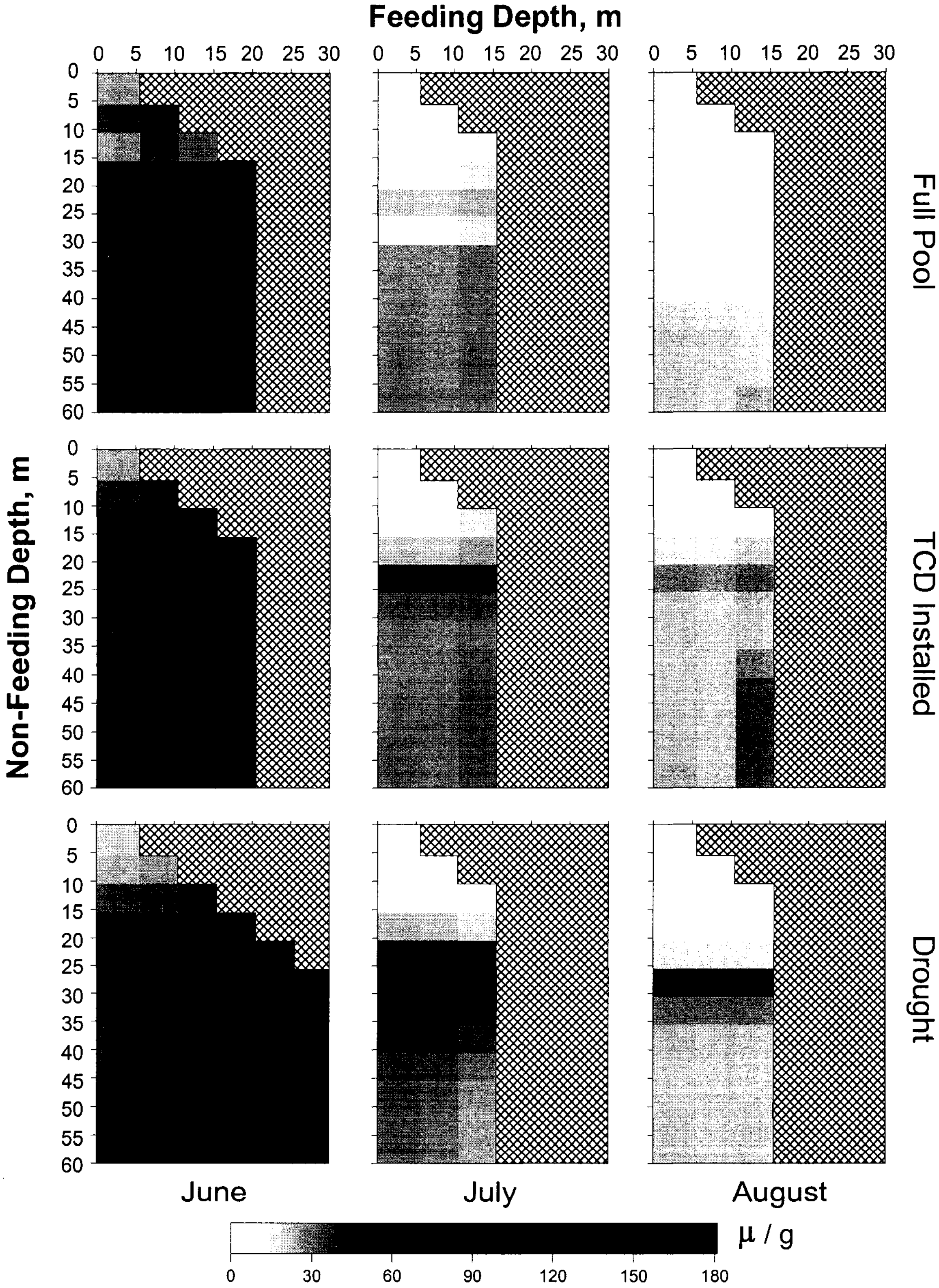
Feeding Depth, m
0 5 10 15 20 25 30
Non-Feeding Depth, m
0 5 10 15 20 25 30 35 40 45 50 55 60
Full Pool
TCD Installed
Drought
June
July
August
0 30 60 90 120 150 180
µ / g

Figure 2.6

CHAPTER 3

STRESSOR INTERACTIONS AND LANDLOCKED SALMON GROWTH: CLIMATE CHANGE AND EUTROPHICATION

Abstract

A bioenergetics-based foraging model was utilized to predict the interactive effects of environmental stressors (eutrophication and climate warming) on the growth of juvenile kokanee salmon (*Oncorhynchus nerka*). Daily growth was calculated for different sized fish (1, 5, 10, and 15-g) in June, July, and August under nine scenarios consisting of three trophic states (mesotrophic, eutrophic, and hypereutrophic) and three climate scenarios (current temperatures, and increased surface temperatures of 3 and 6 °C). Model inputs (temperatures, Secchi depths and zooplankton densities) for mesotrophic, eutrophic and hypereutrophic scenarios were derived from measurements at representative systems. Climate warming and eutrophication alone did not greatly affect daily growth for any sized fish during any month, and in fact increased daily growth (up to 0.5% body weight) in some cases. However, the interactions of these two stressors reduced kokanee growth, especially for larger (10 and 15-g) fish, which lost up to 3% of their body weight per day in July and August. Eutrophication reduced water clarity, requiring that kokanee move to shallower, warmer water to see their prey, resulting in decreased growth. Fishery managers may be able to mitigate some of the effects of

climate warming and eutrophication by altering dam operations to create a more suitable thermal environment in the reservoir, protecting water quality in the reservoir from excess nutrient input, or by changing fishery harvest regulations and stocking programs. These simulations demonstrate the need to examine interactive effects of ecosystem perturbations. By studying the effects of one stressor alone, potential effects of environmental change on aquatic ecosystems may be severely underestimated.

Introduction

As human activities progressively increase our impact on the environment, we strive to understand the important interplay between abiotic processes and living elements in ecosystems. The presence of multiple stressors makes it more difficult to predict ecosystem responses for a number of reasons (Breitburg et al. 1998): first, aquatic organisms have a wide range of sensitivity to any given stressor, and responses will depend on factors such as physiology and behavior. Also, exposure to one stressor may make either individual organisms or entire communities more susceptible to other stressors. Furthermore, predicted responses to stressors may be affected by trophic interactions (e.g., predation risk). Two contemporary anthropogenic stressors that threaten the quality of aquatic ecosystems are eutrophication and climate change. Much work has focused on predicting the effects of each issue separately, but little has been done to forecast how their interactive effects may influence aquatic ecosystems.

While climate change may present problems for aquatic ecosystems in the near future, eutrophication has plagued some systems for decades (Carpenter et al. 1998). In lentic systems, excess nutrient inputs (especially N and P) can increase trophic state

(Downing and McCauley 1992), resulting in phytoplankton blooms, decreased water clarity, hypolimnetic oxygen depletion, increased frequency of fish kills, loss of native species, and taste and odor problems (Lee and Jones 1992; Carpenter et al. 1998). The effects of eutrophication can reach far into food webs: at moderate levels of nutrient enhancement, phytoplankton growth can sustain a higher forage base of zooplankton for planktivores (e.g., the deliberate fertilization of the British Columbia Lake Enrichment Programme (Stockner and MacIsaac 1996)). The opposite is also true; higher nutrient levels may result in reduced water clarity (Canfield and Bachmann 1981; Portielje and Van der Molen 1999), or the production of toxic cyanobacteria that restrict zooplankton abundance (Kotak et al. 1996; Watson et al. 1997; Carpenter et al. 1998). Large-bodied zooplankton, such as *Daphnia*, are important prey items for planktivorous fish; however, the presence of cyanobacteria can decrease fecundity and clog the filtering apparatus of these animals (DeMott 1999; Ferrão-Filho et al. 2000; DeMott et al. 2001). Cladocerans such as *Daphnia* are not only an important prey base for foraging fish, but can graze phytoplankton down to increase water clarity (Deneke and Nixdorf 1999; Jeppesen et al. 1999; Stemberger and Miller 2003) which is beneficial to planktivorous fish searching for prey. Eutrophication can potentially decrease the amount of zooplankton available for fish, and decrease water clarity so that what zooplankton is available becomes harder to find.

Unlike eutrophication, the effects that climate warming will have are not obvious. Average global surface temperatures are expected to increase by up to 5.8 °C within the next 100 years, having important consequences for aquatic ecosystems (Houghton et al. 2001; Poff et al. 2002). Thermal suitability of aquatic habitats will change in many places as temperatures warm, causing habitats that were previously cool- or cold-water environments to disappear and change to warm-water environments open to invasive, non-native, or warm-water species (Carpenter et al. 1992; Hauer et al. 1997). In addition, lake warming also increases the potential for nuisance algae blooms, reduces dissolved oxygen, and generally favors the eutrophic condition (Poff et al. 2002). As a result of these changes, climate warming will affect food web interactions in lentic systems. Warmer temperatures generally increase zooplankton reproductive rates by decreasing egg development time (Orcutt and Porter 1984; Gabriel et al. 1987), and can result in smaller-bodied zooplankton populations as age at first reproduction occurs earlier (Moore et al. 1996). Size-selective planktivorous fish may have to spend more time foraging because smaller zooplankton will be more difficult to find (i.e., reaction distance will be shorter), and they may have to consume more individuals to meet energetic demands. Increased temperatures will affect fish as well; changes in thermal stratification within a lake may either segregate or aggregate predators and prey (e.g., Magnuson et al. (1990) and Brandt et al. (2002)). Furthermore, warmer temperatures will affect the energy budget of fish directly, increasing metabolic rates (Brett 1971; Brett and Glass 1973).

Salmonids are one of the many aquatic organisms that can be greatly affected by changes in their environment. Sockeye salmon and kokanee (*Oncorhynchus nerka*) are both important sport and market fish, and some sockeye stocks are listed as federally endangered or threatened. Salmon returns have dropped dramatically over the past century as a result of overexploitation, dams on natal rivers, and habitat degredation (Williams et al. 1999). One way that managers are hoping to preserve salmon stocks is to better understand their limitations and requirements for survival. Because both sockeye and kokanee rely on zooplankton exclusively throughout their juvenile life cycle (and for kokanee, their entire life) (Finnell and Reed 1969; Hoag 1972; Eggers 1978), the availability of zooplankton is an important indicator of a lake or reservoir's ability to support this species. Kokanee and sockeye have developed complex and efficient behaviors to exploit available zooplankton prey in a range of systems, but their growth rates are tied to environmental conditions.

Kokanee often exhibit diel vertical migrations (DVMs) in order to find and consume prey, digest meals at metabolically favorable temperatures, and avoid predators (Clark and Levy 1988; Levy 1990; Bevelhimer and Adams 1993). A bioenergetics-based foraging model has been used to explain observed DVMs and growth patterns of kokanee (Stockwell and Johnson 1997, 1999). This model has been enhanced with a light-dependent functional response (Chapter 1), which makes it ideal for examining the effects of changing environmental conditions on kokanee growth. The functional response is affected by prey density and light level (Koski and Johnson 2002), which is a function of time of year, geographic location, incident light and water clarity. At higher light levels, kokanee utilize a Type II functional response, at low light levels they utilize a Type I functional response, and when light is less than 0.001 lux fish do not feed (Ali 1959; Koski and Johnson 2002). Both prey density and water clarity can change with eutrophication and climate warming. The model's energy budget calculates the amount of energy left for growth after accounting for energy available through consumption, and energy excreted or egested as waste products and spent on metabolism; all of these rates are a function of fish mass and ambient temperature (Stockwell and Johnson 1997, 1999). A thorough description of the model can be found in Chapter 1.

In this study, the foraging model was utilized to predict the effects of eutrophication and climate warming on the growth of age 0 kokanee. I assumed two main effects of eutrophication: decreased water clarity and altered zooplankton abundance. I also assumed two main effects of climate warming: direct effects on the kokanee's energy budget, and increased zooplankton abundance. While many studies have examined the effects of eutrophication or climate warming on fish alone, this study is one of the first to examine the interactive effects of these stressors. To sustain sport fish populations that are sensitive to environmental change, fishery managers may need to consider options that will mitigate the predicted effects of multiple stressors.

Methods

Model Inputs

A 3 x 3 factorial design was employed to model the effects of eutrophication and climate warming on kokanee growth; there were three trophic states (mesotrophic, eutrophic, and hypereutrophic) and three climate warming scenarios (current temperatures, and air temperature increases of 3 and 6 °C). First, I examined the effects of eutrophication without any temperature change by conducting simulations for June though August, 2002. I altered Secchi depths and zooplankton densities to reflect changes in trophic state, progressing from mesotrophic to hypereutrophic. Next, for each of these trophic states, I simulated the effects of climate warming by increasing water temperature and zooplankton production. For each month (June, July, and August 2002), there were nine suites of simulations representing three trophic states (mesotrophic, eutrophic, and hypereutrophic), three temperature scenarios (current temperatures, and increased air temperatures of 3 and 6 °C), and their interactions. Because age 0 fish size varies across systems containing kokanee and sockeye, I simulated daily growth for a range of fish sizes (1, 5, 10, and 15-g) so that fish size could be eliminated as a confounding factor. This range of fish sizes is typical of the size of both age 0 kokanee and sockeye throughout their geographical range (e.g., Woodey (1972), Hume et al. (1996), Luecke et al. (1996), and Chapter 1). So, for each trophic state – climate warming scenario, simulations were executed using four fish sizes for a total of 108 simulations.

Inputs for baseline simulations (mesotrophic conditions and current temperatures) were collected from Blue Mesa Reservoir (BMR), Colorado, during the summer of 2002. Blue Mesa is a 3,700 ha, 101-m deep reservoir located in southwestern Colorado, and was chosen as the baseline system because it has a well-studied kokanee population and much limnological data has been collected from BMR during the past decade (Johnson 2004). The foraging model was calibrated to BMR conditions using generalized DVMs, Secchi depths, zooplankton densities, and kokanee growth rates measured at BMR (Chapter 1). I used the same monthly zooplankton calibration factor calculated in Chapter 1, which accounts for the difference in average zooplankton densities detected with sampling gear vs. zooplankton patch densities that kokanee likely experience while foraging. Cladoceran zooplankton are abundant and *Daphnia pulex* compose approximately 97% of the kokanee diet in this system, resulting in kokanee growth rates well above average for the species (Stockwell and Johnson 1999). Lake trout (*Salvelinus namaycush*) are the kokanee's main predator in BMR. In baseline simulations (one simulation for each of the summer months of June, July, and August), kokanee performed

DVMs that were derived from hydrouacoustic surveys and gill netting (Hardiman et al. in press, Figure 3.1). Additional field data used as model inputs included information on zooplankton abundance (Figure 3.2), temperature-depth profiles (Figure 3.3), and Secchi depths (Table 3.1) (Hardiman et al. in press).

Effects of Eutrophication

To examine the effects of eutrophication on kokanee, I assumed that increasing trophic state would have two main effects. First, increased algal abundance would decrease water clarity (i.e., reduce Secchi depth), lowering the amount of light available for foraging. I assumed that kokanee DVMs were triggered by light level because observed DVMs were symmetrical around noon; therefore, I changed the depths of the DVMs in eutrophic and hypereutrophic simulations so that 1) the functional responses utilized (i.e, Type I, Type II, or no feeding) during the simulations matched those in the baseline scenarios, and 2) the magnitude of light at each time and depth was approximately the same as in the baseline scenarios. The second effect of eutrophication on kokanee growth was that of changed prey availability. When available, kokanee feed exclusively on large-bodied *Daphnia* (Eggers 1982; Stockwell et al. 1999) but zooplankton species composition, size distribution, and density may change with trophic state. I obtained water clarity data (Secchi depths) and zooplankton densities for eutrophic and hypereutrophic scenarios from data collected from representative systems: Lake Mendota, Wisconsin, and Lake Washington, Seattle, ca. 1963, when the lake was most productive (Edmondson 1970, 1974). While zooplankton were not collected below 20-30 m in each of these three systems, their density usually declines rapidly with depth

(Wissel and Ramacharan 2003) and a decaying power function was used to calculate zooplankton densities below sampled depths (Appendix III).

Lake Mendota is a large eutrophic lake located in Madison, WI, that has high phosphorus loading from agricultural and urban runoff (Soranno et al. 1997) and substantial algal blooms during the summer months (Lathrop et al. 1996; Lathrop et al. 1999). The lake has a food web that is functionally similar to BMR. Cisco (*Coregonus artedi* Lesueur) and yellow perch (*Perca flavescens* Mitchell) are among the dominant planktivores, and are preyed upon by walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*). In eutrophic simulations, I used average monthly Secchi depths and *D. galeata* densities collected from Lake Mendota (Lathrop et al. 1999); zooplankton densities below 20 m were calculated in a similar manner as for BMR (Appendix III).

Data collected from Lake Washington in the 1960's was used to represent the hypereutrophic state in simulations. Between 1941 and 1968 sewage had been released directly into the lake, causing a steady increase in primary productivity, with maximum nutrient inputs occurring in 1963 (Edmondson 1974). Lake Washington contains sockeye salmon, which in the 1960's had a diet consisting of approximately 70% copepods (*Epischura nevadensis*) and 30% cladocerans (*Diaphanosoma birgei*) (Woodey 1972). This ratio was used to calculate the average size of prey consumed and prey energy density (Appendix III). Copepods can be more evasive than cladocerans and require more time to capture (O'Brien 1979), so I adjusted the functional response in the foraging model (Koski and Johnson 2002) as follows. Because pursuit is included in handling time (T_h, s/prey), I increased T_h to incorporate higher handling times required for a mixed diet of copepods (1 s/prey) and cladocerans (0.36 s/prey) (Wissmar and Simenstad 1988;

Koski and Johnson 2002). Equation 3.1 was used to calculate new parameter values (β_0 and β_1 in Equation 3.2) for a mixed diet Type II functional response:

(3.1) $$N = \frac{(a \cdot P)}{(1 + a \cdot T_h \cdot P)}$$

In the above equation, N is the total number of prey eaten per minute, and P is prey density (number/L). Rate of successful search, a, is equal to the volume of foraging habitat a predator can search during a unit of time (3.86 L/min) (Houck and Strauss 1985; Koski and Johnson 2002). I assumed that a did not change for different prey types because both copepods and cladocerans are readily detected by planktivores, either visually or through the lateral line system (O'Brien 1979; Janssen et al. 1995). Using equation 3.1 and an average handling time for a mixed prey diet of 0.808 s/prey, a new Type II functional response was calculated, given that $\beta_1 = (a \cdot T_h)^{-1}$ and $\beta_0 = \beta_1 \cdot a$ (Gotelli 1998):

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

where β_0 was 74.3 prey/min (the maximum consumption rate) and β_1 was 19.2 prey/L (the prey density at which consumption reaches half its maximum rate). Because the handling time for prey consisting solely of cladocerans was decreased by 55% after incorporating copepods into the diet, I decreased the slope of the original Type I functional response by 55% as well, resulting in a new Type I functional response for the copepod-cladoceran prey mix:

$$N = 0.775 \cdot P \tag{3.3}$$

I assumed that the zooplankton calibration factor would not change for different prey types or trophic states, as both copepods and cladocerans exhibit patchy distributions (Malone and McQueen 1983; Pinel-Alloul et al. 1988; Pinel-Alloul 1995; Folt and Burns 1999).

Effects of Climate Warming

I assumed that there would be two main effects of climate warming that would affect kokanee: direct thermal effects on the fish's energy budget, and increased food resources. The Canadian Climate Centre and Hadley general circulation models forecast an average air temperature increase of 3 to 6 °C in southwestern Colorado (Kittel et al. 2000). Air temperature is a significant driver of epilimnetic water temperatures in lakes and reservoirs (Wetzel 2001; Johnson et al. 2004). I calculated new temperature-depth profiles in which I proportionally changed water temperatures by depth; that is, if a 6 °C increase in the surface temperature represented a 30% change from baseline, I increased temperature at other depths by 30% as well. Resulting profiles were consistent with those predicted by Johnson et al. (2004), who modeled the effects of increased air temperature on thermal profiles in BMR.

Increased water temperature (T) increased zooplankton densities in the model via decreased egg development time (D, in days) (Equations 3.4 – 3.6) (Cooley et al. 1986; Gabriel et al. 1987):

(3.4) $$D_{Da} = (0.00041T^2 + 0.0108T - 0.0163)^{-1}$$

(3.5) $$D_{Co} = \frac{38{,}474 \cdot (T + 3.7)^{-2}}{24}$$

(3.6) $$D_{Di} = \frac{1{,}767 \cdot (T + 1.9)^{-1.08}}{24}$$

where D_{Da}, D_{Co}, and D_{Di} is egg development time for *Daphnia*, copepods, and *Diaphanosoma*, respectively; and N_{egg} is the number of eggs per female in BMR (Wise 1997). Finite per capita birth rate (δ) should increase, along with overall prey density (P), which was calculated using observed zooplankton densities from different depth strata of varying temperatures (Equations 3.7 and 3.8) (Rigler and Downing 1984):

(3.7) $$\delta = N_{egg} / D$$

(3.8) $$P_{T+} = (P_{T0} \cdot \delta_{T+}) / \delta_{T0}$$

where P_{T0} and δ_{T0} are prey densities and finite per capita birth rates at baseline temperatures, and P_{T+} and δ_{T+} are prey densities and finite per capita birth rates at elevated temperatures under climate warming scenarios.

Results

Effects of Eutrophication

Eutrophication decreased Secchi depths (Table 3.1), so I altered kokanee DVMs such that they located at depths with light levels similar to those in baseline DVMs (Figure 3.1). In eutrophic scenarios, kokanee were at shallower depths than in mesotrophic conditions during all months. In June, midday depths reached a maximum of 42.5 m, but by August, no DVMs occurred and kokanee spent all their time at a depth of 7.5 m. Similarly, kokanee in hypereutrophic scenarios went to a maximum depth of 12.5 m during midday in June, but spent all their time in July and August at a depth of 2.5 m.

Zooplankton densities from Lakes Mendota and Washington were extrapolated to 60 m for each trophic state (Figure 3.2). In the epilimnion, Lake Mendota had the highest zooplankton densities (25-30 *Daphnia*/L in June), whereas maximum zooplankton densities for BMR and Lake Washington were approximately 13 and 8 per L, respectively. In general, zooplankton densities were highest in June for BMR and Lake Mendota, and both systems had noticeable declines in August especially. In Lake Washington, however, zooplankton densities did not change as much throughout the summer.

Effects of Climate Warming

New temperature-depth profiles were generated for BMR for June, July, and August based on surface temperature increases of 3 and 6 °C (Figure 3.3). With a 3 °C surface temperature change, maximum epilimnetic temperatures were approximately 18

°C in June, and 23 °C in July and August. With a 6 °C surface temperature, maximum epilimnetic temperatures were approximately 21 °C in June, and 26 °C in July and August. Temperatures in the hypolimnion did not increase by more than approximately 2 °C under the warmest climate scenarios.

I used these new temperatures and Equations 3.4 – 3.8 to predict zooplankton abundances for depth strata down to 60 m (Figure 3.2). Zooplankton densities increased with temperature, but *Daphnia* densities in BMR and Lake Mendota exhibited a greater response to temperature than the mixed copepod-cladoceran zooplankton assemblage of Lake Washington. The maximum epilimnetic zooplankton density in Lake Washington was approximately 11 individuals/L (in July under the 6 °C surface temperature increase scenario), whereas the maximum density in Lake Mendota was almost 52 *Daphnia*/L (in June, also with a 6 °C surface temperature increase).

Interactive Effects - Daily Growth Rates

In general, under baseline temperatures, age 0 kokanee in mesotrophic conditions grew at faster rates than in either the eutrophic or hypereutrophic conditions (Figure 3.4). In June, growth was unaffected by trophic state and fish size. In July, larger fish (10 and 15-g) grew more in eutrophic and hypereutrophic conditions than in mesotrophic conditions. The 1-g fish grew at slower rates in July and August in the eutrophic and hypereutrophic scenarios. Fish weighing between 5 and 15-g grew more in July and August in the hypereutrophic scenarios than in the eutrophic scenarios.

Temperature increases did not greatly affect kokanee growth in the mesotrophic system (Figure 3.4); however, increased temperatures in conjunction with higher trophic states yielded changes in fish growth, with the most change occurring in July and August. Under mesotrophic scenarios, 1-g fish grew less in August with a 6 °C surface temperature increase (-0.6% body weight change per day), and larger fish grew up to 0.9% body weight increase per day. However, in the eutrophic and hypereutrophic scenarios, all fish grew less in July and August under a 3 °C surface temperature increase, with 1-g fish having the greatest change in percent body weight growth (up to -1.3% body weight change). When surface temperatures increased by 6 °C, 1-g fish still grew, but fish weighing 5 – 15-g lost weight (up to -3.0% body mass) in July and August in the eutrophic scenarios. In the hypereutrophic scenarios, 5-g fish did not lose weight, but 15-g fish lost weight in all months (between -0.5 and -2.6% body weight per day). In July and August, 10 and 15-g fish in the hypereutrophic scenarios did not lose as much weight as fish in the eutrophic scenarios.

Discussion

The effects of either eutrophication or climate warming alone may not alter kokanee growth to a large degree in mesotrophic systems such as BMR. However, the interactions between climate warming and eutrophication may have strong negative effects on kokanee growth, causing fish to lose up to 3% body weight per day. Few studies have addressed the interactive effects of major environmental stressors, and these simulations suggest that studies examining only one aspect of environmental change may underestimate actual impacts because it is likely that a combination of factors will occur, or that one change will trigger or exacerbate the effects of others (Schindler 2001).

Increasing trophic state enhanced prey resources but decreased visibility and the ability of kokanee to see their food. In eutrophic and hypereutrophic simulations where DVM depths were not altered from those observed in the mesotrophic system, kokanee lost weight (between 0.4 and 1.4% body weight per day) even at baseline temperatures because they were unable to see their prey (i.e., light level was less than 0.001 lx at all times during the simulation). When kokanee were relocated to depths where they could see their prey, they were much closer to the surface, especially in the hypereutrophic scenarios (e.g., in July and August, fish in hypereutrophic conditions stayed at depths between 0 and 5 m during the entire 24-h simulation period). While surface waters had much higher zooplankton densities, prey consumption was limited by the maximum consumption rate (β_0) in the functional response (Koski and Johnson 2002). In addition, if kokanee moved to shallower depths they were exposed to warmer temperatures, even in the absence of climate warming (up to 19.5 °C in July and August). Higher temperatures in the surface water negatively affected small fish because the amount of energy available to meet increased metabolic expenses was limited by their small stomach capacity. On the other hand, energy consumption of larger fish was more limited by C_{max} (the maximum amount of food that can be consumed in one day (Beauchamp et al. 1989)), so warmer epilimnetic temperatures in some cases actually increased growth because of high zooplankton abundance (e.g., 15-g fish in August in hypereutrophic conditions grew 2.2% under baseline temperatures, as opposed to only 1.5% in eutrophic conditions).

Climate warming did not affect growth of fish in the mesotrophic system because light availability and hence kokanee DVMs were not changed. The fish were able to stay in relatively cooler and deeper water and still find prey. Admittedly, the effects of climate warming on phytoplankton and water clarity were not addressed in this study, and it was assumed that climate warming alone would not affect DVMs. Warmer temperatures could possibly increase phytoplankton in the surface waters (Hassan et al. 1998; Ghadouani et al. 2003) and reduce light availability at greater depths, potentially changing kokanee DVMs. However, it is unclear as to how climate warming would change phytoplankton in a system like BMR; results from studies addressing the effects of warming on algal abundance and species composition have been idiosyncratic. Nevertheless, when water clarity was reduced via increased trophic state and kokanee had to move further up in the water column, higher temperatures in the climate warming scenarios negatively affected kokanee growth. Larger fish were especially affected by warmer temperatures because as fish size increases, respiration rates increase rapidly with temperature (Beauchamp et al. 1989).

I assumed that light levels triggered kokanee DVMs in BMR, dictating the depths at which the fish foraged and rested, and presumably, hid from predators. Bioenergetics modeling indicates that predator avoidance alone does not drive kokanee behavior (Chapter 1), and observed DVMs do not entirely shield kokanee from predators, as kokanee are exposed to light levels at which predators can see them. Diel vertical migration patterns could change in a manner different from what was predicted here; that is, the timing of DVMs was not changed, only the depths. In response to increased temperatures, kokanee could spend nights at greater depths to reduce energetic demands instead of staying in the warm epilimnion (as observed). In addition, kokanee may opt to stay in surface waters for shorter periods of time (i.e., for short feeding bouts during dawn and dusk) because prey abundance is greater with warmer temperatures and higher trophic states. With increased food resources fish can consume prey faster and spend more time in cooler waters below, simultaneously reducing energetic expenses and avoiding predators during the day.

I initially expected growth rates in the eutrophic system to be lower than those in the mesotrophic system, and even lower in the hypereutrophic system, especially since zooplankton abundances in hypereutrophic scenarios were often lower than both the mesotrophic and eutrophic systems. However, growth rates in the hypereutrophic system were higher than in the eutrophic system (up to a difference of 1.8% body weight per day), especially in July and August in both climate warming scenarios. While maximum consumption rate was reduced because of increased handling time required for copepods, it was still possible for kokanee to grow more in hypereutrophic scenarios than in eutrophic scenarios. This is because, depending on species, copepods can be larger than cladocerans and can also have higher energy densities (Table 3.1); therefore, kokanee having a diet consisting mostly of copepods may have higher growth rates than kokanee feeding exclusively on large-bodied cladocerans such as *Daphnia*.

Because the Lake Washington zooplankton community was dominated by copepods during the 1960's, the effects of eutrophication using this system should be interpreted with caution. I chose to use the conditions of Lake Washington because it is a large, deep system that is physically comparable to BMR; hypereutrophic systems of this nature are extremely rare. However, differences in their food webs may make direct comparisons between BMR and Lake Washington difficult. If prey in this system consisted entirely of *Daphnia* kokanee may have grown less, but it is difficult to say whether or not these conditions could exist. Lake Washington is a unique system that has a zooplankton community unlike that of Lake Mendota and BMR; in 1963, at the height of its eutrophication, Lake Washington contained few large-bodied cladocerans. In the sixties, kokanee consumed mostly large copepods and some smaller cladocerans (Woodey 1972). Highly eutrophic conditions with abundant toxic cyanobacteria can favor copepods over cladocerans (Ghadouani et al. 2003) because copepods can select non-toxic algae for consumption whereas *Daphnia* can not (Lampert 1981; DeMott 1986; DeMott and Moxter 1991). Thus, the hypereutrophic condition may yield planktivore food resources that are different from, and difficult to compare to, zooplankton communities in systems having lower trophic states.

In addition to growth, predation risk may also change for kokanee under different environmental conditions. In BMR, lake trout, cold-water predators, cause significant mortality to kokanee (Johnson and Martinez 2000). On one hand, increased temperatures may require that kokanee forage in risky environments (i.e., well-lit surface waters where prey items are most abundant) for longer periods of time in order to meet energetic demands. If water clarity does not decrease, this may not be a problem because kokanee would not need to relocate at shallower depths in order to find their prey. If water clarity decreases due to higher turbidity levels, kokanee may also have to spend more time in surface waters in order to locate prey, although there is some evidence to indicate that in moderately turbid environments the ability of planktivores to find zooplankton prey is not reduced as much as the ability of piscivores to find fish (De Robertis et al. 2003). On the other hand, increased temperatures may help to prevent predation by cold-water predators by creating a thermal barrier. In later summer months, lake trout may be inhibited by warmer temperatures in spending significant amounts of time above the hypolimnion (Crockett 2004; Hardiman et al. in press). Especially in eutrophic and hypereutrophic scenarios when kokanee were forced into depths above 10 m in July and August, water temperatures may be high enough to greatly reduce predation on kokanee from lake trout. In other systems, however, forcing fish into a warmer thermal environment closer to the surface may put them at risk to other predators such as warm-water piscivores or birds. Nevertheless, in BMR, spending longer periods of time in warm epilimnetic waters may increase kokanee mortality through the physiological stress of being in a suboptimal environment regardless of any decrease in predation by coldwater predators.

Assessing the effects of changing environmental conditions on growth and predation risk to vertically migrating planktivores can be facilitated with this model in many different systems. Oligotrophic systems present a different suite of issues for age 0 kokanee and sockeye (e.g., those found in the nursery lakes of British Columbia and Alaska). These systems are nutrient-limited and have lower zooplankton abundances to sustain young sockeye. Colder temperatures and low food availability constrain the amount of growth sockeye can achieve before smolting, and in many systems, sockeye smolt at sizes not greater than 10-g (Hume et al. 1996; Bradford et al. 2000; Mazumder and Edmundson 2002). In recent decades, lake fertilization has been used as a possible method to increase phytoplankton productivity, boosting food resources for juvenile sockeye and increasing growth during their first year to enhance survival at sea (Hyatt and Stockner 1985; Budy et al. 1998; Mazumder and Edmundson 2002). Organic turbidity (e.g., phytoplankton) may increase in these fertilized systems, which can affect the vertical migrations of sockeye and limit the ability of sockeye to find and consume their prey; however, the increase of zooplankton prey presumably offsets reduced-quality foraging conditions. Similarly, lakes that have high volumes of glacial till may also be somewhat turbid due to inorganic particles; in these cases, phytoplankton production may be limited by light and nutrients (Koenings et al. 1990), and sockeye may have more difficulty finding what prey is there without the benefit of having more prey as a result of higher productivity (as in fertilized systems). Climate warming may impact northern systems in ways similar to those described here. Increased temperatures will intensify energetic demands of fish, but in these oligotrophic systems, prey may not be sufficient to support their needs even if prey resources also increase in response to warmer temperatures. This model may be used as a way to determine whether or not lake fertilization could mitigate the effects of climate warming by increasing energy resources for juvenile sockeye. Lake fertilization has been successful in many places in bolstering juvenile sockeye growth, and may become more necessary with climatic changes.

The effects of climate warming and eutrophication can have severe consequences for planktivorous fish that vertically migrate. While predation risk may ultimately decrease because of warmer temperatures above the hypolimnion, warmer temperatures may also make it impossible for kokanee to meet increased energetic demands, regardless of prey abundance. The upper lethal temperature of kokanee is approximately 25 °C (Brett et al. 1969), and in some of the simulations presented kokanee could only find food at these temperatures due to low water clarity. Plasticity in DVM behavior could allow kokanee to compensate for increased energetic demands induced by climate warming, but when climate warming and eutrophication act together they may restrict kokanee to a narrow range of depths limited by warm water above and insufficient light to feed below.

Fishery and reservoir managers may be able to mitigate some of the effects of environmental change, in addition to behavioral changes that kokanee themselves may make. Kokanee are popular sport fish and are highly valued fishery resources because they are relatively innocuous outside of their native range, and support multi-million dollar fisheries in several large reservoirs. Furthermore, stocking kokanee for maintenance of a population is cost-effective, as opposed to other sport fish such as lake trout (Johnson and Martinez 2000). If kokanee are to be protected in the face of multiple stressors such as these, management options must include actions that will address a warmer, more turbid environment. Temperature control devices (TCDs) can be installed on dams to regulate downstream release temperatures, and research has shown that TCDs can also alter reservoir thermal profiles (Chapter 2). Releases from different depths and times using a TCD could create more suitable thermal habitats for kokanee. To control water clarity, managers may have to look towards resources outside of the reservoir. Land use change and population growth often result in eutrophication problems (Carpenter et al. 1998), and monitoring the local population, land use, and inflow water quality may be an important measure in assessing sources of excess nutrients. Furthermore, harvest regulations may alleviate some of the pressures associated with changes in predation risk to kokanee as a result of environmental change; if predation risk increases, restrictions on lake trout harvesting could be lifted, whereas kokanee could become more protected. And lastly, stocking programs could be altered so that fish entered the reservoir at a size that would be more appropriate for existing reservoir conditions.

Many studies have examined the potential effects of single environmental issues on fish habitat and growth. However, the combination of eutrophication and climate warming as agents of environmental change will not occur in isolation; it is likely that they will occur together. In the future, models with a strong link to environmental characteristics will be necessary to quantify and predict the interactions of multiple environmental stressors, especially in systems that are physically heterogeneous and have complex trophic interactions within the food web. Research that examines the interactive effects of multiple agents of environmental change will be necessary to determine the likely impacts on organisms such as kokanee, and aquatic environments as a whole. Lacking a multi-factor approach, we may be underestimating the extent to which our actions are influencing the world around us.

Acknowledgements

I'd like to thank Cindy Keough and Dr. Steven Del Grosso (Natural Resources Ecology Lab, Colorado State University) for providing CCC and Hadley model data supplied by VEMAP and the Ecosystem Dynamics and the Atmosphere Section, National Center for Atmospheric Research. Dr. Daniel Schindler and Jennifer Scheuerell (Department of Biology, University of Washington) supplied data from the Lake Washington long-term monitoring database. The U.S. Bureau of Reclamation (Upper Colorado Region, Salt Lake City Office) provided financial support for this project, and the U.S.D.A. provided funding through a National Needs Fellowship in Water Sciences.

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Table 3.1. Model inputs for different trophic states. Prey length is for *Daphnia* in the mesotrophic and eutrophic systems, and a combination of *Diaphanosoma* (30%) and *Epischura* (70%) for the hypereutrophic system.

	Trophic State		
	Mesotrophic	Eutrophic	Hypereutrophic
Prey length (mm)	1.84[a]	1.31*	1.835*
Energy density (cal/mg wet)	0.578[b]	0.578[b]	0.675*
Handling time (s/prey)	0.36[c]	0.36[c]	0.81*
Zooplankton calibration factor - June	2.1[d]	2.4[d]	12.5[d]
Zooplankton calibration factor - July	2.4[d]	2.4[d]	2.4[d]
Zooplankton calibration factor - August	12.5[d]	12.5[d]	12.5[d]
Secchi depth – June (m)	5.1[d]	3.6[e]	1.1[f]
Secchi depth – July (m)	7.0[d]	1.6[e]	0.9[f]
Secchi depth – August (m)	5.6[d]	1.4[e]	1.0[f]

[a] Stockwell et al. (1999)
[b] Cummins and Wuycheck (1971)
[c] Koski and Johnson (2002)
[d] Chapter 1
[e] Lathrop et al. (1999)
[f] Madison Park sampling station, Lake Washington, 1963. (D. Schindler, University of Washington, unpublished data)
* Calculated – Appendix III

List of Figures

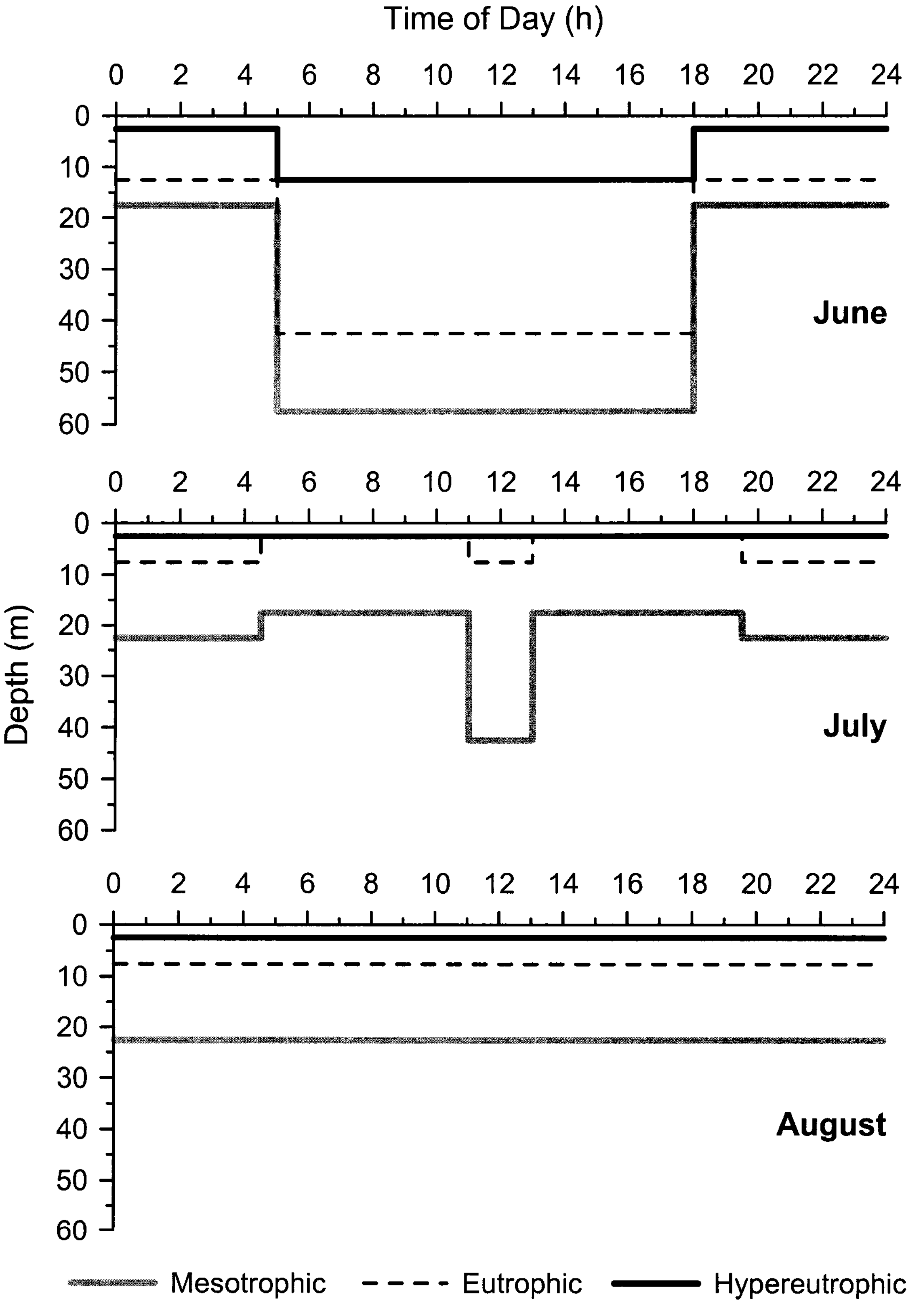

Time of Day (h)
0
2
4
6
8
10
12
14
16
18
20
22
24
Depth (m)
0
10
20
30
40
50
60
June
July
August
Mesotrophic
Eutrophic
Hypereutrophic

Figure 3.1

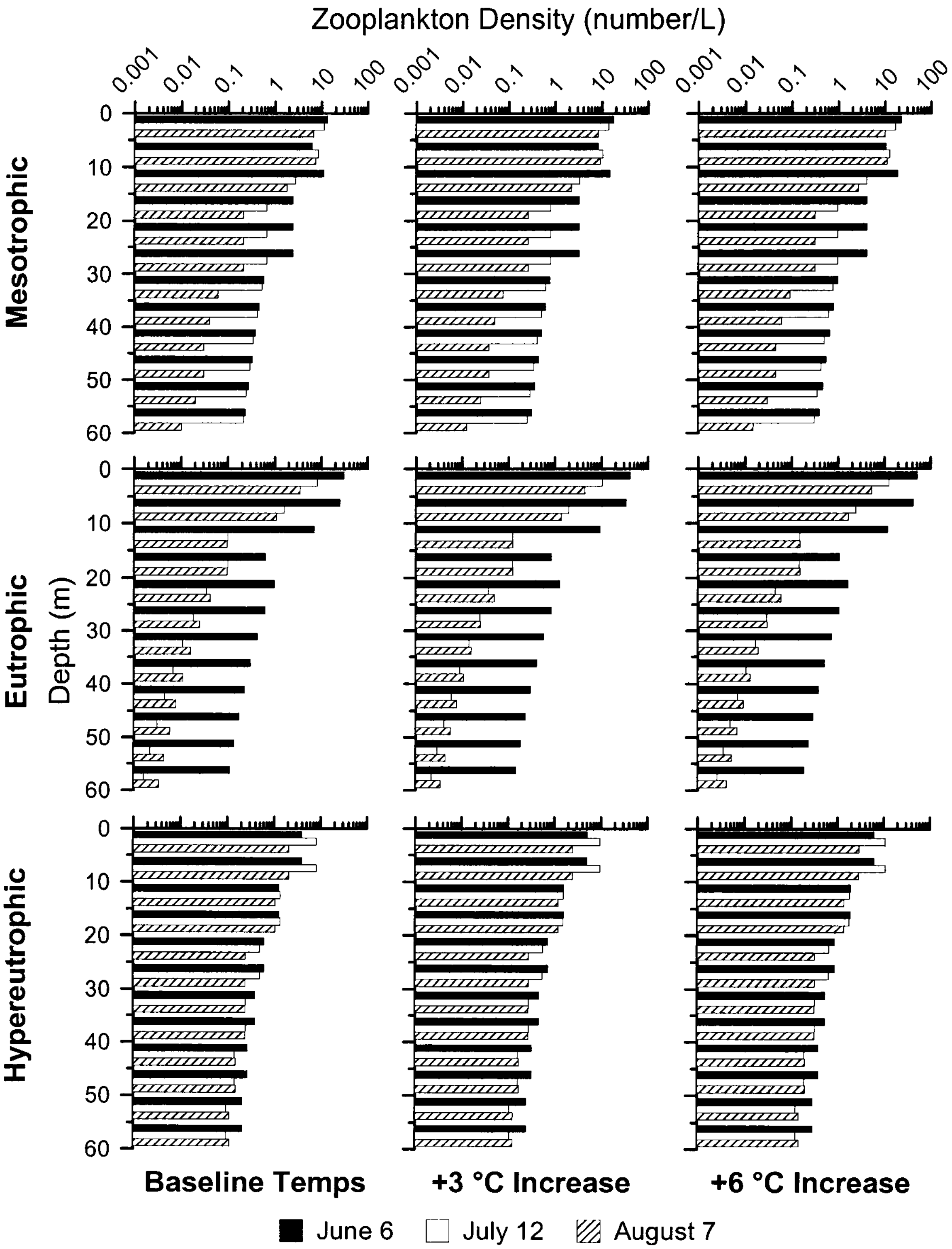
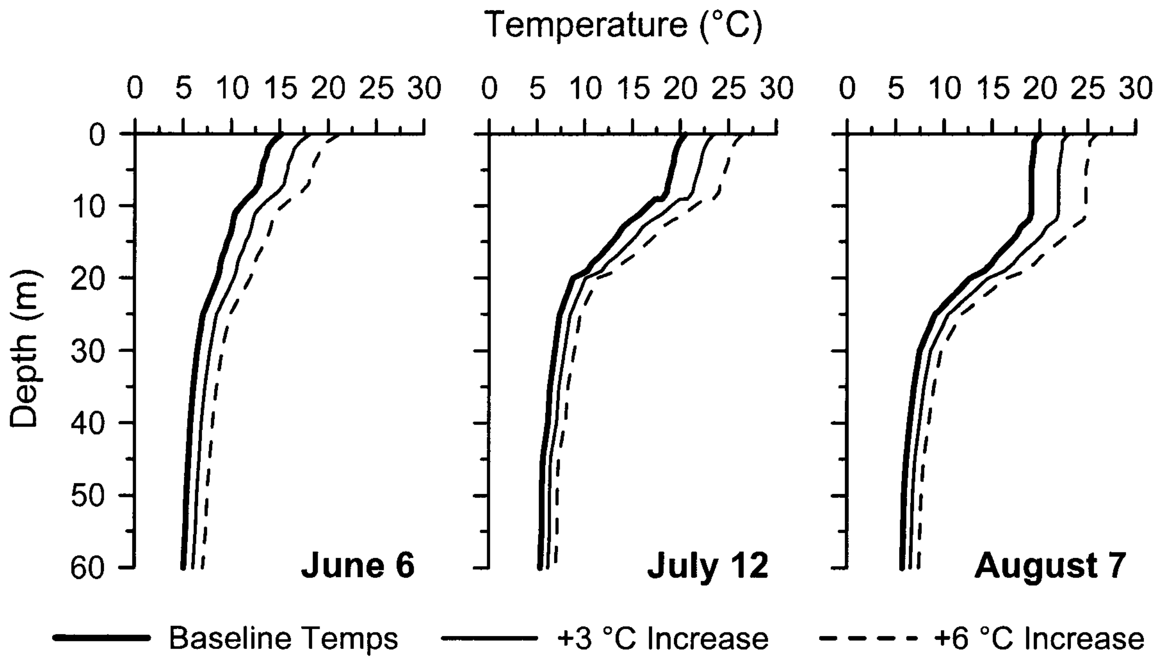

Zooplankton Density (number/L)
0.001
0.01
0.1
1
10
100
Mesotrophic
Eutrophic
Hypereutrophic
Depth (m)
0
10
20
30
40
50
60
Baseline Temps
+3 °C Increase
+6 °C Increase
June 6
July 12
August 7

Figure 3.2


Temperature (°C)
0 5 10 15 20 25 30
0 5 10 15 20 25 30
0 5 10 15 20 25 30
Depth (m)
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10
20
30
40
50
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July 12
August 7
Baseline Temps
+3 °C Increase
+6 °C Increase

Figure 3.3

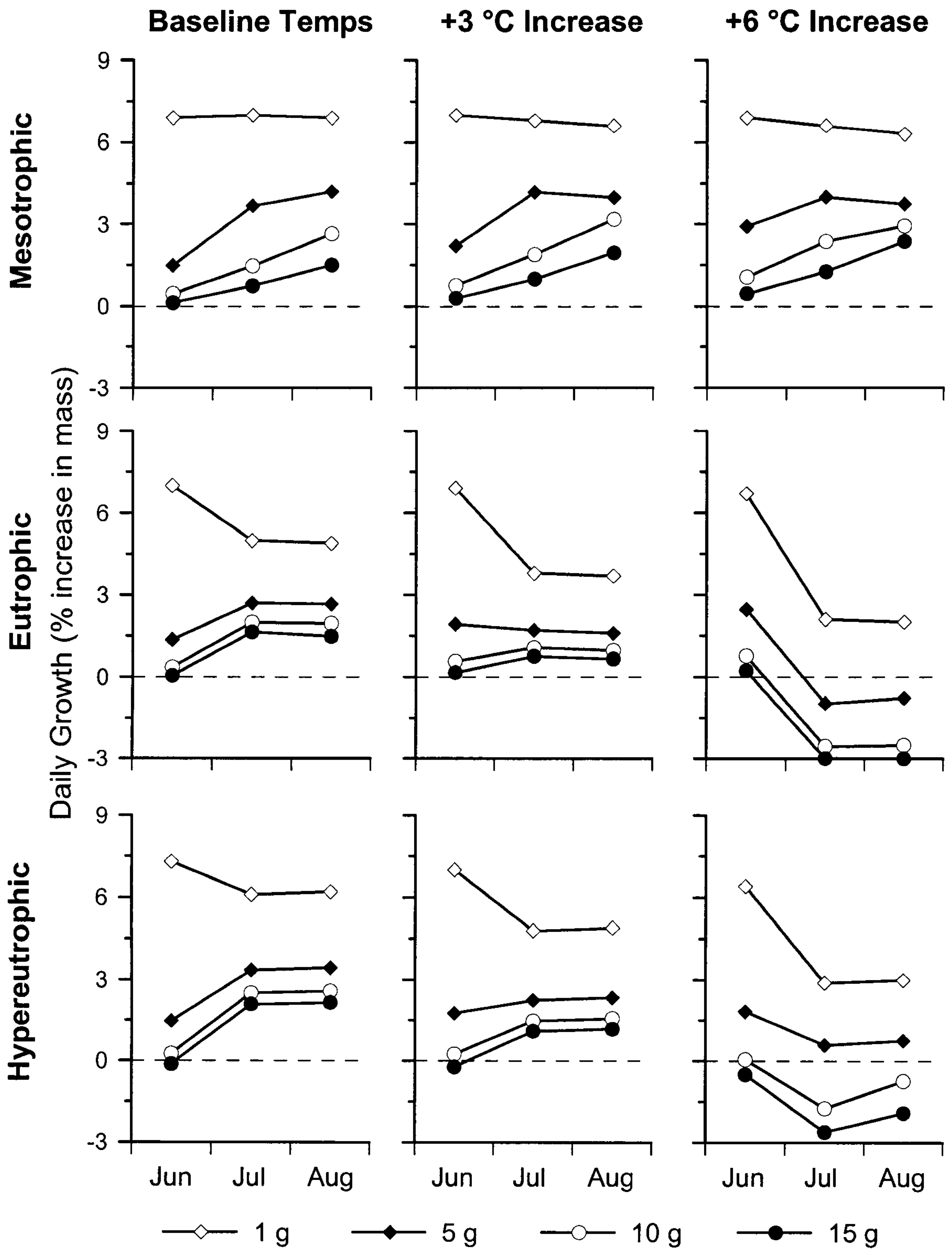

Baseline Temps
+3 °C Increase
+6 °C Increase
Mesotrophic
Eutrophic
Hypereutrophic
Daily Growth (% increase in mass)
9
6
3
0
-3
Jun
Jul
Aug
1 g
5 g
10 g
15 g

Figure 3.4

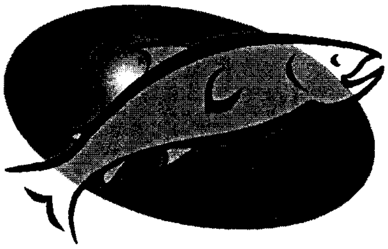
APPENDICES

APPENDIX I

KokanEat v. 1.0 USER MANUAL

Developed by:
Marci L. Koski, Department of Fishery and Wildlife Biology
Colorado State University

Sathish Chittibabu, Department of Electrical and Computer Engineering
Colorado State University



Introduction

KokanEat models the daily energetics of juvenile kokanee salmon (*Oncorhynchus nerka*). In its most basic sense, KokanEat is a bioenergetics-based foraging model that balances energy consumed from food against energy spent through metabolism, waste, and growth. KokanEat differs from other bioenergetics models in that a wider range of environmental conditions are considered in calculating a fish's energy budget; in addition to parameters such as temperature and prey availability, KokanEat now incorporates light intensity and water clarity as a major factor in determining feeding rate, which in turn, determines how much energy a fish can use for growth.

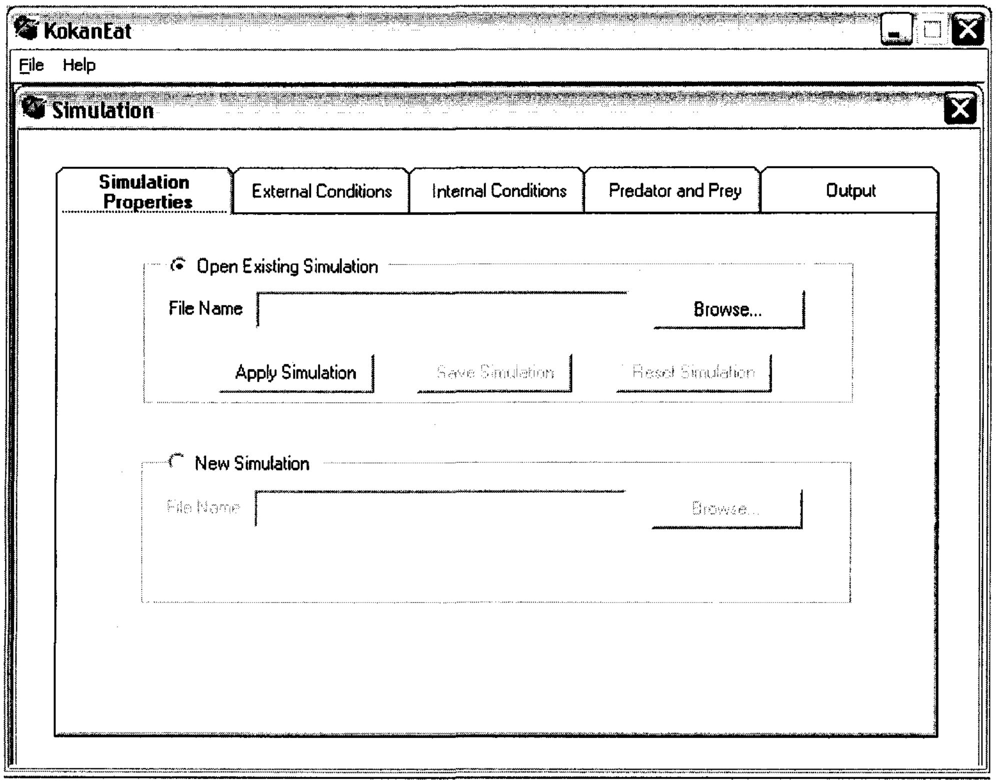
KokanEat has evolved from several models. The work of Beauchamp et al. (1989) and Bevelhimer and Adams (1993) were integral in the development of the Stockwell and Johnson (1997, 1999) model. KokanEat is similar to the Stockwell and Johnson (1999) model except that it now has a light-dependent functional response (Koski and Johnson 2002) and a user-interface that makes setting up simulations easier than entering data in a spreadsheet. For a detailed look at bioenergetics models, please read the manual for Fish Bioenergetics 3.0, which was developed for numerous fish species (Hanson et al. 1997).

KokanEat has a unique user-interface, which is described in this manual. There are two main sections: using the model and interpreting output. Within each section, underlined subsections denote instructions for each page in the model and output; italicized words correspond directly to fields in the model.

Using the Model

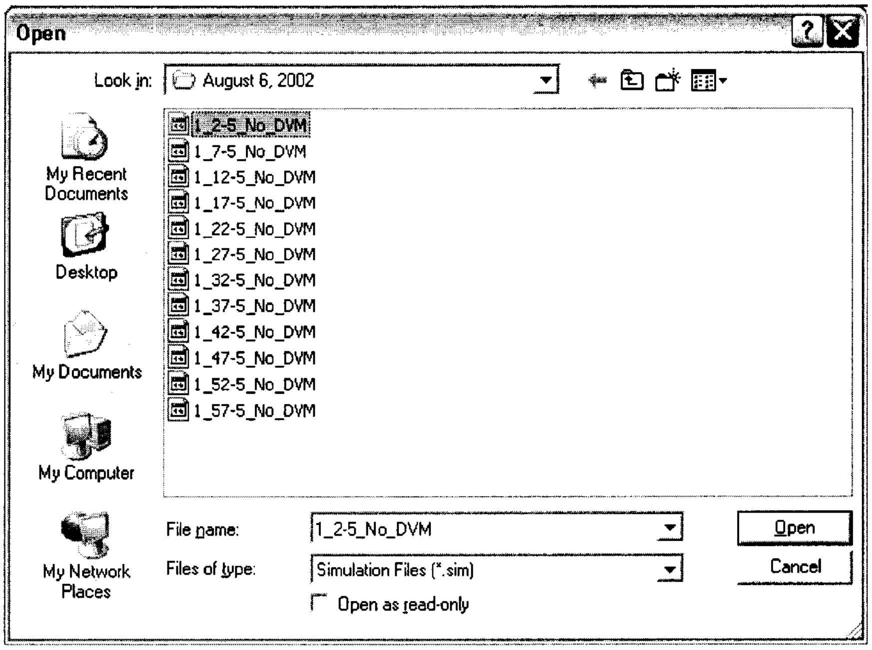
Copy the KokanEat folder from the CD onto your computer; you may wish to make a copy of KokanEat.exe on your Desktop. Double-click the KokanEat icon and choose “Simulation Setup” from the File Menu. You will be presented with five “pages” in the Simulation window, each with their own tab at the top. The first page is called “Simulation Properties”

Simulation Properties



The Simulation Properties page allows the user to either open up an existing simulation or create a new simulation.

To open an existing simulation, click the “*Open Existing Simulation*” radio button, then click the “Browse” button to locate the file. After the file is located, press the “Open” button; the location and file name of the desired file should be in the “file name” field. Click the “*Apply Simulation*” button to populate all the fields in the simulation. If you click on any of the other four tabs you will see that the fields have been filled according to the contents of the simulation (*.sim) file you just opened. In the example below, the file “1_2-5_No_DVM.sim” will be opened.



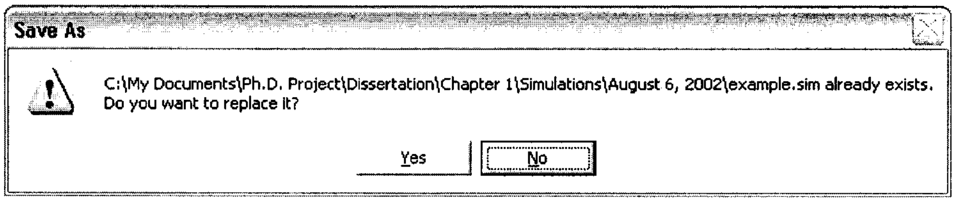
Look in: August 6, 2002

File name: 1_2-5_No_DVM

Files of type: Simulation Files (*.sim)

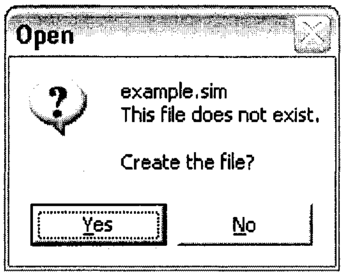
☐ Open as read-only

To save an existing file with another file name (e.g. so that you can change one or more fields in the simulation without having to create a whole new file), follow the procedures above. After clicking the "*Apply Simulation*" button the "*Save Simulation*" button will become active; click it to open the "Save As" dialog box. After renaming the file (making sure it is in the proper location), click "Save". The new file name will now appear in the "New Simulation" section. If you plan on making changes to the simulation file but would like to keep the existing file name, enter the existing file name in the "File name" field; you will receive a message asking to confirm that you would like to overwrite the existing file; click "Yes":



C:\My Documents\Ph.D. Project\Dissertation\Chapter 1\Simulations\August 6, 2002\example.sim already exists.
Do you want to replace it?

To create a new file from scratch, click the "*New Simulation*" radio button, then click the "browse" button to determine the location of the file. Type the file name to be created in the file name box and click "Open". You will get a message stating that the file does not exist. Answer "Yes" when asked if you'd like to create the file. The new file and its location will now appear in the file name field in the "*New Simulation*" section.



example.sim
This file does not exist.

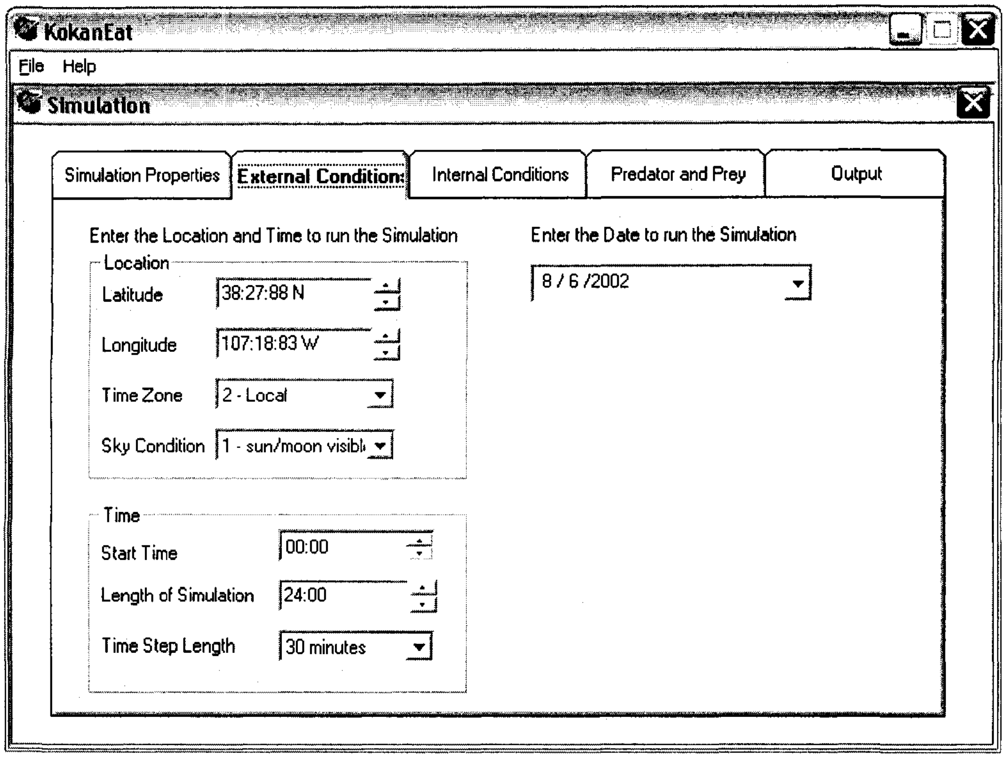
Create the file?

Click "Yes" to create the new (blank) simulation file called "example.sim".

The .sim file will not actually be created (i.e., saved to your computer) until you save the simulation from the "Output" page (described below). The "*Reset Simulation*" button simply depopulates all field values without saving the simulation. All fields in the "Simulation Properties" page will be blank, and you will have to either open an existing file or create a new one. Resetting the simulation does not delete the contents of a *.sim file.

External Conditions

After the simulation properties are specified (file name and location), the user must now give KokanEat some information about when and where the simulated fish exists. The "External Conditions" page requires the user to input geographic coordinates and a date so that a submodel can calculate surface light levels; the submodel can calculate surface light levels for any location on earth and for almost any date, past or present. There are two exceptions; the model cannot calculate light levels correctly for both summer and winter solstices, which occur on June 21 and December 21 respectively. The model uses secchi depth and surface light levels to calculate light levels at the depths that our virtual fish is located, thereby determining which functional response (feeding rate) the fish uses to consume prey.



Enter the Location and Time to run the Simulation

Location
Latitude: 38:27:88 N
Longitude: 107:18:83 W
Time Zone: 2 - Local
Sky Condition: 1 - sun/moon visibl

Time
Start Time: 00:00
Length of Simulation: 24:00
Time Step Length: 30 minutes

Enter the Date to run the Simulation: 8 / 6 /2002

In the above example, the *latitude* and *longitude* coordinates are for Blue Mesa Reservoir, Colorado. There are three options for "*Time Zone*"; click the drop-down menu to choose the appropriate designation. "*0 – UT*" utilizes Universal Time, which is Greenwich Mean Time. This is basically the time in Greenwich, England, and is the same everywhere; Universal Time is mostly commonly used by astronomers. "*1 – Std*" is Standard Time, based on time zones; within each time zone it is the same hour and minute everywhere, and adjacent zones differ by exactly one hour. On the globe there are 24 time zones of approximately 15 degrees longitude. "*2 – Local*", Local Time, is similar to Standard Time except that time will vary within each time zone; within a zone, minutes will decrease as you travel in a direction away from Greenwich, England. So, for example, in the center of the time zone which is at 4:30 p.m. in Standard Time, it could be 4:30 p.m. in Local Time. At this same time however, if you are on the eastern boundary of the time zone it will be 4:59 p.m. (local) and if you are on the western boundary of the time zone it will be 4:01 p.m. (local). Standard time will probably be the most appropriate notation for use in the model, although results will be similar to those using local time. It is important to note that Daylight Saving Time is <u>not</u> incorporated in this model. That is, while in Colorado during the summer you might observe that fish are at a particular depth at 6 a.m. on a certain day according to your own clock, in order use your data for a simulation you should tell the model that the fish was at a particular depth at 5 a.m., one hour earlier. You will not have to make this adjustment for winter dates; most states in the U.S. set clocks ahead at 2 a.m. on the first Sunday in April and set them back at 2 a.m. on the first Sunday in October.

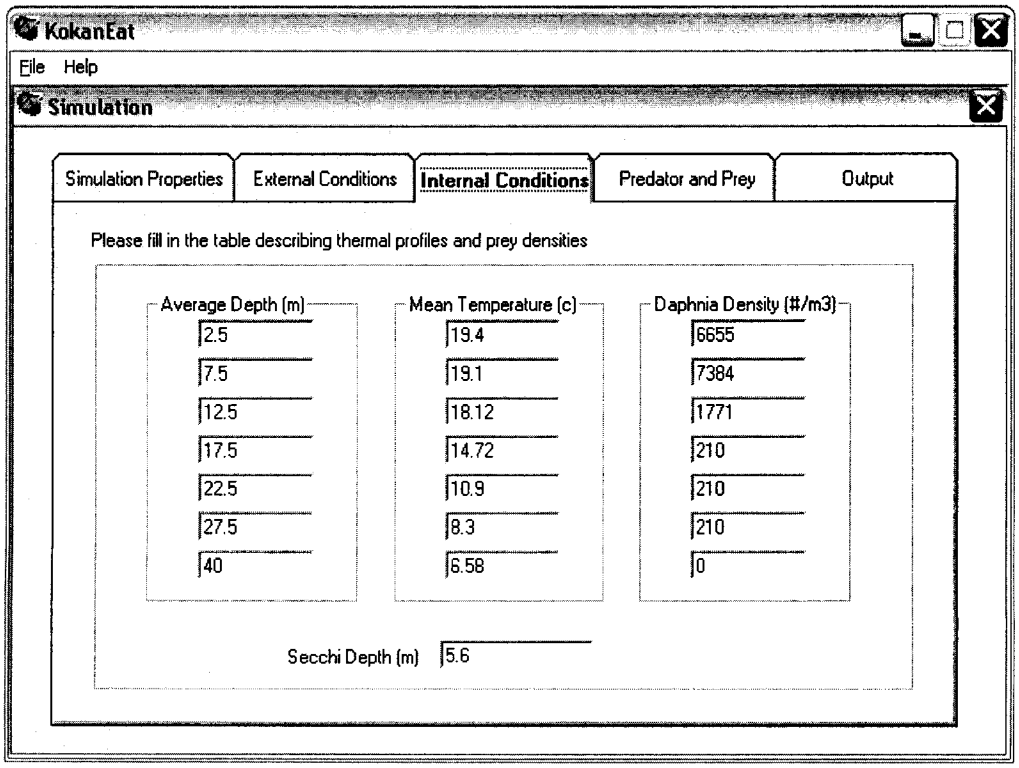
In addition, you can also specify your "*Sky Condition*" to fit a range of visibilities that incorporate cloudiness. Choose "*1*" if the sun and moon are visible, with the sky being less than 70% overcast. Choose "*2*" if the sun and moon are obscured by thin clouds; choose "*3*" if they are obscured by average clouds. Finally, choose "*10*" if the sun and moon are blocked by dark stratus clouds (rare).

To set the *date* for the simulation you can either type the date directly into the date field, or choose the date from a calendar by clicking on the drop-down menu arrow.

KokanEat version 1.0 runs for 24 hours by breaking the day into 48 thirty-minute time steps. In the "Time" section of the "External Conditions" page, you must set the "*Start Time*" at 00:00 (midnight), and choose 24:00 for the "*Length of Simulation*". While there are other options for "*Time Step Length*", "*30 minutes*" is the only option that is currently enabled. In future versions of the model we will expand the "Time" utilities so that the model can start running at any hour, for any number of hours, and be broken down by several other time step lengths.

Internal Conditions

The "Internal Conditions" page is where the user tells the model about some of the environmental conditions that the fish will experience during a simulation. On this page, the user will enter information about temperature and prey density depth profiles and secchi depth. The model uses this information to create a reference table where temperature and prey densities are found according to depth.



Please fill in the table describing thermal profiles and prey densities

Average Depth (m)	Mean Temperature (c)	Daphnia Density (#/m3)
2.5	19.4	6655
7.5	19.1	7384
12.5	18.12	1771
17.5	14.72	210
22.5	10.9	210
27.5	8.3	210
40	6.58	0

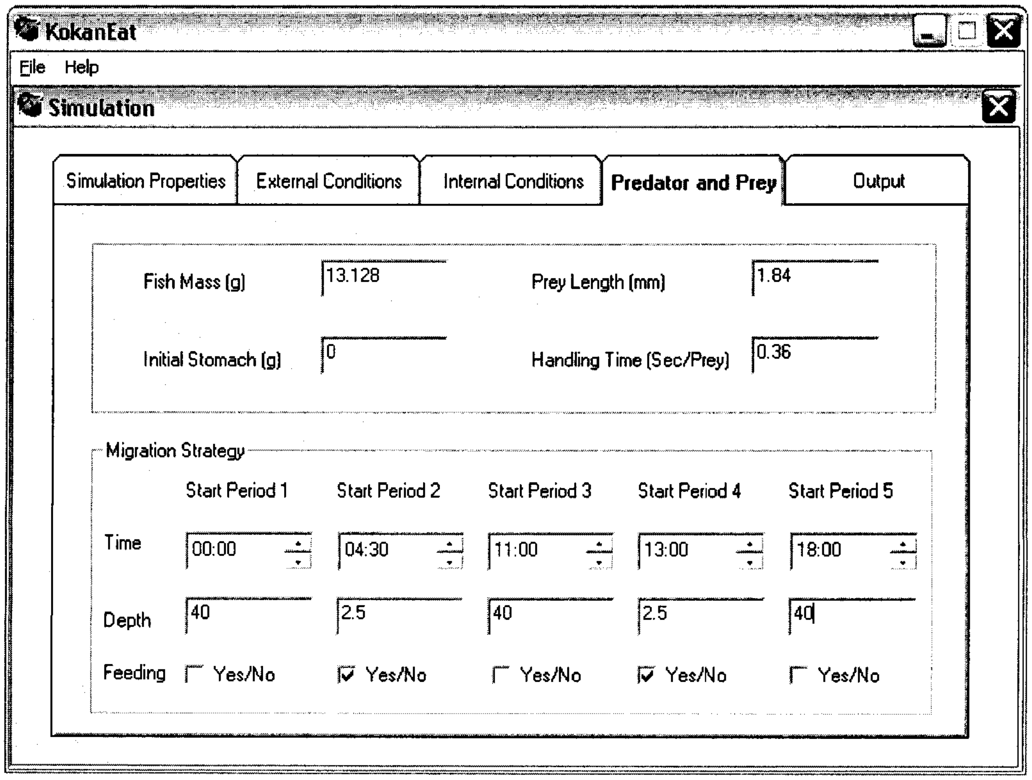
Secchi Depth (m) 5.6

There are seven rows in the table on the "Internal Conditions" page. It is not necessary that you fill in all seven rows, but you must enter data for temperature and prey density if you enter a depth for that row. Enter "*Average Depth*" in meters, "*Mean Temperature*" in degrees Celsius, and "*Daphnia Density*" in numbers per cubic meter (if you have data in numbers per liter, simply multiply by 1000 to get numbers per cubic meter). In the above example, the data represent information obtained from sampling depths from 0-5 m, 5-10 m, 10-15 m, 15-30 m, and 40 m.

Finally, enter *secchi depth* in meters at the bottom of this page. This will enable the model to calculate ambient light level as a function of water clarity and surface light intensity.

Predator and Prey

The "Predator and Prey" page allows the user to tell the model about the fish and its food, and which of the information entered in the "Internal Conditions" page to use for each simulation. In this version of KokanEat, our virtual fish is the kokanee (*Oncorhynchus nerka*) and the model uses physiological parameters specific to this fish. Similarly, its prey is the cladoceran *Daphnia pulex*, and the model uses an energy density specific to this species. Any changes in prey species can be modified in the program code.



Fish Mass (g): 13.128

Prey Length (mm): 1.84

Initial Stomach (g): 0

Handling Time (Sec/Prey): 0.36

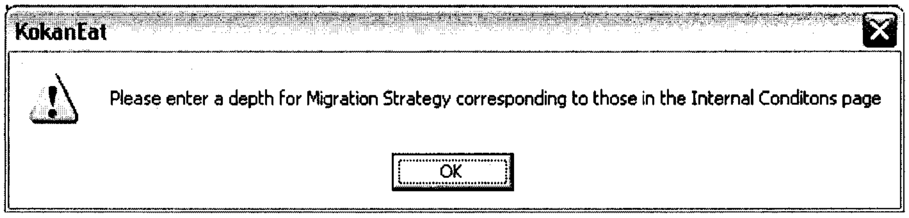
Migration Strategy

	Start Period 1	Start Period 2	Start Period 3	Start Period 4	Start Period 5
Time	00:00	04:30	11:00	13:00	18:00
Depth	40	2.5	40	2.5	40
Feeding	☐ Yes/No	☑ Yes/No	☐ Yes/No	☑ Yes/No	☐ Yes/No

First, enter the mass of the fish in grams in the "*Fish Mass*" field. This model is most useful for smaller (age-0) fish because the functional response it utilizes was derived using fish under 50 g in laboratory experiments (Koski and Johnson 2002). Next, enter the initial stomach contents in grams in the "*Initial Stomach*" field. Usually, 0 g will produce valid results; when the model runs, it starts with no stomach contents, then uses the amount of food in the fish's stomach at the end of the simulation (after 24 hours) as the initial stomach contents and the model runs a second time. Therefore, the initial stomach contents and the end stomach contents will usually be equal, which makes sense because we're trying to simulate how a fish typically behaves on an average day (which is bounded by a day before and a day after) and not just on one individual day.

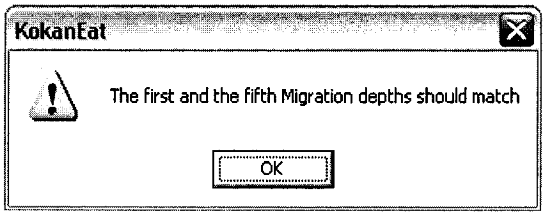
Next, enter the average length of the prey in millimeters in the "*Prey Length*" field. This is the length of the *Daphnia* from the tip of the helmet to the base of the spine. Enter the amount of time it takes for the fish to find, capture, and consume its prey in the "*Handling Time*" field, in seconds per prey item (currently, this version does not use handling time in any calculations).

The data that is entered in the "Migration Strategy" section must match the information that you entered in the "Internal Conditions" page. For example, in the figure above, 2.5 m and 40 m are both listed as depths on the "Internal Conditions" page. If you enter a value of 20 m you will get an error message when you try to run the model:



Please enter a depth for Migration Strategy corresponding to those in the Internal Conditons page

Settings in the "Migration Strategy" area tell the model where the fish is at particular times during the day. In this version of the model, the *depth* of the fish at the start of periods 1 and 5 must be the same, or else you will receive an error message when you run the model:



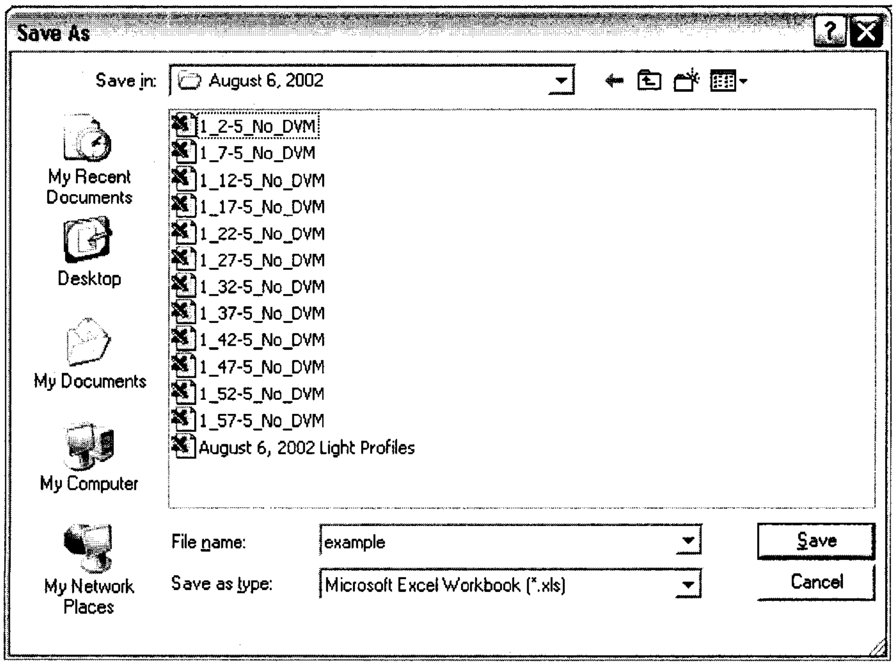
The first and the fifth Migration depths should match

The *time* for "Start Period 1" must be 00:00. Because the model runs for 24 hours in thirty minute time steps, minutes must be in multiples of 30, and the time for "Start Period 5" cannot exceed 23:30. In the above example, the fish makes two foraging trips to 2.5 m: the first trip is 4:30 and 11:00, and the second trip is from 13:00 through 18:00. At all other times the fish resides at a depth of 40 m. It is not necessary that the fish changes depth at the beginning of each period. If you'd like the fish to stay at a depth, simply enter a "dummy" time with a depth equal to the depth in the previous period.

Note also the check boxes for "*Feeding*". The model utilizes a functional response that is dependent upon light level. If you check the box for the corresponding time period, this means that if there is sufficient light and if prey are present then the fish will feed. If the box is left unchecked, the fish will not feed, regardless of light level and prey availability. In our example, the fish is feeding only when at a depth of 2.5 m; at all other times the fish is at a lower depth and is not foraging.

Output

The model creates output as a Microsoft Excel spreadsheet. The user must specify where the spreadsheet will be created; you can either create a new spreadsheet or overwrite an existing one. To create a new spreadsheet, click the "Browse" button next to the "*Spread Sheet*" field and navigate to the desired folder that will contain the file. Type the file name in the "File Name" box and click "Save".

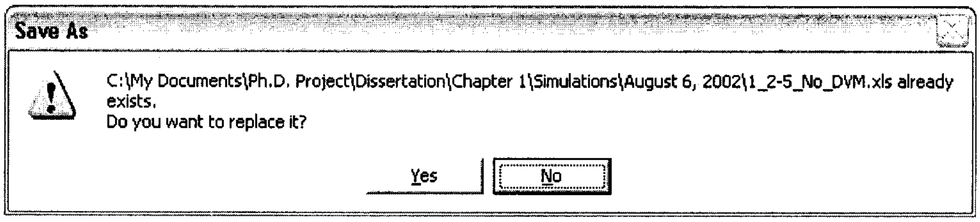


Save in: August 6, 2002

1_2-5_No_DVM
1_7-5_No_DVM
1_12-5_No_DVM
1_17-5_No_DVM
1_22-5_No_DVM
1_27-5_No_DVM
1_32-5_No_DVM
1_37-5_No_DVM
1_42-5_No_DVM
1_47-5_No_DVM
1_52-5_No_DVM
1_57-5_No_DVM
August 6, 2002 Light Profiles

File name: example
Save as type: Microsoft Excel Workbook (*.xls)

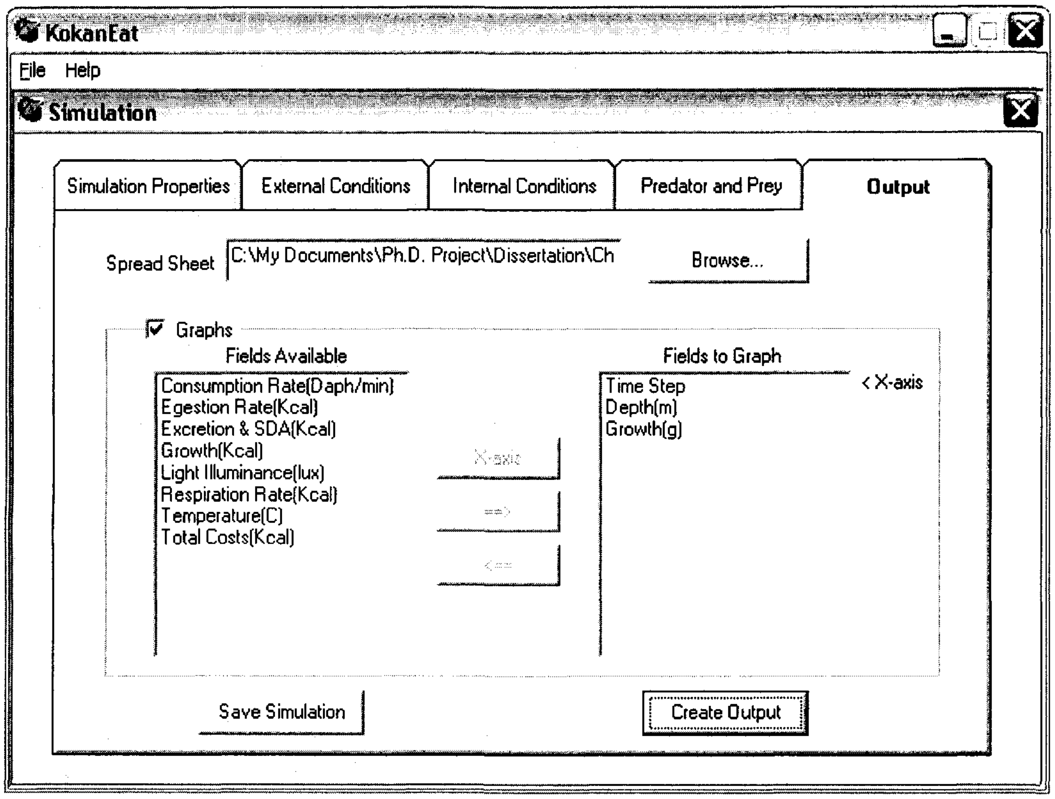
If you wish to overwrite an existing file, click the "Browse" button and then click on the file to be replaced. When you click "Save", you will get a confirmation message:



C:\My Documents\Ph.D. Project\Dissertation\Chapter 1\Simulations\August 6, 2002\1_2-5_No_DVM.xls already exists.
Do you want to replace it?

Click "Yes" if you want to overwrite the file.

If you wish, the model can create graphs as separate worksheets in the output file. Should you require graphs, click the box next to the "*Graph*" field and the list of graph choices in the "*Fields Available*" box will become active. Only one of the fields in the list can serve as the x-axis for all the graphs; all other selected fields will be used for y-axis data on separate graphs. In the example below, we will create two graphs: time vs. depth, and time vs. growth. To create these graphs, click on "Time Step" in the "*Fields Available*" box, then click the "*X-axis*" button. Now, "Time Step" appears in the first row (labeled "X-axis") of the "*Fields to Graph*" box. Next, select "Depth (m)" and click the button marked with the right-pointing arrow. Do the same with "Growth (g)"; now, both fields are below "Time Step" in the "*Fields to Graph*" box. If you wish to remove or replace any of these fields, simply highlight the field to be removed, click the button marked with the left-pointing arrow and the field will be placed back in the list in the "*Fields Available*" box.



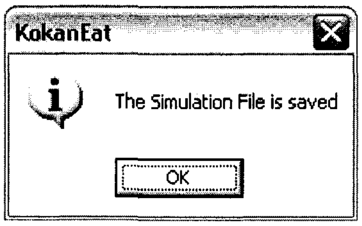
Spread Sheet C:\My Documents\Ph.D. Project\Dissertation\Ch

☑ Graphs

Fields Available
Consumption Rate(Daph/min)
Egestion Rate(Kcal)
Excretion & SDA(Kcal)
Growth(Kcal)
Light Illuminance(lux)
Respiration Rate(Kcal)
Temperature(C)
Total Costs(Kcal)

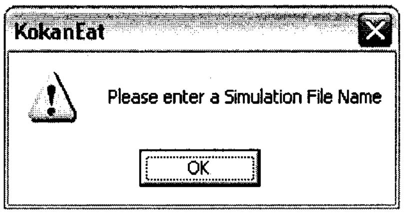
Fields to Graph
Time Step < X-axis
Depth(m)
Growth(g)

You're now done creating the simulation. If you have created a new simulation (there will be a file name in the "New Simulation" section on the "Simulation Properties" page), click the "*Save Simulation*" button and the simulation will be saved as a new file. You will receive a confirmation message; click "Ok":



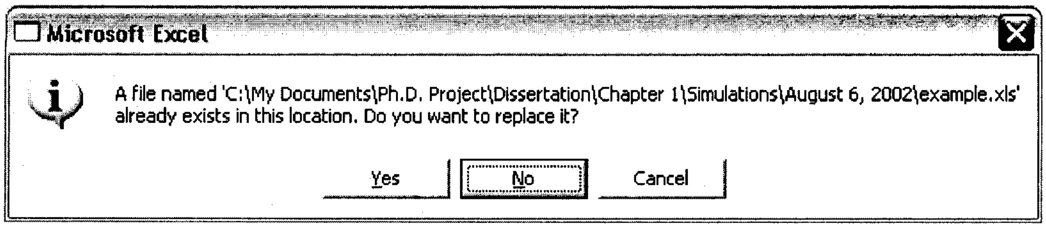
The Simulation File is saved

If you make any changes to an existing file and wish to save the changes with the same file name you must follow the "*Save As*" procedures outlined in the "Simulation Properties" section. Simply enter the same file name and confirm that you would like to replace the existing file. If you do not do this, you will receive the following message:



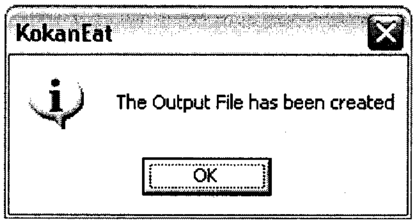
Please enter a Simulation File Name

The model will direct you to the "Simulation Properties" page where you can save the file as a new simulation or as a new simulation with the old file name. After your simulation is saved, execute the model by clicking the "*Create Output*" button. After a few seconds, you may receive a message saying that the output file has the same name as an existing file, click "Yes" to continue and overwrite the existing file:



A file named 'C:\My Documents\Ph.D. Project\Dissertation\Chapter 1\Simulations\August 6, 2002\example.xls' already exists in this location. Do you want to replace it?

After the model has finished generating output, you will receive a message confirming that the model was successful; click "Ok":



The Output File has been created

Congratulations – you have just completed a simulation! IMPORTANT: Close the KokanEat application completely before opening output in Excel.

Interpreting Output

KokanEat produces output in the form of a Microsoft Excel file, the location of which is specified by the user in the "Output" page when setting up a simulation. Each output file contains at least two spreadsheets; the first one summarizes the data input by the user, and the second one summarizes the output. There may be other spreadsheets in the file, one for each graph that the user may have created.

Input Summary Sheet

The first page (or worksheet) in the output file is named "Input" (see tab at the bottom left of the page). In addition to summarizing all the information that was specified by the user to create the *.sim file, you will also see that the model has calculated the "*Maximum Stomach Capacity (g)*" in cell E4. This is particularly useful if you wish to move the fish to a different depth depending on stomach fullness.

Output Summary Sheet

The second worksheet in the output file is named "Output", and contains a summary of all the calculations the model performs during a simulation. We will explain each calculation in a moment, but first, there are a few things to take note of. In general, numbers in row 8 are cumulative values, totaling each parameter over all 48 time steps in the 24 hour simulation period. For example, cell R8 is the total amount that the fish grew during the 24 hour period in grams, while the numbers in column R below cell R8 are the amounts the fish grew during each 30 minute time step. Two of the numbers in row 8 are not cumulative totals; these are the numbers in cells H8 and P8, "*Initial Stomach Contents*" and "*End Stomach Contents*", respectively. The number in H8 is the amount of food in the stomach at the beginning of the simulation (time 00:00), and the number in P8 is the amount of food in the stomach at the end of the simulation (time 24:00). Recall that the model actually runs twice; even though you probably told the model to start the fish with an empty stomach (0 g), the model runs once to determine the amount of food at the end of 24 hours, then uses that value as the initial stomach contents for the second run. If the values in cells H8 and P8 are the same to three decimal places, the *equilibrium* value in cell E9 will be "True". If these values are not equal, equilibrium will be "False".

The following is a list of fields in the output page of the output file:

Time Step (min):	Column A lists time steps in thirty-minute intervals. Because time 00:00 should be the same as 24:00, 00:00 is the last time step listed.
Time Period:	The time period is defined by the user in the "Migration Strategy" section of the "Predator and Prey" page. It is important to note that the time period (and all other subsequent fields) correspond to the previous time step. In our example, time period 2 starts at 4:30

	am. However, on the output, 4:30 still lists time period 1; this is the time period just before 4:30 (i.e., from 4:00 to 4:29). Similarly, if we were to look at initial stomach contents, the stomach contents for any time step correspond to fullness at the very end of the previous time step (equal to fullness at the very beginning of the current time step, which is why the spreadsheet is set up like this). On the "Input" page, the migration strategy is summarized so that the user can verify that time periods correspond with the correct time step.
Depth (m):	This is the depth of the fish, in meters, at the end of the previous time step.
Surface Light (lux):	Surface light (in lux) is calculated using a submodel derived from an algorithm that incorporates geographic location, date, and sky conditions (Kaplan 1981; Janiczek and DeYoung 1987).
Light at Depth (lux):	This is the ambient light level that the virtual fish experiences at a particular depth. Light at depth is calculated using the surface light level, secchi depth, and a light extinction factor (Idso and Gilbert 1974; Horne and Goldman 1994).
Temperature (C):	This is the temperature at the depth of the fish at the end of the previous time step.
T-L Rate Multiplier:	The Thornton-Lessem function modifies the biomass of *Daphnia* consumed as temperature approaches the kokanee's upper tolerance limit, when they stop feeding (Thornton and Lessem 1978); Stockwell and Johnson 1997).
Initial Stomach (g):	This is the mass of *Daphnia* in the fish's stomach at the very beginning of the corresponding time step (or the very end of the previous time step).
Consumption Rate:	Consumption rate, in number of *Daphnia* eaten per minute, is calculated as a function of light level and prey density (Koski and Johnson 2002). If light level is below 0.001 lux, the kokanee does not feed; if light level is between 0.001 and 3.4 lux the kokanee feeds at a minimum rate (Type I functional response); if light level is above 3.4 lux the kokanee feeds at a maximum rate (Type II functional response). For any given time step, this is the rate that the kokanee had to feed at during the previous time step in order to reach the initial stomach fullness of the current time period.
Consumption (g):	This is simply the mass of *Daphnia* consumed in the previous time step, calculated from the number of *Daphnia* eaten in thirty

minutes. It is thought that kokanee are able to squeeze water from cladocerans, and mass is calculated taking this into consideration (Stockwell et al. 1999). The total amount of food consumed in one day is limited by C_{max}, which is a function of body mass (Beauchamp et al. 1989; Hanson et al. 1997). Once the sum in cell J8 reaches C_{max}, the fish does not eat for the remainder of the simulation.

Amount Processed:	The amount of food processed is a function of how much energy (Kcal) was consumed in the previous time step, and digestion rate as a function of temperature (Stockwell and Johnson 1999).
Egestion:	Egestion is energy (Kcal) lost through fecal waste, and is dependent on mass, temperature, and the amount of food consumed (Hanson et al. 1997). Physiological parameters used for egestion rates can be found in Beauchamp et al. (1989).
Excretion & SDA:	Excretion is energy (Kcal) lost through nitrogenous waste, and SDA (Specific Dynamic Action) is the amount of energy spent during the digestion process (Hanson et al. 1997). Physiological parameters used for both excretion rates and SDA can be found in Beauchamp et al. (1989).
Respiration:	Respiration is the amount of energy (Kcal) that is used by the fish for routine metabolism, and is a function of body mass, temperature, and activity costs (Hanson et al. 1997). Physiological parameters used for respiration can be found in Beauchamp et al. (1989).
Total Costs:	This is the sum total amount of energy (Kcal) that the fish has spent on egestion, excretion & SDA, and respiration.
End Stomach (g):	This is the mass of undigested food left in the kokanee's stomach at the end of the time step. This is equal to the initial stomach contents in the next time step.
Growth (Kcal):	This is the amount of energy left over for growth after subtracting total costs from the amount of energy processed.
Growth (g):	This is the mass that the fish gained (or lost) during the previous time step.
Gross Efficiency:	Gross efficiency is calculated by dividing total growth (Kcal) by the total amount processed (Kcal).

Graphs

KokanEat may have created one or more graphs, depending on the information that the user supplied on the "Output" page when setting up a simulation. Each graph is created on separate worksheets, which can be found after the "Output" sheet in the output file. In our example, we created two graphs; the model named them according to the y-axis (the x-axis, time step, is the same for both graphs) – "Chart-Growth_g" and "Chart-Depth". Each chart is fully customizable in Excel; you can reverse the numbers on the axes, change the title or chart element colors, and add additional data series by specifying output from the "Output" worksheet.

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APPENDIX II

KOKANEAT V. 1.0 MODEL CODE

KokanEat v. 1.0 was written in Microsoft Visual Basic 6.0. There are three modules, each separated by a bold horizontal line in the following code. FunctionalResponse.bas contains the code that calculates kokanee bioenergetics, and was written by Marci L. Koski and Satish Kumar Chittibabu. Some of the calculations in FunctionalResponse.bas were derived from a Corel QuattroPro spreadsheet constructed by Jason Stockwell (Stockwell and Johnson 1997, 1999). Mr. Chittibabu also constructed the other two modules, FileSimulation.bas and Illuminance.bas. FileSimulation.bas contains the code for reading and writing a simulation file, and Illumination.bas calculates incident light levels depending on geographic location, date, and sky condition. Illumination.bas was derived from code provided by Mark Kershner, who developed his program fromJaniczek and DeYoung (1987).

The user-interface was also constructed in Microsoft Visual Basic 6.0 by Marci L. Koski and Satish Kumar Chittibabu, and contains several forms. These forms are referenced in the code, as well as in Appendix I, the user manual.

Literature Cited

Janiczek, P. M., and J. A. DeYoung. 1987. Computer programs for sun and moon illuminance with contingent tables and diagrams. U.S. Naval Observatory, Circular No. 171, Washington, D.C.

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Stockwell, J. D., and B. M. Johnson. 1999. Field evaluation of a bioenergetics-based foraging model for kokanee (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Science 56(Suppl. 1):140-151.

FunctionalResponse.bas

```
' **************************************************
' *** This program contains the code for         ***
' *** bioenergetics calculations.                ***
' ***                                            ***
' **************************************************

Option Explicit

Dim Kmass As Double         'Kokanee mass, g

Dim D_1 As Double           'Depth strata 1
Dim D_2 As Double           'Depth strata 2
Dim D_3 As Double           'Depth strata 3
Dim D_4 As Double           'Depth strata 4
Dim D_5 As Double           'Depth strata 5
Dim D_6 As Double           'Depth strata 6
Dim D_7 As Double           'Depth strata 7

Dim T_1 As Double           'Temperature at depth strata 1
Dim T_2 As Double           'Temperature at depth strata 2
Dim T_3 As Double           'Temperature at depth strata 3
Dim T_4 As Double           'Temperature at depth strata 4
Dim T_5 As Double           'Temperature at depth strata 5
Dim T_6 As Double           'Temperature at depth strata 6
Dim T_7 As Double           'Temperature at depth strata 7

Dim S_1 As Double           'Swimming speed at depth strata 1
Dim S_2 As Double           'Swimming speed at depth strata 2
Dim S_3 As Double           'Swimming speed at depth strata 3
Dim S_4 As Double           'Swimming speed at depth strata 4
Dim S_5 As Double           'Swimming speed at depth strata 5
Dim S_6 As Double           'Swimming speed at depth strata 6
Dim S_7 As Double           'Swimming speed at depth strata 7

Dim Z_1 As Double           'Daphnia Density at depth strata 1
Dim Z_2 As Double           'Daphnia Density at depth strata 2
Dim Z_3 As Double           'Daphnia Density at depth strata 3
Dim Z_4 As Double           'Daphnia Density at depth strata 4
Dim Z_5 As Double           'Daphnia Density at depth strata 5
Dim Z_6 As Double           'Daphnia Density at depth strata 6
Dim Z_7 As Double           'Daphnia Density at depth strata 7
Dim Z_t As Double           'Daphnia Density at time t

Dim N_1 As Double           'Consumption rate at depth strata 1 (>=90g)
Dim N_2 As Double           'Consumption rate at depth strata 2 (>=90g)
Dim N_3 As Double           'Consumption rate at depth strata 3 (>=90g)
Dim N_4 As Double           'Consumption rate at depth strata 4 (>=90g)
Dim N_5 As Double           'Consumption rate at depth strata 5 (>=90g)
Dim N_6 As Double           'Consumption rate at depth strata 6 (>=90g)
Dim N_7 As Double           'Consumption rate at depth strata 7 (>=90g)

Dim handtime As Double      'Handling time (user input)
Dim Pi As Double            'PI function
Dim length As Double        'Length of kokanee, cm
Dim Log10Kmass As Double    'Log base 10 ("Log" = natural log) for Kmass
'Dim timestep As Double     'Length of timestep in minutes
Dim timestep As Integer     'Length of timestep in minutes
Dim total_ts As Integer     'Total number of timesteps
Dim total_mins As Double    'Product of timestep and total_ts
Dim Dsize As Double         'Daphnia length, mm
Dim dark As Double          'Number of minutes in simulation in darkness (no feeding)
Dim duration As Double      'Number of minutes in simulation spent feeding
Dim t As Integer            'Current timestep
Dim total_t As Double       'Total minutes at time t
Dim TimePer_t As Double     'Time period at time t

Dim PerStartTime1 As String 'Start Time of period 1
Dim PerStartTime2 As String 'Start Time of period 2
Dim PerStartTime3 As String 'Start Time of period 3
```

```
Dim PerStartTime4 As String 'Start Time of period 4
Dim PerStartTime5 As String 'Start Time of period 5

Dim Min1 As Double          'Minutes spent feeding during period 1
Dim Min2 As Double          'Minutes spent feeding during period 2
Dim Min3 As Double          'Minutes spent feeding during period 3
Dim Min4 As Double          'Minutes spent feeding during period 4
Dim Min5 As Double          'Minutes spent feeding during period 5

Dim Depth1 As Double        'Depth of fish during period 1
Dim Depth2 As Double        'Depth of fish during period 2
Dim Depth3 As Double        'Depth of fish during period 3
Dim Depth4 As Double        'Depth of fish during period 4
Dim Depth5 As Double        'Depth of fish during period 5
Dim depth_t As Double       'Depth at time t in meters

Dim Feed1 As Integer        'Feeding status during period 1
Dim Feed2 As Integer        'Feeding status during period 2
Dim Feed3 As Integer        'Feeding status during period 3
Dim Feed4 As Integer        'Feeding status during period 4
Dim Feed5 As Integer        'Feeding status during period 5
Dim Feed_t As Integer       'Feeding status during time period t

Dim LightRange As Range     'Search range for light by time period
Dim Light_t As Double       'Light level (lux) during time t at depth
Dim LightSurf_t As Double   'Light level (lux) during time t at surface
Dim DaphDensRange As Range  'Search range for Daphnia density by depth
Dim eat_t As Double         'Feeding status during time t
Dim temp_t As Double        'Temperature at depth at time t
Dim temp_2 As Double
Dim TL_t As Double          'Thornton-Lessem function at time t

Dim TempRange As Range      'Search range for temperature
Dim ConsumeRange As Range   'Search range for consumption rate by depth (>90g)
Dim c_rate_t As Double      'Feeding rate at time t
Dim consume_t As Double     'Mass of Daphnia eaten during each time step
Dim consume_2 As Double
Dim in_stom_t As Double     'Mass of Daphnia in stomach of kokanee at the beginning of
time t
Dim in_stom_2 As Double
Dim squeeze As Double           'Number of Daphnia per gram WITH water squeezed out
Dim no_squeeze As Double        'Number of Daphnia per gram WITHOUT water squeezed out
Dim Fish_Multiplier As Double   'Multiplier based on kokanee mass, in Sub Consume
Dim amt_proc_t As Double        'Amount of Daphnia processed from stomach, Kcal
Dim amt_proc_2 As Double
Dim end_stom_0 As Double    'The amount of Daphnia left over at time step 1
Dim in_stom_0 As Double     'The amount of Daphnia in stomach before time step 1
Dim end_stom_t As Double    'Mass of Daphnia left in stomach at end of time step
Dim end_stom_2 As Double
Dim max_stom_cap As Double  'Maximum Stomach Capacity
Dim Cmax As Double          'Maximum amount of food to be eaten in one day, g

Dim egest_t As Double       'Egestion costs at time t
Dim excrete_t As Double     'Excretion & SDA costs at time t
Dim aWb_t As Double
Dim epT_t As Double
Dim evUopt_t As Double
Dim resp_t As Double        'Respiration costs at time t
Dim growth_t As Double      'Amount of energy left for growth at time t (Kcals)
Dim growth_2 As Double
Dim total_costs_t As Double 'Total costs at time t
Dim Kgrowth_t As Double     'Growth of kokanee in grams
Dim Kgrowth_2 As Double
Dim sum_consume As Double   'Sum of consumption over all time steps
Dim s_cons_Range As Range
Dim sum_process As Double   'Sum of amount processed over all time steps
Dim s_proc_Range As Range
Dim sum_egest As Double     'Sum of total egestion over all time steps
Dim s_egest_Range As Range
Dim sum_excrete As Double   'Sum of amount excreted over all time steps
Dim s_excrete_Range As Range
```

```
Dim sum_resp As Double      'Sum of all respiration costs over all time steps
Dim s_resp_Range As Range
Dim sum_growth As Double    'Sum of all growth (kcals) over all time steps
Dim s_growth_Range As Range
Dim sum_endstom As Double
Dim sum_costs As Double     'Sum of all costs over all time steps
Dim sum_Kgrowth As Double   'Sum of all kokanee growth in grams
Dim Gross_Efficiency As Double
Dim equilibrium As Boolean
Dim instom_round As Range
Dim endstom_round As Range

Dim Secchi As Double          'Secchi depth, m
Dim LightExtCoeff As Double   'Light Extinction Coefficient
'Dim CummKokMass  As Double   'Cummulative Kokanee Mass
Dim strSimDate As String      'Date of Simulation
Dim Latitude As String        'Latitude
Dim Longitude As String       'Longitude
Dim TimeZone As String        'TimeZone
Dim SkyCondition As String    'SkyCondition
Dim strSimStartTime As String 'Simulation Start Time
Dim intSimStartMin As Integer 'Simulation start minutes
Dim strSimLength  As String   'Simulation Length
Dim strChartName As String    'Chart Name
Dim intIter As Integer        'Number of iterations

'CONSTANTS USED BY THE PROGRAM

Const Time1 = 1                 'Name of period 1
Const Time2 = 2                 'Name of period 2
Const Time3 = 3                 'Name of period 3
Const Time4 = 4                 'Name of period 4
Const Time5 = 5                 'Name of period 5

Const EGa = 0.212               'Egestion constant
Const EGc = -0.222              'Egestion constant
Const EGf = 0.631               'Egestion constant
Const EXa = 0.0314              'Excretion constant
Const EXc = 0.58                'Excretion constant
Const EXf = -0.299              'Excretion constant
Const SDA = 0.14                'SDA constant
Const CQ = 3                    'TL parameter
Const CTO = 20                  'TL parameter
Const CTM = 20                  'TL parameter
Const CTL = 24                  'TL parameter
Const CK1 = 0.58                'TL parameter
Const CK4 = 0.5                 'TL parameter
Const G1 = 0.209943935638093    'TL parameter
Const G2 = 0.972955074527657    'TL parameter

'Excel objects

Private xlApp As Excel.Application
Private xlWorkBook As Excel.Workbook
Private xlOutputWorkSheet As Excel.Worksheet
Private xlInputWorkSheet As Excel.Worksheet
Private xlChart As Excel.Chart

'For formatting the title and border in the excel output file

Const O_TITLEROW = 5
Const O_TITLECOL = 1
Const O_VALROW = O_TITLEROW + 5
Const O_VALCOL = 1
Const O_GRAPHROW = O_VALROW + 1

Const I_TITLEROW1 = 3
Const I_TITLECOL = 1
Const I_TITLEROW2 = I_TITLEROW1 + 11
Const I_TITLEROW3 = I_TITLEROW1 + 23
Const I_TITLEROW4 = I_TITLEROW1 + 16
```

```
Const C_MARKERSIZE = 4
Const C_COLORINDEX = 3

Const HYPHEN = "-"

'Border and title ranges

Private rOutTitleRange As Range
Private rOutBorderRange As Range
Private rInTitleRange1 As Range
Private rInTitleRange2 As Range
Private rInTitleRange3 As Range
Private rInTitleRange4 As Range
Private rInBorderRange1 As Range
Private rInBorderRange2 As Range
Private rInBorderRange3 As Range
Private rInBorderRange4 As Range

'This subroutine creates an excel file
Sub Setup(i_obForm As frmSimulation)

    Dim intCount As Integer

    Set xlApp = CreateObject("Excel.Application")
    Set xlWorkBook = xlApp.Workbooks.Add    'creates new excel workbook

    xlApp.Visible = False
    xlApp.DisplayAlerts = True

    intCount = xlWorkBook.Worksheets.Count

    Do While intCount > 1
        xlWorkBook.Worksheets(intCount).Delete
        intCount = xlWorkBook.Worksheets.Count

    Loop

    xlWorkBook.Application.ActiveWindow.DisplayGridlines = False

    Set xlOutputWorkSheet = xlWorkBook.ActiveSheet
    xlOutputWorkSheet.Name = "Output"

    Set xlInputWorkSheet = xlWorkBook.Worksheets.Add
    xlInputWorkSheet.Name = "Input"
    xlWorkBook.Application.ActiveWindow.DisplayGridlines = False

    Call FormatInputWorkSheet

     xlWorkBook.SaveAs i_obForm.txtOutSpreadSheet.Text

End Sub

'This subroutine the unloads the xlapplication
Sub Cleanup()

     xlInputWorkSheet.Activate

     Set xlOutputWorkSheet = Nothing
     Set xlInputWorkSheet = Nothing
     Set xlChart = Nothing
     xlWorkBook.Save
     xlWorkBook.Close
     'xlApp.Workbooks.Close
     Set xlWorkBook = Nothing

     Application.Workbooks.Close

     xlApp.Application.Quit
     Set xlApp = Nothing
End Sub
```

```
' This subroutine sets the values of the controls to the variables
' to be used in the program

Sub SetValues(ByVal i_obForm As frmSimulation)

Dim strMonth As String
Dim strDay As String
Dim strYear As String

If (i_obForm.dtpExtSimDate.Month < 10) Then
    strMonth = "0" & i_obForm.dtpExtSimDate.Month
Else
    strMonth = i_obForm.dtpExtSimDate.Month
End If

If (i_obForm.dtpExtSimDate.Day < 10) Then
    strDay = "0" & i_obForm.dtpExtSimDate.Day
Else
    strDay = i_obForm.dtpExtSimDate.Day
End If

strYear = i_obForm.dtpExtSimDate.Year
strSimDate = strMonth & "/" & strDay & "/" & strYear

Latitude = i_obForm.mskExtLatitude.Text
Longitude = i_obForm.mskExtLongitude.Text
TimeZone = i_obForm.cboExtTimeZone.Text

If (i_obForm.cboExtSkyCondition.ListIndex = 0) Then
            SkyCondition = "1"
ElseIf (i_obForm.cboExtSkyCondition.ListIndex = 1) Then
            SkyCondition = "2"
ElseIf (i_obForm.cboExtSkyCondition.ListIndex = 2) Then
            SkyCondition = "3"
ElseIf (i_obForm.cboExtSkyCondition.ListIndex = 3) Then
            SkyCondition = "10"
End If

strSimStartTime = i_obForm.dtpExtStartTime.Hour & ":" & i_obForm.dtpExtStartTime.Minute
strSimLength = i_obForm.mskExtSimLength.Text

Kmass = CDbl(i_obForm.txtPreFishMass.Text)            'Fish Mass
Cmax = Kmass * (0.303 * (Kmass ^ (-0.275)))
Log10Kmass = Log(Kmass) / Log(10#)
max_stom_cap = ((14.1 - (4.95 * Log10Kmass)) * Kmass) / 100

If (i_obForm.txtIntMeanTemp1.Text = "") Then
    T_1 = 0
Else
    T_1 = CDbl(i_obForm.txtIntMeanTemp1.Text)
End If

If (i_obForm.txtIntMeanTemp2.Text = "") Then
    T_2 = 0
Else
    T_2 = CDbl(i_obForm.txtIntMeanTemp2.Text)
End If

If (i_obForm.txtIntMeanTemp3.Text = "") Then
    T_3 = 0
Else
    T_3 = CDbl(i_obForm.txtIntMeanTemp3.Text)
End If

If (i_obForm.txtIntMeanTemp4.Text = "") Then
    T_4 = 0
Else
    T_4 = CDbl(i_obForm.txtIntMeanTemp4.Text)
End If
```

```
If (i_obForm.txtIntMeanTemp5.Text = "") Then
    T_5 = 0
Else
    T_5 = CDbl(i_obForm.txtIntMeanTemp5.Text)
End If

If (i_obForm.txtIntMeanTemp6.Text = "") Then
    T_6 = 0
Else
    T_6 = CDbl(i_obForm.txtIntMeanTemp6.Text)
End If

If (i_obForm.txtIntMeanTemp7.Text = "") Then
    T_7 = 0
Else
    T_7 = CDbl(i_obForm.txtIntMeanTemp7.Text)
End If

'Setting the Depth

If (i_obForm.txtIntAvgDepth1.Text = "") Then
    D_1 = 0
Else
    D_1 = CDbl(i_obForm.txtIntAvgDepth1.Text)
End If

If (i_obForm.txtIntAvgDepth2.Text = "") Then
    D_2 = 0
Else
    D_2 = CDbl(i_obForm.txtIntAvgDepth2.Text)
End If

If (i_obForm.txtIntAvgDepth3.Text = "") Then
    D_3 = 0
Else
    D_3 = CDbl(i_obForm.txtIntAvgDepth3.Text)
End If

If (i_obForm.txtIntAvgDepth4.Text = "") Then
    D_4 = 0
Else
    D_4 = CDbl(i_obForm.txtIntAvgDepth4.Text)
End If

If (i_obForm.txtIntAvgDepth5.Text = "") Then
    D_5 = 0
Else
    D_5 = CDbl(i_obForm.txtIntAvgDepth5.Text)
End If

If (i_obForm.txtIntAvgDepth6.Text = "") Then
    D_6 = 0
Else
    D_6 = CDbl(i_obForm.txtIntAvgDepth6.Text)
End If

If (i_obForm.txtIntAvgDepth7.Text = "") Then
    D_7 = 0
Else
    D_7 = CDbl(i_obForm.txtIntAvgDepth7.Text)
End If

If (i_obForm.txtIntDaphDensity1.Text = "") Then
    Z_1 = 0
Else
    Z_1 = CDbl(i_obForm.txtIntDaphDensity1.Text)
End If

If (i_obForm.txtIntDaphDensity2.Text = "") Then
    Z_2 = 0
Else
```

```
    Z_2 = CDbl(i_obForm.txtIntDaphDensity2.Text)
End If

If (i_obForm.txtIntDaphDensity3.Text = "") Then
    Z_3 = 0
Else
    Z_3 = CDbl(i_obForm.txtIntDaphDensity3.Text)
End If

If (i_obForm.txtIntDaphDensity4.Text = "") Then
    Z_4 = 0
Else
    Z_4 = CDbl(i_obForm.txtIntDaphDensity4.Text)
End If

If (i_obForm.txtIntDaphDensity5.Text = "") Then
    Z_5 = 0
Else
    Z_5 = CDbl(i_obForm.txtIntDaphDensity5.Text)
End If

If (i_obForm.txtIntDaphDensity6.Text = "") Then
    Z_6 = 0
Else
    Z_6 = CDbl(i_obForm.txtIntDaphDensity6.Text)
End If

If (i_obForm.txtIntDaphDensity7.Text = "") Then
    Z_7 = 0
Else
    Z_7 = CDbl(i_obForm.txtIntDaphDensity7.Text)
End If

Feed1 = i_obForm.chkPreMSFeeding1.Value
Feed2 = i_obForm.chkPreMSFeeding2.Value
Feed3 = i_obForm.chkPreMSFeeding3.Value
Feed4 = i_obForm.chkPreMSFeeding4.Value
Feed5 = i_obForm.chkPreMSFeeding5.Value

End Sub

' This subroutine contains the code for the energetics of the fish

Sub Bioenergetics_Model(ByVal i_obForm As frmSimulation)

Setup i_obForm
SetValues i_obForm

S_1 = 9.9 * Kmass ^ 0.13 * Exp(0.0405 * T_1) / 100
S_2 = 9.9 * Kmass ^ 0.13 * Exp(0.0405 * T_2) / 100
S_3 = 9.9 * Kmass ^ 0.13 * Exp(0.0405 * T_3) / 100
S_4 = 9.9 * Kmass ^ 0.13 * Exp(0.0405 * T_4) / 100
S_5 = 9.9 * Kmass ^ 0.13 * Exp(0.0405 * T_5) / 100
S_6 = 9.9 * Kmass ^ 0.13 * Exp(0.0405 * T_6) / 100
S_7 = 9.9 * Kmass ^ 0.13 * Exp(0.0405 * T_7) / 100

handtime = CDbl(i_obForm.txtPreHandlingTime.Text)
Pi = 3.14

N_1 = (Pi * 0.08 ^ 2 / 3) * (3 * S_1 ^ 2 / S_1) * Z_1 / (1 + (Pi * 0.08 ^ 2 / 3) * (3 *
S_1 ^ 2 / S_1) * Z_1 * handtime) * 60 + 0.499
N_2 = (Pi * 0.08 ^ 2 / 3) * (3 * S_2 ^ 2 / S_2) * Z_2 / (1 + (Pi * 0.08 ^ 2 / 3) * (3 *
S_2 ^ 2 / S_2) * Z_2 * handtime) * 60 + 0.499
N_3 = (Pi * 0.08 ^ 2 / 3) * (3 * S_3 ^ 2 / S_3) * Z_3 / (1 + (Pi * 0.08 ^ 2 / 3) * (3 *
S_3 ^ 2 / S_3) * Z_3 * handtime) * 60 + 0.499
N_4 = (Pi * 0.08 ^ 2 / 3) * (3 * S_4 ^ 2 / S_4) * Z_4 / (1 + (Pi * 0.08 ^ 2 / 3) * (3 *
S_4 ^ 2 / S_4) * Z_4 * handtime) * 60 + 0.499
N_5 = (Pi * 0.08 ^ 2 / 3) * (3 * S_5 ^ 2 / S_5) * Z_5 / (1 + (Pi * 0.08 ^ 2 / 3) * (3 *
S_5 ^ 2 / S_5) * Z_5 * handtime) * 60 + 0.499
N_6 = (Pi * 0.08 ^ 2 / 3) * (3 * S_6 ^ 2 / S_6) * Z_6 / (1 + (Pi * 0.08 ^ 2 / 3) * (3 *
S_6 ^ 2 / S_6) * Z_6 * handtime) * 60 + 0.499
```

```
N_7 = (Pi * 0.08 ^ 2 / 3) * (3 * S_7 ^ 2 / S_7) * Z_7 / (1 + (Pi * 0.08 ^ 2 / 3) * (3 *
S_7 ^ 2 / S_7) * Z_7 * handtime) * 60 + 0.499

Call Time_Interval(i_obForm)            ' sets value of timestep, total_ts and Dsize

length = 10 ^ ((5.2006 + Log10Kmass) / 3.085) / 10

total_mins = timestep * total_ts                        ' Calculates total minutes in
simulation

squeeze = 1 / ((0.052 * Dsize ^ 3.012) / (2 * 1000))    ' Calculates squeeze

no_squeeze = 1 / ((0.052 * Dsize ^ 3.012) / 1000)       ' Calculates no_squeeze


' Sets the minutes for migration strategy

Call Minutes(i_obForm)                                  ' Calculates the
Min1,Min2,Min3,Min4,Min5

in_stom_0 = CDbl(i_obForm.txtPreInitialStomach.Text)    ' Initial and End Stomach
end_stom_0 = 0

' Sets the secchi depth and calculates the Light Extinction Coefficient

Secchi = CDbl(i_obForm.txtIntSecchiDepth.Text)
LightExtCoeff = 1.7 / Secchi

Call Depth(i_obForm)

Call SetUserInputs

For intIter = 1 To 2

in_stom_t = in_stom_0
end_stom_t = end_stom_0

t = 1
For t = 1 To total_ts
    total_t = (t * timestep) + intSimStartMin
    Call Output_TI

Call Feeding

Call TimePer
    Call Output_TimePer

Call Output_D                   ' calculates the depth at time and sets the value in
                                  output file

Call Light(i_obForm)
    Call Output_Light

Call SetDensityTempAtTime       ' sets the daphniadensity and temperature at time t
                                ' based on the depth at the time t

Call FunResp
    Call Output_FunResp
    Call Output_Temp

    TL_t = ((CK1 * Exp(G1 * (temp_t - CQ))) / (1 + CK1 * (Exp(G1 * (temp_t - CQ)) - 1)))
* ((CK4 * Exp(G2 * (CTL - temp_t))) / (1 + CK4 * (Exp(G2 * (CTL - temp_t)) - 1))) / ((CK1
* Exp(G1 * (10 - CQ))) / (1 + CK1 * (Exp(G1 * (10 - CQ)) - 1))) * ((CK4 * Exp(G2 * (CTL -
10))) / (1 + CK4 * (Exp(G2 * (CTL - 10)) - 1)))
    Call Output_TL

Call Consume
    Call Output_Consume

Call Rent
    Call Output_Rent
```

```
Next t

Call Sums
    in_stom_0 = Round(sum_endstom, 3)
    Call Output_Sums
    Call Clear_Sums

Next intIter

Call FormatOutputWorkSheet

If (i_obForm.chkOutGraphs.Value = 1) Then
    DrawGraphs i_obForm
End If
Cleanup
End Sub

' This subroutine clears the sum variables
Sub Clear_Sums()

    sum_consume = 0
    sum_process = 0
    sum_egest = 0
    sum_excrete = 0
    sum_resp = 0
    sum_growth = 0
    sum_endstom = 0
    sum_costs = 0
    sum_Kgrowth = 0
    End Sub

' This subroutine calculates the time step for duration of simulation

Sub Time_Interval(ByRef i_obForm As frmSimulation)

    Dim intSimLen As Integer

    If (i_obForm.cboExtTimeStepLength.ListIndex = 0) Then
            timestep = 10
        ElseIf (i_obForm.cboExtTimeStepLength.ListIndex = 1) Then
            timestep = 20
        ElseIf (i_obForm.cboExtTimeStepLength.ListIndex = 2) Then
            timestep = 30
        ElseIf (i_obForm.cboExtTimeStepLength.ListIndex = 3) Then
            timestep = 60
    End If

    intSimStartMin = i_obForm.dtpExtStartTime.Hour * 60 + i_obForm.dtpExtStartTime.Minute

    intSimLen = CInt(Left(strSimLength, 2)) * 60 + CInt(Right(strSimLength, 2))

    'simulation length entered should be a multiple of timestep selected

    total_ts = intSimLen / timestep

    Dsize = CDbl(i_obForm.txtPrePreyLength.Text)        'sets the length of the Daphnia

End Sub

' This subroutine writes the Time interval in the output file

Sub Output_TI()

    Dim strHour As String
    Dim strMin As String
    Dim strTime As String

    If (total_t = 1440) Then
        strTime = "00:00"
    Else
```

```
        strHour = CStr(total_t \ 60)
        strMin = CStr(total_t Mod 60)
        strTime = strHour + ":" + strMin
    End If

    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL) = strTime

End Sub

' This subroutine calculates the Minutes for the Migration periods

Sub Minutes(ByRef i_obForm As frmSimulation)

    Dim intPerStartTime1 As Integer
    Dim intPerStartTime2 As Integer
    Dim intPerStartTime3 As Integer
    Dim intPerStartTime4 As Integer
    Dim intPerStartTime5 As Integer

    PerStartTime1 = SetTime(i_obForm.dtpPreMSTime1.Hour, i_obForm.dtpPreMSTime1.Minute)
    PerStartTime2 = SetTime(i_obForm.dtpPreMSTime2.Hour, i_obForm.dtpPreMSTime2.Minute)
    PerStartTime3 = SetTime(i_obForm.dtpPreMSTime3.Hour, i_obForm.dtpPreMSTime3.Minute)
    PerStartTime4 = SetTime(i_obForm.dtpPreMSTime4.Hour, i_obForm.dtpPreMSTime4.Minute)
    PerStartTime5 = SetTime(i_obForm.dtpPreMSTime5.Hour, i_obForm.dtpPreMSTime5.Minute)

    intPerStartTime1 = (CInt(Left(PerStartTime1, 2)) * 60) + (CInt(Right(PerStartTime1,
2)))
    intPerStartTime2 = (CInt(Left(PerStartTime2, 2)) * 60) + (CInt(Right(PerStartTime2,
2)))
    intPerStartTime3 = (CInt(Left(PerStartTime3, 2)) * 60) + (CInt(Right(PerStartTime3,
2)))
    intPerStartTime4 = (CInt(Left(PerStartTime4, 2)) * 60) + (CInt(Right(PerStartTime4,
2)))
    intPerStartTime5 = (CInt(Left(PerStartTime5, 2)) * 60) + (CInt(Right(PerStartTime5,
2)))

    Min1 = Abs(intPerStartTime1 - intPerStartTime2)
    Min2 = Abs(intPerStartTime2 - intPerStartTime3)
    Min3 = Abs(intPerStartTime3 - intPerStartTime4)
    Min4 = Abs(intPerStartTime4 - intPerStartTime5)
    Min5 = Abs(intPerStartTime5 - (24 * 60))


End Sub

' This function sets the time of simulation to the variables

Function SetTime(i_strHour As String, i_strMin As String) As String

Dim strHour As String
Dim strMin As String

If (i_strHour < 10) Then
    strHour = "0" & i_strHour
Else
    strHour = i_strHour
End If

If (i_strMin < 10) Then
    strMin = "0" & i_strMin
Else
    strMin = i_strMin
End If

SetTime = strHour & ":" & strMin

End Function
```

```
' This subroutine sets the feeding status for the time interval t

Sub Feeding()

    If total_t <= Min1 Then Feed_t = Feed1
    If total_t > Min1 And total_t <= (Min1 + Min2) Then Feed_t = Feed2
    If total_t > (Min1 + Min2) And total_t <= (Min1 + Min2 + Min3) Then Feed_t = Feed3
    If total_t > (Min1 + Min2 + Min3) And total_t <= (Min1 + Min2 + Min3 + Min4) Then
Feed_t = Feed4
    If total_t > (Min1 + Min2 + Min3 + Min4) And total_t <= (Min1 + Min2 + Min3 + Min4 +
Min5) Then Feed_t = Feed5

End Sub

' This subroutine sets the time period for the time interval t

Sub TimePer()

    If total_t <= Min1 Then TimePer_t = Time1
    If total_t <= (Min2 + Min1) And total_t > Min1 Then TimePer_t = Time2
    If total_t <= (Min3 + Min2 + Min1) And total_t > (Min1 + Min2) Then TimePer_t = Time3
    If total_t <= (Min4 + Min3 + Min2 + Min1) And total_t > (Min1 + Min2 + Min3) Then
TimePer_t = Time4
    If total_t <= (Min5 + Min4 + Min3 + Min2 + Min1) And total_t > (Min1 + Min2 + Min3 +
Min4) Then TimePer_t = Time5

End Sub

' This subroutine writes the Time period in the output file

Sub Output_TimePer()

    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 1) = TimePer_t

End Sub

' This subroutine sets the Migration depths to the variables

Sub Depth(ByRef i_obForm As frmSimulation)   'Lists depth at each time step in simulation

    Depth1 = CDbl(i_obForm.txtPreMSDepth1.Text)
    Depth2 = CDbl(i_obForm.txtPreMSDepth2.Text)
    Depth3 = CDbl(i_obForm.txtPreMSDepth3.Text)
    Depth4 = CDbl(i_obForm.txtPreMSDepth4.Text)
    Depth5 = CDbl(i_obForm.txtPreMSDepth5.Text)

End Sub

' This subroutine writes the Depth in the output file

Sub Output_D()

    If total_t <= Min1 Then depth_t = Depth1
    If total_t > Min1 And total_t <= (Min1 + Min2) Then depth_t = Depth2
    If total_t > (Min1 + Min2) And total_t <= (Min1 + Min2 + Min3) Then depth_t = Depth3
    If total_t > (Min1 + Min2 + Min3) And total_t <= (Min1 + Min2 + Min3 + Min4) Then
depth_t = Depth4
    If total_t > (Min1 + Min2 + Min3 + Min4) And total_t <= (Min1 + Min2 + Min3 + Min4 +
Min5) Then depth_t = Depth5

    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 2) = depth_t

End Sub
```

```
' This subroutine calculates the light illumination in the depth and also on the
' surface

Sub Light(i_obForm As frmSimulation)

    LightSurf_t = CalTotalIllum(Latitude, Longitude, strSimDate, SkyCondition, TimeZone,
total_t)
    Light_t = LightSurf_t * Exp(-LightExtCoeff * depth_t)

End Sub

' This subroutine writes the light illuminance in the output file

Sub Output_Light()

    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 3) = LightSurf_t
    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 4) = Light_t

End Sub

' This subroutine sets the density values at the time interval t

Sub SetDensityTempAtTime()

    If (depth_t = D_1) Then
        Z_t = Z_1
        temp_t = T_1
    ElseIf (depth_t = D_2) Then
        Z_t = Z_2
        temp_t = T_2
    ElseIf (depth_t = D_3) Then
        Z_t = Z_3
        temp_t = T_3
    ElseIf (depth_t = D_4) Then
        Z_t = Z_4
        temp_t = T_4
    ElseIf (depth_t = D_5) Then
        Z_t = Z_5
        temp_t = T_5
    ElseIf (depth_t = D_6) Then
        Z_t = Z_6
        temp_t = T_6
    ElseIf (depth_t = D_7) Then
        Z_t = Z_7
        temp_t = T_7
    End If

End Sub

' This subroutine calculates the function response (consumption rate) at
' time interval t

Sub FunResp()

    If sum_consume < Cmax Then
    If Light_t >= 3.3994 Then c_rate_t = Feed_t * (163.6 * (Z_t / 1000)) / (42.2 + (Z_t /
1000))
    If Light_t < 3.3994 And Light_t >= 0.001 And Z_t <= 52000 Then c_rate_t = Feed_t *
(1.74 * (Z_t / 1000))
    If Light_t < 3.3994 And Light_t >= 0.001 And Z_t > 52000 Then c_rate_t = Feed_t *
(163.6 * (Z_t / 1000)) / (42.2 + (Z_t / 1000))
    If Light_t < 0.001 Then c_rate_t = 0

    Else: c_rate_t = 0
    End If

End Sub
```

```
' This subroutine writes the consumption rate in the ouput file

Sub Output_FunResp()

    If (c_rate_t < 0) Then c_rate_t = 0
    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 8) = c_rate_t

End Sub

' This subroutine writes the temperature in the output file

Sub Output_Temp()

    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 5) = temp_t

End Sub

' This subroutine writes the TL multiplier value in the output file

Sub Output_TL()

    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 6) = TL_t

End Sub

' This subroutine mass of daphnia eaten by the fish (consumption)

Sub Consume()

    If t = 1 Then amt_proc_2 = (((in_stom_t - consume_2 * 2 / (0.11 + 0.01401 * temp_t))
* (1 - Exp(-(0.11 + 0.01401 * temp_t) * timestep / 60))) + consume_t) * 0.578
    If t > 1 Then amt_proc_2 = (((end_stom_t - consume_2 * 2 / (0.11 + 0.01401 * temp_t))
* (1 - Exp(-(0.11 + 0.01401 * temp_t) * timestep / 60))) + consume_t) * 0.578

    If Kmass >= 253.5 Then Fish_Multiplier = 2.2
    If Kmass < 253.5 Then Fish_Multiplier = (14.1 - 4.95 * Log10Kmass)

    If c_rate_t / squeeze * timestep * TL_t + end_stom_t > Kmass * Fish_Multiplier / 100
Then consume_2 = (Kmass * Fish_Multiplier / 100 - end_stom_t)
    If c_rate_t / squeeze * timestep * TL_t + end_stom_t <= Kmass * Fish_Multiplier / 100
Then consume_2 = c_rate_t / squeeze * timestep * TL_t

    If consume_2 + sum_consume > Cmax Then consume_2 = Cmax - sum_consume

    in_stom_2 = consume_2 + end_stom_t
    amt_proc_t = amt_proc_2
    in_stom_t = in_stom_2

    If t = 1 Then in_stom_t = in_stom_0
    consume_t = consume_2
    end_stom_t = in_stom_t - amt_proc_t / 0.578

End Sub


' This subroutine sets ConsumpRate if fish mass > 90g

Sub SetConsumpRate()

    If (depth_t = D_1) Then
        c_rate_t = N_1
    ElseIf (depth_t = D_2) Then
        c_rate_t = N_2
    ElseIf (depth_t = D_3) Then
        c_rate_t = N_3
    ElseIf (depth_t = D_4) Then
        c_rate_t = N_4
    ElseIf (depth_t = D_5) Then
        c_rate_t = N_5
    ElseIf (depth_t = D_6) Then
        c_rate_t = N_6
```

```
    ElseIf (depth_t = D_7) Then
        c_rate_t = N_7
    End If

End Sub

' This subroutine writes the consumption in the output file

Sub Output_Consume()

    If (consume_t < 0) Then consume_t = 0
    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 9) = consume_t

    sum_consume = sum_consume + consume_t

    If (in_stom_t < 0) Then in_stom_t = 0
    If (in_stom_t > max_stom_cap) Then in_stom_t = max_stom_cap
    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 7) = in_stom_t

    If (amt_proc_t < 0) Then amt_proc_t = 0
    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 10) = amt_proc_t

    sum_process = sum_process + amt_proc_t

    If (end_stom_t < 0) Then end_stom_t = 0
    If (end_stom_t > max_stom_cap) Then end_stom_t = max_stom_cap
    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 15) = end_stom_t

End Sub

' This subroutine calculates the growth of the fish

Sub Rent()
    aWb_t = 0.00143 * Kmass ^ (-0.209)
    epT_t = Exp(0.086 * temp_t)
    evUopt_t = Exp(0.0234 * 9.9 * Kmass ^ 0.13 * Exp(0.0405 * temp_t))

    egest_t = EGa * temp_t ^ EGc * Exp(EGf) * amt_proc_t

    excrete_t = EXa * temp_t ^ EXc * Exp(EXf) * (amt_proc_t - egest_t) + SDA *
(amt_proc_t - egest_t)

    resp_t = aWb_t * epT_t * evUopt_t * Kmass * 13560 * 0.239 / 1000 / 48

    growth_2 = amt_proc_t - egest_t - excrete_t - resp_t

    total_costs_t = egest_t + excrete_t + resp_t

    growth_t = growth_2

    If Kmass > 196 Then Kgrowth_t = growth_t / (1588 + (0.1254 * Kmass)) * 1000
    If Kmass <= 196 Then Kgrowth_t = growth_t / (1250 + (1.851 * Kmass)) * 1000

End Sub

' This subroutine outputs the growth of the fish in the output file

Sub Output_Rent()

    If (egest_t < 0) Then egest_t = 0
    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 11) = egest_t

    sum_egest = sum_egest + egest_t

    If (excrete_t < 0) Then excrete_t = 0
    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 12) = excrete_t

    sum_excrete = sum_excrete + excrete_t

    If (resp_t < 0) Then resp_t = 0
    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 13) = resp_t
```

```
    sum_resp = sum_resp + resp_t

    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 16) = growth_t

    sum_growth = sum_growth + growth_t

    If (total_costs_t < 0) Then total_costs_t = 0
    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 14) = total_costs_t

    xlOutputWorkSheet.Cells(O_VALROW + t, O_VALCOL + 17) = Kgrowth_t

End Sub

' This subroutine calculates the sums

Sub Sums()

    sum_endstom = sum_consume + in_stom_0 - sum_process / 0.578
    sum_costs = sum_egest + sum_excrete + sum_resp

    If Kmass > 196 Then sum_Kgrowth = sum_growth / (1588 + 0.1254 * Kmass) * 1000
    If Kmass <= 196 Then sum_Kgrowth = sum_growth / (1250 + 1.851 * Kmass) * 1000

    If (sum_process = 0) Then
        Gross_Efficiency = 0
    Else
        Gross_Efficiency = sum_growth / sum_process
    End If

    If ((Round(in_stom_0, 3) = Round(sum_endstom, 3)) Or (Round(in_stom_0, 2) =
Round(sum_endstom, 2))) Then equilibrium = True Else: equilibrium = False

End Sub

' This subroutine outputs the sums

Sub Output_Sums()

    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 9) = sum_consume
    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 7) = in_stom_0
    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 10) = sum_process
    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 11) = sum_egest
    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 12) = sum_excrete
    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 13) = sum_resp
    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 16) = sum_growth

    If (sum_endstom < 0) Then sum_endstom = 0
    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 15) = sum_endstom

    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 14) = sum_costs
    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 17) = sum_Kgrowth

    If (Gross_Efficiency = 0) Then
        xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 18) = "NA"
    Else
        xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL + 18) = Gross_Efficiency
    End If

    xlOutputWorkSheet.Cells(O_VALROW - 1, O_VALCOL + 4) = equilibrium

End Sub

' This subroutine formats the output worksheet in the output file

Sub FormatOutputWorkSheet()

    Dim rTotalsRange As Range

    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL) = "Time Step"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 1) = "Time Period"
```

```
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 2) = "Depth"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 3) = "Surface Light"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 4) = "Light at Depth"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 5) = "Temp"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 6) = "T-L Rate Multiplier"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 7) = "Initial Stomach"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 8) = "Consumption Rate"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 9) = "Consumption"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 10) = "Amount Processed"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 11) = "Egestion"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 12) = "Excretion & SDA"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 13) = "Respiration"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 14) = "Total Costs"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 15) = "End Stomach"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 16) = "Growth"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 17) = "Growth"
    xlOutputWorkSheet.Cells(O_TITLEROW, O_TITLECOL + 18) = "Gross"

    'Writing units in separate row

    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL) = "(min)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 1) = ""
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 2) = "(m)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 3) = "(lux)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 4) = "(lux)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 5) = "(C)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 6) = ""
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 7) = "(g Daph)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 8) = "(Daph/min)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 9) = "(g Daph)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 10) = "(Kcal)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 11) = "(Kcal)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 12) = "(Kcal)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 13) = "(Kcal)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 14) = "(Kcal)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 15) = "(g Daph)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 16) = "(Kcal)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 17) = "(g)"
    xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 18) = "Efficiency"

    xlOutputWorkSheet.Cells(O_VALROW - 2, O_VALCOL) = "Totals"
    xlOutputWorkSheet.Cells(O_VALROW - 1, O_VALCOL + 3) = "Equilibrium?"

    'Makes the totals row bold
    Set rTotalsRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_VALROW - 2,
O_VALCOL), xlOutputWorkSheet.Cells(O_VALROW - 1, O_VALCOL + 18))
    rTotalsRange.Font.Bold = True

    'Border is drawn for the selected range

    Set rOutBorderRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_TITLEROW,
O_TITLECOL), xlOutputWorkSheet.Cells(O_VALROW + total_ts, O_TITLECOL + 18))
    rOutBorderRange.Font.ColorIndex = 1
    rOutBorderRange.Borders.ColorIndex = 0
    rOutBorderRange.BorderAround ColorIndex:=0, Weight:=xlMedium


'    Makes the title of the fields bold and apply blue color

    Set rOutTitleRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_TITLEROW,
O_TITLECOL), xlOutputWorkSheet.Cells(O_TITLEROW + 1, O_TITLECOL + 18))
    rOutTitleRange.Font.Bold = True
    rOutTitleRange.Font.ColorIndex = 5         ' blue color

    'Setting properties for the fields

xlOutputWorkSheet.Cells(O_TITLEROW + total_ts, O_TITLECOL + 19)).HorizontalAlignment =
xlCenter
```

```
    rOutBorderRange.EntireColumn.AutoFit
    rOutBorderRange.HorizontalAlignment = xlCenter

    xlWorkBook.Save

End Sub

' This subroutine formats the input worksheet in the output file

Sub FormatInputWorkSheet()

    Dim rMGHeader As Range

    xlInputWorkSheet.Cells(I_TITLEROW1, I_TITLECOL) = "Date"
    xlInputWorkSheet.Cells(I_TITLEROW1, I_TITLECOL + 1) = "Depth (m)"
    xlInputWorkSheet.Cells(I_TITLEROW1, I_TITLECOL + 2) = "Temp (C)"
    xlInputWorkSheet.Cells(I_TITLEROW1, I_TITLECOL + 3) = "Daphnia Density (#/cu.m)"
    xlInputWorkSheet.Cells(I_TITLEROW1, I_TITLECOL + 4) = "Max Stomach Capacity (g)"
    xlInputWorkSheet.Cells(I_TITLEROW1, I_TITLECOL + 5) = "Secchi Depth (m)"

    xlInputWorkSheet.Cells(I_TITLEROW2, I_TITLECOL) = "Time Step (min)"
    xlInputWorkSheet.Cells(I_TITLEROW2, I_TITLECOL + 1) = "Number of Time Steps"
    xlInputWorkSheet.Cells(I_TITLEROW2, I_TITLECOL + 2) = "Kokanee Mass (g)"
    xlInputWorkSheet.Cells(I_TITLEROW2, I_TITLECOL + 3) = "Handling Time (sec/Daph)"
    xlInputWorkSheet.Cells(I_TITLEROW2, I_TITLECOL + 4) = "Mean Daph Length (mm)"
    xlInputWorkSheet.Cells(I_TITLEROW2, I_TITLECOL + 5) = "Initial Stomach (g)"

    'Migration Strategy

    xlInputWorkSheet.Cells(I_TITLEROW3, I_TITLECOL) = "Period Start Time"
    xlInputWorkSheet.Cells(I_TITLEROW3, I_TITLECOL + 1) = "Duration of Period (min)"
    xlInputWorkSheet.Cells(I_TITLEROW3, I_TITLECOL + 2) = "Time Period"
    xlInputWorkSheet.Cells(I_TITLEROW3, I_TITLECOL + 3) = "Depth (m)"

    xlInputWorkSheet.Cells(I_TITLEROW3 - 2, I_TITLECOL + 2) = "MIGRATION STRATEGY"

    xlInputWorkSheet.Cells(I_TITLEROW4, I_TITLECOL) = "Latitude"
    xlInputWorkSheet.Cells(I_TITLEROW4, I_TITLECOL + 1) = "Longitude"
    xlInputWorkSheet.Cells(I_TITLEROW4, I_TITLECOL + 2) = "Time Zone"
    xlInputWorkSheet.Cells(I_TITLEROW4, I_TITLECOL + 3) = "Sky Condition"
    xlInputWorkSheet.Cells(I_TITLEROW4, I_TITLECOL + 4) = "Simulation Start Time"
    xlInputWorkSheet.Cells(I_TITLEROW4, I_TITLECOL + 5) = "Simulation Length"

    'Border is drawn for the selected range

    Set rInBorderRange1 = xlInputWorkSheet.Range(xlInputWorkSheet.Cells(I_TITLEROW1,
I_TITLECOL), xlInputWorkSheet.Cells(I_TITLEROW1 + 7, I_TITLECOL + 5))
    Set rInBorderRange2 = xlInputWorkSheet.Range(xlInputWorkSheet.Cells(I_TITLEROW2,
I_TITLECOL), xlInputWorkSheet.Cells(I_TITLEROW2 + 1, I_TITLECOL + 5))
    Set rInBorderRange3 = xlInputWorkSheet.Range(xlInputWorkSheet.Cells(I_TITLEROW3,
I_TITLECOL), xlInputWorkSheet.Cells(I_TITLEROW3 + 5, I_TITLECOL + 3))
    Set rInBorderRange4 = xlInputWorkSheet.Range(xlInputWorkSheet.Cells(I_TITLEROW4,
I_TITLECOL), xlInputWorkSheet.Cells(I_TITLEROW4 + 1, I_TITLECOL + 5))

    rInBorderRange1.Font.ColorIndex = 1
    rInBorderRange2.Font.ColorIndex = 1
    rInBorderRange3.Font.ColorIndex = 1
    rInBorderRange4.Font.ColorIndex = 1

    rInBorderRange1.Borders.ColorIndex = 0
    rInBorderRange2.Borders.ColorIndex = 0
    rInBorderRange3.Borders.ColorIndex = 0
    rInBorderRange4.Borders.ColorIndex = 0

    rInBorderRange1.BorderAround ColorIndex:=0, Weight:=xlMedium
    rInBorderRange2.BorderAround ColorIndex:=0, Weight:=xlMedium
    rInBorderRange3.BorderAround ColorIndex:=0, Weight:=xlMedium
    rInBorderRange4.BorderAround ColorIndex:=0, Weight:=xlMedium
```

```
    ' Makes the title of the fields bold and apply blue color

    Set rInTitleRange1 = xlInputWorkSheet.Range(xlInputWorkSheet.Cells(I_TITLEROW1,
I_TITLECOL), xlInputWorkSheet.Cells(I_TITLEROW1, I_TITLECOL + 5))
    Set rInTitleRange2 = xlInputWorkSheet.Range(xlInputWorkSheet.Cells(I_TITLEROW2,
I_TITLECOL), xlInputWorkSheet.Cells(I_TITLEROW2, I_TITLECOL + 5))
    Set rInTitleRange3 = xlInputWorkSheet.Range(xlInputWorkSheet.Cells(I_TITLEROW3,
I_TITLECOL), xlInputWorkSheet.Cells(I_TITLEROW3, I_TITLECOL + 3))
    Set rInTitleRange4 = xlInputWorkSheet.Range(xlInputWorkSheet.Cells(I_TITLEROW4,
I_TITLECOL), xlInputWorkSheet.Cells(I_TITLEROW4, I_TITLECOL + 5))

    ' Sets the heading "Migration Strategy" bold

    Set rMGHeader = xlInputWorkSheet.Cells(I_TITLEROW3 - 2, I_TITLECOL + 2)

    rInTitleRange1.Font.Bold = True
    rInTitleRange2.Font.Bold = True
    rInTitleRange3.Font.Bold = True
    rInTitleRange4.Font.Bold = True
    rMGHeader.Font.Bold = True

    rInTitleRange1.Font.ColorIndex = 5      'blue color
    rInTitleRange2.Font.ColorIndex = 5      'blue color
    rInTitleRange3.Font.ColorIndex = 5      'blue color
    rInTitleRange4.Font.ColorIndex = 5      'blue color
    rMGHeader.Font.ColorIndex = 5

    ' Setting the properties for the fields

    xlInputWorkSheet.Range(xlInputWorkSheet.Cells(I_TITLEROW1, I_TITLECOL),
xlInputWorkSheet.Cells(I_TITLEROW3 + 5, I_TITLECOL + 5)).EntireColumn.AutoFit
    xlInputWorkSheet.Range(xlInputWorkSheet.Cells(I_TITLEROW1, I_TITLECOL),
xlInputWorkSheet.Cells(I_TITLEROW3 + 5, I_TITLECOL + 5)).HorizontalAlignment = xlCenter

    rMGHeader.HorizontalAlignment = xlCenter
    rMGHeader.VerticalAlignment = xlCenter

End Sub


'This subroutine draws graphs based on the information available in
'the output worksheet

Sub DrawGraphs(i_obForm As frmSimulation)

    Dim xlChartSeries As Excel.Series
    Dim xlChartSeriesCollec As Excel.SeriesCollection
    Dim xlAxis As Excel.Axis
    Dim xlCatAxis As Excel.Axis
    Dim rXRange As Range
    Dim rYRange As Range

    Dim intList As Integer
    Dim strFieldName As String
    Dim strXAxisTitle As String

    intList = 1

    While (intList <> i_obForm.lstOutFieldsToGraph.ListCount)

        Set xlChart = xlWorkBook.Charts.Add(xlInputWorkSheet)

        xlChart.Move _
           after:=xlWorkBook.Worksheets(2)

        xlChart.Activate

        strXAxisTitle = i_obForm.lstOutFieldsToGraph.List(0)
        Set rXRange = XGraphRange(strXAxisTitle)

        strFieldName = i_obForm.lstOutFieldsToGraph.List(intList)
```

```
        Set rYRange = YGraphRange(strFieldName)

        xlChart.ChartType = xlLine
        xlChart.Name = "Chart" + HYPHEN + strChartName
        xlChart.HasLegend = False

        Set xlChartSeriesCollec = xlChart.SeriesCollection
        Set xlChartSeries = xlChartSeriesCollec.NewSeries

        xlChartSeries.XValues = rXRange
        xlChartSeries.Values = rYRange

        xlChartSeries.Name = strFieldName

        xlChartSeries.MarkerSize = C_MARKERSIZE
        xlChartSeries.Border.ColorIndex = C_COLORINDEX
        xlChartSeries.Border.Weight = xlThick

        Set xlAxis = xlChart.Axes(XlAxisType.xlValue, xlPrimary)
        Set xlCatAxis = xlChart.Axes(XlAxisType.xlCategory, xlPrimary)

        xlAxis.HasMajorGridlines = True
        xlAxis.HasMinorGridlines = False
        xlAxis.MajorUnitIsAuto = True

        xlAxis.HasTitle = True
        xlAxis.MinimumScale = 0
        xlAxis.AxisTitle.Text = strFieldName
        xlAxis.AxisTitle.Font.FontStyle = "Bold"

        xlCatAxis.HasTitle = True
        xlCatAxis.TickLabels.NumberFormatLinked = True
        xlCatAxis.TickLabels.Orientation = xlTickLabelOrientationUpward
        xlCatAxis.AxisTitle.Text = strXAxisTitle
        xlCatAxis.AxisTitle.Font.FontStyle = "Bold"

        intList = intList + 1

    Wend

End Sub

' This subroutine sets the range for the x-axis for the graphs

Function XGraphRange(i_strXAxis As String) As Range

     Dim rXGraphRange As Range

     If (i_strXAxis = "Consumption Rate(Daph/min)") Then

        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 8), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 8))

    ElseIf (i_strXAxis = "Depth(m)") Then

        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 2), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 2))

    ElseIf (i_strXAxis = "Egestion Rate(Kcal)") Then

        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 11), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 11))

    ElseIf (i_strXAxis = "Excretion & SDA(Kcal)") Then

        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 12), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 12))

    ElseIf (i_strXAxis = "Growth(g)") Then
```

```
        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 17), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 17))

    ElseIf (i_strXAxis = "Growth(Kcal)") Then

        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 16), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 16))

    ElseIf (i_strXAxis = "Light Illuminance(lux)") Then

        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 4), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 4))

    ElseIf (i_strXAxis = "Respiration Rate(Kcal)") Then

        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 13), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 13))

    ElseIf (i_strXAxis = "Temperature(C)") Then

        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 5), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 5))

    ElseIf (i_strXAxis = "Time Step") Then

        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL))

    ElseIf (i_strXAxis = "Total Costs(Kcal)") Then

        Set rXGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 14), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 14))

    End If

    Set XGraphRange = rXGraphRange

End Function

' This subroutine selects the range for the y-axis for the graphs

Function YGraphRange(i_strYAxis As String) As Range

    Dim rYGraphRange As Range

     If (i_strYAxis = "Consumption Rate(Daph/min)") Then

        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 8), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 8))
        strChartName = "ConsmpRate"

    ElseIf (i_strYAxis = "Depth(m)") Then

        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 2), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 2))
        strChartName = "Depth"

    ElseIf (i_strYAxis = "Egestion Rate(Kcal)") Then

        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 11), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 11))
        strChartName = "EgesRate"

    ElseIf (i_strYAxis = "Excretion & SDA(Kcal)") Then

        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 12), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 12))
        strChartName = "ExcreSDA"

    ElseIf (i_strYAxis = "Growth(g)") Then
```

```
        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 17), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 17))
        strChartName = "Growth_g"

    ElseIf (i_strYAxis = "Growth(Kcal)") Then

        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 16), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 16))
        strChartName = "Growth_Kcal"

    ElseIf (i_strYAxis = "Light Illuminance(lux)") Then

        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 4), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 4))
        strChartName = "LightIllum"

    ElseIf (i_strYAxis = "Respiration Rate(Kcal)") Then

        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 13), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 13))
        strChartName = "RespRate"

    ElseIf (i_strYAxis = "Temperature(C)") Then

        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 5), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 5))
        strChartName = "Temperature"

    ElseIf (i_strYAxis = "Time Step") Then

        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL))
        strChartName = "TimeStep"

    ElseIf (i_strYAxis = "Total Costs(Kcal)") Then

        Set rYGraphRange = xlOutputWorkSheet.Range(xlOutputWorkSheet.Cells(O_GRAPHROW,
O_VALCOL + 14), xlOutputWorkSheet.Cells(O_GRAPHROW + total_ts, O_VALCOL + 14))
        strChartName = "TotalCosts"

    End If

    Set YGraphRange = rYGraphRange

End Function

' This subroutine sets the user inputs to the input worksheet of the output file

Sub SetUserInputs()

    xlInputWorkSheet.Cells(I_TITLEROW1 + 1, I_TITLECOL) = strSimDate

    xlInputWorkSheet.Cells(I_TITLEROW1 + 1, I_TITLECOL + 1) = D_1
    xlInputWorkSheet.Cells(I_TITLEROW1 + 2, I_TITLECOL + 1) = D_2
    xlInputWorkSheet.Cells(I_TITLEROW1 + 3, I_TITLECOL + 1) = D_3
    xlInputWorkSheet.Cells(I_TITLEROW1 + 4, I_TITLECOL + 1) = D_4
    xlInputWorkSheet.Cells(I_TITLEROW1 + 5, I_TITLECOL + 1) = D_5
    xlInputWorkSheet.Cells(I_TITLEROW1 + 6, I_TITLECOL + 1) = D_6
    xlInputWorkSheet.Cells(I_TITLEROW1 + 7, I_TITLECOL + 1) = D_7

    xlInputWorkSheet.Cells(I_TITLEROW1 + 1, I_TITLECOL + 2) = T_1
    xlInputWorkSheet.Cells(I_TITLEROW1 + 2, I_TITLECOL + 2) = T_2
    xlInputWorkSheet.Cells(I_TITLEROW1 + 3, I_TITLECOL + 2) = T_3
    xlInputWorkSheet.Cells(I_TITLEROW1 + 4, I_TITLECOL + 2) = T_4
    xlInputWorkSheet.Cells(I_TITLEROW1 + 5, I_TITLECOL + 2) = T_5
    xlInputWorkSheet.Cells(I_TITLEROW1 + 6, I_TITLECOL + 2) = T_6
    xlInputWorkSheet.Cells(I_TITLEROW1 + 7, I_TITLECOL + 2) = T_7

    xlInputWorkSheet.Cells(I_TITLEROW1 + 1, I_TITLECOL + 3) = Z_1
    xlInputWorkSheet.Cells(I_TITLEROW1 + 2, I_TITLECOL + 3) = Z_2
    xlInputWorkSheet.Cells(I_TITLEROW1 + 3, I_TITLECOL + 3) = Z_3
```

```
xlInputWorkSheet.Cells(I_TITLEROW1 + 4, I_TITLECOL + 3) = Z_4
xlInputWorkSheet.Cells(I_TITLEROW1 + 5, I_TITLECOL + 3) = Z_5
xlInputWorkSheet.Cells(I_TITLEROW1 + 6, I_TITLECOL + 3) = Z_6
xlInputWorkSheet.Cells(I_TITLEROW1 + 7, I_TITLECOL + 3) = Z_7
xlInputWorkSheet.Cells(I_TITLEROW1 + 1, I_TITLECOL + 4) = max_stom_cap
xlInputWorkSheet.Cells(I_TITLEROW1 + 1, I_TITLECOL + 5) = Secchi

xlInputWorkSheet.Cells(I_TITLEROW2 + 1, I_TITLECOL) = timestep
xlInputWorkSheet.Cells(I_TITLEROW2 + 1, I_TITLECOL + 1) = total_ts
xlInputWorkSheet.Cells(I_TITLEROW2 + 1, I_TITLECOL + 2) = Kmass
xlInputWorkSheet.Cells(I_TITLEROW2 + 1, I_TITLECOL + 3) = handtime
xlInputWorkSheet.Cells(I_TITLEROW2 + 1, I_TITLECOL + 4) = Dsize
xlInputWorkSheet.Cells(I_TITLEROW2 + 1, I_TITLECOL + 5) = in_stom_0

xlInputWorkSheet.Cells(I_TITLEROW3 + 1, I_TITLECOL) = PerStartTime1
xlInputWorkSheet.Cells(I_TITLEROW3 + 2, I_TITLECOL) = PerStartTime2
xlInputWorkSheet.Cells(I_TITLEROW3 + 3, I_TITLECOL) = PerStartTime3
xlInputWorkSheet.Cells(I_TITLEROW3 + 4, I_TITLECOL) = PerStartTime4
xlInputWorkSheet.Cells(I_TITLEROW3 + 5, I_TITLECOL) = PerStartTime5

xlInputWorkSheet.Cells(I_TITLEROW3 + 1, I_TITLECOL + 1) = Min1
xlInputWorkSheet.Cells(I_TITLEROW3 + 2, I_TITLECOL + 1) = Min2
xlInputWorkSheet.Cells(I_TITLEROW3 + 3, I_TITLECOL + 1) = Min3
xlInputWorkSheet.Cells(I_TITLEROW3 + 4, I_TITLECOL + 1) = Min4
xlInputWorkSheet.Cells(I_TITLEROW3 + 5, I_TITLECOL + 1) = Min5

xlInputWorkSheet.Cells(I_TITLEROW3 + 1, I_TITLECOL + 2) = Time1
xlInputWorkSheet.Cells(I_TITLEROW3 + 2, I_TITLECOL + 2) = Time2
xlInputWorkSheet.Cells(I_TITLEROW3 + 3, I_TITLECOL + 2) = Time3
xlInputWorkSheet.Cells(I_TITLEROW3 + 4, I_TITLECOL + 2) = Time4
xlInputWorkSheet.Cells(I_TITLEROW3 + 5, I_TITLECOL + 2) = Time5

xlInputWorkSheet.Cells(I_TITLEROW3 + 1, I_TITLECOL + 3) = Depth1
xlInputWorkSheet.Cells(I_TITLEROW3 + 2, I_TITLECOL + 3) = Depth2
xlInputWorkSheet.Cells(I_TITLEROW3 + 3, I_TITLECOL + 3) = Depth3
xlInputWorkSheet.Cells(I_TITLEROW3 + 4, I_TITLECOL + 3) = Depth4
xlInputWorkSheet.Cells(I_TITLEROW3 + 5, I_TITLECOL + 3) = Depth5

xlInputWorkSheet.Cells(I_TITLEROW4 + 1, I_TITLECOL) = Latitude
xlInputWorkSheet.Cells(I_TITLEROW4 + 1, I_TITLECOL + 1) = Longitude
xlInputWorkSheet.Cells(I_TITLEROW4 + 1, I_TITLECOL + 2) = TimeZone
xlInputWorkSheet.Cells(I_TITLEROW4 + 1, I_TITLECOL + 3) = SkyCondition
xlInputWorkSheet.Cells(I_TITLEROW4 + 1, I_TITLECOL + 4) = strSimStartTime
xlInputWorkSheet.Cells(I_TITLEROW4 + 1, I_TITLECOL + 5) = strSimLength
End Sub
```

Illuminance.bas

```
' **************************************************
' *** This program contains the code for         ***
' *** light illuminance.                         ***
' ***                                            ***
' **************************************************

' Constants used in the program
Const RD = 57.29577951
Const DR = 0.017453293
Const CE = 0.91775
Const SE = 0.39715
Const C = 360

Dim dLat As Double
Dim dLong As Double
Dim dSI As Double
Dim dCI As Double
Dim intYear As Integer
Dim intMon As Integer
Dim intDay As Integer
Dim intTZ As Integer
Dim intSky As Integer
Dim dTime As Double
Dim bTimeFlag As Boolean
Dim bSplTimeFlag1 As Boolean
Dim bSplTimeFlag2 As Boolean
Dim intTimeFlag As Integer

' This function calculates the arcsin
Function ArcSin(i_dNum As Double) As Double

    ArcSin = Atn(i_dNum / Sqr(-i_dNum * i_dNum + 1))

End Function

' This function calculates the arccos
Function ArcCos(i_dNum As Double) As Double

    ArcCos = Atn(-i_dNum / Sqr(-i_dNum * i_dNum + 1)) + 2 * Atn(1)

End Function

' This function sets the values required for calculating the light illuminance
Function SetData(i_strLatitude As String, i_strLongitude As String, _
                        i_strSimDate As String, i_strSky As String, _
                        i_strTimeZone As String, i_dTime As Double)

    SetLatitude i_strLatitude
    SetLongitude i_strLongitude
    SetDate i_strSimDate

    Select Case intTimeFlag

    Case 1
            If (i_dTime <= 720) Then
                dTime = (i_dTime + 720) / 60
            Else
                dTime = (i_dTime - 720) / 60
            End If
    Case 2
            dTime = i_dTime / 60

    Case 3
            If (i_dTime <= 720) Then
                If (i_dTime > 30) Then
                    dTime = (i_dTime + 720) / 60
                Else
                    dTime = i_dTime / 60
                End If
```

```
            Else
                dTime = (i_dTime - 720 + 30) / 60
            End If

    Case 4
            If (i_dTime <= 720) Then
                dTime = (720 - i_dTime + 30) / 60
            Else
                dTime = i_dTime / 60
            End If

    End Select

    intTZ = CInt(Left(i_strTimeZone, 1))
    intSky = CInt(i_strSky)

End Function


' This function sets the date of simulation
Function SetDate(i_strSimDate As String)

    intMon = CInt(Left(i_strSimDate, 2))
    intDay = CInt(Mid(i_strSimDate, 4, 2))
    intYear = CInt(Right(i_strSimDate, 4))

    If ((intMon > 6) And (intMon < 12)) Then
        intTimeFlag = 1
    ElseIf (intMon = 6) Then
        If (intDay >= 22) Then
            intTimeFlag = 1
        ElseIf (intDay = 21) Then
            intTimeFlag = 3
        ElseIf (intDay < 21) Then
            intTimeFlag = 2
        End If
    ElseIf (intMon = 12) Then
        If (intDay <= 20) Then
            intTimeFlag = 1
        ElseIf (intDay = 21) Then
            intTimeFlag = 4
        ElseIf (intdat > 21) Then
            intTimeFlag = 2
        End If
    Else
        intTimeFlag = 2
    End If

End Function

' This functions sets the latitude
Function SetLatitude(i_strLat As String)
    Dim dDeg As Double
    Dim dMin As Double
    Dim dSec As Double
    Dim strSign As String

    dDeg = CDbl(Left(i_strLat, 2))
    dMin = CDbl(Mid(i_strLat, 4, 2))
    dSec = CDbl(Mid(i_strLat, 7, 2))
    strSign = Right(i_strLat, 1)

    dLat = (((dSec / 60) + dMin) / 60) + dDeg

    If (strSign = "S") Then
        dLat = -dLat
    End If

End Function
```

```
' This functions sets the longitude
Function SetLongitude(i_strLong As String)
    Dim dDeg As Double
    Dim dMin As Double
    Dim dSec As Double
    Dim strSign As String

    dDeg = CDbl(Left(i_strLong, 3))
    dMin = CDbl(Mid(i_strLong, 5, 2))
    dSec = CDbl(Mid(i_strLong, 8, 2))
    strSign = Right(i_strLong, 1)

    dLong = (((dSec / 60) + dMin) / 60) + dDeg

    If (strSign = "W") Then
        dLong = -dLong
    End If

End Function

' This function calculates the total light illuminance
Function CalTotalIllum(i_strLatitude As String, i_strLongitude As String, _
                        i_strSimDate As String, i_strSky As String, _
                        i_strTimeZone As String, i_dTime As Double) As Double

    Dim dLI As Double
    Dim dDT As Double
    Dim dJ As Double
    Dim dE As Double
    Dim dD As Double
    Dim dSunIllum As Double
    Dim dMoonIllum As Double

    'SetData i_obForm
    SetData i_strLatitude, i_strLongitude, i_strSimDate, i_strSky, i_strTimeZone, i_dTime

    dSI = Sin(dLat * DR)
    dCI = Cos(dLat * DR)
    dLI = Abs(dLong)

    dJ = 367 * CLng(intYear) - Int(7 * (intYear + Int((intMon + 9) / 12)) / 4) + Int(275
* intMon / 9) + intDay - 730531

    If (intTZ = 0) Then
            dDT = -dLong / C
    ElseIf (intTZ = 1) Then
            'dDT = -(dLI - 15 * Int((dLI + 7.5) / 15)) / C * Sgn(dLong)
            dDT = (dLI - 15 * Int((dLI + 7.5) / 15)) / C * Sgn(-dLong)
    End If

    dE = dTime / 24 - dDT - dLong / C
    dD = dJ - 0.5 + dE

    dSunIllum = CalSunIllum(dD, dE, dSI, dCI)
    dMoonIllum = CalMoonIllum(dD, dSI, dCI)

    CalTotalIllum = dSunIllum + dMoonIllum

End Function

' This function calculates the sun illuminance
Function CalSunIllum(i_dD As Double, i_dE As Double, _
                     i_dSI As Double, i_dCI As Double) As Double

    Dim dT As Double
    Dim dAS As Double
    Dim dSD As Double
    Dim dDS As Double
    Dim dH As Double
    Dim dCD As Double
    Dim dCS As Double
```

```
    Dim dMval As Double

    Sun i_dD, dT, dAS, dSD, dDS

    dT = dT + C * i_dE + dLong

    dH = dT - dAS
    dCD = Cos(dDS)
    dCS = Cos(dH * DR)

    dH = ArcSin(dSD * i_dSI + dCD * i_dCI * dCS) * RD

    dMval = Atmos(dH)

    CalSunIllum = 133775 * dMval / CDbl(intSky)

End Function

' This function calculates the moon illuminance
Function CalMoonIllum(i_dD As Double, i_dSI As Double, i_dCI As Double) As Double

    Dim dT As Double
    Dim dAS As Double
    Dim dSD As Double
    Dim dDS As Double
    Dim dH As Double
    Dim dLS As Double
    Dim dV As Double
    Dim dCB As Double
    Dim dCD As Double
    Dim dCS As Double
    Dim dZ As Double
    Dim dMval As Double
    Dim dEval As Double
    Dim dPval As Double

    Moon i_dD, dV, dT, dAS, dSD, dDS, dLS, dCB

    dH = dT - dAS
    dCD = Cos(dDS)
    dCS = Cos(dH * DR)

    dH = ArcSin(dSD * i_dSI + dCD * i_dCI * dCS) * RD
    dZ = dH * DR

    dH = dH - 0.95 * Cos(dH * DR)

    dMval = Atmos(dH)

    dEval = ArcCos(Cos(dV - dLS) * dCB)

    dPval = 0.892 * Exp(-3.343 / ((Tan(dEval / 2)) ^ 0.632)) + 0.0344 * (Sin(dEval) -
dEval * Cos(dEval))
    dPval = 0.418 * dPval / (1 - 0.005 * Cos(dEval) - 0.03 * Sin(dZ))

    CalMoonIllum = dPval * dMval / CDbl(intSky)

End Function
Function Moon(ByVal i_dD As Double, ByRef io_dV As Double, ByRef io_dT As Double, _
              ByRef io_dAS As Double, ByRef io_dSD As Double, ByRef io_dDS As Double, _
              ByRef io_dLS As Double, ByRef io_dCB As Double)

    Dim dG As Double
    Dim dY As Double
    Dim dOval As Double
    Dim dW As Double
    Dim dSB As Double
    Dim dX As Double
    Dim dS As Double
    Dim dCD As Double
    Dim dSV As Double
```

```
    Dim dQ As Double
    Dim dP As Double


    io_dV = 218.32 + 13.1764 * i_dD
    io_dV = io_dV - Int(io_dV / C) * C

    If (io_dV < 0) Then
        io_dV = io_dV + 360
    End If

    io_dT = 280.46 + 0.98565 * i_dD
    io_dT = io_dT - Int(io_dT) * C

    If (io_dT < 0) Then
        io_dT = io_dT + C
    End If

    dG = (357.5 + 0.9856 * i_dD) * DR
    io_dLS = (io_dT + 1.91 * Sin(dG)) * DR

    dY = (134.96 + 13.06499 * i_dD) * DR
    dOval = (93.27 + 13.22935 * i_dD) * DR
    dW = (235.7 + 24.3815 * i_dD) * DR

    dSB = Sin(dY)
    io_dCB = Cos(dY)
    dX = Sin(dOval)
    dS = Cos(dOval)
    io_dSD = Sin(dW)
    dCD = Cos(dW)

    io_dV = (io_dV + (6.29 - 1.27 * dCD + 0.43 * io_dCB) * dSB + (0.66 + 1.27 * io_dCB) *
io_dSD - 0.19 * Sin(dG) - 0.23 * dX * dS) * DR

    dY = ((5.13 - 0.17 * dCD) * dX + (0.56 * dSB + 0.17 * io_dSD) * dS) * DR

    dSV = Sin(io_dV)
    dSB = Sin(dY)
    io_dCB = Cos(dY)
    dQ = io_dCB * Cos(io_dV)
    dP = CE * dSV * io_dCB - SE * dSB

    io_dSD = SE * dSV * io_dCB + CE * dSB
    io_dAS = Atn(dP / dQ) * RD

    If (dQ < 0) Then
        io_dAS = io_dAS + 180
    End If

    io_dDS = ArcSin(io_dSD)
    io_dT = io_dT - 180

End Function
Function Sun(ByVal i_dD As Double, ByRef io_dT As Double, ByRef io_dAS As Double, _
            ByRef io_dSD As Double, ByRef io_dDS As Double)

    Dim dG As Double
    Dim dLS As Double
    Dim dY As Double

    io_dT = 280.46 + 0.98565 * i_dD
    io_dT = io_dT - Int(io_dT) * C

    If (io_dT < 0) Then
        io_dT = io_dT + C
    End If

    dG = (357.5 + 0.9856 * i_dD) * DR
    dLS = (io_dT + 1.91 * Sin(dG)) * DR
```

```
    io_dAS = Atn(CE * Tan(dLS)) * RD

    dY = Cos(dLS)
    If (y < 0) Then
        io_dAS = io_dAS + 180
    End If

    io_dSD = SE * Sin(dLS)
    io_dDS = ArcSin(io_dSD)

    io_dT = io_dT - 180

End Function
Function Atmos(i_dH As Double) As Double

    Dim dHA As Double
    Dim dU As Double
    Dim dX As Double
    Dim dS As Double
    Dim dM As Double

    If (i_dH < (-5 / 6)) Then
        dHA = i_dH
    Else
        dHA = i_dH + 1 / (Tan((i_dH + 8.6 / (i_dH + 4.42)) * DR)) / 60
    End If

    dU = Sin(dHA * DR)
    dX = 753.66156
    dS = ArcSin(dX * Cos(dHA * DR) / (dX + 1))

    dM = dX * (Cos(dS) - dU) + Cos(dS)

    dM = Exp(-0.21 * dM) * dU + 0.0289 * Exp(-0.042 * dM) * (1 + (dHA + 90) * dU / RD)

    Atmos = dM

End Function
```

FileSimulation.bas

```
' ************************************************
' *** This program contains the code for writing ***
' *** & reading from the *.sim file and updating ***
' *** the simulation setup dialog box whenever   ***
' *** open existing simulation (*.sim) file      ***
' *** option is used.                            ***
' ************************************************

Option Explicit

' Constants used in the program

Const LATI = "Latitude"
Const LONGI = "Longitude"
Const TZ = "Time Zone"
Const SKY = "Sky Condition"
Const ST = "Start Time"
Const SIMLEN = "Length of Simulation"
Const SIMDATE = "Simulation Date"
Const TSLEN = "Time Step Length"
Const SECCHIDEPTH = "Secchi Depth"
Const AVGDEPTH1 = "Depth1"
Const AVGDEPTH2 = "Depth2"
Const AVGDEPTH3 = "Depth3"
Const AVGDEPTH4 = "Depth4"
Const AVGDEPTH5 = "Depth5"
Const AVGDEPTH6 = "Depth6"
Const AVGDEPTH7 = "Depth7"
Const TEMP1 = "Temperature1"
Const TEMP2 = "Temperature2"
Const TEMP3 = "Temperature3"
Const TEMP4 = "Temperature4"
Const TEMP5 = "Temperature5"
Const TEMP6 = "Temperature6"
Const TEMP7 = "Temperature7"
Const DEN1 = "Density1"
Const DEN2 = "Density2"
Const DEN3 = "Density3"
Const DEN4 = "Density4"
Const DEN5 = "Density5"
Const DEN6 = "Density6"
Const DEN7 = "Density7"
Const FISHMASS = "Fish Mass"
Const HANDLINGTIME = "Handling Time"
Const PREYLEN = "Prey Length"
Const INSTOM = "Initial Stomach"
Const MSTIME1 = "Time1"
Const MSTIME2 = "Time2"
Const MSTIME3 = "Time3"
Const MSTIME4 = "Time4"
Const MSTIME5 = "Time5"
Const MSDEPTH1 = "Depth1"
Const MSDEPTH2 = "Depth2"
Const MSDEPTH3 = "Depth3"
Const MSDEPTH4 = "Depth4"
Const MSDEPTH5 = "Depth5"
Const MSFEED1 = "Feeding Status1"
Const MSFEED2 = "Feeding Status2"
Const MSFEED3 = "Feeding Status3"
Const MSFEED4 = "Feeding Status4"
Const MSFEED5 = "Feeding Status5"
Const SSHEET = "SpreadSheet"
Const GRAPHS = "Graphs"
Const FIELDSAVAIL = "Fields Available"
Const EQLTO = "="

Dim strFileName As String
Dim strSectionName As String
Dim strKeyName As String
```

```
Dim strDefault As String
Dim strReturnedString As String
Dim strString As String
Dim strNull As String

Declare Function GetPrivateProfileInt Lib "KERNEL32" _
           Alias "GetPrivateProfileIntA" _
                 (ByVal strSectionName As String, _
                  ByVal strKeyName As String, _
                  ByVal lDefault As Long, _
                  ByVal strFileName As String) As Long
Declare Function GetPrivateProfileString Lib "KERNEL32" _
           Alias "GetPrivateProfileStringA" _
                 (ByVal strSectionName As String, _
                  ByVal strKeyName As String, _
                  ByVal strDefault As String, _
                  ByVal strReturnedString As String, _
                  ByVal lSize As Long, _
                  ByVal strFileName As String) As Long
Declare Function GetPrivateProfileSection Lib "KERNEL32" _
          Alias "GetPrivateProfileSectionA" _
                (ByVal strSectionName As String, _
                 ByVal strReturnedString As String, _
                 ByVal lSize As Long, _
                 ByVal strFileName As String) As Long
Declare Function WritePrivateProfileSection Lib "KERNEL32" _
           Alias "WritePrivateProfileSectionA" _
                 (ByVal strSectionName As String, _
                  ByVal strString As String, _
                  ByVal strFileName As String) As Long
Declare Function WritePrivateProfileString Lib "KERNEL32" _
           Alias "WritePrivateProfileStringA" _
                 (ByVal strSectionName As String, _
                  ByVal strKeyName As String, _
                  ByVal strString As String, _
                  ByVal strFileName As String) As Long

' This function writes the values of the controls in the simulation file
Public Function WriteSimulationFile(ByVal i_obForm As frmSimulation)
'This function is called on click of create button

    strFileName = i_obForm.txtSimNewFileName.Text

    WriteExtCondPage i_obForm
    WriteIntCondPage i_obForm
    WritePredAndPreyPage i_obForm
    'WriteOutputPage i_obForm

End Function

' This function reads the values of the controls from the simulation file
Public Function ReadSimulationFile(ByVal io_obForm As frmSimulation) As Boolean

    strFileName = io_obForm.txtSimOpenFileName.Text

    If (ReadExtCondPage(io_obForm) = True) Then GoTo FnBreak_ReadSimulationFile
    ReadIntCondPage io_obForm
    ReadPredAndPreyPage io_obForm
    ReadSimulationFile = False
    Exit Function
FnBreak_ReadSimulationFile:
    ReadSimulationFile = True
    Exit Function

End Function

' This function writes the values of the controls in the External conditions
' page in the simulation file
Public Function WriteExtCondPage(ByVal i_obForm As frmSimulation)

    Dim bReturn As Boolean
```

```
    strNull = Chr$(0)

    strSectionName = "External Conditions"

    strString = LATI & EQLTO & i_obForm.mskExtLatitude.Text & strNull _
            & LONGI & EQLTO & i_obForm.mskExtLongitude.Text & strNull _
            & TZ & EQLTO & i_obForm.cboExtTimeZone.Text & strNull _
            & SKY & EQLTO & i_obForm.cboExtSkyCondition.Text & strNull _
            & ST & EQLTO & i_obForm.dtpExtStartTime.Hour & ":" &
i_obForm.dtpExtStartTime.Minute & strNull _
            & SIMLEN & EQLTO & i_obForm.mskExtSimLength.Text & strNull _
            & TSLEN & EQLTO & i_obForm.cboExtTimeStepLength.Text & strNull _
            & SIMDATE & EQLTO & i_obForm.dtpExtSimDate.Month & "/" &
i_obForm.dtpExtSimDate.Day & "/" & i_obForm.dtpExtSimDate.Year & strNull & strNull &
strNull

    bReturn = WritePrivateProfileSection(strSectionName, strString, strFileName)

End Function

' This function writes the values of the controls in the Internal conditions
' page in the simulation file
Public Function WriteIntCondPage(ByVal i_obForm As frmSimulation)

    Dim bReturn As Boolean
    strNull = Chr$(0)

    strSectionName = "Internal Conditions"

    strString = SECCHIDEPTH & EQLTO & i_obForm.txtIntSecchiDepth.Text & strNull _
                & AVGDEPTH1 & EQLTO & i_obForm.txtIntAvgDepth1.Text & strNull _
                & AVGDEPTH2 & EQLTO & i_obForm.txtIntAvgDepth2.Text & strNull _
                & AVGDEPTH3 & EQLTO & i_obForm.txtIntAvgDepth3.Text & strNull _
                & AVGDEPTH4 & EQLTO & i_obForm.txtIntAvgDepth4.Text & strNull _
                & AVGDEPTH5 & EQLTO & i_obForm.txtIntAvgDepth5.Text & strNull _
                & AVGDEPTH6 & EQLTO & i_obForm.txtIntAvgDepth6.Text & strNull _
                & AVGDEPTH7 & EQLTO & i_obForm.txtIntAvgDepth7.Text & strNull _
                & TEMP1 & EQLTO & i_obForm.txtIntMeanTemp1.Text & strNull _
                & TEMP2 & EQLTO & i_obForm.txtIntMeanTemp2.Text & strNull _
                & TEMP3 & EQLTO & i_obForm.txtIntMeanTemp3.Text & strNull _
                & TEMP4 & EQLTO & i_obForm.txtIntMeanTemp4.Text & strNull _
                & TEMP5 & EQLTO & i_obForm.txtIntMeanTemp5.Text & strNull _
                & TEMP6 & EQLTO & i_obForm.txtIntMeanTemp6.Text & strNull _
                & TEMP7 & EQLTO & i_obForm.txtIntMeanTemp7.Text & strNull _
                & DEN1 & EQLTO & i_obForm.txtIntDaphDensity1.Text & strNull _
                & DEN2 & EQLTO & i_obForm.txtIntDaphDensity2.Text & strNull _
                & DEN3 & EQLTO & i_obForm.txtIntDaphDensity3.Text & strNull _
                & DEN4 & EQLTO & i_obForm.txtIntDaphDensity4.Text & strNull _
                & DEN5 & EQLTO & i_obForm.txtIntDaphDensity5.Text & strNull _
                & DEN6 & EQLTO & i_obForm.txtIntDaphDensity6.Text & strNull _
                & DEN7 & EQLTO & i_obForm.txtIntDaphDensity7.Text & strNull & strNull &
strNull

    bReturn = WritePrivateProfileSection(strSectionName, strString, strFileName)

End Function

' This function writes the values of the controls in the Predator and Prey
' page in the simulation file
Private Function WritePredAndPreyPage(ByVal i_obForm As frmSimulation)

    Dim bReturn As Boolean
    strNull = Chr$(0)
    strSectionName = "Predator and Prey"

    strString = FISHMASS & EQLTO & i_obForm.txtPreFishMass.Text & strNull _
                & PREYLEN & EQLTO & i_obForm.txtPrePreyLength.Text & strNull _
                & HANDLINGTIME & EQLTO & i_obForm.txtPreHandlingTime.Text & strNull _
                & INSTOM & EQLTO & i_obForm.txtPreInitialStomach.Text & strNull & strNull

    bReturn = WritePrivateProfileSection(strSectionName, strString, strFileName)
```

```
    strSectionName = "Migration Strategy"

    strString = MSTIME1 & EQLTO & i_obForm.dtpPreMSTime1.Hour & ":" &
i_obForm.dtpPreMSTime1.Minute & strNull _
                & MSTIME2 & EQLTO & i_obForm.dtpPreMSTime2.Hour & ":" &
i_obForm.dtpPreMSTime2.Minute & strNull _
                & MSTIME3 & EQLTO & i_obForm.dtpPreMSTime3.Hour & ":" &
i_obForm.dtpPreMSTime3.Minute & strNull _
                & MSTIME4 & EQLTO & i_obForm.dtpPreMSTime4.Hour & ":" &
i_obForm.dtpPreMSTime4.Minute & strNull _
                & MSTIME5 & EQLTO & i_obForm.dtpPreMSTime5.Hour & ":" &
i_obForm.dtpPreMSTime5.Minute & strNull _
                & MSDEPTH1 & EQLTO & i_obForm.txtPreMSDepth1.Text & strNull _
                & MSDEPTH2 & EQLTO & i_obForm.txtPreMSDepth2.Text & strNull _
                & MSDEPTH3 & EQLTO & i_obForm.txtPreMSDepth3.Text & strNull _
                & MSDEPTH4 & EQLTO & i_obForm.txtPreMSDepth4.Text & strNull _
                & MSDEPTH5 & EQLTO & i_obForm.txtPreMSDepth5.Text & strNull _
                & MSFEED1 & EQLTO & i_obForm.chkPreMSFeeding1.Value & strNull _
                & MSFEED2 & EQLTO & i_obForm.chkPreMSFeeding2.Value & strNull _
                & MSFEED3 & EQLTO & i_obForm.chkPreMSFeeding3.Value & strNull _
                & MSFEED4 & EQLTO & i_obForm.chkPreMSFeeding4.Value & strNull _
                & MSFEED5 & EQLTO & i_obForm.chkPreMSFeeding5.Value & strNull & strNull

    bReturn = WritePrivateProfileSection(strSectionName, strString, strFileName)


End Function

' This function writes the values of the controls in the Output
' page in the simulation file
Private Function WriteOutputPage(ByVal i_obForm As frmSimulation)

    Dim bReturn As Boolean
    Dim i As Integer
    Dim tempstrString As String
    Dim strComma As String
    strComma = ", "

    strNull = Chr$(0)
    strSectionName = "Output"

    strString = i_obForm.txtOutSpreadSheet.Text
    bReturn = WritePrivateProfileString(strSectionName, SSHEET, strString, strFileName)

    If (i_obForm.chkOutGraphs.Value = 0) Then
        strString = "No"
    Else
        strString = "Yes"
    End If

    bReturn = WritePrivateProfileString(strSectionName, GRAPHS, strString, strFileName)

    strString = i_obForm.lstOutFieldsAvailable.List(1)

    For i = 2 To 8

        tempstrString = i_obForm.lstOutFieldsAvailable.List(i)
        strString = strString & strComma & tempstrString

    Next

    bReturn = WritePrivateProfileString(strSectionName, FIELDSAVAIL, strString,
strFileName)

End Function
```

```
' This function reads the values of the controls in the External conditions
' page from the simulation file
Private Function ReadExtCondPage(ByRef io_obForm As frmSimulation) As Boolean

    strSectionName = "External Conditions"

    If (ReadSection(strSectionName) = "") Then GoTo FnBreak_ReadExtCondPage

    If (ReadValue(strSectionName, LATI) <> "") Then
        io_obForm.mskExtLatitude.Text = ReadValue(strSectionName, LATI)
    End If

    If (ReadValue(strSectionName, LONGI) <> "") Then
        io_obForm.mskExtLongitude.Text = ReadValue(strSectionName, LONGI)
    End If

    If (ReadValue(strSectionName, SKY) <> "") Then
            io_obForm.cboExtSkyCondition.Text = ReadValue(strSectionName, SKY)
    End If

    If (ReadValue(strSectionName, TZ) <> "") Then
        io_obForm.cboExtTimeZone.Text = ReadValue(strSectionName, TZ)
    End If

    If (ReadValue(strSectionName, TSLEN) <> "") Then
        io_obForm.cboExtTimeStepLength.Text = ReadValue(strSectionName, TSLEN)
    End If

    If (ReadValue(strSectionName, SIMLEN) <> "") Then
        io_obForm.mskExtSimLength.Text = ReadValue(strSectionName, SIMLEN)
    End If

    If (ReadValue(strSectionName, SIMDATE) <> "") Then
        io_obForm.dtpExtSimDate.Value = ReadValue(strSectionName, SIMDATE)
    End If

    If (ReadValue(strSectionName, ST) <> "") Then
        io_obForm.dtpExtStartTime.Value = ReadValue(strSectionName, ST)
    End If

    ReadExtCondPage = False
    Exit Function

FnBreak_ReadExtCondPage:

     ReadExtCondPage = True
     Exit Function

End Function

' This function reads the values of the controls in the Internal conditions
' page from the simulation file
Private Function ReadIntCondPage(ByRef io_obForm As frmSimulation)

      Dim i As Integer

      strSectionName = "Internal Conditions"

      If (ReadValue(strSectionName, AVGDEPTH1) <> "") Then
            io_obForm.txtIntAvgDepth1.Text = ReadValue(strSectionName, AVGDEPTH1)
      End If

      If (ReadValue(strSectionName, AVGDEPTH2) <> "") Then
            io_obForm.txtIntAvgDepth2.Text = ReadValue(strSectionName, AVGDEPTH2)
      End If

      If (ReadValue(strSectionName, AVGDEPTH3) <> "") Then
            io_obForm.txtIntAvgDepth3.Text = ReadValue(strSectionName, AVGDEPTH3)
      End If

      If (ReadValue(strSectionName, AVGDEPTH4) <> "") Then
```

```
        io_obForm.txtIntAvgDepth4.Text = ReadValue(strSectionName, AVGDEPTH4)
  End If

  If (ReadValue(strSectionName, AVGDEPTH5) <> "") Then
        io_obForm.txtIntAvgDepth5.Text = ReadValue(strSectionName, AVGDEPTH5)
  End If

  If (ReadValue(strSectionName, AVGDEPTH6) <> "") Then
        io_obForm.txtIntAvgDepth6.Text = ReadValue(strSectionName, AVGDEPTH6)
  End If

  If (ReadValue(strSectionName, AVGDEPTH7) <> "") Then
        io_obForm.txtIntAvgDepth7.Text = ReadValue(strSectionName, AVGDEPTH7)
  End If

  If (ReadValue(strSectionName, TEMP1) <> "") Then
        io_obForm.txtIntMeanTemp1.Text = ReadValue(strSectionName, TEMP1)
  End If

  If (ReadValue(strSectionName, TEMP2) <> "") Then
        io_obForm.txtIntMeanTemp2.Text = ReadValue(strSectionName, TEMP2)
  End If

  If (ReadValue(strSectionName, TEMP3) <> "") Then
        io_obForm.txtIntMeanTemp3.Text = ReadValue(strSectionName, TEMP3)
  End If

  If (ReadValue(strSectionName, TEMP4) <> "") Then
        io_obForm.txtIntMeanTemp4.Text = ReadValue(strSectionName, TEMP4)
  End If

  If (ReadValue(strSectionName, TEMP5) <> "") Then
        io_obForm.txtIntMeanTemp5.Text = ReadValue(strSectionName, TEMP5)
  End If

  If (ReadValue(strSectionName, TEMP6) <> "") Then
        io_obForm.txtIntMeanTemp6.Text = ReadValue(strSectionName, TEMP6)
  End If

  If (ReadValue(strSectionName, TEMP7) <> "") Then
        io_obForm.txtIntMeanTemp7.Text = ReadValue(strSectionName, TEMP7)
  End If

  If (ReadValue(strSectionName, DEN1) <> "") Then
        io_obForm.txtIntDaphDensity1.Text = ReadValue(strSectionName, DEN1)
  End If

  If (ReadValue(strSectionName, DEN2) <> "") Then
        io_obForm.txtIntDaphDensity2.Text = ReadValue(strSectionName, DEN2)
  End If

  If (ReadValue(strSectionName, DEN3) <> "") Then
        io_obForm.txtIntDaphDensity3.Text = ReadValue(strSectionName, DEN3)
  End If

  If (ReadValue(strSectionName, DEN4) <> "") Then
        io_obForm.txtIntDaphDensity4.Text = ReadValue(strSectionName, DEN4)
  End If

  If (ReadValue(strSectionName, DEN5) <> "") Then
        io_obForm.txtIntDaphDensity5.Text = ReadValue(strSectionName, DEN5)
  End If

  If (ReadValue(strSectionName, DEN6) <> "") Then
        io_obForm.txtIntDaphDensity6.Text = ReadValue(strSectionName, DEN6)
  End If

  If (ReadValue(strSectionName, DEN7) <> "") Then
        io_obForm.txtIntDaphDensity7.Text = ReadValue(strSectionName, DEN7)
  End If
```

```
        If (ReadValue(strSectionName, SECCHIDEPTH) <> "") Then
              io_obForm.txtIntSecchiDepth.Text = ReadValue(strSectionName, SECCHIDEPTH)
        End If

  End Function

  ' This function reads the values of the controls in the Predator and Prey
  ' page from the simulation file
  Private Function ReadPredAndPreyPage(ByRef io_obForm As frmSimulation)

      strSectionName = "Predator and Prey"


      If (ReadValue(strSectionName, FISHMASS) <> "") Then
          io_obForm.txtPreFishMass.Text = ReadValue(strSectionName, FISHMASS)
      End If

      If (ReadValue(strSectionName, HANDLINGTIME) <> "") Then
          io_obForm.txtPreHandlingTime.Text = ReadValue(strSectionName, HANDLINGTIME)
      End If

      If (ReadValue(strSectionName, PREYLEN) <> "") Then
          io_obForm.txtPrePreyLength.Text = ReadValue(strSectionName, PREYLEN)
      End If

      If (ReadValue(strSectionName, INSTOM) <> "") Then
          io_obForm.txtPreInitialStomach.Text = ReadValue(strSectionName, INSTOM)
      End If

      strSectionName = "Migration Strategy"

      If (ReadValue(strSectionName, MSTIME1) <> "") Then
          io_obForm.dtpPreMSTime1 = ReadValue(strSectionName, MSTIME1)
      End If

      If (ReadValue(strSectionName, MSTIME2) <> "") Then
          io_obForm.dtpPreMSTime2 = ReadValue(strSectionName, MSTIME2)
      End If

      If (ReadValue(strSectionName, MSTIME3) <> "") Then
         io_obForm.dtpPreMSTime3 = ReadValue(strSectionName, MSTIME3)
      End If

      If (ReadValue(strSectionName, MSTIME4) <> "") Then
          io_obForm.dtpPreMSTime4 = ReadValue(strSectionName, MSTIME4)
      End If

      If (ReadValue(strSectionName, MSTIME5) <> "") Then
          io_obForm.dtpPreMSTime5 = ReadValue(strSectionName, MSTIME5)
      End If

      If (ReadValue(strSectionName, MSDEPTH1) <> "") Then
          io_obForm.txtPreMSDepth1.Text = ReadValue(strSectionName, MSDEPTH1)
      End If

      If (ReadValue(strSectionName, MSDEPTH2) <> "") Then
          io_obForm.txtPreMSDepth2.Text = ReadValue(strSectionName, MSDEPTH2)
      End If

      If (ReadValue(strSectionName, MSDEPTH3) <> "") Then
          io_obForm.txtPreMSDepth3.Text = ReadValue(strSectionName, MSDEPTH3)
      End If

      If (ReadValue(strSectionName, MSDEPTH4) <> "") Then
          io_obForm.txtPreMSDepth4.Text = ReadValue(strSectionName, MSDEPTH4)
      End If

      If (ReadValue(strSectionName, MSDEPTH5) <> "") Then
         io_obForm.txtPreMSDepth5.Text = ReadValue(strSectionName, MSDEPTH5)
      End If
```

```
    If (ReadValue(strSectionName, MSFEED1) <> "") Then
        io_obForm.chkPreMSFeeding1.Value = ReadValue(strSectionName, MSFEED1)
    End If

    If (ReadValue(strSectionName, MSFEED2) <> "") Then
        io_obForm.chkPreMSFeeding2.Value = ReadValue(strSectionName, MSFEED2)
    End If

    If (ReadValue(strSectionName, MSFEED3) <> "") Then
        io_obForm.chkPreMSFeeding3.Value = ReadValue(strSectionName, MSFEED3)
    End If

    If (ReadValue(strSectionName, MSFEED4) <> "") Then
        io_obForm.chkPreMSFeeding4.Value = ReadValue(strSectionName, MSFEED4)
    End If

    If (ReadValue(strSectionName, MSFEED5) <> "") Then
        io_obForm.chkPreMSFeeding5.Value = ReadValue(strSectionName, MSFEED5)
    End If


End Function

' This function reads the values of the controls in the Output
' page from the simulation file
Private Function ReadOutputPage(ByRef io_obForm As frmSimulation)

    strSectionName = "Output"

    If (ReadValue(strSectionName, SSHEET) <> "") Then
        io_obForm.txtOutSpreadSheet.Text = ReadValue(strSectionName, SSHEET)
    End If

End Function
Private Function ReadValue(ByVal i_strSectionName As String, _
                                      ByVal i_strKeyName As String) As String

    Dim lReturn As Long

    strDefault = ""
    strReturnedString = String(255, Chr$(0))

    lReturn = GetPrivateProfileString(i_strSectionName, i_strKeyName, strDefault, _
                                      strReturnedString, Len(strReturnedString), _
                                      strFileName)

    ReadValue = Left(strReturnedString, lReturn)

End Function
Private Function ReadSection(ByVal i_strSectionName As String) As String

    Dim lReturn As Long

    strReturnedString = String(255, Chr$(0))

    lReturn = GetPrivateProfileSection(i_strSectionName, strReturnedString,
Len(strReturnedString), _
                                        strFileName)
    If (lReturn = 0) Then

        ReadSection = ""
    Else
        ReadSection = strReturnedString
    End If

End Function
```

APPENDIX III

CALCULATING ZOOPLANKTON DENSITIES AND LENGTHS FOR MODEL INPUTS

1. *Daphnia* densities in Blue Mesa Reservoir, 2002 (Chapters 1 and 2)

Very few measurements have been made of *Daphnia pulex* densities below 30 m in Blue Mesa Reservoir, Colorado. Evidence indicates that *Daphnia* do exist in deeper waters, and that abundance may decline exponentially below the thermocline (Wissel and Ramacharan 2003). Average *D. pulex* densities sampled during the summer of 2002 are listed in Table III.1. To extrapolate *Daphnia* densities below 30 m during 2002, I calculated average zooplankton densities in the upper 30 m of the water column from 1994-1997 and 2002 (Johnson et al. 1997; Wise 1997; Johnson et al. 2002) (Table III.2). I then fit decaying power functions to the averaged data for June, July, and August (Figure III.1), and used these equations to extrapolate *Daphnia* densities from 30-60 m (Table III.1). Equation III.1 was used to calculate *Daphnia* densities (number/L) from 30-60 m in June 2002, Equation III.2 for July 2002, and Equation III.3 for August 2002. For each equation "Depth" refers to the maximum depth in the depth interval (e.g. Depth = 10 for the depth interval 5-10 m).

(Eq. III.1) $$\text{Density} = 219.23 \cdot \text{Depth}^{-1.6728} \qquad R^2 = 0.89$$

(Eq. III.2) $$\text{Density} = 212.29 \cdot \text{Depth}^{-1.6887} \qquad R^2 = 0.89$$

(Eq. III.3) $$\text{Density} = 1492.1 \cdot \text{Depth}^{-2.8693} \qquad R^2 = 0.83$$

2. Zooplankton densities for representative mesotrophic, eutrophic, and hypereutrophic lakes (Chapter 3)

Zooplankton densities for each of the lakes in Chapter 3 were calculated much the same way that they were in Chapter 1; the mesotrophic system in Chapter 3 is Blue Mesa Reservoir, and the *Daphnia* densities used in Chapter 3 are the same as in Chapter 1. I used Lake Mendota, Wisconsin, as the eutrophic system, and Lake Washington in Seattle as the hypereutrophic system.

Lake Mendota *Daphnia* densities were derived from twenty year averages; data was collected between 1976 and 1995, and were divided into *D. pulex* and *D. galeata* years (Lathrop et al. 1999). I used zooplankton averages from *D. galeata* years, as these were years with lower water clarity, higher algae abundance, and more representative of a eutrophic system. Average *D. galeata* densities were 15.9/L in June, 2.5/L in July, and 1.2/L in August. *Daphnia* densities were averaged over 20 m, the approximate depth of Lake Mendota, so I had to calculate the vertical distribution of *D. galeata* based on the average *Daphnia* density. Lathrop (1998) calculated the percentage of the *D. galeata* population distributed in 5 m depth intervals (Table III.3). Using these percentages and the average *Daphnia* density I calculated *Daphnia* densities for depths between 0 and 20 m (Table III.4).

Lake Mendota is not as deep as Blue Mesa Reservoir, but because I was not trying to model conditions in Lake Mendota per se, I needed to have zooplankton densities below 20 m. *Daphnia* densities for depths between 20 and 60 m were calculated in the same way as for Blue Mesa Reservoir; decaying power functions were fit to *Daphnia* densities by depth for each month (Figure III.2). Equation III.4 was used to calculate *Daphnia* densities (number/L) from 20-60 m for June, Equation III.5 for July, and Equation III.6 for August. For each equation "Depth" refers to the maximum depth in the depth interval (e.g. Depth = 10 for the depth interval 5-10 m). Extrapolated *Daphnia* densities below 20 m are also in Table III.4.

$$\text{(Eq. III.4)} \qquad \text{Density} = 3193.4 \cdot \text{Depth}^{-2.5092} \qquad R^2 = 0.71$$

$$\text{(Eq. III.5)} \qquad \text{Density} = 2704.8 \cdot \text{Depth}^{-3.4974} \qquad R^2 = 0.93$$

$$\text{(Eq. III.6)} \qquad \text{Density} = 425.2 \cdot \text{Depth}^{-2.8645} \qquad R^2 = 0.91$$

Zooplankton densities for Lake Washington, the representative hypereutrophic system, were calculated slightly differently. Raw data from the long-term monitoring database initiated by T. Edmondson was generously supplied by Dr. Daniel Schindler at the Department of Zoology, University of Washington, Seattle; and compiled by Jennifer Scheuerell, of the same lab. Zooplankton were collected at various depth intervals with a Clark-Bumpus sampler, and data resolution was by 10 m depth intervals instead of 5 m intervals (Table III.5). Furthermore, sockeye in Lake Washington consumed two main prey items in the 1960's: about 30% of their diet was the cladoceran *Diaphanosoma birgei*, and about 70% of their diet was the copepod *Epischura nevadensis* (Woodey 1972). I used data from 1963 in the hypereutrophic simulations because 1963 marked the height of eutrophication in Lake Washington.

Calculations for the Lake Washington 1963 zooplankton densities were slightly complicated because either few depth intervals were sampled (e.g., June 1963) or depth intervals overlapped (e.g., July and August 1963). For both *Epischura* and *Diaphanosoma*, the most data was collected in August. Because I had average zooplankton density values for 0-10, 0-20 and 0-40 m depth intervals, I could calculate the "unknown intervals" (i.e., 10-20, 20-30, and 30-40 m intervals). For example, the densities for each unknown interval were calculated the following way:

$$\text{“0-20”} = (\text{“0-10”} + \text{“10-20”}) / 2$$

$$\text{“10-20”} = (2 \cdot \text{“0-20”}) - \text{“0-10”}$$

$$\text{“0-40”} = (\text{“0-10”} + \text{“10-20”} + \text{“20-40”}) / 4$$

$$\text{“20-40”} = (4 \cdot \text{“0-40”}) - \text{“0-10”} - \text{“10-20”}$$

I first computed densities for unknown intervals for August (10-20, 20-30, and 30-40 m), and then for July (10-20 m). I only had one measurement for June, but I needed at least two depths so that I could fit a decaying power function to calculate densities for each depth. I averaged the proportional change in zooplankton densities between 0-10 and 10-20 m for July and August for each zooplankton species and used that proportional change to calculate the zooplankton density for the 10-20 m depth interval in June.

Finally, I fit decaying power functions for each date and zooplankter to calculate density as a function of depth. Equations III.7 through III.9 calculate *Epischura* density as a function of depth for June, July, and August 1963 respectively; equations III.10

through III.12 calculate *Diaphanosoma* density as a function of depth for June, July, and August 1963. For each equation "Depth" refers to the maximum depth in the depth interval (e.g. Depth = 10 for the depth interval 0-10 m). R^2 values were 1.0 because there are only two measured data points. Calculated densities of *Epischura* and *Diaphanosoma* are listed in Table III.6. Total zooplankton numbers used in the hypereutrophic scenarios are the sum of the copepod and cladoceran densities for each date.

(Eq. III.7) $$\text{Density} = 539.37 \cdot \text{Depth}^{-2.4871}$$

(Eq. III.8) $$\text{Density} = 67.805 \cdot \text{Depth}^{-1.7879}$$

(Eq. III.9) $$\text{Density} = 43.337 \cdot \text{Depth}^{-1.9794}$$

(Eq. III.10) $$\text{Density} = 4.439 \cdot \text{Depth}^{-1.3823}$$

(Eq. III.11) $$\text{Density} = 4094.3 \cdot \text{Depth}^{-2.7649}$$

(Eq. III.12) $$\text{Density} = 61.292 \cdot \text{Depth}^{-1.5685}$$

3. Zooplankton lengths and energy densities for representative eutrophic, and hypereutrophic lakes (Chapter 3)

Kokanee are size-selective planktivores when prey are abundant (Koski et al. 2003) and the size of *Daphnia* found in kokanee guts is greater than the average found in the environment (Stockwell et al. 1999; Stockwell and Johnson 1999). The foraging model uses prey size to calculate mass of food consumed, and transforms mass to energy using energy densities (cal/mg wet weight) for different zooplankton species. I multiplied the average length of *D. galeata* in Lake Mendota by a factor calculated from BMR data (Stockwell et al. 1999) to obtain the length of *Daphnia* that would be found in kokanee guts if they were feeding exclusively on *D. galeata* and selecting the largest prey. The average size of *Daphnia* consumed by kokanee in BMR was 1.84 mm, but the average size of *Daphnia* in the environment was 1.34 mm (Stockwell et al. 1999); thus, kokanee consumed *Daphnia* that were approximately 37% larger than the average *Daphnia*. The average length *D. galeata* in the environment was 0.953 mm (Dumont et al. 1975; Hawkins and Evans 1979). I increased this length by 37% to obtain the average size of *Daphnia* consumed by kokanee in eutrophic scenarios (1.31 mm).

Lake Washington contains sockeye salmon, which in the 1960's had a diet consisting of approximately 70% copepods (*Epischura nevadensis*) and 30% cladocerans (*Diaphanosoma birgei*) (Woodey 1972). This ratio was used to calculate the average size of prey consumed and prey energy density. The average length of *Epishura* found in age 0 sockeye stomachs in Lake Washington in 1975 was 1.97 mm (Eggers 1982). Based on *Daphnia* sizes in sockeye stomachs and the environment (Eggers 1982), I predicted that the average size of *Diaphanosoma* ingested would be approximately 1.52 mm, using average ambient *Diaphaonosoma* lengths from Eggers (1982). I transformed these lengths into wet weights using equations derived by Dumont et al. (1975). Using an energy density of 0.717 cal/mg (wet weight) for *Epischura* and 0.578 cal/mg (wet weight) for the cladoceran (Cummins and Wuycheck 1971), the average energy density of a prey item was 0.675 cal/mg (wet weight) (Table 3.1). I added *Epischura* and *Diaphanosoma* densities to get total prey densities for each depth interval sampled.

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Woodey, J. 1972. Distribution, feeding, and growth of juvenile sockeye salmon in Lake Washington. Ph.D. Dissertation. University of Washington, Seattle.

Table III.1. Sampled and calculated *Daphnia* densities (number/L) for Blue Mesa Reservoir during the summer of 2002. Italicized densities were calculated using equations III.1 through III.3. *Note that this depth interval is 15 m, instead of 5 m.

Depth Interval, m	June 8, 2002	July 12, 2002	August 8, 2002
0-5	13.3	11.2	6.7
5-10	6.2	8.4	7.4
10-15	11.1	2.7	1.8
15-30*	2.4	0.7	0.2
30-35	*0.57*	*0.52*	*0.06*
35-40	*0.46*	*0.42*	*0.04*
40-45	*0.38*	*0.34*	*0.03*
45-50	*0.32*	*0.29*	*0.02*
50-55	*0.27*	*0.24*	*0.02*
55-60	*0.23*	*0.21*	*0.01*

Table III.2. Average *Daphnia* densities (number/L) by month for 1994-1997 and 2002; standard deviations are in parentheses. *Note that this depth interval is 15 m, instead of 5 m.

Depth Interval, m	June	July	August
0-5	11.1 (4.4)	11.7 (2.04)	7.1 (2.18)
5-10	8.8 (2.68)	8.3 (2.93)	5.7 (1.28)
10-15	2.5 (3.83)	1.6 (0.77)	1.6 (0.96)
15-30*	0.9 (0.71)	0.9 (0.55)	0.1 (0.06)

Table III.3. Proportion of the *D. galeata* population that each depth strata contains (adapted from Figure 3-1 in Lathrop (1998))

Depth Interval, m	June 19, 1987	July 22, 1987	August 14, 1987
0-5	0.48	0.82	0.73
5-10	0.40	0.16	0.23
10-15	0.11	0.01	0.02
15-20	0.01	0.01	0.02

Table III.4. Sampled and calculated *D. galeata* densities (number/L) for a eutrophic system, based on data collected at Lake Mendota. Italicized densities were calculated using equations III.4 through III.6.

Depth Interval, m	June	July	August
0-5	30.53	8.20	3.50
5-10	25.44	1.60	1.10
10-15	7.00	0.10	0.10
15-20	0.64	0.10	0.10
20-25	*0.99*	*0.03*	*0.04*
25-30	*0.63*	*0.02*	*0.02*
30-35	*0.43*	*0.01*	*0.02*
35-40	*0.31*	*0.01*	*0.01*
40-45	*0.23*	*0*	*0.01*
45-50	*0.17*	*0*	*0.01*
50-55	*0.14*	*0*	*0*
55-60	*0.11*	*0*	*0*

Table III.5. Raw data from Lake Washington, sampled during 1963. Zooplankton densities are in number/L. All samples were taken from the Madison Park sampling station, over the deepest part of the lake; each density is the average value from nets 10 and 20. *Epischura* measurements include adult male and females and immature copepodites. *Diaphanosoma* measurements are of total females (mature and immature).

	Epischura			*Diaphanosoma*		
Tow Depths, m	6/14/63	7/1/63	8/16/63	6/14/63	7/1/63	8/16/63
0-20	1.035			1.590		
0-10		1.105			7.035	
10-20		0.320			1.025	
0-10			0.715			1.345
0-20			0.280			1.175
0-40			0.215			0.685

Table III.6. Raw and calculated data from Lake Washington, sampled during 1963. Italicized numbers were calculated using equations III.13 through III.18. Zooplankton densities are in number/L. All samples were taken from the Madison Park sampling station, over the deepest part of the lake; each density is the average value from nets 10 and 20. *Epischura* measurements include adult male and females and immature copepodites. *Diaphanosoma* measurements are of total females (mature and immature). *Indicates June values for the 10-20 m depth interval that were calculated using July and August's averaged proportional changes from 0-10 and 10-20 m intervals.

	Epischura			*Diaphanosoma*		
Depth Interval, m	6/14/63	7/1/63	8/16/63	6/14/63	7/1/63	8/16/63
0-10	1.76	1.11	0.72	2.20	7.04	1.35
10-20	0.31*	0.32	0.05	0.98*	1.04	1.01
20-30	*0.11*	*0.16*	0.05	*0.49*	*0.34*	0.20
30-40	*0.06*	*0.09*	0.05	*0.33*	*0.15*	0.20
40-50	*0.03*	*0.06*	*0.02*	*0.24*	*0.08*	*0.13*
50-60	*0.02*	*0.05*	*0.01*	*0.19*	*0.05*	*0.10*

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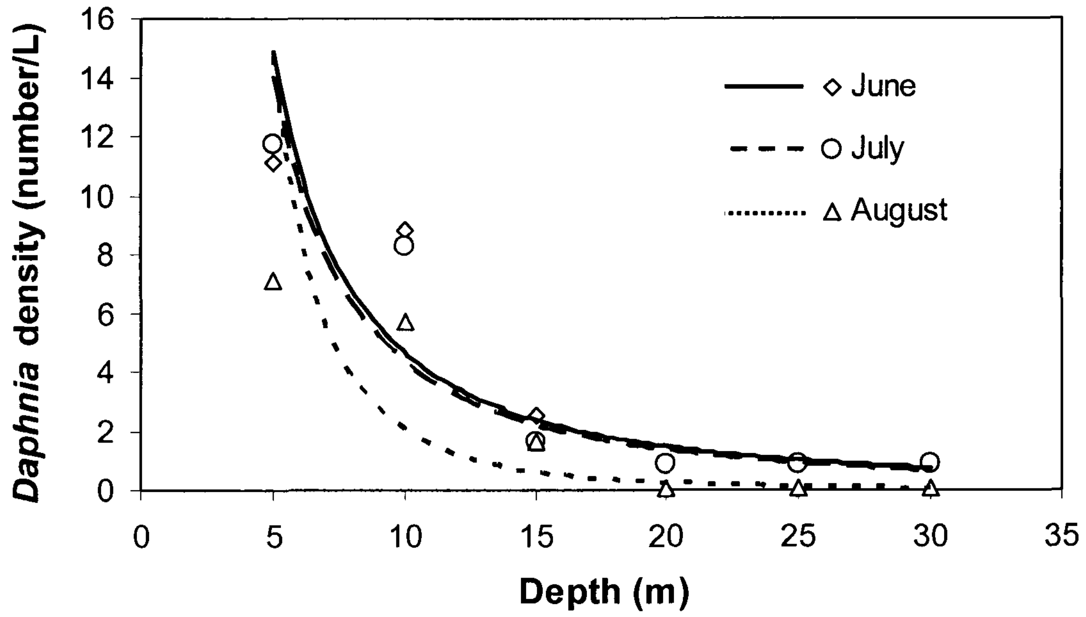

Daphnia density (number/L)
16
14
12
10
8
6
4
2
0
0
5
10
15
20
25
30
35
Depth (m)
◇ June
○ July
△ August

Figure III.1

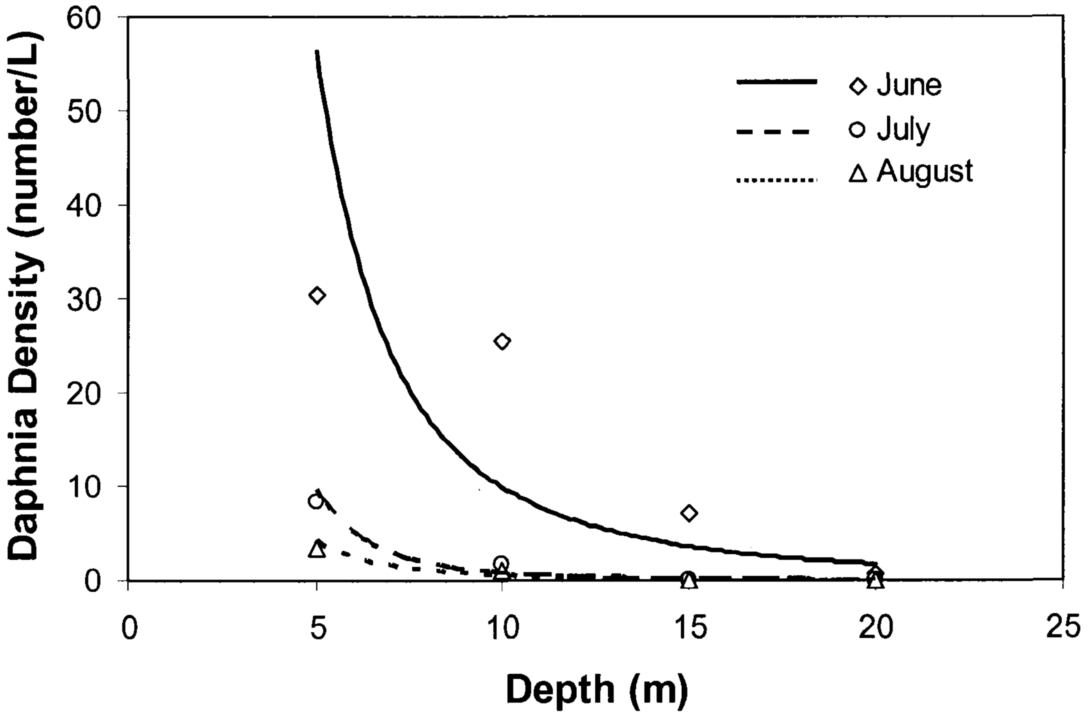
Daphnia Density (number/L)
0
10
20
30
40
50
60
0
5
10
15
20
25
Depth (m)
◇ June
○ July
△ August

Figure III.2

APPENDIX IV

SENSITIVITY ANALYSIS FOR AN IMPROVED FUNCTIONAL RESPONSE OF KOKANEE FEEDING ON *DAPHNIA*

I performed a sensitivity analysis on the parameters in the two functional response equations, X, β_0, and β_1, by calculating 10% upper and lower bounds for each parameter. The resulting ± 10% parameter values yielded equations that approximated the 90% confidence intervals of the functional response equations developed by Koski and Johnson (2002). I then executed the baseline simulations from Chapter 1 using the bioenergetics model and the parameter values that created the largest change in the functional response (that is, using the -10% value for β_0 with the +10% value for β_1, and vice-versa, and ±10% the original value of *X*). I performed this sensitivity analysis for the three sampling dates that reflected changes in temperature profiles, water clarity, and zooplankton abundance. Sensitivity analyses for the other parameters in the bioenergetics model have been addressed in Kitchell et al. (1977), Bartell et al. (1986), and Stockwell and Johnson (1997).

Calculated daily growth increments for kokanee are much more sensitive to changes in the Type II functional response parameters than to changes in the Type I functional response. This is because fish utilize the Type I functional response during periods of low light levels, which occur when light level changes as a result of the sun rising or setting, or from a vertical migration. These times are temporary, and the fish spends more time feeding under Type II conditions than Type I conditions in the baseline simulations. Figures IV.1 and IV.2 show the maximum change in the functional response when the parameters X, β_0, and β_1 were varied by ± 10%. For the June 5 sensitivity analysis simulations, a ± 10% change in the slope of the Type I functional response resulted in a ± 5-6% change in daily incremental growth; however, when β_0 and β_1 where changed by ± 10% (in a combination to yield the greatest change in the functional response curve) daily fish growth rate varied by ± 15-18% (Table IV.1). For the July 10 sensitivity analysis simulations, daily incremental growth changed by less than one percent with a ± 10% change in the slope of the Type I functional response; however, when β_0 and β_1 where changed by ± 10% daily fish growth rate changed by up to 30% (Table IV.2). For the August 6 sensitivity analysis simulations, daily incremental growth changed by 1-2% with a ± 10% change in the slope of the Type I functional response; when β_0 and β_1 where changed by ± 10% daily fish growth rate changed by up to approximately 30% (Table IV.3).

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Table IV.1. Maximum changes in daily growth increment for ± 10% changes in X, β_0, and β_1 in the Type I and Type II functional response parameters for the June 5, 2002 baseline simulation. The first value listed for each parameter combination is the simulated growth increment (g), followed by the percent change from the baseline simulation run with no change in any of the parameter values.

		Type II parameters, β_0 and β_1		
		-10% β_0 and +10% β_1	Mean β_0 and β_1	+10% β_0 and -10% β_1
Type I parameter, X	-10% X	0.063 (-19.23%)	0.074 (-5.13%)	0.088 (12.82%)
	Mean X	0.067 (-14.10%)	0.078 (0.0%)	0.092 (17.95%)
	+10% X	0.071 (-8.97%)	0.083 (6.41%)	0.097 (24.36%)

Table IV.2. Maximum changes in daily growth increment for ± 10% changes in X, β_0, and β_1 in the Type I and Type II functional response parameters for the July 10, 2002 baseline simulation. The first value listed for each parameter combination is the simulated growth increment (g), followed by the percent change from the baseline simulation run with no change in any of the parameter values.

		Type II parameters, β_0 and β_1		
		-10% β_0 and +10% β_1	Mean β_0 and β_1	+10% β_0 and -10% β_1
Type I parameter, X	-10% X	0.116 (-25.64%)	0.155 (-0.64%)	0.203 (30.13%)
	Mean X	0.117 (-25.00%)	0.156 (0%)	0.204 (30.77%)
	+10% X	0.118 (-24.36%)	0.157 (0.64%)	0.204 (30.77%)

Table IV.3. Maximum changes in daily growth increment for ± 10% changes in X, β_0, and β_1 in the Type I and Type II functional response parameters for the August 6, 2002 baseline simulation. The first value listed for each parameter combination is the simulated growth increment (g), followed by the percent change from the baseline simulation run with no change in any of the parameter values.

		Type II parameters, β_0 and β_1		
		-10% β_0 and +10% β_1	Mean β_0 and β_1	+10% β_0 and -10% β_1
Type I parameter, X	-10% X	0.178 (-25.52%)	0.237 (-0.84%)	0.309 (29.29%)
	Mean X	0.181 (-24.27%)	0.239 (0%)	0.311 (30.13%)
	+10% X	0.183 (-23.42%)	0.242 (1.26%)	0.313 (30.96%)

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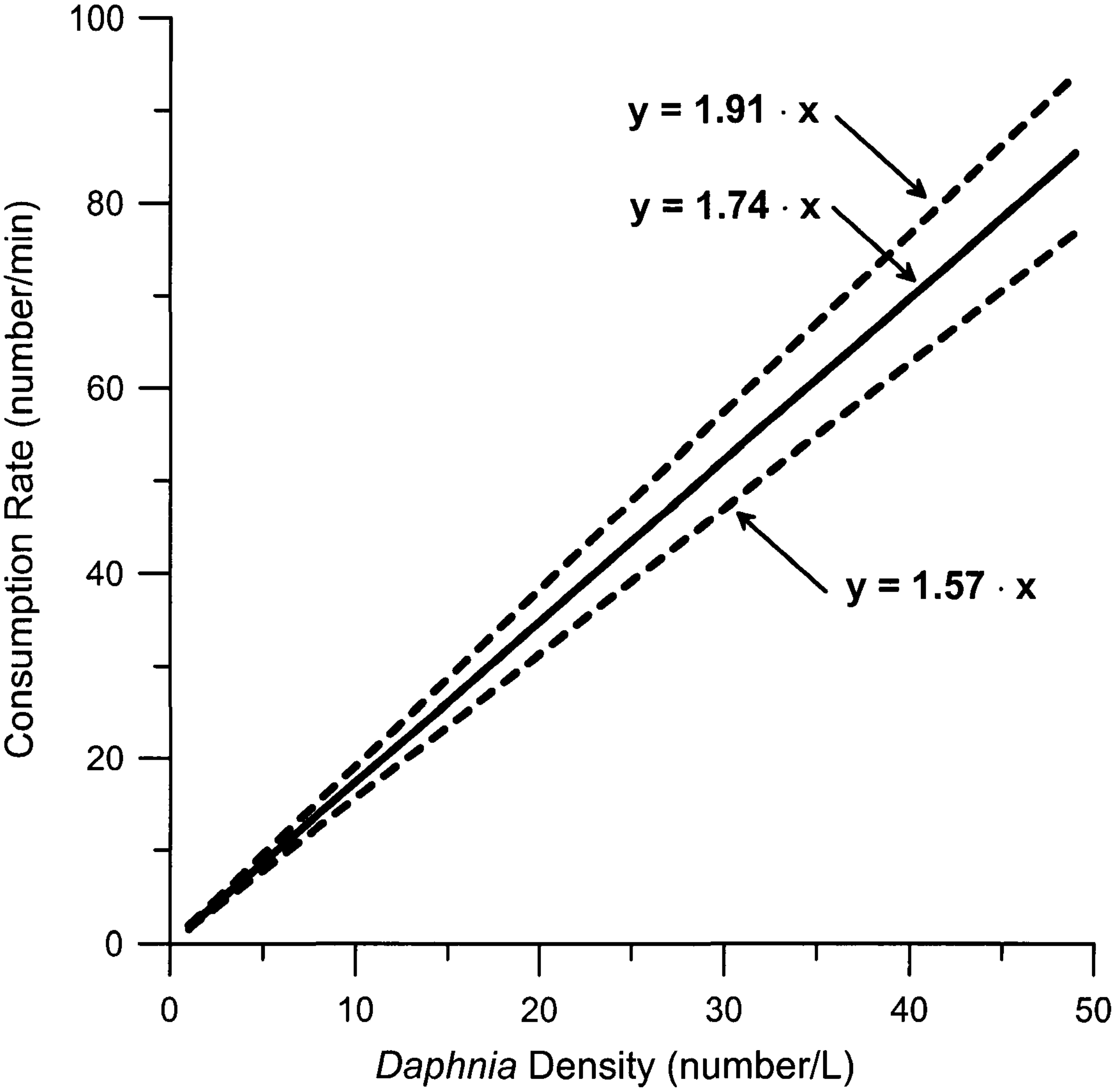
100
80
60
40
20
0
Consumption Rate (number/min)
0
10
20
30
40
50
Daphnia Density (number/L)
y = 1.91 · x
y = 1.74 · x
y = 1.57 · x

Figure IV.1

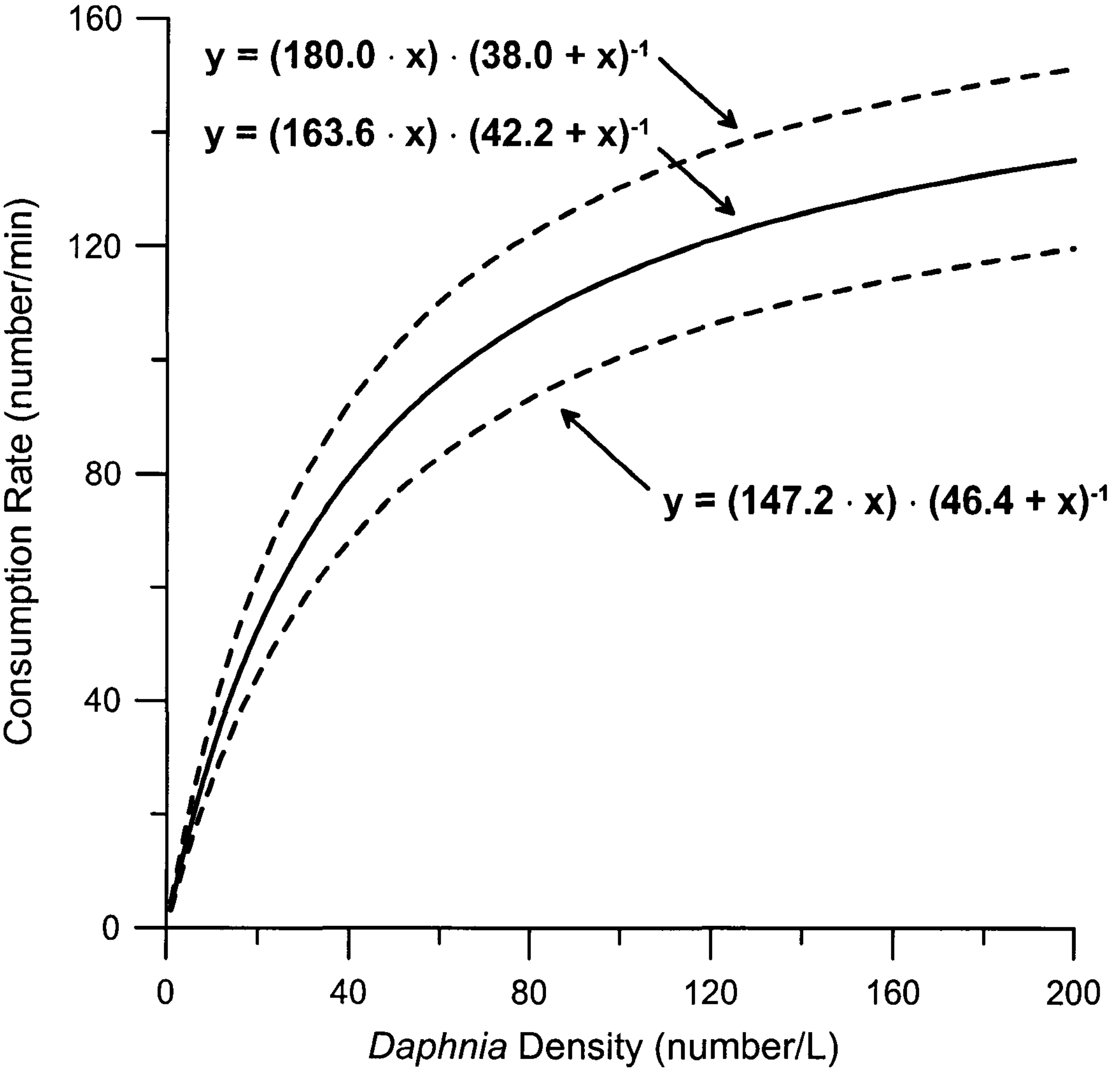
160
120
80
40
0
0
40
80
120
160
200
Consumption Rate (number/min)
Daphnia Density (number/L)
y = (180.0 · x) · (38.0 + x)-1
y = (163.6 · x) · (42.2 + x)-1
y = (147.2 · x) · (46.4 + x)-1

Figure IV.2