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Habitat Selection by Kokanee Salmon and Smallmouth Bass in Thermally Heterogeneous Environments: The Importance of Growth Maximization to Diel Habitat Shifts

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HABITAT SELECTION BY KOKANEE SALMON AND SMALLMOUTH BASS IN THERMALLY HETEROGENEOUS ENVIRONMENTS: THE IMPORTANCE OF GROWTH MAXIMIZATION TO DIEL HABITAT SHIFTS[1]

M.S. Bevelhimer, S.M. Adams, and L.J. Gross[2]

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[1]Submitted as a thesis by M.S. Bevelhimer to the Graduate Council of The University of Tennessee in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Diel habitat shifts consisting of vertical or horizontal movements are common in both marine and freshwater fishes. Hypotheses proposed to explain this behavior include maximizing food consumption, minimizing risk of predation, and maximizing bioenergetic efficiency. The bioenergetic hypothesis is often considered under conditions of thermal heterogeneity within the environment. The general objective of this study was to evaluate the importance of bioenergetic efficiency (i.e., maximization of net energy assimilation) as an influence on habitat selection and diel habitat shifts of two fishes.

The vertical distribution and movement patterns of the planktivorous kokanee salmon (*Oncorhynchus nerka*) were monitored in Nantahala Lake, North Carolina, with vertical gill nets and hydroacoustics surveys. The hydroacoustics surveys indicated only limited movement (about 8 m) by adults on one occasion, but a substantial vertical migration (up to 45 m) for juveniles at another time. A bioenergetics model was developed to simulate diel vertical migrations by kokanee to examine the energetic advantages and consequences of different migratory strategies. The model demonstrated that vertical migrations can be energetically advantageous when a predator and its prey are thermally segregated. The model also predicts ontogenetic and seasonal differences in the optimal migration strategy.

The daily movement patterns of adult smallmouth bass (*Micropterus dolomieu*) were monitored in Melton Hill Reservoir,

Tennessee, with temperature-sensitive ultrasonic transmitters so that habitat selection and daily movements could be determined with regard to temperature, depth, and nearness to shore and physical structure. The expected offshore migrations were not evident in the tracked fish, and a high affinity for nearshore cover was observed even when temperatures exceeded preferred levels. Based on the field observations, laboratory experiments with a thermal gradient tank were designed to evaluate the relative importance of temperature, food availability, and cover on habitat section by smallmouth bass. Both food and cover affected the habitat selection of the fish within the thermal gradient, and cover was often selected with apparent disregard for bioenergetic efficiency. These results demonstrate the importance of bioenergetic efficiency to daily movements under certain conditions, but also demonstrate that several factors can have a simultaneous effect on diel habitat shifts.

CHAPTER I

DAILY HABITAT SHIFTS IN FISHES

Diel habitat shifts of fishes are common in both marine and freshwater systems. In order to make accurate estimates of population size and to understand species interactions an understanding of these daily migration patterns is necessary. In most cases, movement involves leaving one habitat for another around dusk and then returning around dawn, resulting in a day/night utilization pattern of two different habitats. The spatial pattern of these movements is generally vertical (shallow to deep) or horizontal (inshore to offshore), although in some cases vertical movements might contain a slight horizontal component and vice versa. Some fish migrate vertically up to 600 m in a day (Carey and Robison 1981), and others have been reported to move horizontally up to 2-3 km (DeMartini et al. 1985), though the average range of daily migrations is normally less than these extremes. Habitat shifts representing all temporal-spatial combinations (offshore, inshore, shallow, and deep by night or day) have been reported and representative studies are listed in Table I-1. Habitat shifts among more than two habitats in a day are rare but have been reported by Narver (1970) and Begg (1976) who observed fish in deep water during the day, at the surface at dusk, partially descending during the night, and back at the surface at dawn for a short time before returning to deep water.

Table I-1. Summary of reported occurrences of diel migrations. Feeding activity was categorized as D=diurnal, N=nocturnal, C=crepuscular, A=throughout the 24-h day, or U=unknown. A list of scientific names of fishes used in this work is found in Table I-3.

Movement Pattern	Species (source)	Feeding Pattern
Shallow by day - deep by night	Kokanee salmon (Northcote et al. 1964)	U
Deep by day - shallow by night	Sculpin (Wurtsbaugh and Neverman 1988)	D
	Alewife (Janssen and Brandt 1980)	N
	Sardine (Begg 1976)	N
	Vendace and smelt (Dembinski 1971)	C
	Vendace (Hamrin 1986; Munk et al. 1989)	N
	Sockeye salmon (Narver 1970; Eggers 1978)	C
	Peamouth chub (Northcote et al. 1964)	A
	Swordfish (Carey and Robinson 1981)	U
Offshore by day - inshore by night	Tidewater silverside (Wurtsbaugh and Li 1985)	D[1]
	Bluegill (Bauman and Kitchell 1974)	D
	Troutperch (Emery 1973)	D
Inshore by day - offshore by night	Northern redbelly dace (Naud and Magnan 1988)	A
	Queenfish (DeMartini et al. 1985)	N
	Golden shiner (Hall et al. 1979)	N
	Roach, rudd, bream, and bleak (Bohl 1980)	N
	Mimic shiner and smallmouth bass (Helfman 1981)	D
	Smallmouth bass (Emery 1973)	D

[1]When not feeding during the day returned to nearshore.

The variation in daily migration patterns described in Table I-1 is represented by a wide range of sizes and ages of fish. Within a single species, variation in migration patterns among different sizes and ages might also be expected considering the size-related differences in food and habitat requirements found in many species. DeMartini et al. (1985) found such size-related differences in queenfish migrations. In addition to the effects of size and age, one might also expect to find differences in daily migration patterns due to differences in foraging types (i.e., piscivore versus planktivore). Piscivores generally consume a few large prey per day while planktivores consume many relatively small prey per day. These differences between piscivore and planktivore foraging probably result in differences in the migration strategies (time of day, duration, and locality) between these two foraging types.

Much of the early work on the vertical migration of aquatic organisms was performed on zooplankton. Many of the ideas and theories on the diel migration of fishes have been borrowed from these studies and modified for fish. McLaren (1963) provided a good review of this information. More recent studies of zooplankton diel migrations that are pertinent to this study include Swift (1976), Enright (1977), Enright and Honegger (1977), Orcutt and Porter (1983), and Stich and Lampert (1984).

Activity patterns that accompany these habitat shifts are normally either diurnal, nocturnal, or crepuscular, but do not always coincide precisely with the habitat shifts. That is, a fish may reside in the habitat where food is located for 12 hours of the day

but actual feeding may be accomplished in the first few hours, after which time activity decreases.

The primary cue for the timing of these diel shifts has most often been attributed to light intensity (Blaxter 1974; Bohl 1980). Diel migration of food organisms has been proposed as the cue in other situations (Dembinski 1971; Janssen and Brandt 1980). Even in these cases light has an indirect effect in that it probably cues the movement of the food organisms. Temperature has been described as the cue for the fish movements in small desert pools where noticeable temperature changes occur daily at the surface and nearshore (Barlow 1958). As the nearshore temperatures rise, they become physiologically sub-optimal. In this case temperature is not only a cue, but also a physiological stimulus.

Although light and sometimes food have been identified as the primary cues for diel migrations, they are not necessarily the underlying reason for such movement patterns. Several hypotheses have been suggested for diel migration of aquatic organisms. Baumann and Kitchell (1974), Hall et al. (1979), Bohl (1980), and Munk et al. (1989) proposed that daily migrations from one habitat to another permit fish to maximize food consumption by moving to areas where food density and/or capture rates are highest. Stich and Lampert (1981) and Clark and Levy (1988) proposed that predator avoidance controlled diel migrations in the systems they studied. The presence of predators forced potential prey to reside at depths where daytime light intensity was low enough to appreciably decrease the probability of predation. McLaren (1963), Brett (1971a), and Enright

(1977) argued that diel habitat shifts are a means of energetic efficiency via thermoregulation. This last hypothesis states that organisms move to deeper, colder water after feeding to achieve more efficient assimilation of consumed food as a result of reduced metabolic rates at lower temperature. Evidence to support this view comes from several laboratory studies which suggest that increased growth can be achieved by fish experiencing cyclic temperature regimes as opposed to those maintained at constant temperatures (Hokanson et al. 1977; Biette and Geen 1980; Cox and Coutant 1981; Diana 1984; Konstantinov and Zdanovich 1987). An additional explanation of diel habitat shifts was reported by Dembinski (1971) who found that spawning behavior was partly responsible for daily inshore migrations that he observed. Naud and Magnan (1988) suggested that a combination of factors, both food consumption and predator avoidance, was responsible for diel migrations that they observed.

The above hypotheses all have merit, but do not directly address the underlying reason for diel habitat shifts which I argue is a relatively simple one. By spending time in two habitats, a fish is able to satisfy more of its basic needs (food, protection, reproduction, etc.) than if it were to remain in a single habitat throughout the day. Satisfying all basic needs to the highest level possible translates to maximum reproductive fitness. The potential adaptive advantages of diel habitat shifts can be summarized into four major habitat "selection strategies" which incorporate those hypotheses mentioned above. These four selection strategies are:

1) to maximize growth, 2) to maximize reproductive success, 3) to minimize mortality due to predation, and 4) to minimize chronic or lethal exposure to abiotic environmental factors.

Growth maximization can be achieved by maximizing food intake and/or minimizing energetic costs, such as those related to activity, food capture, and metabolism. Reproductive success is dependent on mate selection, nest site selection, parental care, egg viability, and other factors. Minimizing predation entails the development of behavioral or physical characteristics that reduce the probability of being captured by a predator. Predator avoidance behaviors include moving to habitats devoid of predators, limiting activity to times of the day when predators are absent or inactive, and schooling with conspecifics. Minimizing exposure to harmful abiotic factors includes avoiding habitats where temperature exceeds a critical maximum or dissolved oxygen falls below a critical minimum. Whereas it is useful to discuss these selection strategies as separate entities they are not totally independent. Similar discussions of proposed hypotheses regarding the adaptive significance of diel habitat shifts are found in McLaren (1963), Enright (1977), and Clark and Levy (1988).

Each of these four selection strategies is affected by a different suite of habitat variables (Table I-2), though the effects of many variables are included in more than one strategy. A single habitat is normally affected by variables associated with all of these selection strategies. The choice of a habitat, or the choice

Table I-2. Common variables of aquatic habitats listed by habitat selection strategy.

Maximize growth	Maximize reproductive success	Minimize predation	Minimize lethal exposure
Cover	Cover	Cover	pH
Depth	Depth	Depth	Oxygen
Temperature	Temperature	Light	Temperature
Light	Substrate	Predators	Depth
Oxygen	Oxygen		
Competitors	Competitors		
Food	Mates		
	Nest sites		

to use two habitats, is based on the differences in the suite of variables that compose each available habitat.

The mechanism by which a fish chooses one habitat (or a combination of habitats) over another is not well understood, but several hypotheses can be generated. The simplest is that habitat selection is based on a priority for a single variable such as temperature or food. This single-variable approach has been used with regarded to temperature in studies on thermoregulation based on optimal temperature preference (Brandt et al. 1980; Coutant and Carroll 1980) and with regarded to food in studies of food patch selection based on optimal foraging theory (for reviews see Pyke 1984 and Gross 1986). With this single variable approach, the effect of other variables is considered to be constant among habitats or is simply ignored.

The single variable hypothesis can be extended to include other variables in some hierarchy of importance. For example, first consideration in habitat selection might be based on temperature, then food, then dissolved oxygen, etc. This type of approach was used for striped bass (see Table I-3 for the common and scientific names of all fishes cited in this dissertation) by Coutant (1986).

Analogous to the single variable approach is habitat choice based on satisfying the requirements of one of the selection strategies. For example, a habitat may be selected based only on its potential for maximum growth. The single strategy approach can also be expanded to include the other strategies in some hierarchy of importance. For example, first consideration might be for growth

Table I-3. Common and scientific names of all fish species mentioned in this dissertation.

Common name	Scientific name
Alewife	*Alosa pseudoharengus*
Atlantic salmon	*Salmo salar*
Bleak	*Alburnus alburnus*
Bluegill	*Lepomis macrochirus*
Bream	*Abramis brama*
Brook trout	*Salvelinus fontinalis*
Channel catfish	*Ictalurus punctatus*
Desert pupfish	*Cyprinodon nevadensis*
Fathead minnow	*Pimephales promelas*
Golden shiner	*Notemigonus crysoleucas*
Kokanee salmon	*Oncorhynchus nerka*
Lake charr	*Salvelinus namaycush*
Largemouth bass	*Micropterus salmoides*
Mimic shiner	*Notropis volucellus*
Northern redbelly dace	*Phoxxinus eos*
Peamouth chub	*Mylocheilus caurinus*
Queenfish	*Seriphus politus*
Rainbow trout	*Oncorhynchus mykiss*
Redbreast sunfish	*Lepomis auratus*
Roach	*Rutilus rutilus*
Rock bass	*Ambloplites rupestris*
Rudd	*Scardinius erythrophtalamus*
Sardine	*Limnothrissa miodon*
Sculpin	*Cottus extensus*
Smallmouth bass	*Micropterus dolomieu*
Smelt	*Osmerus eperlanus*
Sockeye salmon	*Oncorhynchus nerka*
Striped bass	*Morone saxatilis*
Tidewater silverside	*Menidia beryllina*
Troutperch	*Percopsis omiscomaycus*
Vendace	*Coregonus albula*
Walleye	*Stizostedion vitreum vitreum*
White crappie	*Pomoxis annularis*
White sucker	*Catostomus commersoni*
Yellow perch	*Perca flavescens*

maximization, then predator avoidance, then spawning requirements. Handling the analysis of all of these strategies concurrently either involves setting up a single currency (McNamara and Houston 1986), doing vector optimization (Mesterton-Gibbons 1988), or using statistical decision theory (Mangel and Clark 1986).

A more complex mechanism for habitat selection would be based on some overall value or worth of a habitat based on all variables considered simultaneously. Whereas such a mechanism seems theoretically most advantageous, its complexity may make it less likely to occur in reality.

Of the studies on diel habitat shifts, the most useful for the research reported here are those that discuss habitat selection in terms of its adaptive significance (Brett 1971a; Clark and Levy 1988). These studies typically begin by promoting the importance of one strategy (such as predator avoidance) while minimizing the importance of another (such as growth maximization) and then briefly conclude that in reality more than one of these major influences are probably involved in habitat selection.

Not only are more than one of the selective strategies operating at a time, but the relative importance of the different strategies is probably not fixed or constant. Because of daily and seasonal changes in the habitats themselves and ontogenetic and size-related changes in a fish's requirements, the relative importance of the selection strategies should have a strong temporal component. For example, for many fishes, spawning requirements are very important at certain times of the year and of little or no importance at other

times. For juvenile fish the habitat selection pressure of spawning is non-existent altogether. Likewise, for many adult fishes, the threat of mortality due to predation is negligible thus minimizing the pressures of predator avoidance. Such ontogenetic changes in diel migrations were noted by DeMartini et al. (1985) who found that the adult fish they studied migrated further offshore at night than did the juveniles.

To better understand the underlying mechanisms of diel habitat shifts with particular emphasis on the energetic costs and benefits, I designed a study with a research approach that integrated field observation, laboratory experimentation, and computer simulation. The major objectives of this study were:

1) to determine the extent of diel habitat shifts in two fishes, the kokanee salmon and the smallmouth bass, with particular reference to temperature differences among habitats,

2) to evaluate the importance of the growth maximization strategy by comparing diel migration predictions of a bioenergetics model with the observed migration patterns in the field, and

3) to determine the relative importance of a few key habitat variables to better understand the relative importance of the selection strategies with which those variables are associated.

To accomplish these objectives, the vertical distribution and movement patterns of kokanee salmon in Nantahala Lake, North Carolina, were monitored with vertical gill nets and hydroacoustic surveys. The vertical distribution and densities of the zooplankton (the primary prey of kokanee) as well as temperature profiles were

also determined. A bioenergetics model was developed to simulate diel vertical migrations by the fish to predict the energetic advantages of different migratory strategies. These predictions were tested against the results of the hydroacoustics survey. This study comprises Chapter II.

In the second part of the study, the daily movement patterns of smallmouth bass in Melton Hill Reservoir, Tennessee, were monitored with underwater telemetry. Adult smallmouth bass were implanted with temperature-sensitive ultrasonic transmitters so that natural movements with regard to temperature, depth, and nearness to shore and physical structure could be determined. Based on the field observations, laboratory experiments were designed to evaluate the relative importance of three habitat variables to habitat selection. An electronically-monitored thermal gradient tank was used to contrast the effects of temperature, food availability, and cover on habitat section by smallmouth bass. This study comprises the third chapter.

The final chapter (IV) summarizes the two studies and uses the conclusions of each to discuss in broader terms the ecological adaptiveness of diel habitat shifts in aquatic organisms. A discussion of the differences in migration strategies between two fishes of different foraging types, a planktivore and a piscivore, is also included.

CHAPTER II

A BIOENERGETICS ANALYSIS OF DIEL VERTICAL MIGRATIONS OF KOKANEE SALMON IN NANTAHALA LAKE, NORTH CAROLINA

INTRODUCTION

Diel vertical migration has been observed and extensively studied in sockeye salmon (Narver 1970; Brett 1971a; Eggers 1978; Clark and Levy 1988; Levy 1989) and in the landlocked variety of this species, kokanee salmon (Northcote et al. 1964). Proposed explanations of this behavior for juvenile sockeye include predator avoidance (Eggers 1978; Clark and Levy 1988) and bioenergetic efficiency (Brett 1971a).

The bioenergetics hypothesis, first proposed for zooplankton by McLaren (1963) and then for fish by Brett (1971a), states that vertical migration of aquatic organisms through a wide range of temperatures can serve to maximize food consumption and minimize metabolic costs, thereby maximizing growth. The environmental conditions that would produce such movements according to this hypothesis are a spatial separation between preferred food densities and preferred thermal habitat.

Nantahala Lake in western North Carolina provides an ideal situation to examine this phenomenon and test the bioenergetics hypothesis. The forager of interest, the kokanee salmon, is an introduced cold-water planktivore. Nantahala Lake is characterized by a wide range of well-oxygenated thermal habitats with summer surface temperatures exceeding those normally experienced by this fish in the Pacific northwest. In summer, large zooplankton, the primary food of

kokanee (Northcote and Lorz 1966; Cordone et al. 1971; Richards et al. 1975; Doble and Eggers 1978; Schneidervin and Hubert 1987), are concentrated in the upper portion of the water column where temperatures are typically higher than the physiologically optimal temperature (15°C) of this species (Brett 1971a) (Figure II-1).

Most of the previous work on the vertical migration of this species has been done with juvenile sockeye salmon in nursery lakes before their oceanic migration (Narver 1970; Brett 1971a; Levy 1989). The most common summer migratory pattern described in these studies is a rapid ascent to the surface at dusk from depths of 30-50 m followed by a 5-15 m descent at night to the thermocline. At dawn the salmon return to the surface briefly and then descend to 30-50 m where they reside throughout the day. The exact depths vary from system to system. Feeding occurs mainly during the dusk and dawn movements to the surface (Narver 1970). Occasional exceptions to this general pattern have been observed. Levy (1989) noted that in two lakes juvenile sockeye were at the surface during the day and at greater depths at night. Vertical migrations at seasons other than summer, when thermal stratification is less pronounced, are of lesser magnitude or absent altogether (Narver 1970). The vertical migration of adult sockeye at sea is not as well documented, although Pearcy et al. (1984) reported increased catches of adults at the surface at night. Less is known about the vertical migration of the landlocked kokanee salmon. Northcote et al. (1964) reported that adult kokanee were in the upper portion of the water column during the day and at greater depths at night. No information was found in the literature pertaining to juvenile migration.

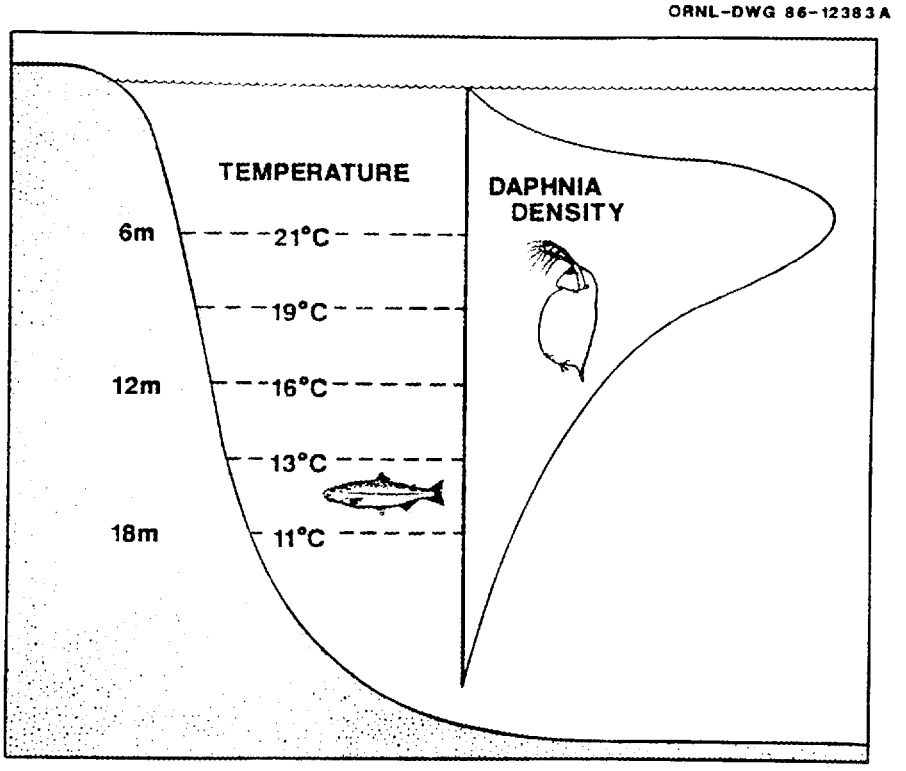

Figure II-1. Typical early summer distributions of kokanee salmon, zooplankton, and temperature in Nantahala Lake.

In order to evaluate the importance of growth maximization as a contributing factor to vertical migration, the effects of predator avoidance and reproduction must be taken into account. The effect of predator avoidance was minimized by concentrating on adult kokanee (> 300 mm), whose risk of predation in Nantahala Lake is negligible. It is unlikely that the large piscivores in this system (largemouth bass, walleye, and channel catfish) would regularly consume fish larger than 250 mm. To minimize the effects of spawning, which occurs around the second week of October in this population of kokanee, most of the sampling was performed from May to August.

The objectives of this study were: (1) to document the depth distribution and vertical migration of adult kokanee in relation to their prey and to the temperature profile, and (2) to use a bioenergetics model along with actual data on prey and temperature distributions to predict the expected vertical migration patterns (with regards to depths utilized) based on those patterns that maximize growth.

METHODS

Lake Description

Kokanee salmon were sampled in Nantahala Lake (Macon County, NC) from 1985 to 1988 (Figure II-2). Nantahala Lake, located in the southern Appalachian Mountains of western North Carolina at an elevation of 918 m, was impounded in 1942 for the main purpose of hydroelectric generation. The watershed of the lake is composed mainly of national forest land. Total surface area is 650 ha, maximum depth is 69 m, and

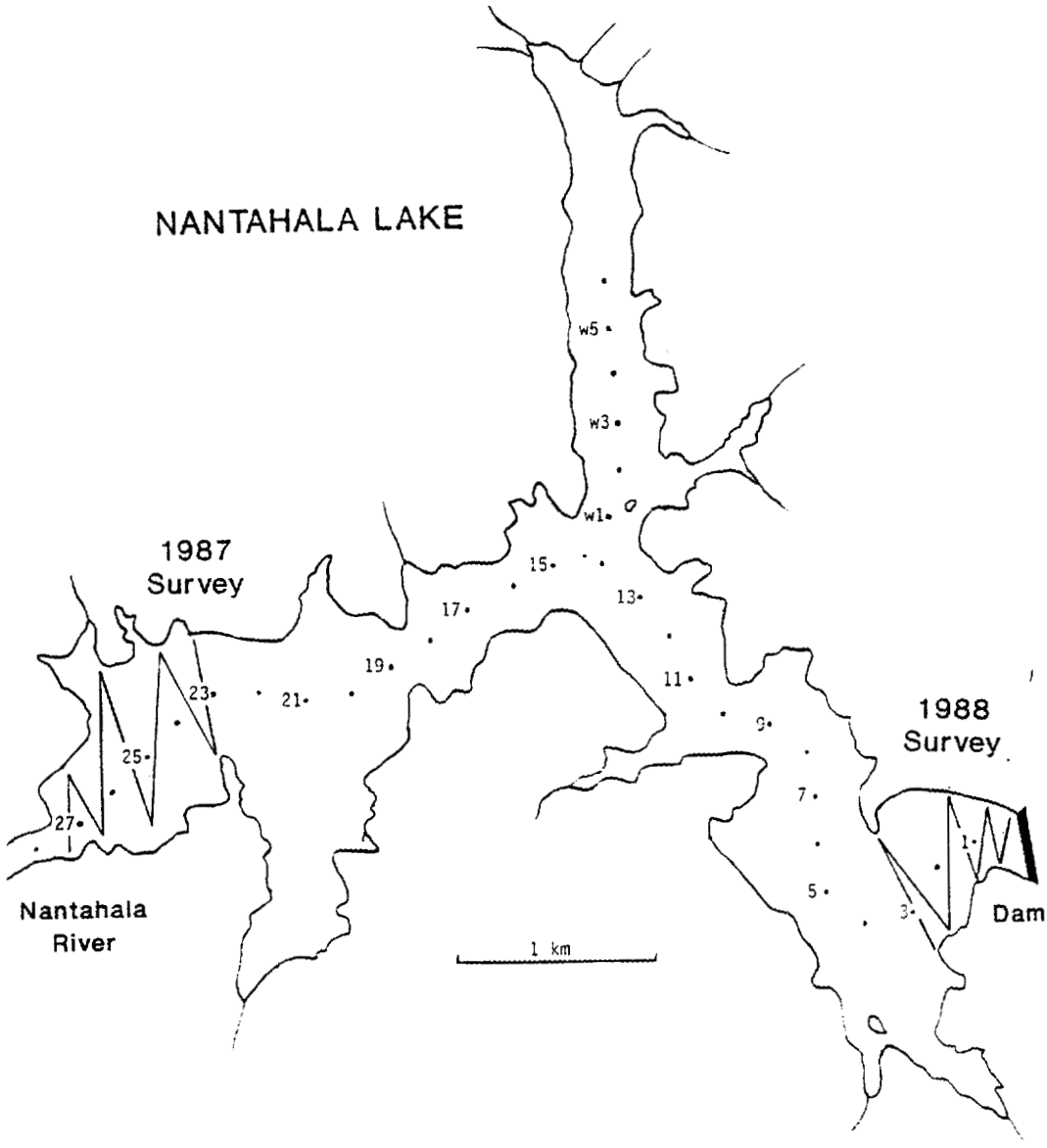

Figure II-2. Map of Nantahala Lake with location of 1987 and 1988 hydroacoustics surveys. Numbers were used as reference points for sampling locations.

average depth is 26 m. Nantahala Lake is oligotrophic and has steep rocky or sandy sides with a relatively small littoral zone. Because of regular water withdrawal for hydroelectric operation, annual drawdown of 10-15 m by late fall is normal. In years of extremely low rainfall, drawdown may exceed 35 m.

Kokanee salmon were stocked in Nantahala Lake for 2 or 3 yr in the early 1960's, and the population is presently self-supporting. Fall spawning migrations occur in the relatively pristine Nantahala River and its tributaries. Spawning within lakes has been reported for some kokanee salmon populations (Cordone et al. 1971; Kurenkov 1978), but no such evidence exists for Nantahala Lake.

Fish Sampling

Vertical gill nets

Six vertical gill nets (4.6 m wide, 30.5 m long) were used to collect kokanee salmon and determine their depth distribution on 10 occasions (26 total nights) from May 1985 to June 1988. Each net was attached at the top to a rigid flotation bar (PVC pipe fitted with styrofoam cylinders) and at the bottom to an anchor bar (4.6-m steel pipe). To ensure that the net was properly spread, 4.6-m sections of aluminum conduit were placed every 6 m along the length of the net. Lead anchors were attached by ropes to the flotation bar to hold the entire net in place (see Horak and Tanner (1964) for an additional description of this type of net). The nets were sometimes fished in water shallower than 30.5 m by leaving the unneeded portion of the net wrapped around the flotation bar. On one occasion they were also fished

deeper than 30.5 m by attaching the top of the net to the flotation bar with extension ropes instead of directly to the flotation bar. A different mesh size (1.90, 2.54, 3.18, 3.81, 4.44, and 5.08 cm square measure) was used on each of six nets. Sampling dates and locations are summarized in Table A-1 in Appendix A.

Because daytime sets proved ineffective, nets were set overnight, usually in two groups of three. Fish were removed from the nets early in the morning while still fresh and often alive, and the depth of capture was noted. Kokanee salmon stomachs were pumped (Seaburg 1957) and the contents preserved in 10% formalin. They were then tagged for later identification and preserved on dry ice. Although the adult kokanee were of most interest, all kokanee captured in the nets were collected and processed. Depth of capture was also noted for non-target species.

Upon return to the laboratory, kokanee salmon were weighed, measured, sexed, and scales and otoliths removed for aging. Weights of the liver, viscera, and gonads were also determined. Scales were pressed on acetate slides for age and growth determination. Otoliths were stored in glycerol and read with a dissecting microscope.

Hydroacoustic surveys

Hydroacoustic surveys were conducted in August 1987 and June 1988 to estimate the size, distribution, and vertical migration patterns of kokanee salmon. The Biosonics dual-beam/echo integration system was used for acoustic data acquisition and processing. This system consisted of the following equipment: a 120 kHz, 6°/15° dual-beam transducer installed in a towed body, a Model 101 echo sounder with dual

receivers, a Model 121 digital echo integrator, a Model 181 dual-beam processor, a Model 115 chart recorder, a Model V-352 Hitachi-Denshi oscilloscope, a Compaq microcomputer, and a Betamax tape recorder. This equipment was owned by the Tennessee Valley Authority and operated by trained operators from that agency. As data were collected, they were stored on both Betamax tape and computer diskette.

Preliminary surveys were performed in Nantahala Lake to determine the location of highest kokanee salmon concentrations. Once an area with sufficient densities was located, a series of half hour surveys was then conducted during a 24-h period. Each survey consisted of traversing shore to shore transects in a zig-zag pattern in one particular part of the lake. The course was replicated as accurately as possible for each 30-min survey with the use of compass headings and landmarks. The 24-h surveys in 1988 were not in the same area of the lake as in 1987 (Figure II-2).

Kokanee depth distribution and target strength analyses were performed from recorded data. Target strengths (decibels) from each marked fish were roughly translated to fish length (mm) with Love's equation (Love 1971). Simultaneous gill netting data were also used to estimate the size of kokanee salmon being tracked by hydroacoustics. The data were analyzed by 4-m depth intervals in 1987 and by 5.5-m intervals in 1988. Because the volume of water being sampled by this technique is conical (or triangular in two dimensions), a correction was applied to the data so that the estimate of fish located at each depth represented an equal volume of water sampled.

Limnological Measurements

Temperature and dissolved oxygen profiles were determined at least once during each sampling trip to investigate the correlation of kokanee salmon depth distribution to limnological characteristics of the water column. A Hydrolab Surveyor II was used to determine profiles from the surface to the bottom. Secchi depths were determined and light penetration was quantified with a photometer (Li-Cor model LI-188B). Additional light data were obtained from a previous study on Nantahala Lake (B. Kimmel, unpublished data). These temperature profiles comprised the actual prey/temperature databases used in the bioenergetics model.

Zooplankton Sampling

Zooplankton were collected by horizontal tows with a Clarke-Bumpus zooplankton sampler (153 μm mesh) at several depths in the same area of the lake as the net sets to determine seasonal changes in depth distributions and densities of the kokanee prey. Tows were 1 to 2 min in duration, and the water volume sampled was determined with a meter on the sampler. Samples were preserved in 10% formalin for later identification and enumeration. Zooplankton larger than 1 mm (the size most likely to be consumed by kokanee salmon as determined from stomach samples) were counted and identified to genus. Zooplankton densities and vertical distribution were part of the prey/temperature databases used in the bioenergetics model. Sample dates, locations, and depths are summarized in Table A-1 in Appendix A.

Bioenergetics Model

Basic operation of the model

The bioenergetics model is a mass balance equation which accounts for energy from consumed food as it is partitioned among various energetic costs and growth of an organism. Though the model is most commonly used to estimate food consumption given estimates of growth and energetic costs (Kitchell et al. 1977; Stewart et al. 1981), it can also be used to estimate growth given estimates of food consumption (Bevelhimer et al. 1985). The basic equation is

$$G = C - (R + F + U) \quad (1)$$

where G = specific growth rate (g/g/d), C = specific rate of food consumption, R = specific rate of respiration, which includes routine and active metabolism and heat increment components, F = specific rate of egestion, and U = specific rate of excretion.

Most other bioenergetics models operate on daily or longer time steps, but a unique feature of this model is that it operates on 30-min time steps to better reflect the time scale on which changes in thermal exposure and feeding occur as a result of vertical migration.

Figure II-3 illustrates the general structure and operation of the model, the basic relationships among various model components, and the primary habitat variables (e.g., depth, temperature, and prey density) that influence foraging strategy. For each 24-h simulation, the initial input includes a prey/temperature database, the weight of the fish, the depths between which vertical migration occurs, the time spent at each depth, and the time of active feeding. For each 30-min time step,

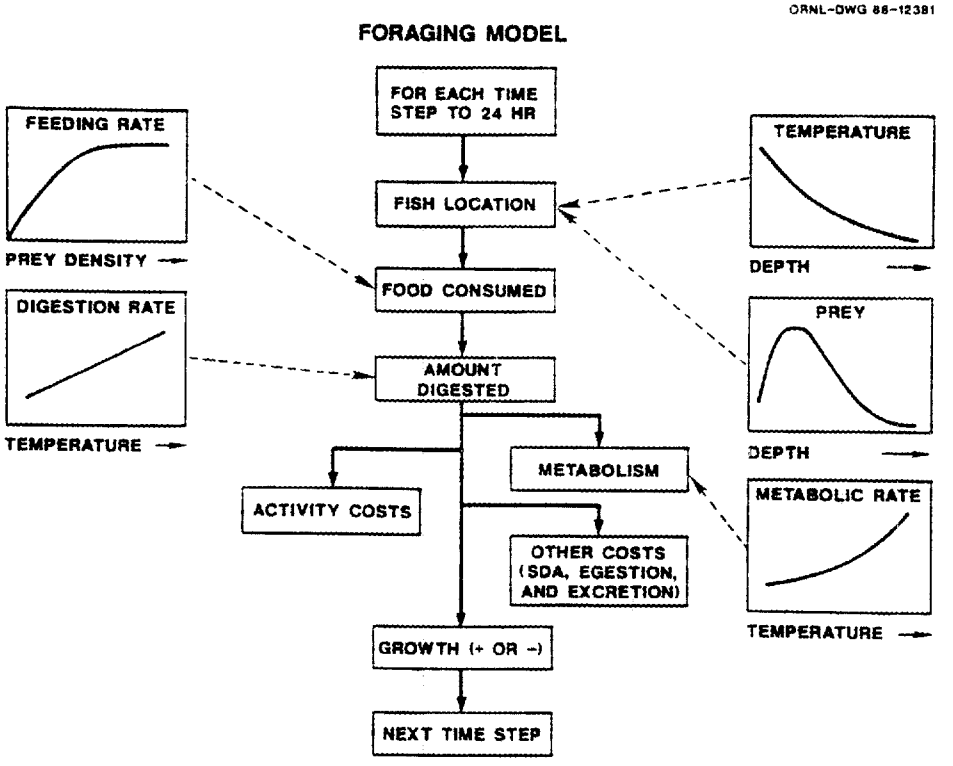

Figure II-3. Flow chart description of bioenergetics model used to measure the resulting growth of various vertical migration strategies of kokanee salmon.

the location (depth) of the kokanee salmon was determined from the initial input. Depth corresponded to a known temperature and prey density from the prey/temperature database that was selected. The prey/temperature databases used in the model included those measured in the field as described above and some hypothetical databases. The feeding status (feeding or not feeding) during the time step was also determined from the initial input. When feeding, the amount of food consumed was determined as a function of the food density at the fish's depth during that time step. Food intake was at times limited by the capacity of the stomach. The amount of food consumed was added to the amount of undigested food remaining in the stomach from the previous time step if any existed. The amount of food digested during a time step was calculated as a function of the amount of food in the stomach at the beginning of the time step and the food intake during the time step. Since all the food that was consumed during a time step was not necessarily digested during that time step, I chose to use D, the amount of food digested (or processed), instead of C, the amount of food consumed, to represent the energy intake during a time step. Under this condition, equation (1) then becomes

$$G = D - (R + F + U). \tag{2}$$

A portion of the processed food is not useful to the fish and is egested as feces (F). Energy not lost in the feces is the amount of useful energy (A) available for assimilation, that is

$$A = D - F. \tag{3}$$

Of the useful energy that is assimilated, a portion is lost through excretion (U) as nitrogenous wastes. The last item to be subtracted as a cost is the respiration component which includes the metabolic costs associated with standard and active metabolism and heat increment (also known as specific dynamic action, SDA). Heat increment is the metabolic cost associated with the biochemical transformation of consumed food to usable energy forms. Subtracting the costs of egestion (F), excretion (U), and respiration (R) from the energy processed (D) resulted in the growth (G) or change in weight (which can be positive or negative) for the time step. The food remaining in the stomach was carried over to the next time step, and calculations were repeated beginning with the input of the depth occupied by the fish during the next time step.

The model continues in 30-min time steps for 24 h. Change in weight for the entire 24 h was summed to provide an estimate of daily growth (g/d). The simulation was repeated using the final stomach content value of the first run for the initial stomach content of the second run. This iterative process was repeated until a steady state was reached (i.e., the final stomach content was equal to the initial stomach content for that 24-h simulation). Normally, only two or three such iterations were necessary. A steady state situation (equal initial and final stomach contents) would occur naturally if the 24-h feeding pattern of the kokanee salmon and the food remained unchanged from day to day. In the long term this is certainly not the case, but in the short term this assumption is reasonable if in fact the feeding pattern is on a daily cycle. The results of the steady state simulation were

those used in the analyses. The data derived from the simulations were daily estimates of consumption rate, energetic costs, growth, and gross conversion efficiency (kcal growth/kcal consumed).

The entire model was constructed as a Lotus 1-2-3 spreadsheet which allowed for easy manipulation of parameters and provided immediate results from those manipulations (see Appendix B for more details on the model construction). Within the model there were 12 prey/temperature databases from which to choose; these are described below. The depths between which vertical migration occurred could be entered automatically with macros or manually one at a time. Once the initial conditions (prey/temperature database, migration depths and times, fish weight, and feeding status) were input, the calculations and iterations were performed automatically. The equations for the various components of the model are described below.

Food consumption

The following function was fit to laboratory data on consumption rates (zooplankton/min) of kokanee salmon at various zooplankton densities (Hyatt 1980):

$$C = Z / (x \cdot Z + y) \tag{4}$$

where C is consumption (prey/min), x and y are constants, and Z is zooplankton density (zooplankton per m^3) (see Appendix B for more details). Whether this rate of food capture varies with size of the fish is unknown, therefore, the rate of capture is assumed equal for all sizes. The values for x and y as well as the other parameters in the model are listed in Table II-1.

Table II-1. Parameters used in the bioenergetics model for kokanee salmon.

Parameter	Description	Value
Consumption (C):		
x	constant	0.0138
y	constant	11.5
Z	zooplankton density (#/m^3)	0 to 7358
Digestion (D):	r (digestion coefficient)	
a1	scaling parameter	0.0154
T	temperature (°C)	5 to 25
c1	exponent for temperature dependence	-0.0140
Egestion (F):		
a2	scaling parameter	0.212
T	temperature (°C)	5 to 25
c2	exponent for temperature dependence	-0.222
f2	parameter for feeding level	0.631
Excretion (U):		
a3	scaling parameter	0.0314
T	temperature (°C)	5 to 25
c3	exponent for temperature dependence	0.580
f3	parameter for feeding level	-0.299
Respiration (R):		
	Maximum Sustainable Swimming Speed	
a4	intercept value	0.909
L	length (cm)	15 to 50
b4	exponent for weight dependence	0.632
T	temperature (°C)	5 to 25
c4	parameter for temperature dependence	-0.00901
d4	parameter for temperature dependence	0.00349
e4	parameter for temperature dependence	-0.000128
	Standard Respiration	
a5	intercept value	-2.47
W	weight (g)	100 to 1000
b5	exponent for weight dependence	0.882
T	temperature (°C)	5 to 25
c5	parameter for temperature dependence	0.00126
d5	parameter for temperature dependence	0.00286
	Active Respiration	
a6	intercept value	-1.19
W	weight (g)	100 to 1000
b6	exponent for weight dependence	0.986
T	temperature (°C)	5 to 25
c6	parameter for temperature dependence	0.111
d6	parameter for temperature dependence	-0.00294
	Heat Increment (SDA)	
sda	proportion of consumed energy for SDA	0.14

The amount of food consumed is not only limited by the density of prey, but also by the maximum stomach capacity. Average maximum stomach capacity of adult (> 500 g) O. nerka at sea was estimated as 2.2% of the fish's weight (Brett 1971b). Values for the stomach capacity of smaller salmon were obtained from Figure 5A of Brett (1971b); a value of 4% of body weight was used for 100 g kokanee in the model.

Daphnia biomass and caloric value

From stomach contents analyses the main prey item of kokanee in Nantahala Lake are large Daphnia sp. of a mean length of about 2.25 mm. The following equation was used to estimate the wet weight of Daphnia:

$$WW = 0.052 \cdot L^{3.012} \quad (5)$$

where WW is wet weight (mg) and L is length (mm) (Dumont et al. 1975). From this equation, a single fresh 2.25-mm Daphnia weighs 0.60 mg. A similar equation describes the relationship between length and dry weight:

$$DW = 1.23 \cdot 10^{-11} \cdot L^{2.61} \quad (6)$$

where DW is dry weight (mg) and L is length (μm) (Dumont et al. 1975). The dry weight of a single 2.25 mm-Daphnia is therefore 0.069 mg. Richman (1958) determined the caloric content of mature Daphnia sp. as 5.08 Kcal/g dry weight which translates to 0.586 Kcal/g wet weight. Possible seasonal changes in caloric density of zooplankton were not considered. The conversion from grams wet weight to Kcal in the model was made after the digestion step.

Digestion

The amount of food digested (D) during a time step is described by the following equation adapted from Elliott and Persson (1978):

$$(7) \qquad D = W_{(0)} + C - (W_{(0)} \cdot \exp(-rt) + C/r \cdot (1-\exp(-rt)))$$

where $W_{(0)}$ is the amount of food (g) in the stomach at the beginning of the time step, C is the food consumed during the time step (g), r is the digestion coefficient, and t is the length of the time step (0.5 h). This digestion model assumes an exponential rate of digestion and constant level of food intake during the time step. Brett and Higgs (1970) described the digestion of sockeye salmon as an exponential function. The digestion coefficient, r, is temperature dependent and is described by the following equation:

$$(8) \qquad r = a_1 + c_1 \cdot T$$

Equation (8) was derived from data in Brett and Higgs (1970); this derivation is described in Appendix B.

Egestion

Egestion (F) was calculated with the following temperature-dependent equation used for salmon species in Hewett and Johnson (1987):

$$(9) \qquad F = a_2 \cdot T^{c2} \cdot e^{f2} \cdot D$$

where a_2 is the scaling parameter, T is temperature, c_2 is the exponent of temperature dependence, f_2 is the parameter of feeding level dependence, and D is the amount of food processed during the time step.

Excretion

Excretion (U) was calculated with a similar temperature-dependent equation for salmon (Hewett and Johnson 1987):

$$U = a_3 \cdot T^{c3} \cdot e^{f3} \cdot A \quad (10)$$

where a_3 is the scaling parameter, T is temperature, c_3 is the exponent of temperature dependence, f_3 is the parameter of feeding level dependence, and A is the amount of assimilated energy.

Respiration

J.R. Brett and colleagues (Brett et al. 1958; Brett 1962; Brett 1964; Brett 1965; Brett and Glass 1973) have done extensive work on the respiration requirements of the ocean-run variety of this species, the sockeye salmon, including the effects of temperature, size, and swimming speed on respiration rate. The difference between the kokanee salmon and sockeye salmon with regards to respiratory function was here assumed to be minimal (J.R. Brett, personal communication). Brett and Glass (1973) determined weight-dependent equations for the maximum sustainable swimming speed (MSS) at five temperatures, and weight-dependent equations for standard ($R_{(std)}$), and active respiration ($R_{(act)}$) at three temperatures. Active respiration rates were determined at the maximum sustainable swimming speed, which was defined as the maximum speed at which swimming could be sustained for 1 h. They present a graphical method by which the respiration rate for any swimming speed can be determined from these equations for three temperatures (5, 15, and 20°C). These equations and a mathematical form of their graphical method were used to derive the following equations for respiration (see

Appendix B for more details of the derivation of these equations). The equations for MSS, $R_{(std)}$, and $R_{(act)}$ are

(11) $MSS = \exp(a_4 + b_4 \cdot \ln(L) + c_4 \cdot T + d_4 \cdot T^2 + e_4 \cdot T^3)$

(12) $R_{(std)} = \exp(a_5 + b_5 \cdot \ln(W) + c_5 \cdot T + d_5 \cdot T^2)$

(13) $R_{(act)} = \exp(a_6 + b_6 \cdot \ln(W) + c_6 \cdot T + d_6 \cdot T^2)$

where a_4, a_5, and a_6 are scaling parameters, L is length (cm), W is weight (g), b_4, b_5, and b_6 are exponents of weight dependence, c_4, c_5, c_6, d_4, d_5, d_6, and e_4 are parameters of temperature dependence, and T is temperature. From these three equations, the respiration at any weight, temperature, and swimming speed can be estimated with the following equation derived from the graphical method of Brett and Glass (1973):

(14) $R = \exp[\ln(R_{(std)}) + ((\ln(R_{(act)}) - \ln(R_{(std)})) \cdot S/MSS)]$

where S is swimming speed (cm/s). Hyatt (1980) observed 15-20 cm kokanee swimming at an average speed of about 20 cm/sec while feeding. Since there is no reason to suspect that larger fish need to swim at a different rate to encounter the same number of prey, this speed was chosen for all sizes in the model. When not feeding the kokanee were assumed to be resting at a swimming speed of 0 cm/sec.

Heat increment or specific dynamic action (SDA) is usually calculated as a constant proportion of consumption. Because no values for this parameter were found that had been determined specifically for

a planktivorous salmonid, a generic value of 14% of food consumed (or assimilated in this model) was used (Brett and Groves 1979).

(15) $$SDA = 0.14 \cdot A$$

where A is the energy available for assimilation.

Model simulations

Simulations were performed to mimic possible patterns of diel vertical migration. Twelve prey/temperature databases were available to evaluate the effects of prey availability and temperature on vertical migration. These databases consisted of the prey density and the temperature from the surface to the bottom (usually at about 30 m) and included six theoretical and six actual databases. The six theoretical databases included high, medium, and low densities of prey distributed uniformly throughout the water column and high, medium, and low densities of prey in a unimodal distribution (Table II-2, Figures II-4 and II-5). In the unimodal distributions, peak prey density occurred at 6 m. For the six theoretical databases the temperature stratification was represented as a linear decrease from 24.5°C at the surface to 9.5°C at 30 m. The databases with the unimodal prey distribution are similar to natural situations in which the heterogeneity in the prey and temperature distributions produce the foraging dilemma mentioned in the introduction and illustrated in Figure II-1. The six actual databases were determined at Nantahala Lake during sampling trips from June 1985 to June 1988 and are discussed further in the results section.

Initial simulations were run without any vertical migration of the

Table II-2. Prey/temperature databases used in the simulation model of vertical migration of kokanee salmon.

Database	Maximum prey density (#/m^3)	Temperature range (°C)	Maximum depth (m)
	Theoretical		
Uniform-High	5000	9.5-24.5	30
Uniform-Medium	2000	9.5-24.5	30
Uniform-Low	500	9.5-24.5	30
Unimodal-High	5400	9.5-24.5	30
Unimodal-Medium	2700	9.5-24.5	30
Unimodal-Low	1350	9.5-24.5	30
	Actual		
May 1986	2274	7.5-17.9	20
June 1985	7358	8.0-22.0	30
June 1987	1233	6.7-22.0	34
June 1988	2491	5.9-21.0	45
July 1987	58	7.5-26.6	33
October 1985	142	6.8-20.4	34

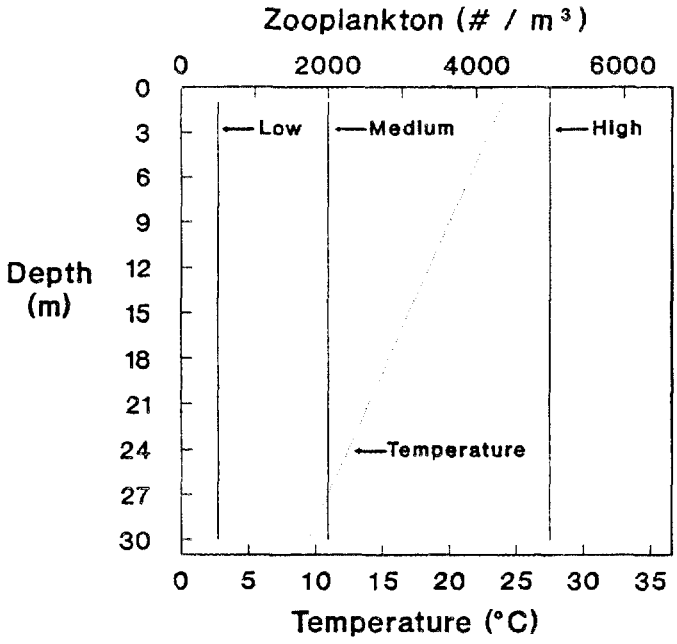

Figure II-4. The uniform prey density distributions used in the bioenergetics model. Three levels of zooplankton densities (high, medium, and low) are represented by solid lines with temperature indicated by a dotted line.

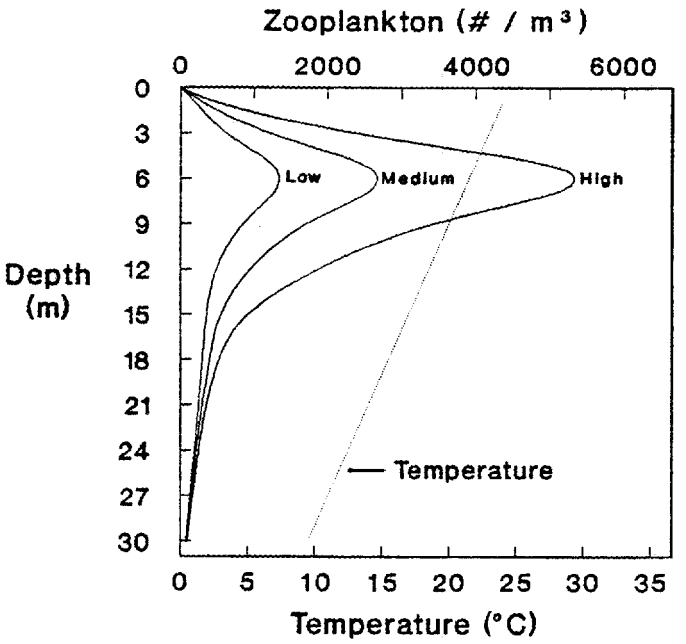

Figure II-5. The unimodal prey density distributions used in the bioenergetics model. Three levels of zooplankton densities (high, medium, and low) are represented by solid lines with temperature indicated by a dotted line.

kokanee to demonstrate the relative values of the various depths in terms of food availability and energy conservation. These simulations were performed with the six theoretical databases.

The bulk of the simulations were run with a combination of two depths, one for feeding and one when not feeding. These depth combinations were chosen to represent all reasonable patterns of diel vertical movements. That is, a fish fed at a particular depth and then remained at that depth or moved to a lower depth when not feeding. Only depths that were multiples of 3 m were used in most simulations. For example, a fish was modeled at 3 m when feeding and either 3, 6, 9, ..., or 30 m when not feeding. For those databases which included data to a depth of 30 m, this resulted in a total of 55 different depth combinations for feeding and resting (note: this included 10 instances of feeding and resting at the same depth). Therefore, for each prey-temperature database, a series of simulations was performed to determine the optimal migration strategy for a fish of a given size with a particular temporal feeding pattern. The total number of simulations varied for the actual databases because not all contained exactly 30 m of data.

The standard simulation consisted of a 500 g kokanee, with a diurnal feeding pattern of 12 h of feeding per day, and the unimodal-high database. Kokanee size, feeding duration, swimming speed, and feeding pattern were varied in other simulations to evaluate their effects on the predictions of the optimal migration strategy. The feeding pattern was usually diurnal, but a crepuscular pattern was also

simulated in a few cases. Table II-3 summarizes those variables that were manipulated in the various simulations.

Whereas the theoretical databases were used in the simulations to evaluate the properties of the model, the actual databases were used to evaluate migration strategies under natural prey densities and temperature stratification. Simulations with the six actual databases were the same as the standard simulation except for the substitution of one of the actual databases for the theoretical database. Table II-4 describes the simulations presented in this paper.

The predictions of the model were tested against the results of the hydroacoustics surveys. The observed kokanee migration patterns were compared to the predictions of simulations with the prey/temperature databases collected at the time of the surveys. Simulations of the 1988 hydroacoustics results had to be adjusted for a smaller fish size and a different feeding pattern (nocturnal instead of diurnal).

RESULTS

Field Sampling

Gill netting

Kokanee salmon were captured over a wide range of depths (5-29 m) and temperatures (7-22°C) during the study. A preference for a narrower range of temperatures is evident in that 87% of the kokanee were captured in an 8°C range (7.5-15.5°C) with a mode at 12°C (Figure II-6A). Seasonal changes in the depth distribution of kokanee reflected the seasonal changes in the thermal profile of the lake. As the summer

Table II-3. Variables used in simulations of the vertical migration of kokanee salmon. The conditions of the standard simulation are highlighted in bold print.

Variable	Range of values
Fish size	100, **500**, or 1000 g
Feeding duration	8, 10, 12, or 16 h/d
Feeding swim speed	**20** or 30 cm/sec
Feeding pattern	**diurnal** or crepuscular

Table II-4. Simulations performed with bioenergetics model to analyze vertical migration of kokanee salmon.

Sim. #	Database	Fish weight	Feeding pattern	Hours Feeding	Other
1	Uniform-high	500	Diurnal	12	
2	Uniform-medium	500	Diurnal	12	
3	Uniform-low	500	Diurnal	12	
4	Unimodal-high	500	Diurnal	12	
5	Unimodal-medium	500	Diurnal	12	
6	Unimodal-low	500	Diurnal	12	
7	Unimodal-high	500	Diurnal	12	1
8	Unimodal-high	500	Diurnal	4	
9	Unimodal-high	500	Diurnal	8	
10	Unimodal-high	500	Diurnal	16	
11	Unimodal-high	100	Diurnal	12	
12	Unimodal-high	1000	Diurnal	12	
13	Unimodal-high	500	Diurnal	12	2
14	Unimodal-high	500	Diurnal	12	3
15	Unimodal-high	500	Crepuscular	12	
16	Unimodal-low	500	Crepuscular	12	
17	May 1986	500	Diurnal	12	
18	June 1985	500	Diurnal	12	
19	June 1987	500	Diurnal	12	
20	June 1988	500	Diurnal	12	
21	July 1987	500	Diurnal	12	
22	October 1985	500	Diurnal	12	
23	June 1988	100	Diurnal	12	
24	June 1988(night)	100	Diurnal	12	

[1]Consumption X 2
[2]Swim spd.=30 cm/s
[3]Swim spd.=30 cm/s and consumption X 1.5

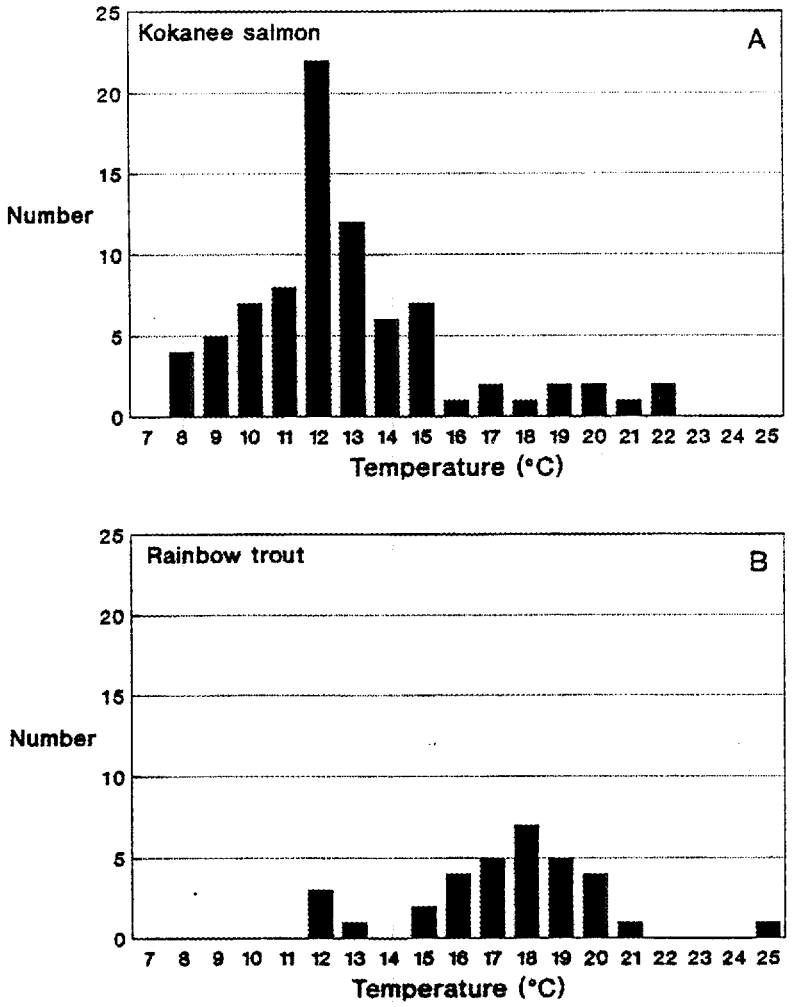

Figure II-6. Temperature distributions of kokanee salmon (panel A) and rainbow trout (panel B) captured in gill nets from 1985 to 1988 in Nantahala Lake.

progressed and water temperatures warmed, the kokanee moved to deeper water. That kokanee were caught at temperatures up to 22°C indicates that they occasionally move into water that is much warmer than their preferred temperature range.

The largest kokanee captured in the nets, a male within a few weeks of spawning, was 551 mm long and weighed 1459 g. This is an indication of the maximum size achieved in Nantahala Lake and is among the largest kokanee salmon reported (Carlander 1968, Cordone et al. 1971). See Table A-2 in Appendix A for more information on captured kokanee.

Other species captured in the nets were rainbow trout, channel catfish, walleye, black crappie, white crappie, rock bass, redbreast sunfish, and common sucker. Very little overlap in depth distribution occurred between these species and the kokanee. Rainbow trout were captured at 16-20°C, and fewer were captured than kokanee (Figure II-6B).

As reported by others, the diets of the kokanee consisted exclusively of zooplankton and included Daphnia sp., chironomid pupae and larvae, Chaoborus sp. larvae, and Leptodora sp. Daphnia accounted for the majority of items in the stomachs both numerically and by weight.

Zooplankton and limnology

The depth distributions of zooplankton and the temperature profiles are shown for six of the sampling dates (Figures II-7 to II-12). The data for these six dates were used as the six actual databases in the model simulations. The databases included values for every 3 m of depth. Linear interpolation provided values at depths that were not

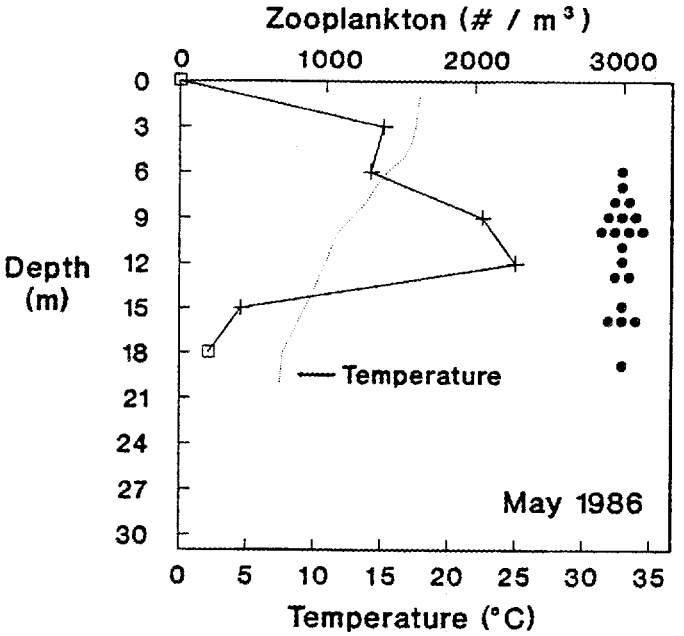

Figure II-7. Prey/temperature distribution measured in Nantahala Lake in May 1986. Plus signs are estimates of zooplankton densities from horizontal zooplankton tows and open squares are projected densities for use in the bioenergetics model. Dots indicate the depths of kokanee salmon captured in gill nets on the same sampling trip.

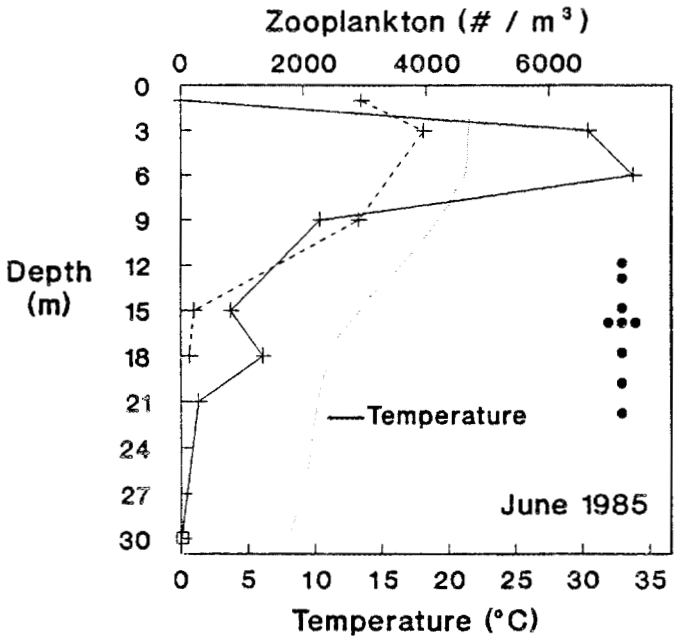

Figure II-8. Prey/temperature distribution measured in Nantahala Lake in June 1985. Plus signs are estimates of zooplankton densities from horizontal zooplankton tows and open square is projected density for use in the bioenergetics model. Zooplankton densities determined at night represented by dashed line. Dots indicate the depths of kokanee salmon captured in gill nets on the same sampling trip.

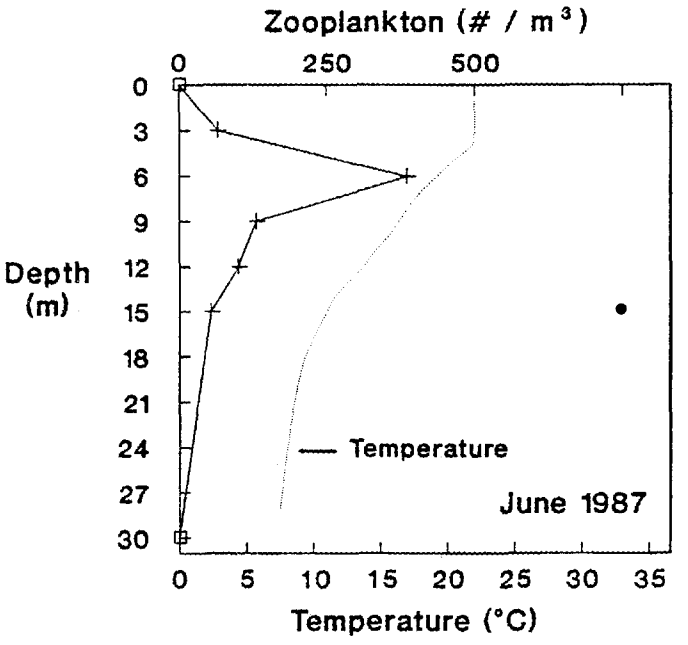

Figure II-9. Prey/temperature distribution measured in Nantahala Lake in June 1987. Plus signs are estimates of zooplankton densities from horizontal zooplankton tows and open squares are projected densities for use in the bioenergetics model. Dot indicates the depth of kokanee salmon captured in gill nets on the same sampling trip.

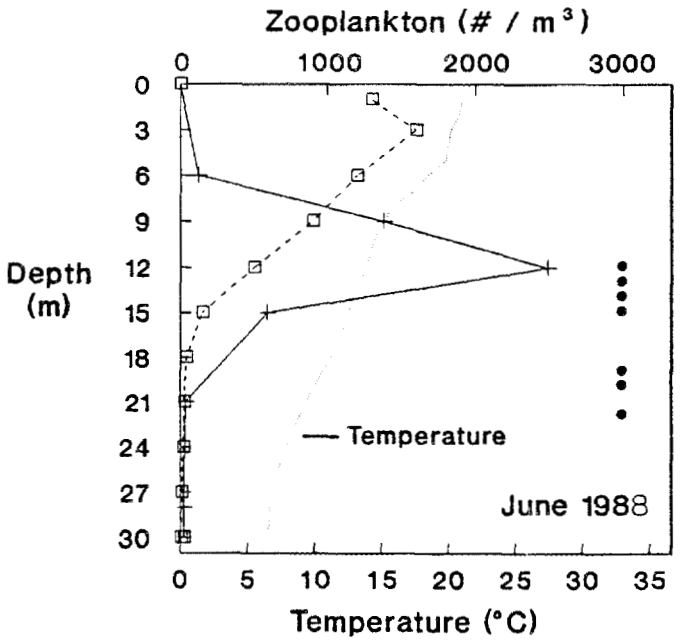

Figure II-10. Prey/temperature distribution measured in Nantahala Lake in June 1988. Plus signs are estimates of zooplankton densities from horizontal zooplankton tows and open squares are projected densities for use in the bioenergetics model. Dashed line represents projected night zooplankton densities. Dots indicate the depth of kokanee salmon captured in gill nets on the same sampling trip.

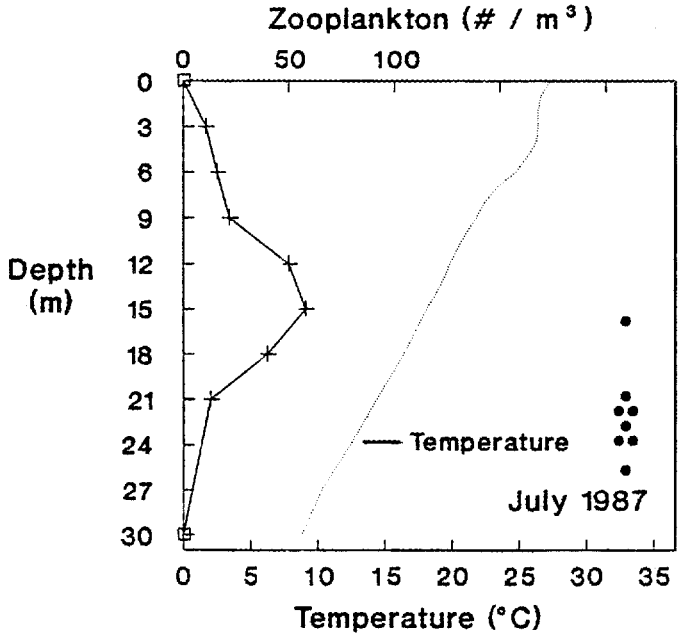

Figure II-11. Prey/temperature distribution measured in Nantahala Lake in July 1987. Plus signs are estimates of zooplankton densities from horizontal zooplankton tows and open squares are projected densities for use in the bioenergetics model. Dots indicate the depth of kokanee salmon captured in gill nets on the same sampling trip.

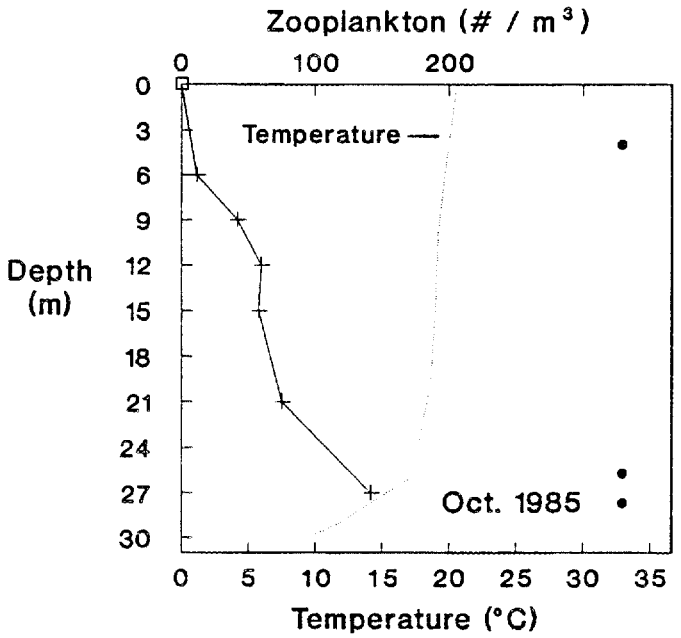

Figure II-12. Prey/temperature distribution measured in Nantahala Lake in October 1985. Plus signs are estimates of zooplankton densities from horizontal zooplankton tows and open square is projected density for use in the bioenergetics model. Dots indicate the depth of capture in gillnets of kokanee salmon on the same sampling trip.

sampled. Values at 30 m and the surface were often projected to provide complete databases for the model simulations. The capture location of kokanee on those dates is also indicated in the figures to illustrate the relationship between kokanee and the zooplankton and temperature.

Daphnia sp. accounted for nearly 95% of the zooplankton > 1 mm with Leptodora, chironomids, Chaoborus, Holopedium sp., and copepods making up smaller proportions of this size class of zooplankton (see Table A-3 in Appendix A for more information on zooplankton distributions). Smaller zooplankton (< 1 mm) were dominated by copepods, Daphnia sp., and Bosmina sp., but were not quantified. Seasonal changes in the density of large zooplankton were obvious. Total numbers increased in the spring from a winter low, peaked in June, and then decreased through July and August to relatively low levels.

The temperature profile of Nantahala Lake can be characterized as gradually decreasing from the surface downward, usually with no distinct thermocline (Figures II-7 to II-12). Because of the altitude and depth of Nantahala Lake, surface and bottom temperatures during the summer are cooler than most reservoirs in the southeastern United States. Dissolved oxygen was seldom below 5 ppm and thus not a limiting factor to kokanee distribution. Secchi depths were normally in the 3-5 m range. Light profiles of the water column for two dates are shown in Figure II-13. The intensity at 30 m (approximately 10^{-1} footcandles) is approximately the same as the lowest level at which Brett and Groot (1963) found no effect on feeding rate ofjuvenile salmon in laboratory experiments; therefore, light should not be a limiting factor on feeding at 30 m during midday. Brett and Groot (1963) also reported that at

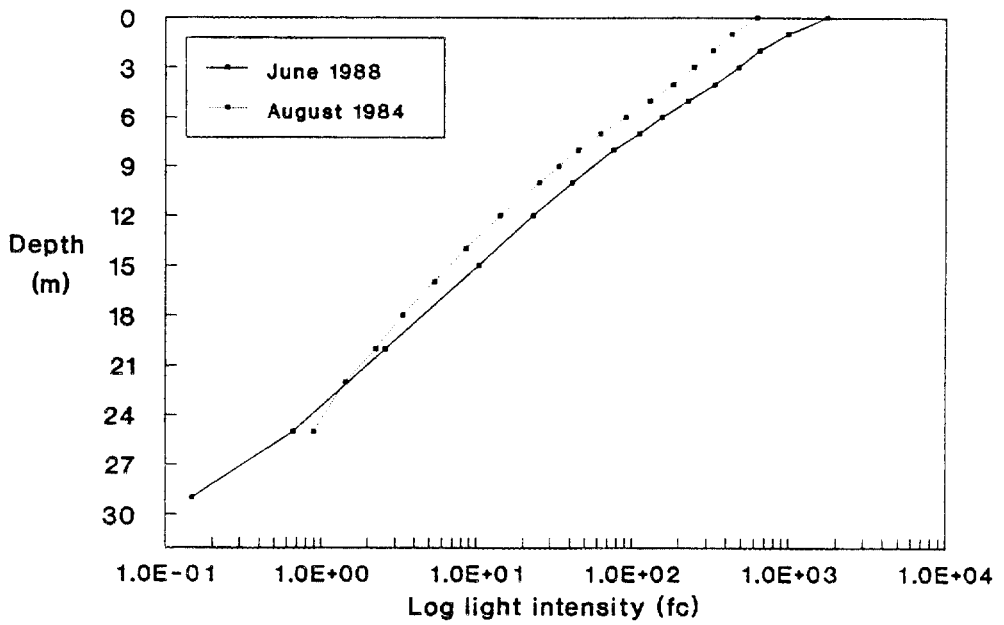

Figure II-13. Light intensity (fc) profiles measured in Nantahala Lake on two occasions in 1984 and 1988.

total darkness the salmon did not feed at all even at high prey densities.

Hydroacoustics

Results of an intensive 24-h hydroacoustics survey in late July 1987 indicated that adult kokanee salmon were undergoing limited vertical migrations at that time (Table II-5 and Figure II-14). Rainbow trout and kokanee were captured in gill nets at depths from 0-21 m and 16-26 m, respectively, during this sampling trip. Because of the depth range differences in these two species and the fact that temperatures in the upper 5 m exceeded 25°C, the fish marked in the upper 8 m of the water column were probably channel catfish and rainbow trout and not kokanee. Fish from 8-20 m could conceivably have been rainbow trout or kokanee, and fish from 20-36 m were probably kokanee. Given these species differences in depth distribution, the hydroacoustics survey results were interpreted as follows. At dusk (sample time 2025 hours; all times are Eastern Daylight Savings) kokanee were located from 8-24 m. During the night (2200 and 2357 hours) they concentrated at 20-28 m. At dawn (0558 hours) they were still at 20-28 m, but some appeared to have begun to move upward. By mid-day (1310 hours) they were at 12-24 m and by late afternoon (1711 hours) they were at 12-24 m. And at the second dusk survey (2042 hours) they were dispersed from 12-32 m, but more were appearing at 20-32 m suggesting a return to those depths during the night. Although the upper limits of the vertical migration are not clear because of possible overlap with rainbow trout, an estimate of the migration patterns during this time would be that most of the kokanee are located from 12-24 m during the day and 20-32 m

Table II-5. Summary of hydroacoustics survey on Nantahala Lake in late July 1987. Values in the top panel are the number of fish of adult kokanee salmon size that were located throughout the water column. In the bottom panel these numbers have been corrected for differential sample volume at each depth so that each number represents the same sample volume.

Depth interval (m)	Time						
	2025	2200	2357	0558	1310	1711	2042
0 - 4	3	2	0	1	14	4	5
4 - 8	6	0	0	0	4	6	0
8 - 12	4	0	0	4	3	8	2
12 - 16	5	0	0	5	5	2	4
16 - 20	5	0	0	9	10	9	11
20 - 24	4	13	10	30	12	6	2
24 - 28	0	1	15	15	1	1	2
28 - 32	1	1	1	2	0	2	6
32 - 36	0	0	0	0	0	0	1
36 - 40	0	0	0	0	0	0	0
Corrected values for equal sample volume.							
0 - 4	57	38	0	19	266	76	95
4 - 8	38	0	0	0	25	38	0
8 - 12	15	0	0	15	11	30	8
12 - 16	14	0	0	14	14	5	11
16 - 20	11	0	0	19	21	19	23
20 - 24	7	22	17	52	21	10	4
24 - 28	0	2	22	22	2	2	3
28 - 32	1	1	1	2	0	2	8
32 - 36	0	0	0	0	0	0	1
36 - 40	0	0	0	0	0	0	0

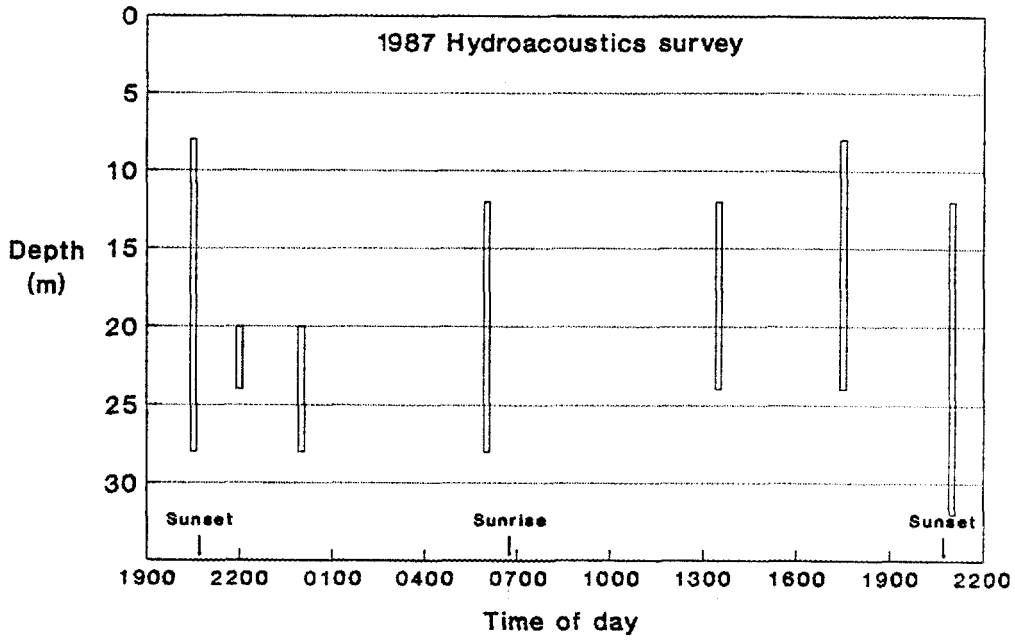

Figure II-14. Estimated depth range of kokanee salmon for seven sampling times over 25-h period as determined with hydroacoustics in July 1987.

during the night for an average daily vertical migration of about 6-8 m. The kokanee appear to be distributed over the greater depth range around sunrise and sunset than during the middle of the night or day. That the kokanee were usually spread over an 8 m or greater range in the water column is an indication of the degree of precision (or lack thereof) with which vertical position is selected. This indicates a fair amount of individual variation and/or asynchrony in the timing of the movements.

In June 1988, reconnaissance surveys prior to the intensive 24-h survey were unable to locate any fish resembling adult kokanee either in location or size, and no adult kokanee were captured in the nets at this time either. A concentration of small fish (presumably juvenile kokanee) were located at depths greater than 40 m during afternoon reconnaissance surveys. In addition, juvenile kokanee (179-197 mm) were captured at 13-22 m in the gill nets during this sampling trip. Unlike the previous year when surface temperatures during the hydroacoustics survey exceeded 25°C, the temperature at 1 m depth was only 21°C, therefore, fish marked in the upper few meters of the water column were not ruled out as kokanee. The results of this survey (Table II-6 and Figure II-15) were interpreted as follows. In the afternoon (starting time 1435 hours), the kokanee were concentrated from 40-50 m deep. Only one fish (probably not kokanee) was marked from 12-40 m. At dusk (2048 hours) the kokanee had left the deepest water and moved to 12-28 m. At night (2123, 2204, and 0002 hours) they were mostly at 1-23 m with some reappearing as deep as 50 m. At some time during the night, fish probably migrate to the surface to feed since that is where moonlight

Table II-6. Summary of hydroacoustics survey on Nantahala Lake in June 1988. Values in the top panel are the number of fish of juvenile kokanee salmon size that were located throughout the water column. In the bottom panel these numbers have been corrected for differential sample volume at each depth so that each number represents the same sample volume.

Depth interval (m)	Time								
	1435	2048	2123	2204	0002	0540	0629	0804	1053
1.0 - 6.5	25	2	6	25	35	1	2	14	12
6.5 - 12.0	4	1	24	9	43	1	3	1	1
12.0 - 17.5	0	26	62	15	16	0	4	0	0
17.5 - 23.0	1	33	38	18	24	1	1	1	1
23.0 - 28.5	0	10	19	6	2	33	0	0	6
28.5 - 34.0	0	5	9	5	0	65	49	6	0
34.0 - 39.5	0	0	4	14	6	42	63	7	0
39.5 - 45.0	33	0	3	4	0	27	15	87	55
45.0 - 50.5	64	0	2	2	1	0	8	20	77
Corrected values for equal sample volume.									
1.0 - 6.5	318	25	76	318	446	13	25	178	153
6.5 - 12.0	21	5	124	46	222	5	15	5	5
12.0 - 17.5	0	84	201	49	52	0	13	0	0
17.5 - 23.0	2	78	90	42	57	2	2	2	2
23.0 - 28.5	0	19	35	11	4	61	0	0	11
28.5 - 34.0	0	8	14	8	0	99	75	9	0
34.0 - 39.5	0	0	5	18	8	55	82	9	0
39.5 - 45.0	37	0	3	5	0	31	17	98	62
45.0 - 50.5	64	0	2	2	1	0	8	20	77

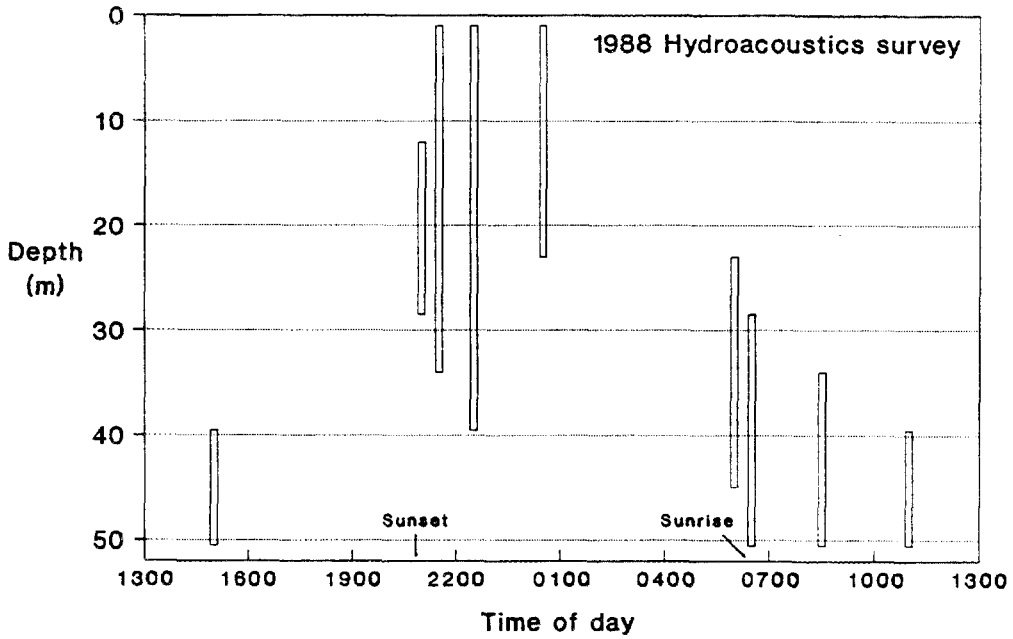

Figure II-15. Estimated depth range of kokanee salmon for nine sampling times over 24-h period as determined with hydroacoustics in June 1988.

would make feeding possible. That all fish were not near the surface at once suggests some asynchrony in feeding. At dawn (0540 hours) few fish remained from 1-23 m, and the kokanee were concentrated at 23-45 m. After sunrise (0629 hours) they were at 28-50 m, and by late morning (0804 and 1053 hours) most of the kokanee were back at 40-50 m. This disappearance and reappearance of kokanee below 40 m was also evident in the echograms that were created during the survey (Figure II-16). To summarize this migration pattern, juvenile kokanee remain at 40-50 m during the daylight, gradually move toward the top 20 m of the water column at dusk where they stay throughout the night, probably feeding near the surface at some point during the night, and then return to 40-50 m at dawn.

Model predictions

In simulations with the uniform-high database (Figure II-5) and no vertical migration, growth for a 500 g kokanee was optimal at 18 m (15.5°C) (Figure II-17). Growth was lower at depths <15 m due to increased metabolic rates associated with higher temperatures. At depths >24 m growth was inhibited because food consumption was limited by slower digestion rates associated with colder temperatures. That is, at the high feeding rate achievable at this high prey density, the maximum stomach content was achieved after several hours, after which the feeding rate was limited by the rate at which the stomach was evacuated. The depth of optimal growth, however, was not the depth of greatest gross conversion efficiency which occurred at 27 m (11°C). Due to a decrease in the feeding rate with the uniform-medium database, the effect of the digestion rate/stomach capacity interaction was only

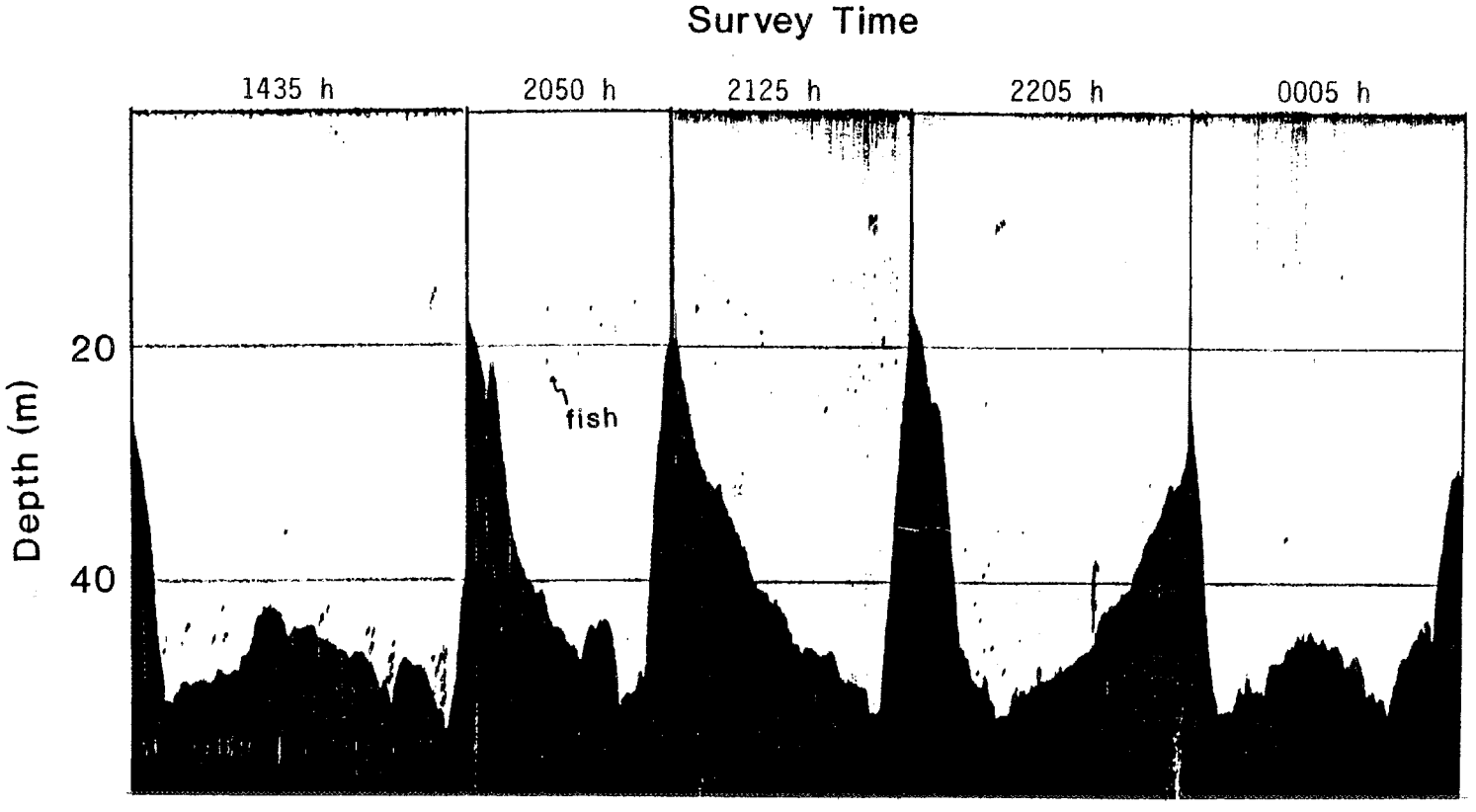

Figure II-16. Echograms recorded during June 1988 hydroacoustics survey showing the location of juvenile kokanee salmon for samples at nine different times of the day (continued on next page).

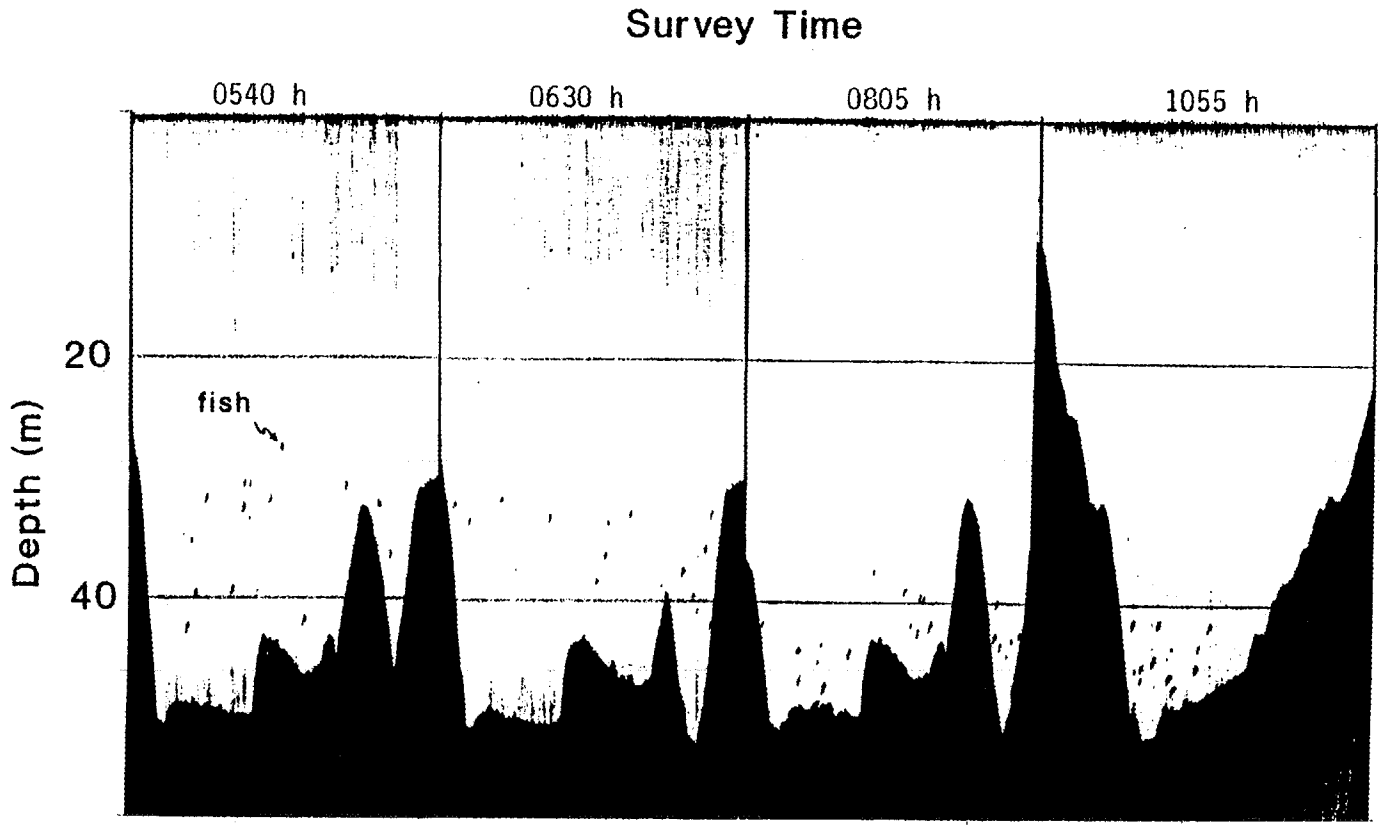

Figure II-16 (continued).

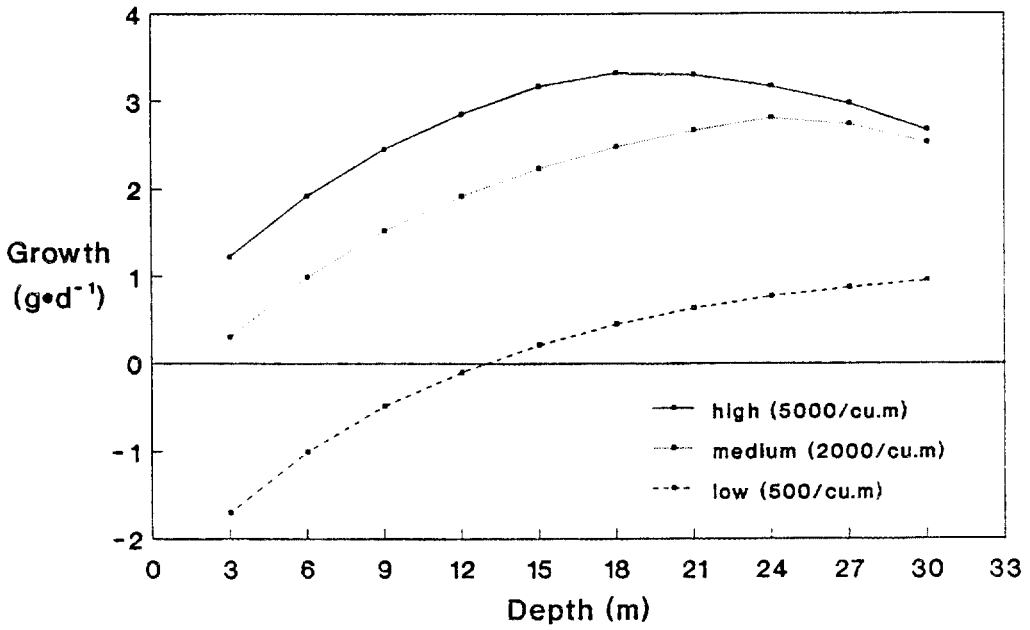

Figure II-17. Results of model simulations for growth at three prey densities with uniform vertical distribution and no vertical migration of kokanee.

important at 27 and 30 m, and the depth of optimal growth was therefore greater (24 m, 12.5°C). With the uniform-low database, the limitations on food consumption by digestion rate and stomach capacity were not important at all, and optimal growth was achieved at 30 m (9.5°C).

In simulations with the unimodal prey distributions (Figure II-6) and no vertical migration, the resulting growth-at-depth distribution was more reflective of the prey distribution (Figure II-18) than the previous example. With the unimodal-high database, maximum growth occurred at 9 m (20°C) even though the greatest prey density (and the highest feeding rate) occurred at 6 m (21.5). The increased food consumption at 6 m as compared to 9 m was offset by an even greater total energetic cost at 6 m due to the warmer temperatures. In addition, the difference in daily consumption between 6 and 9 m is not of the same magnitude as the difference in prey densities due to the effects of the physical limitations of feeding rate and stomach capacity. The most efficient depth for growth with the high prey densities was 12 m (18.5°C) where gross conversion efficiency was highest (28%). With the unimodal-medium and unimodal-low databases the depth of maximum growth is 6 m. At lower levels of food availability and consumption, stomach capacity doesn't have the same limiting effects as at higher prey densities, therefore, the growth-at-depth relationship more closely reflects the prey distribution.

The standard simulation (#4 in Table II-4) with the unimodal-high database generated growth rates ranging from 3.29 to -0.51 g/d (Table II-7). The most obvious result of these simulations is that there is a definite advantage to some type of vertical migration with this

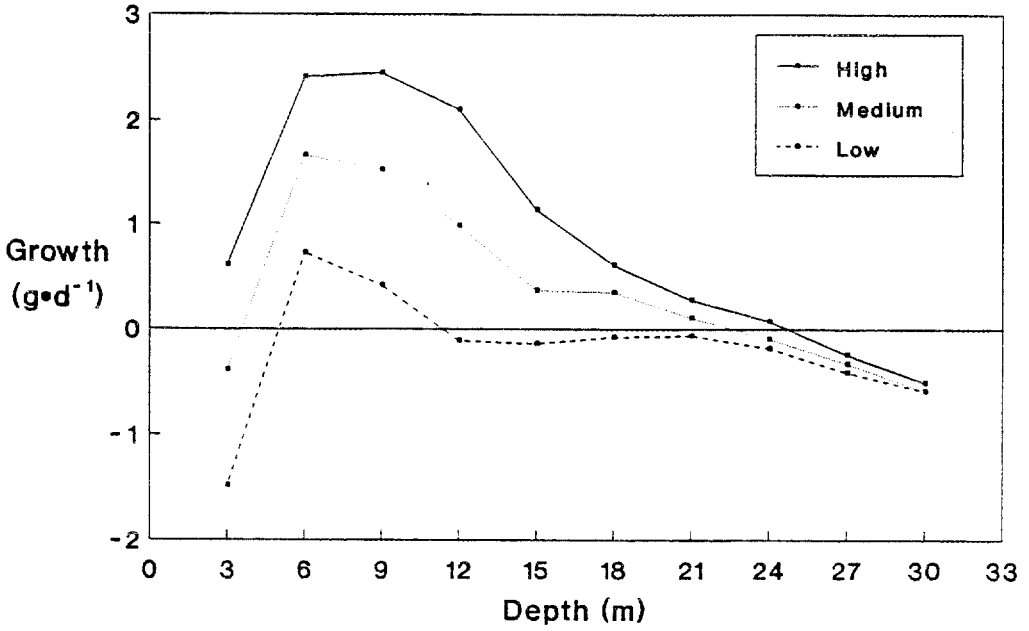

Figure II-18. Results of model simulations for growth at three prey densities with unimodal vertical distribution and no vertical migration of kokanee.

Table II-7. Results of the standard simulation for feeding at any of 10 depths and resting at that depth or lower. The simulation was run with a 500 g fish feeding for 12 h in a diurnal feeding mode with the high density/unimodal prey distribution.

Resting depth	Feeding depth									
	3	6	9	12	15	18	21	24	27	30
3	0.61									
6	0.89	2.41								
9	1.11	2.63	2.45				Growth (g/d)			
12	1.28	2.80	2.62	2.10						
15	1.42	2.94	2.75	2.23	1.14					
18	1.52	3.05	2.86	2.34	1.24	0.61				
21	1.61	3.13	2.95	2.42	1.33	0.69	0.28			
24	1.68	3.20	3.01	2.49	1.40	0.76	0.35	0.08		
27	1.73	3.25	3.07	2.54	1.45	0.81	0.40	0.13	-0.24	
30	1.77	3.29	3.11	2.58	1.49	0.86	0.44	0.17	-0.20	-0.51

prey/temperature database. Though the difference in growth among the 10 most productive migration patterns is slight, these patterns are similar and can be collectively summarized as feeding from 6-9 m and then moving to 15-30 m when not feeding (Figure II-19). The least growth occurred with little or no migration.

Because differences among the top five or ten most productive migration strategies are slight, in the analyses that follow the five migration patterns with the highest growth will be presented for evaluation instead of just the single migration pattern that produces the highest growth.

The effect of prey density was evaluated with the three levels of unimodal prey distributions (Figure II-5). A fourth level was created by multiplying the consumption at the high level by 2. The results indicate that at all prey levels the best strategy is to move to where the food is most abundant to feed and then to the coolest water when not feeding (Figure II-20). The differences in growth were as expected; higher levels of prey resulted in greater growth. The growth advantages of migrating as opposed to not migrating for each of the prey densities is illustrated in Figure II-21.

The effect of the amount of daily feeding was evaluated at durations of 4, 8, 12, and 16 h/d. At 4 h per day, feeding at 6 or 9 m was equally productive (Figure II-22). However, as feeding time increased, feeding at 6 m only produced the highest growth rates. The difference in growth is as expected - those that feed for a longer time grow more. The growth advantages of migration are particularly important at the shorter feeding durations (Figure II-23).

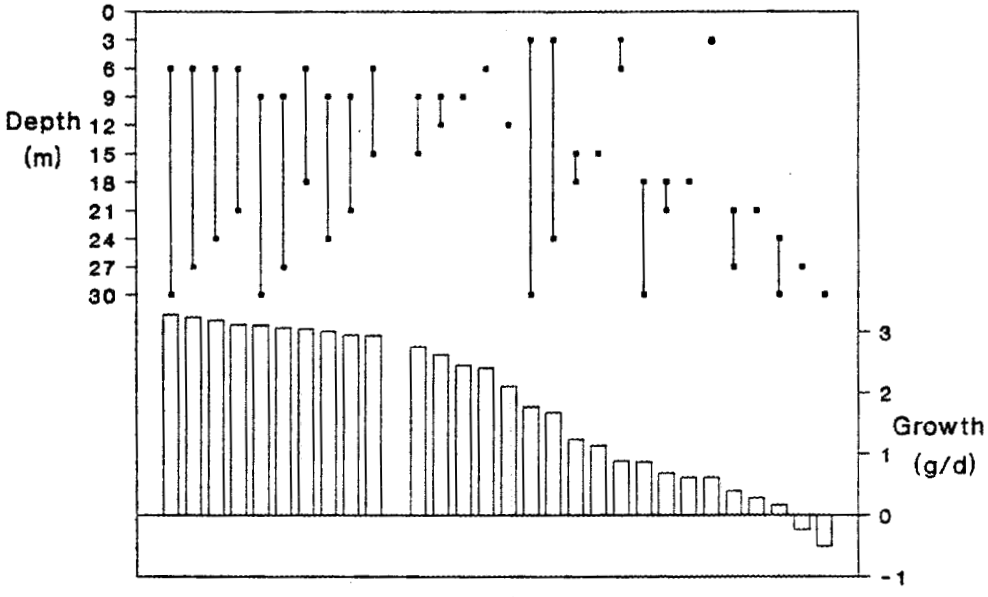

Figure II-19. Results of standard model simulation. Top half of graph indicates the combination of depths (either one or two) between which vertical migration occurred. Each histogram at the bottom indicates the growth resulting from the migration pattern directly above. The top ten producing migration patterns are shown left to right along with 19 other selected patterns.

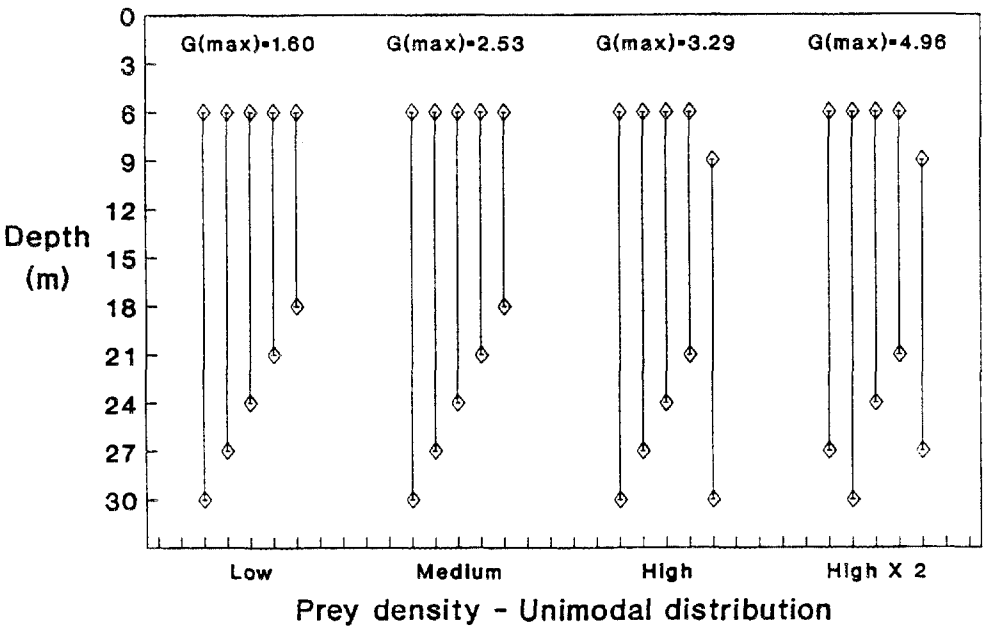

Figure II-20. The top five producing migration patterns (in order left to right) for each of four treatments of prey density. G(max) above each set indicates the daily growth (g) achieved by the highest ranked depth combination (the leftmost of the five patterns).

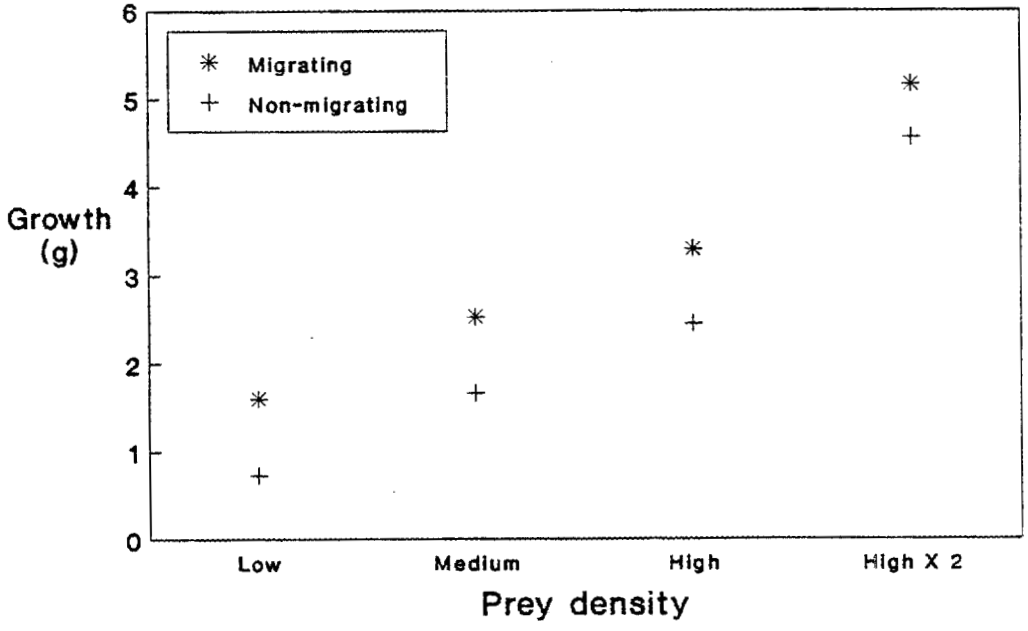

Figure II-21. Daily growth (g) of the highest ranked simulations for migrating and non-migrating kokanee salmon for each of the prey densities modeled.

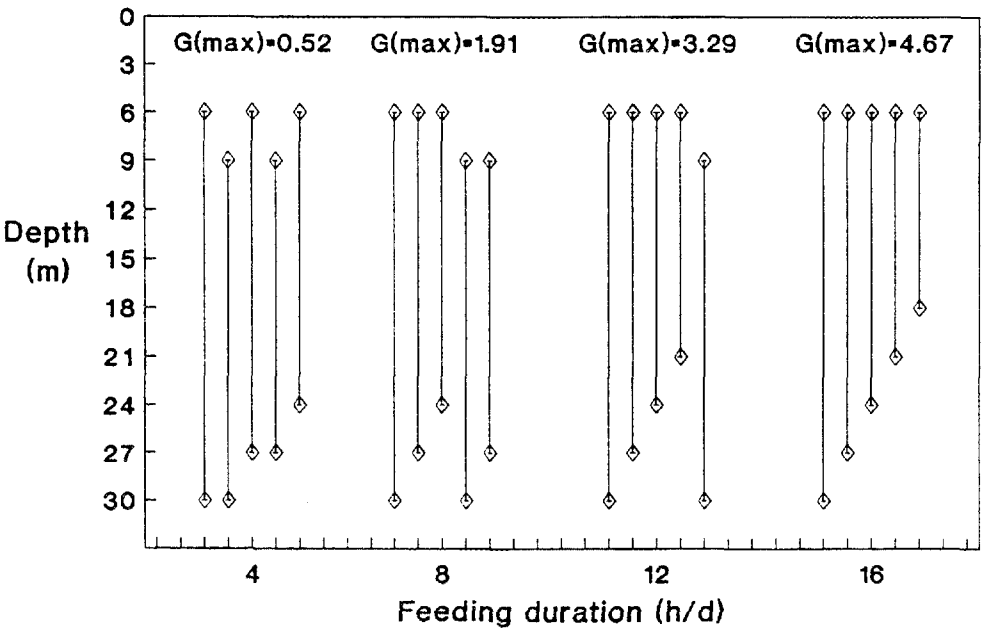

Figure II-22. The top five producing migration patterns (in order left to right) for each of four treatments of feeding time (h/d). G(max) above each set indicates the daily growth (g) achieved by the highest ranked depth combination (the leftmost of the five patterns).

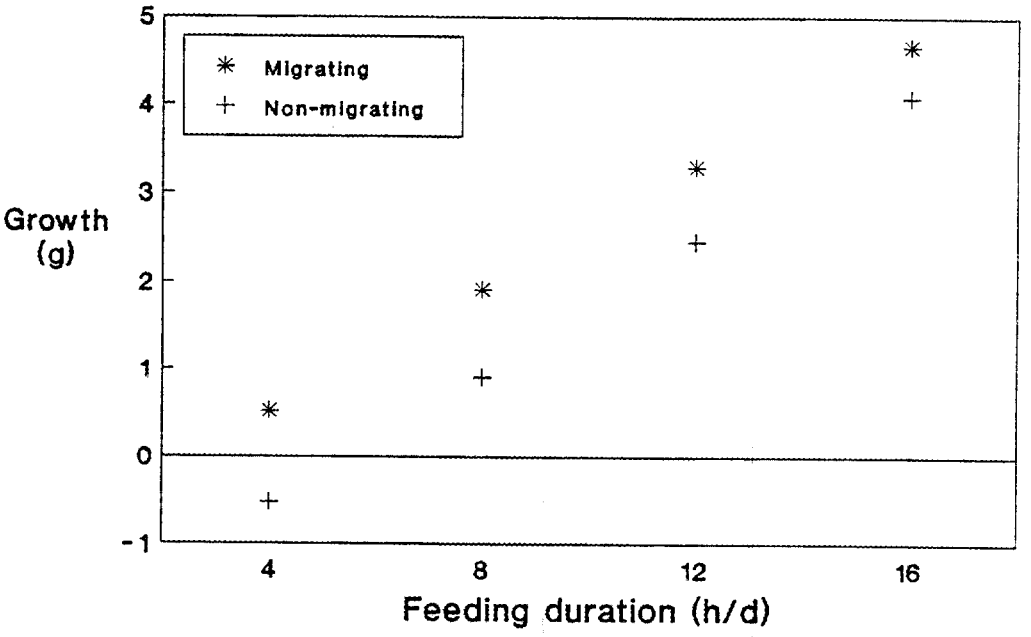

Figure II-23. Daily growth (g) of the highest ranked simulations for migrating and non-migrating kokanee salmon for each of the feeding durations modeled.

The effect of fish size on optimal strategy was evaluated for fish of 100, 500, and 1000 g. These results suggest that as size increases the upper limits of migration should be slightly deeper (Figure II-24). This pattern is largely due to a weight-specific differences in metabolic rate and stomach capacity. The advantages of migration are small for the 100-g fish, but become markedly more important as size increases (Figure II-25).

The effect of swimming speed (i.e., increase in active metabolism) on the migration strategy was evaluated by increasing the swimming speed during feeding from 20 cm/sec to 30 cm/sec. An additional simulation was performed to allow for an increase in consumption of the same magnitude (1.5 X) as the increase in swimming speed assuming that search volume and thus consumption increases proportional to swimming speed. With changes in swimming speed alone, the basic migration strategy remained the same, but growth was lower because of increased metabolic costs (Figure II-26). Increasing consumption along with swimming speed resulted in the same general migration patterns being most productive. Growth in this instance (i.e., increased speed and consumption) was greater than when the fish was at the normal swimming speed and rate of consumption.

To evaluate differences between diurnal and crepuscular feeding modes, comparisons were made between both modes at both low and high modal prey densities. For these simulations the diurnal feeding pattern was 12 h on:12 h off, and the crepuscular pattern was 6 h on:6 h off:6 h on:6 h off. No differences existed in optimal strategies between the

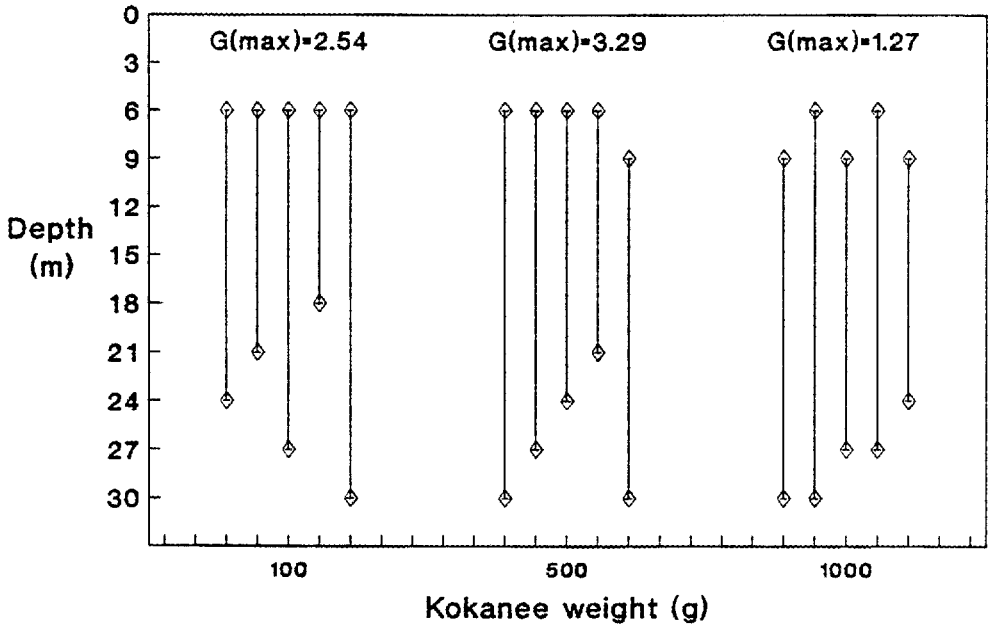

Figure II-24. The top five producing migration patterns (in order left to right) for each of three treatments of fish weight (g). G(max) above each set indicates the daily growth (g) achieved by the highest ranked depth combination (the leftmost of the five patterns).

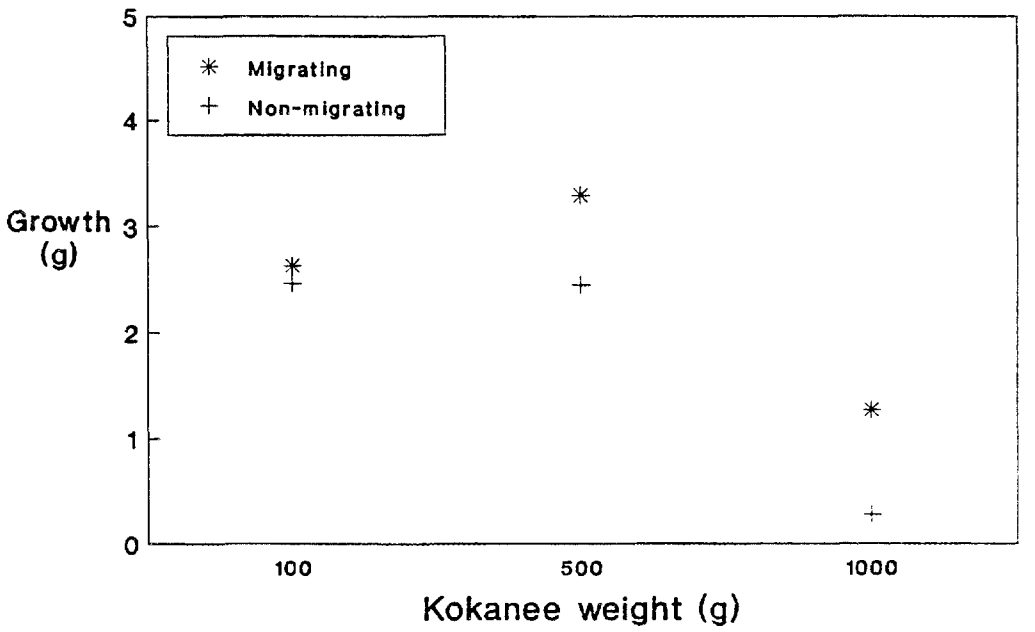

Figure II-25. Daily growth (g) of the highest ranked simulations for migrating and non-migrating kokanee salmon for each of the kokanee sizes modeled.

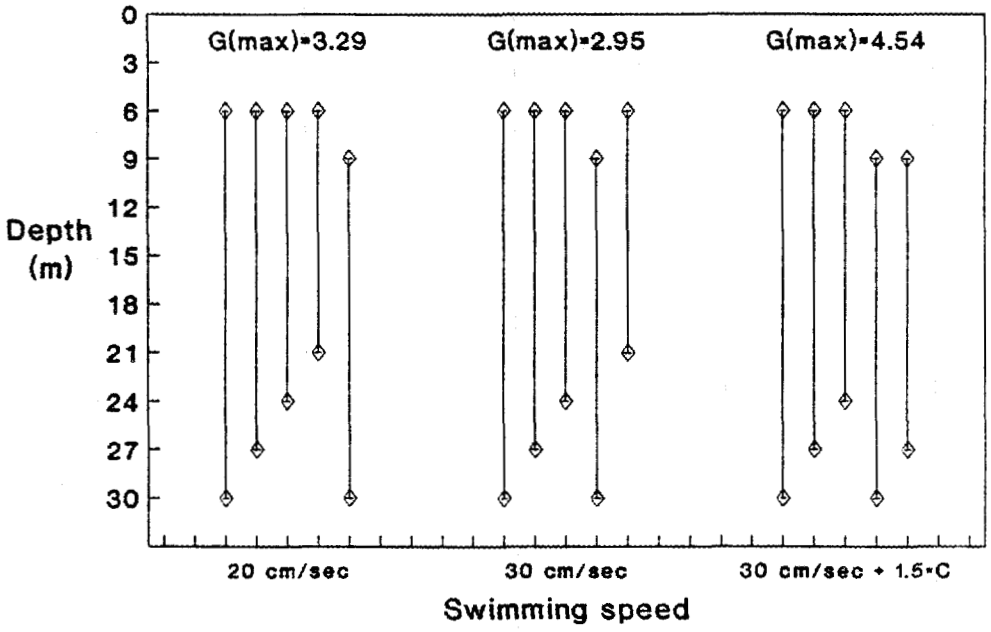

Figure II-26. The top five producing migration patterns (in order left to right) for each of three treatments of swimming speed and consumption. G(max) above each set indicates the daily growth (g) achieved by the highest ranked depth combination (the leftmost of the five patterns).

two feeding modes for either prey density (Figure II-27), and growth rates were nearly identical as well.

The standard simulation was also performed with the six actual prey/temperature databases to evaluate possible seasonal variation in optimal migration strategy. In the spring when water temperatures were < 20°C and a significant thermal stratification had not yet developed, the model predicts that kokanee should be migrating only 9 m or less through the water column (Figure II-28, May 1986). As the lake warmed in late spring and summer and stratification developed, migration distance increased to 9-24 m (Figure II-28, June 1985 and June 1987; Figure II-29, June 1988). In mid-summer and early fall, when prey densities were drastically reduced and the entire water column was warmer, the model predicts only limited migration deep in the water column (Figure II-29, July 1987 and October 1985). The apparent seasonal effect on the growth advantages of vertical migration are illustrated in Figures II-30 and II-31.

Data from the hydroacoustics surveys were used to test the predictions of the model. Model simulations with the July 1987 database predicted limited migrations (vertical range of 0-12 m) with most fish occurring at 18-30 m depth (Figure II-29, July 1987). These predictions and the results of the 1987 survey are quite similar. The gill netting data are also in agreement in that most of the kokanee were captured at 21-26 m (Figure II-11).

The simulations performed with the June 1988 database, which was the date of the 1988 hydroacoustics survey, were done with 500 g fish. Since the fish located in the survey were juveniles, additional

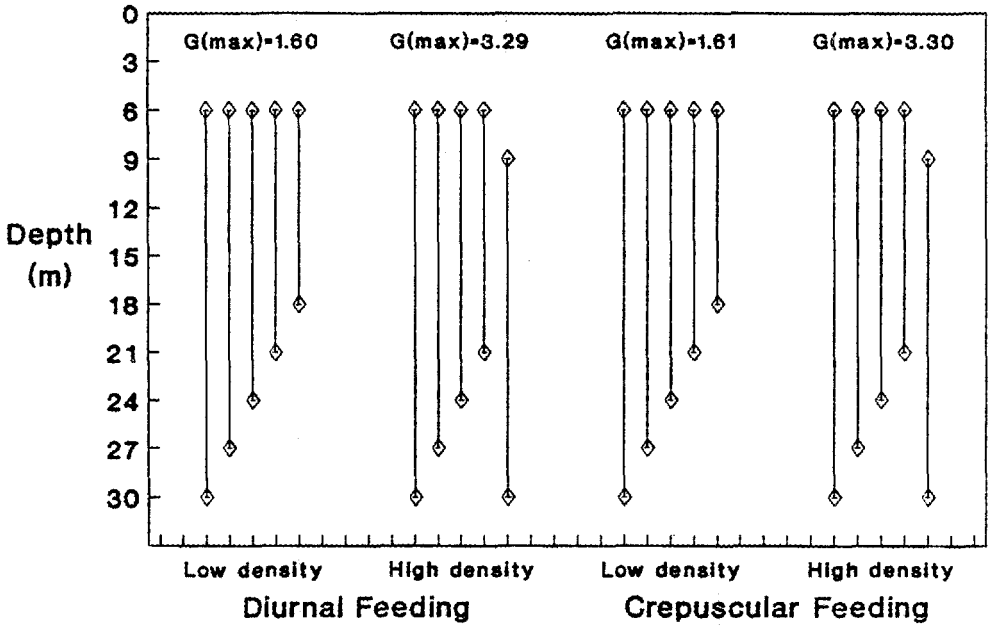

Figure II-27. The top five producing migration patterns (in order left to right) for each of four treatments of prey density and feeding mode (diurnal versus crepuscular). G(max) above each set indicates the daily growth (g) achieved by the highest ranked depth combination (the leftmost of the five patterns).

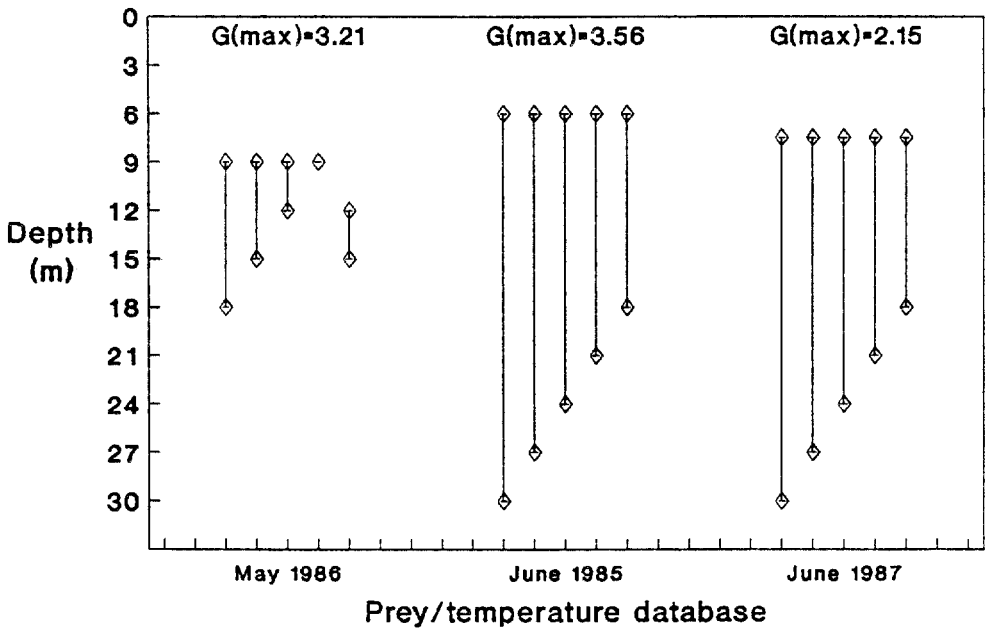

Figure II-28. The top five producing migration patterns (in order left to right) for each of three actual prey/temperature distributions from May 1986, June 1985, and June 1987. G(max) above each set indicates the daily growth (g) achieved by the highest ranked depth combination (the leftmost of the five patterns).

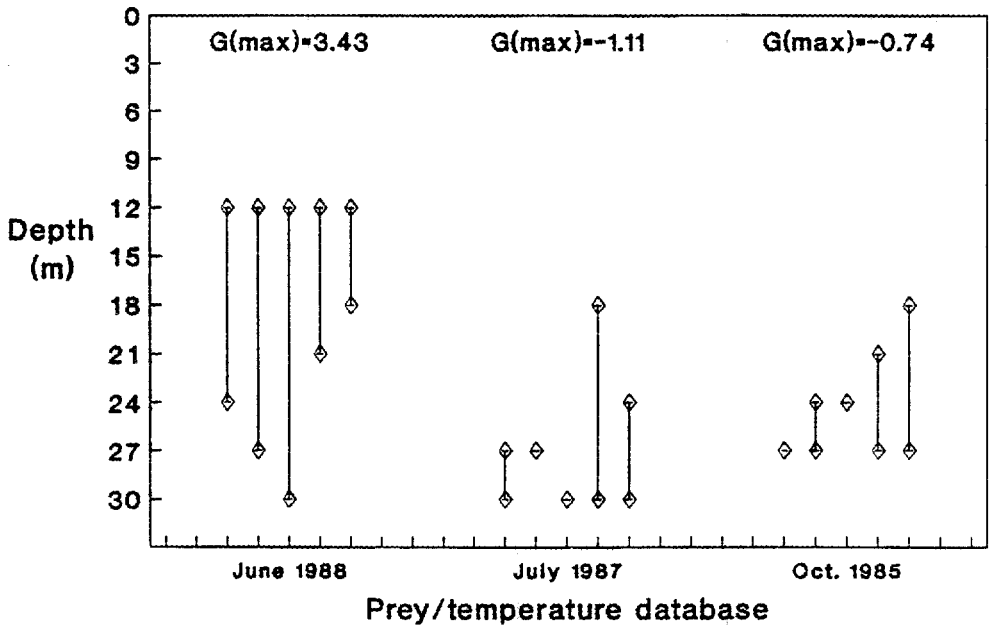

Figure II-29. The top five producing migration patterns (in order left to right) for each of three actual prey/temperature distributions from June 1988, July 1987 and October 1985. G(max) above each set indicates the daily growth (g) achieved by the highest ranked depth combination (the leftmost of the five patterns).

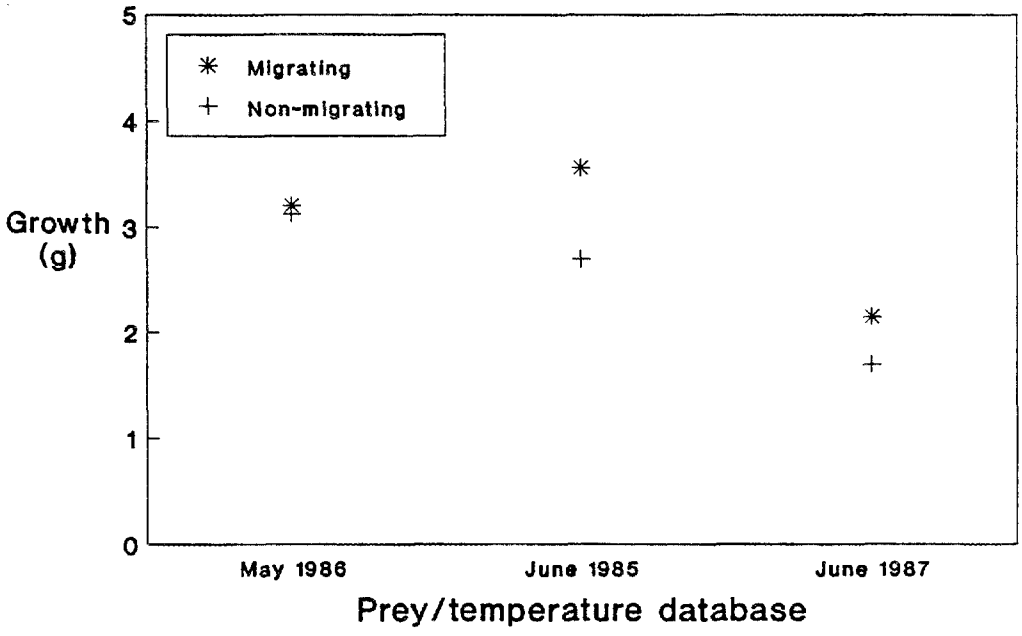

Figure II-30. Daily growth (g) of the highest ranked simulations for migrating and non-migrating kokanee salmon for each of the three actual prey/temperature databases from May 1986, June 1985, and June 1987.

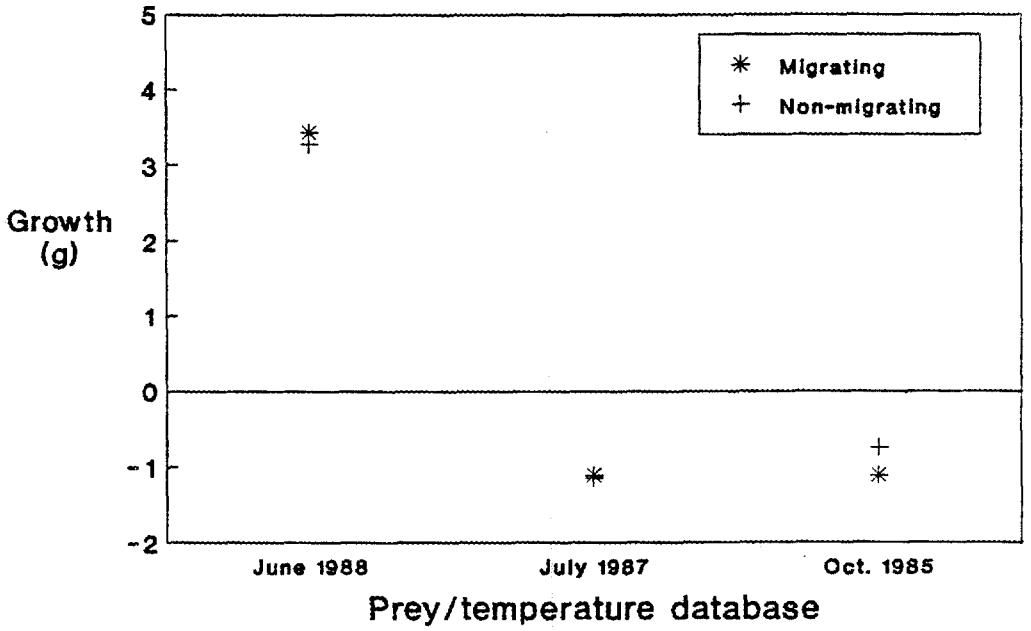

Figure II-31. Daily growth (g) of the highest ranked simulations for migrating and non-migrating kokanee salmon for each of the three actual prey/temperature databases from June 1988, July 1987, and October 1985.

simulations were performed for the June 1988 database with 100 g fish, the general size of the juvenile kokanee at this time. With diurnal migrations simulated, the greatest growth occurred with migration patterns in which feeding took place at 9 m and resting at 9-21 m (Figure II-32). These predictions did not match the observed patterns at all, which is probably a result of the upward migrations occurring at night when the prey distribution is different than at day. To better simulate the observed migration pattern, a night distribution of zooplankton was projected for this date (Figure II-10) based on the shape of the distribution of an actual night sample collected in June 1985 (Figure II-8). Simulations with this projected night prey distribution predicted that the greatest growth occurred when feeding at 3 m and then migrating downward to 9-21 m when not feeding. These are not too different from the observed pattern. Although the observed migration pattern (moving from 3 to 45 m) was not among the top five simulations with respect to growth, the growth achieved by migrating from 3 to 45 m (2.24 g/d) was only 4% less than that achieved by the highest rated migration pattern (2.33 g/d).

DISCUSSION

The principal finding of the modeling exercise was that when the preferred temperature and optimum prey density are spatially separated, some form of vertical migration will result in greater growth than not migrating. Because of the interaction of factors such as feeding rate, stomach evacuation rate, stomach capacity, and respiration rate, the most productive zone for feeding is not always the one with the greatest

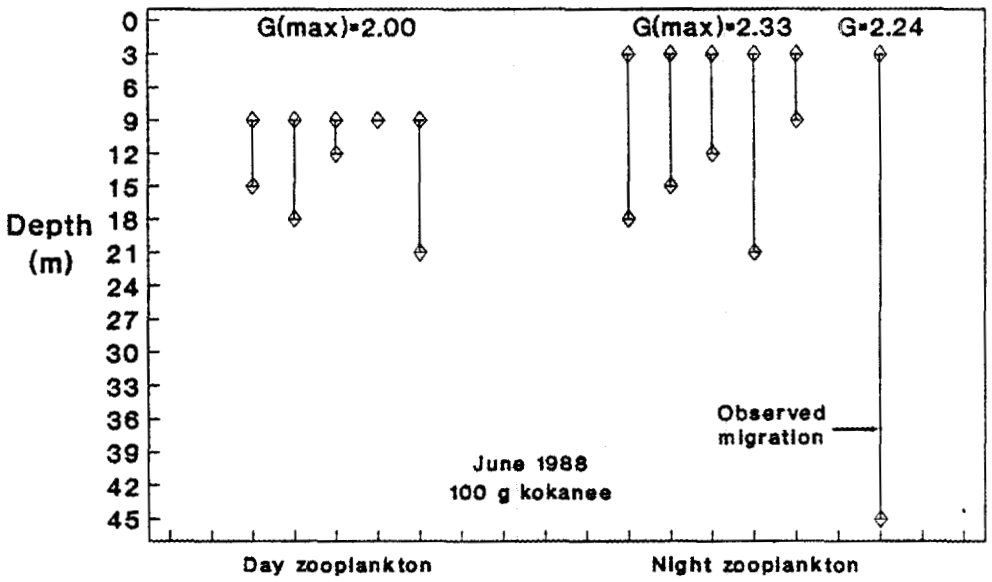

Figure II-32. The top five producing migration patterns (in order left to right) for 100 g fish with day and night prey distributions from June 1988. The pattern shown on the far right is the one most like that observed with hydroacoustics. G(max) above each set indicates the daily growth (g) achieved by the highest ranked depth combination.

food density. Likewise, the most productive zone for resting is not always that with the lowest metabolic cost. In addition the combination of depths that produces the highest growth rates is usually not the same as the combination which produces the highest conversion efficiency. These not so obvious predictions are partially a result of the short time step feature of the model, which allows for more interaction of the physiological processes than if each process were calculated as a single compartment for a 24-h period and then summed.

In general, the model seems to perform well as evidenced by results of the standard simulation where consumption rate was about 4.5% body weight per day, growth rate was slightly less than 1% body weight per day, and gross conversion efficiency was 35%. All of these are within the ranges expected for fish of this size when feeding at a high ration (Brett 1979).

Several assumptions within the model should not be overlooked in its evaluation. The effect of the time lag between a change in ambient water temperature and the body core temperature on respiration and other physiological functions was assumed to be negligible with regards to the predictions of the model since over the course of a day both heating and cooling of the same magnitude are experienced. Although, Weller et al. (1984) found that heat exchange occurred at a faster rate when heating than when cooling, these differences are not expected to have a noticeable effect on the predictions of vertical migration strategy. For more accurate predictions of growth, however, these considerations might need to be included.

Another important assumption in the model was that there was no

additional metabolic cost incurred due to vertical migration other than a change in respiration rate related to the change in temperature and swimming speed that accompanied each vertical migration. As a fish moves up or down in the water column its buoyancy changes due to changes in hydrodynamic pressure. A fish that is not at neutral buoyancy must compensate by active movement or by deflation or inflation of the swimbladder to remain at the same depth. Alexander (1972) estimated the additional cost of swimming activity needed to compensate for negative bouyancy by a shallow-acclimated fish that migrates to deeper water as approximately 25 cc O_2/kg/h (36 mg O_2/kg/h) while at the lower depth. Levy (1989) and Clark and Levy (1988) used this value to refute the energetic advantages of vertical migration. For the standard simulation in this study, this additional cost becomes about 0.7 Kcal/d which would reduce the daily growth by about 20%. This is possibly an overestimate for kokanee, because the swimming activity associated with feeding should account for much of the activity required to maintain position. Even with this reduction, the strategy of vertical migration is still more productive than not migrating at all. Alexander (1972) also estimated the cost of swimbladder inflation for buoyancy compensation as approximately 10 times less costly than active compensation. Though compensation via swimbladder volume control is the more economical, this method may not occur fast enough in salmonids to maintain a steady volume at the rate of depth change that has been observed. Unfortunately, the type of data required to make accurate calculations of the energetic costs of vertical migration of kokanee salmon are not available. Even Alexander (1972) states that there is so much

uncertainty in the data that it is difficult to make firm conclusions about the energetic advantages of vertical migration based only on the physical costs of vertical migration.

Due to a lack of information, it was also assumed that all sizes of kokanee had the same feeding rate to prey density relationship that was determined by Hyatt (1980). This assumption had some effect on the predictions of vertical migration as is discussed below, but is more critical to accurate predictions of growth. Information regarding differences in maximum feeding rate due to size for particulate-feeding fish was not found in a search of the literature. Certainly, fish can increase their effective search volume by increasing their swimming speed thus increasing their encounter rates, and large fish should be able to sustain increased swimming speeds for longer periods than small fish. Therefore, we might expect larger fish to have higher feeding rates especially at lower prey densities. At high prey densities, increasing the encounter rate may not make much difference if the limiting factor is handling time. In this model the swimming speed while foraging was also the same for all sizes. This is reasonable considering the feeding rates were the same for all sizes for any given prey density, but it would be more realistic to use size-dependent and prey density-dependent relationships to determine feeding rate and swimming speed if this information were available.

Several variables in the model were tested to determine their relative importance to the predictions of the model. Changes in the swimming speed within the range that it was varied did not noticeably affect the migration predictions. Varying the prey density from low to

high also did not result in different predictions of optimal migration strategy. However, had the shape of the prey distribution been changed, optimal migration patterns probably would be different as well. No substantial difference between the two feeding modes (diurnal and crepuscular) was evident under the combination of variables that were tested.

Small changes in the optimal migration patterns were predicted when the feeding time was varied from 4 to 16 h. As feeding time increased, consumption increased and migration priority seemed to shift from one of metabolic cost minimization (i.e., residing at the deepest depths, 24-30 m) to one of maximizing food intake (i.e., feeding at the level of highest food concentration, 6 m).

Similar changes were predicted when fish size was varied. Because fixed feeding rates (number of prey captured per minute) were the same for all sizes of fish, the 1000-g fish consumed less relative to its size than did the 100-g fish. This resulted in different migration priorities as above. The priority for the 100-g fish was to maximize food intake since it was able to consume at a high relative rate, while the priority for the 1000-g fish was to minimize metabolic costs.

When simulations were performed with actual prey/temperature distributions a seasonal pattern of migration strategies was predicted. In spring when water temperatures in the upper half of the water column are still relatively cool, migrations are short in distance and maintained within the upper portion of the water column. As temperatures warm and thermal stratification progresses, migrations include nearly the entire water column. As the summer progresses the

upper limit of the migrations becomes deeper due to increased temperatures. And by late summer and early fall when prey densities are greatly reduced, the benefits of vertical migration are greatly diminished as well.

Comparing the predicted range of occurrence (Figures II-28 and II-29) with the depths where kokanee were actually captured in the nets (Figures II-7 to II-12) indicates a relatively good match, especially for the May 1986, June 1988, and July 1987 samples. Unfortunately, no information regarding migration patterns can be obtained from the net data since the precise time of capture of individual fish could not be determined.

A better test of the model is to compare the predictions with the hydroacoustics data. For July 1987 the model predicted generally limited migration in the bottom half of the water column, 12-30 m. The general migration pattern of those fish tracked during the hydroacoustics survey was to concentrate around 24 m at night and then move upward to feed during the day somewhere between 12 and 17 m. In this case the model did a fair job of predicting the actual migration pattern.

To provide testable predictions for the June 1988 data additional simulations were performed with a projected night prey distribution and with 100 g fish. The model correctly predicted ascension to the top of the water column to feed but underestimated the depth when not feeding. However, the correct depth combination (3 to 45 m) was ranked eleventh out of 120 possible combinations, and the resulting growth was only 4% less than that obtained by the top ranked combination. The resulting

growth of the night simulations was slightly higher than that of the day simulations even though the maximum prey density was lower than that during the day. Lower growth occurred during the day because the amount of food that could be processed at the depth of highest prey concentration (12 m) was limited by the cooler temperatures (6°C less than at 3 m). Although predator avoidance is a reasonable explanation for juvenile kokanee to feed at night, these results suggest that there can be energetic advantages as well.

The migrations of the juvenile kokanee observed in this study were similar to those of juvenile sockeye observed by Narver (1970) and Brett (1971a). Although the small descent in the middle of the night displayed by sockeye was not evident in the kokanee surveys, the kokanee data do not preclude such movement. Whether this secondary migration has any energetic benefit is testable with the current model. Simulations were performed with fish moving from 30 m when not feeding to 3 m to feed at dusk and dawn. Between dusk and dawn a secondary migration was simulated to 6, 9, 12, 15, or 30 m or remaining at 3 m and the resulting growths compared (Figure II-33). Highest growth occurred when the secondary migration went to 6 or 9 m, though growth was nearly the same at 3 and 12 m. The differences in this example are small, but this exercise suggests that under some conditions migrations similar to those observed by Narver (1970) can have an energetic basis. Though the growth of this feeding pattern (for a few hours only at dusk and dawn) is less than feeding continuously throughout the night, it is probably more realistic. Small fish can become satiated in a few hours and might stop feeding until dawn when the stomach has partially evacuated.

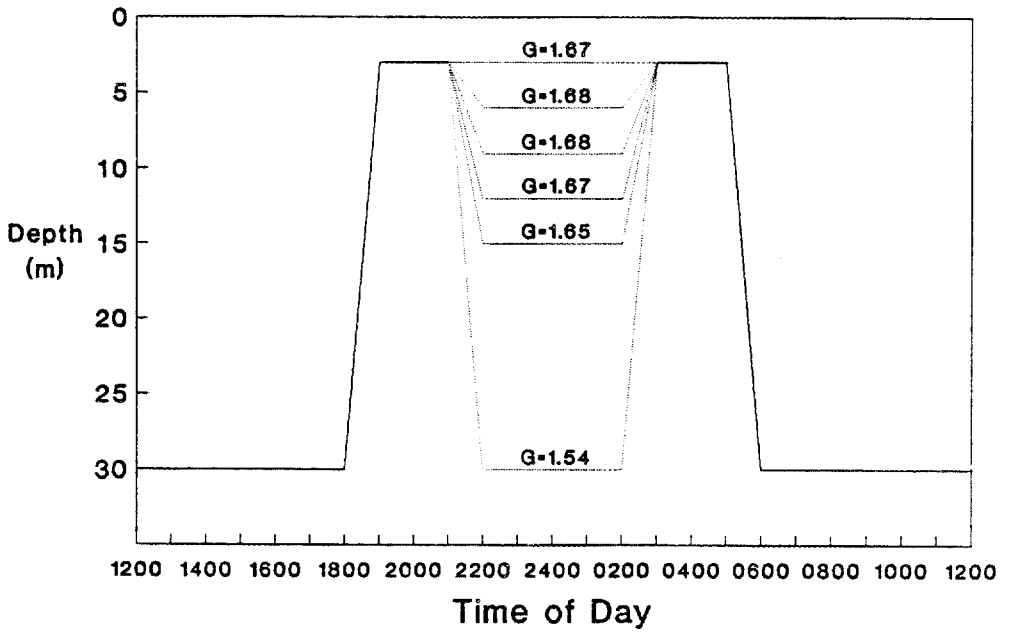

Figure II-33. Results of vertical migration simulations of the possible secondary migration patterns like those observed by Narver (1970). The dotted lines represent the different depths simulated for the night descent. On each line is the resulting daily growth (g) of the simulation using that depth.

The predator avoidance hypothesis is purported by some as the basis for migration patterns observed in sockeye and kokanee salmon (Eggers 1978; Clark and Levy 1988). Certainly this factor can not be discounted for juveniles, particularly in light of the apparent differences in migration patterns between juveniles and adults. Within the constraints imposed by predation (i.e., feeding at night) the migrations observed are energetically sound. However, to consider that a single factor hypothesis can explain the vertical migration of even a single species is unreasonable given the variety of seasonal and size-related differences. A multi-factor approach with individual factors receiving different value depending on seasonal and ontogenetic considerations seems to be the most sensible approach to understanding vertical migration in aquatic organisms.

CHAPTER III

RELATIVE IMPORTANCE OF TEMPERATURE, FOOD, AND PHYSICAL STRUCTURE TO HABITAT CHOICE BY SMALLMOUTH BASS IN THE FIELD AND LABORATORY

INTRODUCTION

As described in Chapter I, habitat selection by fish has a direct effect on its potential growth and survival. Levels of preference and avoidance have been described for many habitat variables for many species. A compilation of this information results in a list of characteristics that supposedly describe the ideal habitat for a species. For example, habitat qualities for lake-dwelling adult smallmouth bass as described by several investigators can be summarized as low turbidity, rock or gravel substrate, 20-25°C temperature, abundant cover (i.e., tree stumps, fallen trees, rock ledges, and boulders), and abundant forage (i.e., small fish and crayfish) (Coble 1975; Coutant 1975; Miller 1975). Realistically, however, all of these ideal components are rarely found in the same place at the same time. In any one habitat some variables may be within this ideal or "preferred" range while others may occur only within a broader "acceptable" range. With different combinations of optimal and sub-optimal features present, selection of the appropriate habitat becomes more difficult.

In this study habitat selection by smallmouth bass was evaluated as it related to those habitat variables that are associated with the growth maximization strategy as described in Chapter I. To minimize

the effects of predator avoidance on habitat choice, as large a fish as possible were used in the field (> 300 mm) and laboratory (>250 mm) studies. To minimize the effects of spawning on habitat selection the field studies were performed after the spawning season in early spring.

Two habitat variables which have a major influence on growth are temperature and food availability. Fish usually demonstrate a preference for a narrow range of temperatures (Reynolds 1977). The preferred temperature range is assumed to be that at which physiological processes, such as digestion and assimilation of food, are most efficient (Crawshaw 1977). Studies by several investigators to determine the preferred temperatures of smallmouth bass have been summarized by Coutant (1975) and Reynolds and Casterlin (1976). Because of a variety of complicating factors (e.g., acclimation temperature, season, age, physical health, geographic origin, field versus laboratory procedures), determination of a single preferred temperature for adult smallmouth bass is difficult if not impossible (Reynolds 1977). Age and size-related differences in temperature preference are well documented (Ferguson 1958). Younger fish prefer higher temperatures than older ones, which probably explains much of the variation between temperature preferences determined in the laboratory (usually with juveniles) and those observed in the field (usually for adults). With these factors taken into consideration, the preferred temperature range of juvenile smallmouth bass is therefore assumed to be 26 to 31°C, and 21 to 26°C for adults.

Because of thermal stratification during summer in most

southeastern reservoirs, the preferred temperature of adult smallmouth bass often occurs in deeper off-shore areas. In Melton Hill Reservoir in Tennessee the 24°C isotherm is normally deeper than 3 m during much of the summer (Figure III-1). Typical prey items, such as small sunfishes and crayfish, are often concentrated in shallow near-shore areas which may exceed 30°C in mid-summer. Therefore, during summer stratification, smallmouth bass that select their preferred temperature are often spatially separated from their preferred prey along a thermal gradient (Figure III-2).

Given the above descriptions of prey and temperature distributions, the choice of a single habitat for smallmouth bass means either residing nearshore where food is abundant but energetic costs (particularly basal metabolism) are high due to warm temperatures, or residing off-shore where energetic costs are low but food is less abundant. An alternative to selecting a single habitat would be to move between habitats on a regular basis. For maximum net energy gain, smallmouth bass could move into the littoral zone to feed and then move offshore to deeper, cooler waters to reduce metabolic costs. Diel movement patterns for the combined purpose of feeding and thermoregulation have been proposed for several fish species (Northcote et al. 1964; Narver 1970; Janssen and Brandt 1980; DeMartini et al. 1985; Wurtsbaugh and Li 1985). Emery (1973) and Helfman (1981) observed smallmouth bass moving from shallow waters to deeper waters at night where activity slowed and eventually stopped.

The first objective of this study was to determine if smallmouth bass in Melton Hill Reservoir displayed the type of diel movement

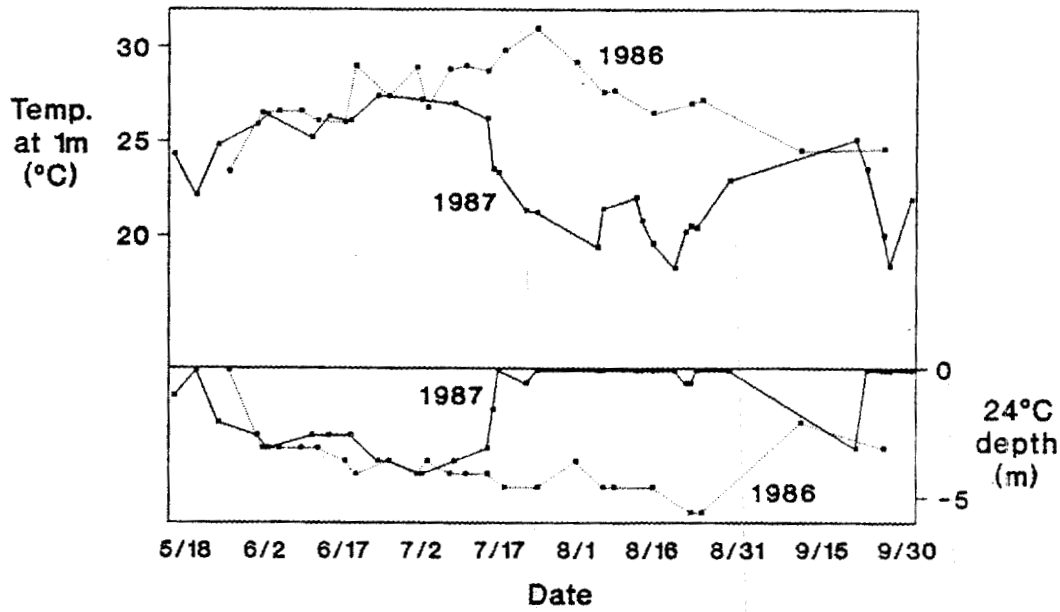

Figure III-1. Summer temperatures (°C) at 1 m of depth (top half of figure) and the depth (m) of the 24°C isotherm (bottom half of figure) in Melton Hill Reservoir in 1986 and 1987.

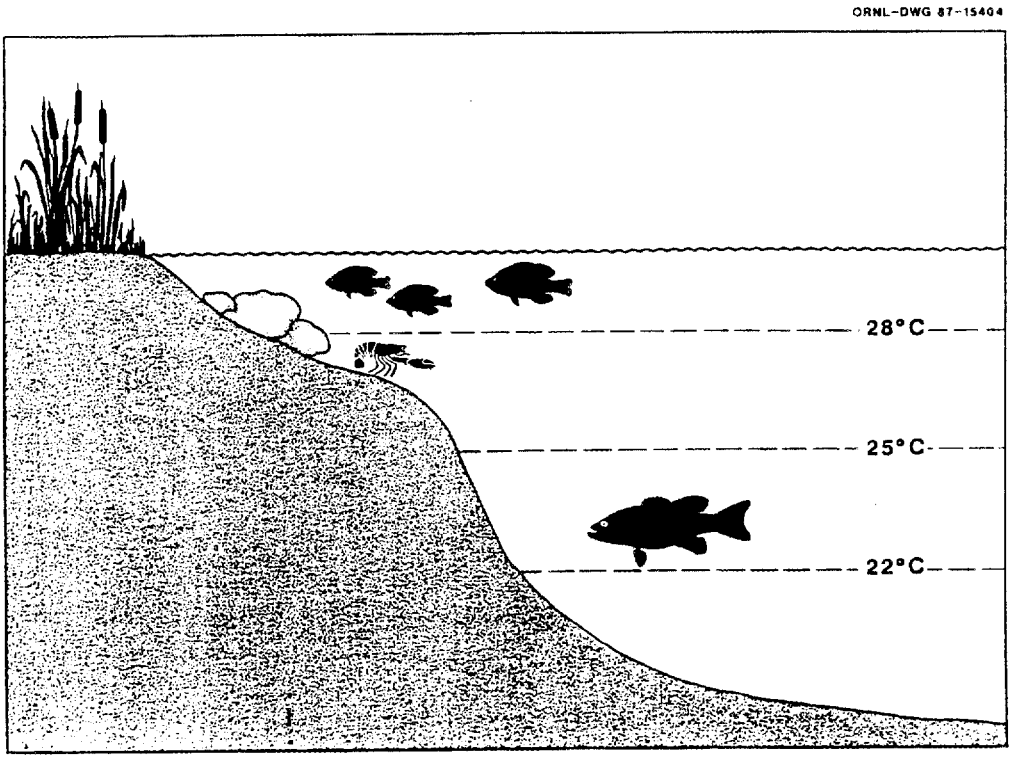

Figure III-2. Typical mid-summer distributions of smallmouth bass, their prey, and temperature in Melton Hill Reservoir. The smallmouth bass is located within its preferred temperature range.

described for smallmouth bass in other systems. Movements of individual smallmouth bass were observed with the use of ultrasonic transmitters implanted into the fish. Telemetry has been used by others to track smallmouth bass movements and habitat selection (Peterson and Myhr 1977; Hubert and Lackey 1980; Gerber and Haynes 1988), but those studies were not designed to observe the short-term daily movements that are of interest in this study.

The initial results of the telemetry study provided data which indicated that some variables might be more important than others in dictating habitat choice. The second objective of this study, therefore, was to investigate the relative importance of some of these variables (temperature, food, and cover) as they relate to habitat selection. This was accomplished with controlled laboratory experiments in a thermal gradient tank. In particular, these experiments evaluated the effect of ration, food availability, and cover on temperature selection. The effect that these variables and their interactions have on activity was also evaluated.

METHODS

Lake Description

The telemetry study was performed in Melton Hill Reservoir, a 2270 ha mesotrophic reservoir on the Clinch River in eastern Tennessee. Melton Hill Reservoir (impounded in 1966) has a mean depth of 6 m and a maximum depth of 21 m. This reservoir can be characterized as riverine in nature with a mean residence time of only 18 d, a length of 71 km, and a maximum width of approximately

0.6 km. The study area was located in the middle of the reservoir (between river miles 34 and 40). Thermal stratification of the reservoir is impacted by a density underflow of cold water from a hypolimnetic discharge from the upstream Norris Reservoir. Because this discharged water becomes well oxygenated after its release, Melton Hill Reservoir offers a wide range of well-oxygenated thermal habitats throughout the summer.

Ultrasonic Telemetry

Temperature-sensitive, ultrasonic transmitters were surgically implanted into the abdominal cavity of adult smallmouth bass (560-2130 g, 368-542 mm) during spring and summer of 1986 and 1987 (Table III-1). Length and weight of one smallmouth bass were inadvertently not measured, but were within the ranges mentioned above. Smallmouth bass were collected by electrofishing, returned to the laboratory after capture, and held for a few days before and after implantation to monitor health and recovery. After surgery, fish were released into Melton Hill Reservoir at their original site of capture. Six smallmouth bass were tagged and released in both 1986 and 1987.

Transmitters were cylindrical in shape (65 mm in length, 16 mm in diameter, and 22.5 g weight in air (10.2 g in water)) with an 85-mm tail and thermistor which extended outside of the body of the fish to monitor ambient water temperature. Transmitter signals were calibrated at known temperatures in the laboratory. The expected life of the transmitters was approximately 1 y.

Tagged fish were located with an underwater directional

hydrophone connected to a sonic receiver (Smith Root model TA25). Signals were received at 71, 75, or 79 kHz. Those tags transmitting on the same frequencies were differentiated by individual codes within the signal. Ambient temperature was determined by measuring time intervals between signal pulses. Transmitters were tested at various depths to ensure that neither depth nor temperature stratification had noticeable effects on signal reception.

Tagged fish were located by employing a mobile survey by boat from the point where a fish was last located. Each day that a fish was located was considered one fix. For example, two fish located on the same day was two fixes, while one fish located twice in one day was just one fix. Once located, a fish was often monitored continuously for several hours during the day. The ambient water temperature of the fish's position was determined from the transmitter signal. The general position relative to the shoreline was estimated by triangulation, and the depth of the fish was estimated by comparison to a vertical temperature profile measured at the location with a Hydrolab Surveyor II temperature/dissolved oxygen meter. The fish's position and temperature were recorded about every 10 min, but more often if the fish was rapidly changing position. All tracking and limnological measurements were performed at a sufficient distance to avoid disturbing the fish. Movement of the fish while being tracked was noted on maps and linear distance was estimated to nearest 5 m with the use of shore markings every 50 m. The length of shoreline travelled over the course of the study was calculated for each fish as an estimate of its linear range of

activity, Activity data, which included the proportion of time spent moving and the distance travelled, were analyzed for each hour of the day for each fish to determine diel patterns of activity.

Laboratory Experiments

Experimental subjects

Smallmouth bass (249-299 mm and 160-332 g) used in the laboratory experiments were collected from Melton Hill Reservoir by electrofishing. Experimental fish were held in individual cages (3 cages per tank) in 1.5-m diameter fiberglass tanks at 20°C. A 14-h light:10-h dark cycle was used for both the gradient tank and the holding tanks. The amount of food (live fish) consumed in the holding tanks and the weight of each smallmouth bass were monitored to maintain the fish on a slightly greater than maintenance ration.

Thermal gradient tank description

Laboratory experiments were performed in a 565-L fiberglass tank (Figure III-3). The actual experimental area of the tank was 5.0 x 0.31 x 0.25 m (volume = 388 L). Four perforated PVC pipes were positioned along the bottom of the tank to supply water of four different temperatures to different areas of the tank. By varying these temperatures, a horizontal gradient of 7°C could be established along the length of the tank. An overflow pipe was located at one end of the tank, and screens were placed 45 cm from each end to prevent fish from moving into the corners of the tank. During the experiments, a top (an inverted fiberglass tank of similar dimensions) was lowered onto the tank to prevent outside

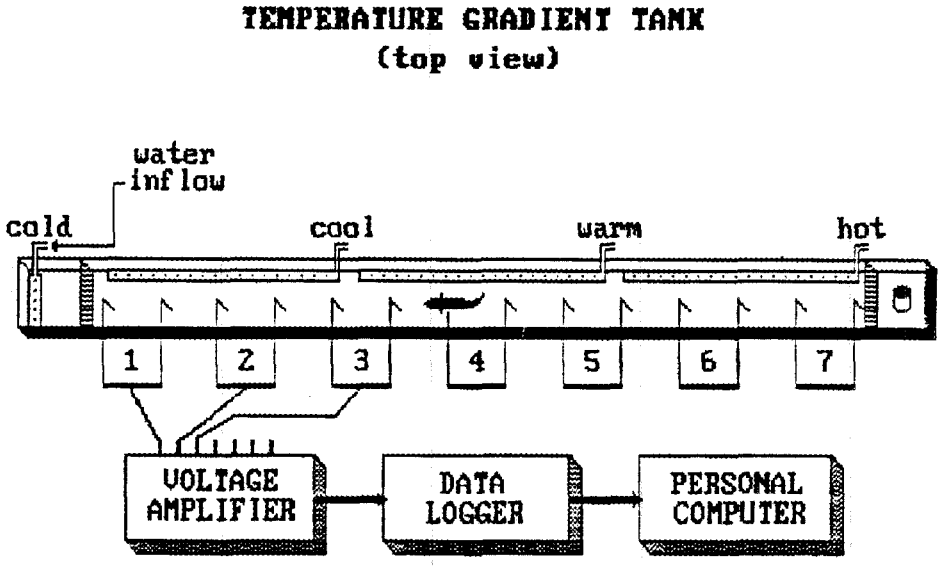

Figure III-3. Diagram of thermal gradient tank used in laboratory experiments.

disturbances. A string of small lights mounted inside the top produced an even light source over the length of the tank. These lights were on a 14:10 h light:dark cycle. Mirrors mounted inside the top allowed visual observation of the fish through peepholes. Temperature was continuously monitored with 12 thermistors placed along the length of the tank and attached to a 12-channel chart recorder.

Fish position in the tank was monitored electronically. This system was modeled after those of Spoor et al. (1971) and Spoor and Drummond (1972). Seven pairs of stainless steel wire probes were placed along the length of the tank (equidistant from the tank sides) and wired to a voltage amplifier which was in turn connected to a microcomputer interface (Omega Engineering Model WB40) connected to a personal computer (Zenith Model Z-181). Each wire probe extended from just above the water surface to within 2 cm of the bottom. That part of the wire that was above the water and extended into the first 2 cm in the water was covered with rubber tubing to insulate it from interference, especially at the water surface. As a fish moved near a wire probe the voltage potential between that pair of probes changed. The variance of the voltage potentials for each pair was calculated every 26 s (approximately 3325 times per day) and recorded to disk. A high variance in the measured voltage potential indicated the fish was at or passed through that position in the tank during the previous 26 s. The position of the fish (+ or - 35 cm) was continuously monitored in this manner for the length of the experiment. For analysis purposes, the tank was considered to be

composed of seven cells or positions to correspond to the seven pairs of probes. This system was periodically tested by visual observation to ensure its accuracy.

Data analyses

The proportion of time spent by the fish at each of the seven positions was calculated for each day. When the fish occurred in more than one position during any 26-s time interval, that time interval was divided equally among those positions. Likewise, when a fish remained between two positions, the system recognized it as being in both positions so the time was split between those two positions. The mean tank position (MeanP) and the percent time spent at the warm end of the tank (PCW, the sum of time spent at positions 5, 6, and 7) were calculated for statistical analyses. Activity was measured as the difference in distance between each successive position reading and summarized as distance moved per hour.

The statistical analysis was similar throughout the various laboratory experiments. Analysis of variance (ANOVA) tests were performed to determine the significance of the effects of interest. When a significant effect was identified the Student-Newman-Keuls (SNK) multiple comparisons test was performed for a more in-depth analysis of the effect. These tests were performed on the three measures of fish position and activity described above (MeanP, PCW, and Activity). All results were analyzed at a significance level of $\alpha=0.1$ unless otherwise noted. For comparisons of the actual distributions of the time spent at the seven positions, simple t-tests were performed to determine if the amount of time spent at

any one position differed from a uniform distribution (14.3% of time at each of seven positions) which would be expected if position was chosen randomly without regard to any features of the tank. Statistical tests will be further described for each experiment below when necessary.

The following experiments were designed to test the effect of three important environmental factors (ration, food availability, and cover) on position (i.e., temperature) selection and activity within the tank. Information from these tests were then used to evaluate and interpret the results of the field telemetry study.

Uniform temperature experiment

To test whether any features of the experimental tank (other than those being manipulated) affected the position selected by the fish, a control experiment was designed with uniform conditions where the temperature was maintained at 24°C throughout the tank. The position of five fish (tested individually) was monitored for 1 d each under the control conditions. This test was primarily conducted to determine fish preference for or avoidance of any particular part of the tank, particularly positions 1 and 7 at the ends of the tank. An analysis of variance (ANOVA) F-test was performed to determine if any differences existed in the amount of time spent at the seven positions.

Ration experiment

This experiment was designed to test the effect of prior ration on temperature selection within a thermal gradient of 21 to 28°C.

With this gradient, positions 1 to 7 correspond to temperatures of 21.5 to 27.5°C by 1°C increments. Five fish were individually tested with each of two treatments. These treatments were administered before the fish was placed in the gradient tank. A low ration treatment was established by withholding food from the fish for 7 d prior to the fish being placed in the gradient tank. The second treatment consisted of maintaining the fish on a high ration (1.5 times maintenance) for 7 d prior to being tested. No feeding took place while the fish was monitored in the gradient tank. Other than the treatment period (7 d prior to experiment) and the experimental period, fish were maintained on a maintenance ration. The order of treatments was alternated among the fish to minimize any possible effect of treatment order. A fish was transferred from the holding tank to the gradient tank and allowed to acclimate for 24 h before commencement of each experiment. The position of the fish within the tank was continuously monitored for 3 d. Each experimental day began and ended at 1200 hours (noon).

The factorial ANOVA included Ration, Day, Time of Day, and Fish as factors. In addition to testing the effect of the ration treatment, the effects of different fish, day of experiment, and time of day (dark versus light) were also tested. Differences in levels of activity were tested for in a similar manner except that time of day was analyzed for four time periods to investigate the presence of crepuscular or diurnal activity patterns. These time periods were morning (0600-1059 hours), midday (1100-1559 hours), late afternoon/evening (1600-2059 hours), and night (2100-0559 hours).

Food availability experiment

This experiment was designed to test the effect of food availability and the level of feeding on temperature selection. The temperature gradient was maintained at 24 to 31°C. With this temperature gradient, positions 1 to 7 correspond to temperatures of 24.5 to 30.5°C by 1°C increments. This range was chosen in an effort to offer temperatures that were noticeably warmer than the expected preferred temperatures. The fish were challenged to spend time in the warmest part of the tank by offering food only at the warm end (position 6).

Eight fish were tested individually in 4-d trials. Experimental days began and ended at 0900 hours. One day of acclimation was allowed before the experiment commenced. The first experimental day consisted of no treatment in order to determine a base temperature selection by the fish. The results of day one served as a control with which to compare the treatment effects from subsequent days of the experiment. On the second day a live prey item was offered three times during the day (0900, 1100, and 1300 hours). Prey items, small sunfishes (Lepomis sp.) or fathead minnows, were tethered with a piece of fine thread so that they remained at a single position (#6) in the tank (Figure III-4). The prey item was easily removed from the thread and consumed by the smallmouth bass. None of the fish had experienced feeding in this manner prior to the actual experiment, but they learned quite quickly. The treatment on day three was the same as that on day two. On both days the combined weight of the three items consumed each day was 1.5 to 2.5% of the weight of the

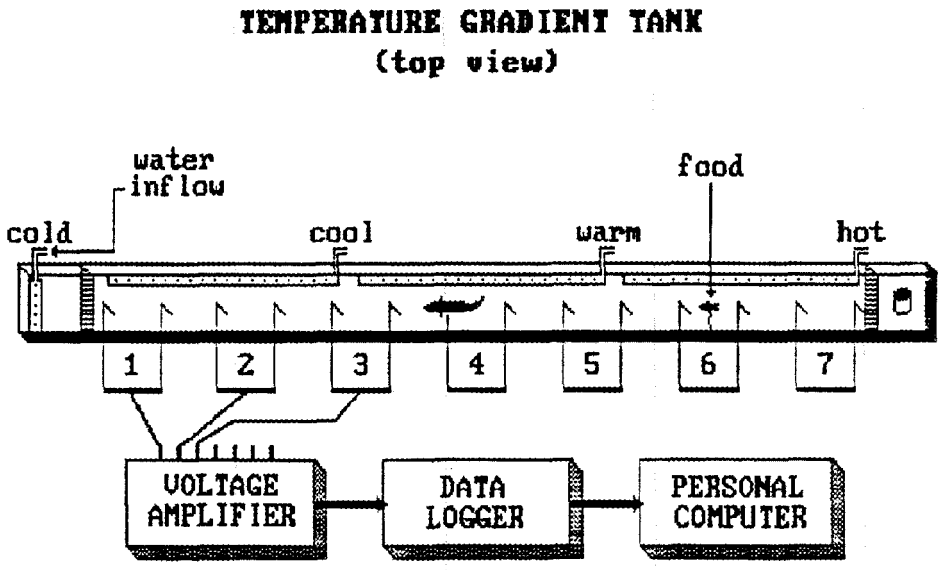

Figure III-4. Diagram of thermal gradient tank as used in the food availability experiment with prey item presented on tether at position 6.

smallmouth bass (i.e., an approximate maintenance ration at the preferred temperature). On day four, prey items were repeatedly presented at position #6 from 0900 to 1200 hours as fast as the smallmouth bass would consume them. Although food was left in the tank till 1200 hours, the fish usually became satiated in the first 1 or 2 h and feeding ceased after that. The amount consumed on day four ranged from 10.1 to 27.3 g or 4.1 to 11.9% the predator's weight. Only the data from the first, third, and fourth days were used in the analysis. Day two was considered as a learning day for the smallmouth bass to learn where prey was presented and how to remove it from the tether.

The ANOVA tests (with factors Treatment, Time of Day, and Fish) were performed to determine the effect of level of feeding (no food, maintenance or satiation), differences among fish, and time of day on position selection and activity. Because of differences in experimental design from the previous experiment, the four time blocks for analyzing activity were changed slightly to early morning (0600-0859 hours), the feeding period (0900-1259 hours), afternoon/evening (1300-1959 hours), and night (2000-0559 hours).

Cover experiment

This experiment was designed to test the effect of cover and temperature on position selection. The temperature gradient was maintained at 24 to 31°C. The treatments in this experiment were the presence of cover(s) at different positions in the tank. The cover was an aluminum cylinder (length = 29 cm, diameter = 20 cm) placed with the open ends toward the ends of the tank (Figure III-5). Six

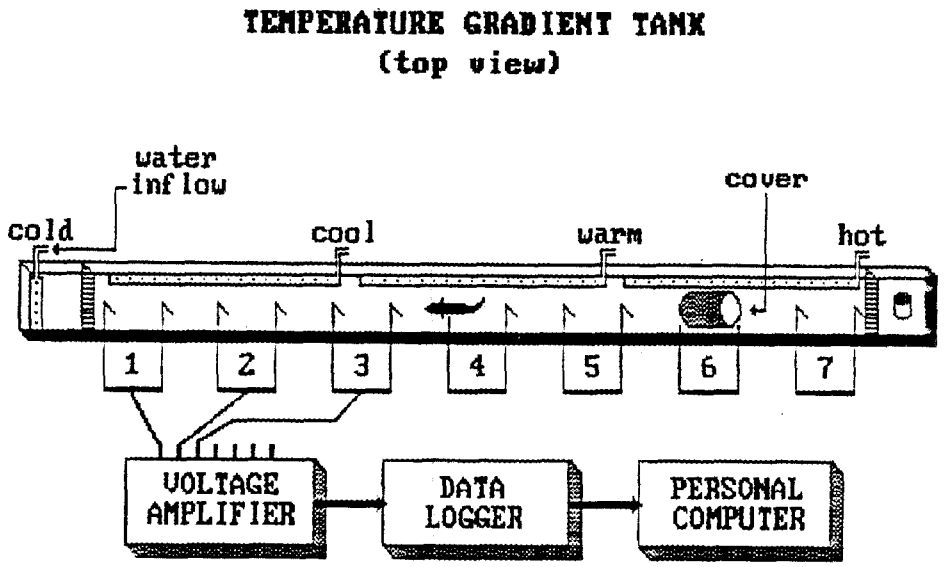

Figure III-5. Diagram of thermal gradient tank as used in the cover experiment with cover at position 6.

smallmouth bass (not previously used) were tested individually in 5-d trials. Experimental days began and ended at 0900 hours. Each smallmouth bass was placed in the tank for 1 d of acclimation before the five days of treatments began. Five randomly assorted daily treatments (1 per day) were as follows: no cover in the tank, cover at position 1 (cool end of tank), cover at position 4 (middle of tank), cover at position 6 (warm end of tank), and covers at positions 1, 4, and 6 simultaneously. This randomized complete blocks design (Sokal and Rohlf 1981) resulted in each of the six fish receiving these five treatments in a different order. Cover positions were changed each day between 0900 and 0930 hours, and the first hour (0900 to 1000 hours) was omitted from the analysis because of possible disturbance to the fish when cover position was changed. The time spent at each position and activity were determined for each day as in previous experiments.

The ANOVA tests (with factors Cover, Time of Day, and Fish) were performed to determine the effect of cover position, differences among fish, and time of day on position selection and activity. Again, because of differences in experimental design from the previous experiments, the four time blocks for analyzing activity were changed slightly to early morning (0600-0859 hours), midday (1000-1459 hours), afternoon/evening (1500-1959 hours), and night (2000-0559 hours).

RESULTS

Ultrasonic Telemetry

Smallmouth bass tagged in 1986 were located on 11 of 19 days of tracking from May 28 to October 29 plus two days in 1987 (February 25 and March 6). Because of limited success due to problems with equipment, transmitters, technique, and loss of fish to anglers, data collected in 1986 were insufficient for appropriate analysis; however, this effort did serve to identify and resolve problems with procedures and equipment. The data that were collected, however, suggested that fish occupied the littoral zone habitats most of the time, including mid-summer when nearshore water temperatures exceeded 28°C. The tracked fish were also often associated with some type of physical structure (i.e., overhanging bushes, fallen trees, and boulders).

Tracking of smallmouth bass tagged in 1987, resulted in 55 fixes during 40 days of tracking from May 18 to November 13 (Table III-1). Only on three of the 40 d were no fish found. Three of the four tags (numbers 249, 258, and 2264) that were still tracked 1 mo after release apparently strayed from calibration as evident by tag-estimated temperatures that were higher than available temperatures. Tag malfunction prevented determination of the exact temperature and depth of these three fish throughout the study, although the general location of the fish with regard to distance from shoreline and proximity to visible physical structure could still be estimated from triangulation. The tags appeared to lose calibration gradually, and

Table III-1. Lengths, weights, and tracking information on smallmouth bass tagged with transmitters in 1987.

Fish no.	Length (mm)	Weight (g)	Date released	Last fix	Total fixes
249	---	----	06-26-87	08-05-87	10
258	425	1004	06-12-87	11-13-87	15
267	542	2130	08-13-87	10-07-87	7
2228	378	560	06-12-87	06-26-87	4
2264	406	760	05-15-87	08-27-87	19
2336	492	1680	06-02-87	06-04-87	1

the data collected during the first month after release were assumed to be reasonably accurate. During the first month following release, 22 fixes were made on the six tagged fish. The temperatures occupied by these fish were within 1°C of the maximum temperature available most of the time (Figure III-6). A comparison of these occupied temperatures to temperature profiles taken on those days indicated that all of the fish were in the top 1.5 m of the water column. Some of the occupied temperatures were greater than the maximum available temperature at that time, but usually within 1°C. This temperature discrepancy probably resulted from using offshore temperature profiles as an estimate of inshore temperatures. Temperatures inshore at less than 1 m of depth were found to differ from temperatures collected 10-100 m from shore at the same depth by up to + or -1.7°C. These differences could be due to several possible factors (e.g., wind speed and direction, presence or absence of direct sunlight, and currents related to hydropower operation). Regardless of the inshore temperatures, tagged fish (including those data collected after the tags lost calibration) appeared to be within 3 m of the surface and 5 m of the shore most of the time. Except for crossings of small embayments, smallmouth bass were not found in the open water or crossing the main channel of the reservoir. The linear range of activity for the four fish tracked on seven or more occasions ranged from 840-1680 m with a mean of 1258 m.

When bass were stationary they were often associated with various types of physical structure that were visible from the

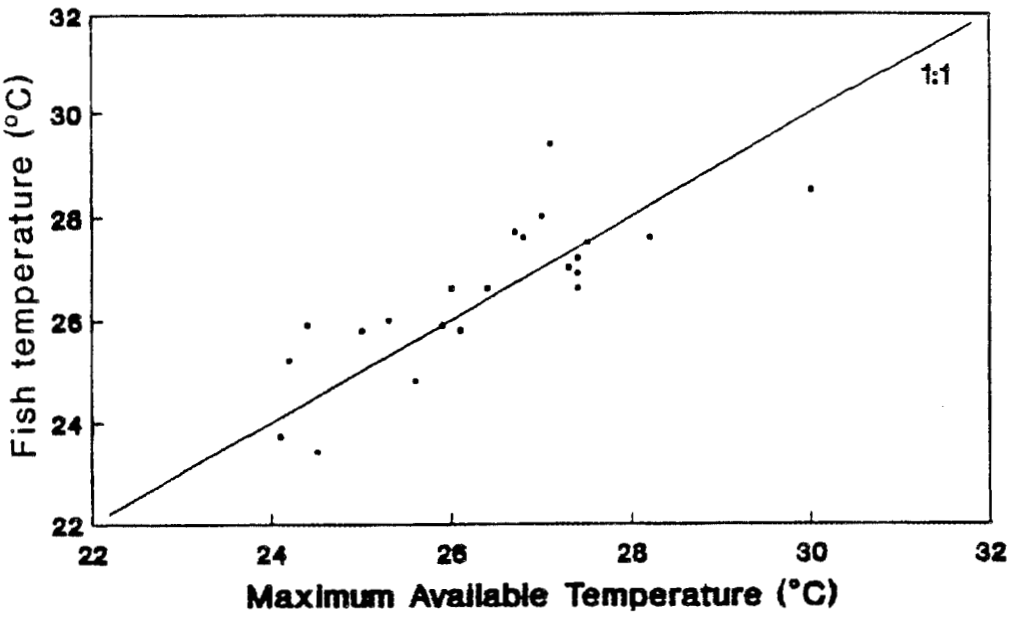

Figure III-6. Temperature (°C) occupied by six tagged smallmouth bass plotted against maximum available temperature in Melton Hill Reservoir during the first month after release (1987 fish only).

surface. These included fallen trees, submerged logs, boulders, over-hanging bushes, and man-made fish attractors.

Abnormal climactic conditions in 1987 probably impacted the movement of the smallmouth bass as well. Several months of less than normal rainfall and hotter than normal air temperatures during August in 1987 created abnormal thermal conditions in Melton Hill Reservoir. As the demand for electrical power in the region increased (due to increased air-conditioner use), hydropower generation increased at the upstream reservoir and at Melton Hill Reservoir. This subjected Melton Hill Reservoir to a greater than normal influx of cold hypolimnetic water which greatly reduced temperatures in the study area at the hottest time of the year (Figure III-1). These low temperatures were probably beneficial to the smallmouth bass populations, but not to the completion of the objectives of this study. Nearshore temperatures did not reach the levels expected during the hottest part of the summer and thus there was less incentive for smallmouth to leave the nearshore areas.

Activity analysis was performed on the data from four fish tracked for more than 12 h each (Table III-2). Total number of hours in direct contact with these four fish was 107 h. Fish were tracked during all hours of the day (Figure III-7), but only one fish tracked on one occasion accounted for the time between 2300 and 0600 hours. Pooling data for all bass showed that they were actively moving about 6.7 h (28%) of the 24-h day. Considering only daylight and twilight hours (roughly 0530 to 0930 hours), bass were active nearly 42% of the time. The mean movement speed (distance travelled per time

Table III-2. Movement and activity of smallmouth bass in Melton Hill Reservoir as determined with ultrasonic telemetry. Rate of movement was calculated as the distance moved per time moving. Daily movement was estimated with values of "Percent time moving" and "Rate of movement".

Tag no.	Time tracked (min)	Time moving (min)	Percent time moving	Rate of movement (m/min)	Daily movement (m)	Shoreline range (m)
249	798	296	37	4.7	2527	840
258	2881	1073	37	6.5	3477	1680
267	1996	288	14	7.5	1555	1510
2264	744	124	17	3.4	825	1000
Totals	6419	1781			1243	
Means	1605	445	28	4.2		1258

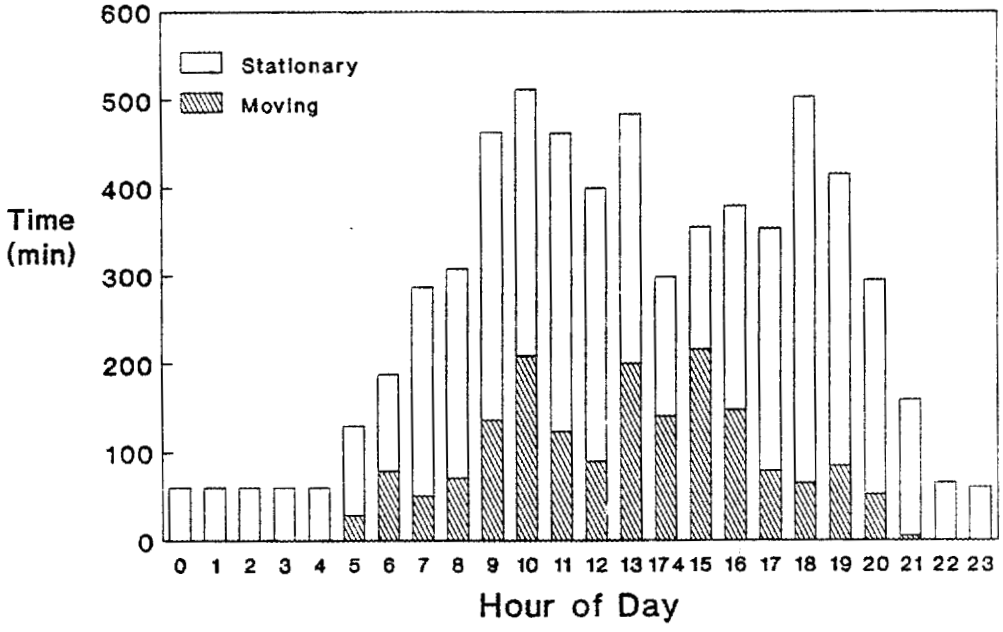

Figure III-7. Total time (min) of actual contact with four tagged smallmouth bass for each hour of the day in 1987 partitioned between time spent stationary and moving.

moving) for all bass was 4.2 m/min. The distance travelled per hour was estimated as the product of the proportion of hour spent moving and the movement speed (m/min) of that hour times 60 min/h. A comparison of distance moved per hour throughout the day suggests that activity peaks at midday and is greatly reduced during the night (Figure III-8). The distance travelled per day was similarly estimated as the product of the proportion of the day spent moving and the movement speed (m/min) times 1440 min/d. Estimates for individual fish ranged from 825 to 3477 m/d and for all fish was 1243 m/d (Table III-2).

Laboratory Experiments

Uniform temperature

Under uniform temperatures, no difference was found in the amount of time spent at any of the seven positions (ANOVA, $p=0.19$, 6 d.f.). According to individual t-tests, the times spent at the ends of the tank, positions 1 (13.1%) and 7 (13.5%) (Table III-3), were not significantly different from the value that would be expected if all positions were selected with equal probability (1/7 or 14.3%) suggesting no end-of-tank effect on position preference or avoidance. Positions 4 and 6 were selected significantly less than expected (4.0% and 7.3%, respectively), but this is probably a result of small sample sizes or short experiment length as there are no apparent physical characteristics of the tank that would explain this result.

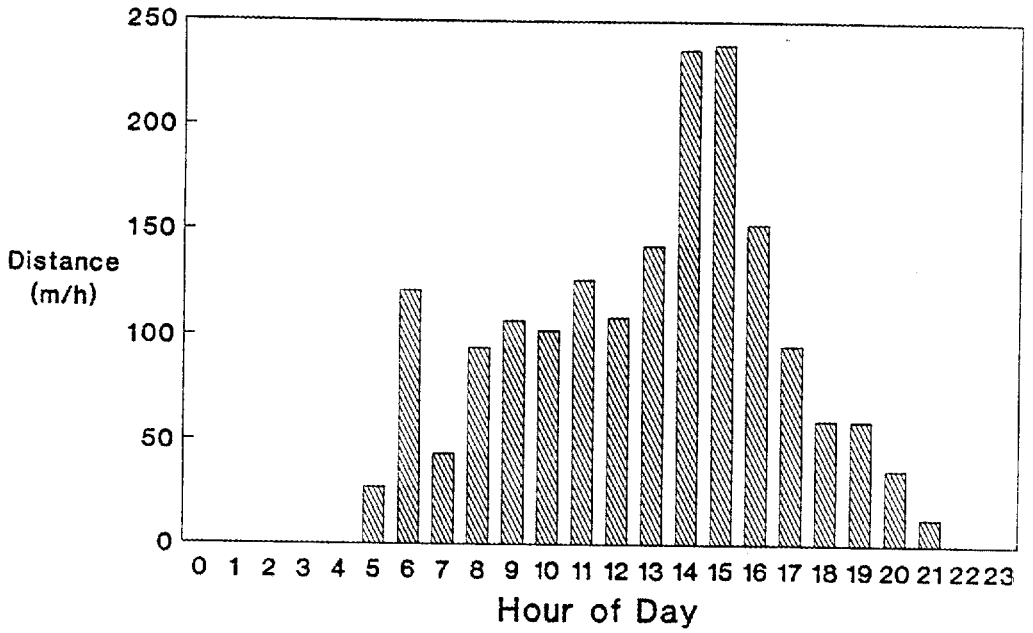

Figure III-8. Average estimated distance moved per hour by four tagged smallmouth bass in 1987.

Table III-3. Mean percent time spent at each of seven positions (standard errors in parenthesis) during the uniform temperature experiment with no treatments. Means with an asterisk (*) are significantly different (α=0.1) from the expected value (14.3) given a random choice of position.

	Tank Position						
	1	2	3	4	5	6	7
No treatment	13.1 (6.5)	10.6 (5.3)	34.9 (15.2)	4.0* (1.2)	16.7 (8.9)	7.3* (2.8)	13.5 (7.6)

Ration

Among fish variation was significant in this experiment, but the effect of the two ration treatments on position selection as measured by PCW or MeanP was not significant (Figure III-9 and Table III-4). There was also no significant time (dark versus light) effect. Day effect was significant, however, for MeanP (but not for PCW) and was interpreted as a possible trend toward the selection of cooler temperatures as the experiment progressed from day 1 to day 3. Since there was no effect of ration on temperature selection, data for both rations, all fish, and all days were pooled to investigate position selection (Figure III-10). The time spent at position 5 (25.5°C) was significantly greater than that expected if choice of tank position was random, and the time spent at positions 1 and 7 was significantly less than expected (Table III-5). There is no difference in the amount of time spent at positions 2 through 6 suggesting that there is a general preference for a range of temperatures (approximately 22.5 to 26.5°C) with a more precise preference for 25.5°C.

The effects of the tested variables on activity (m/h) were similar to those on position selection, that is, no effect of ration, but significant fish and day effects (Table III-4). Whereas no dark/light differences were found in position selection, significant time of day effects on activity were found (Tables III-4 and III-6). Activity peaked in the morning and decreased throughout the day reaching a minimum during the night.

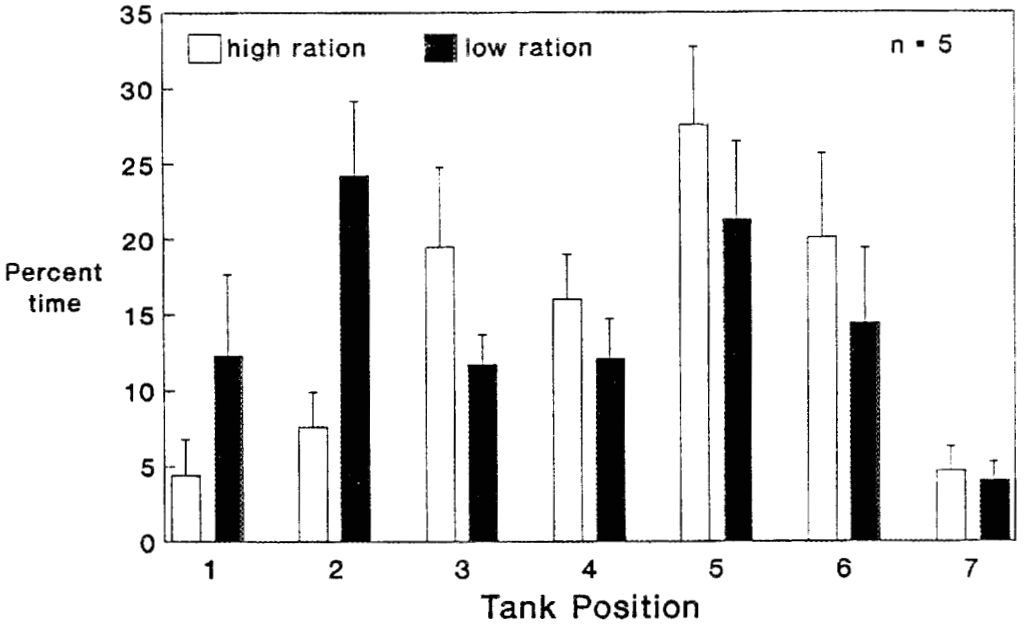

Figure III-9. Percent time spent by smallmouth bass at each of seven positions in thermal gradient tank for two ration treatments. The temperature gradient within the tank was 21-28°C from position 1 to 7. Each bar represents the mean (+1 S.E.) for five fish over three days.

Table III-4. Results of ANOVA for the ration experiment. Asterisks symbolize statistical significance (* significant at α=0.10; ** significant at α=0.05). The time variable for mean position (MeanP) and percent time at the warm end (PCW) consisted of two blocks of time while for Activity (meters moved per hour) it consisted of four blocks of time. The degrees of freedom in parentheses are those for the analysis of activity.

Source of variation	Degrees of freedom	F ratio		
		MeanP	PCW	Activity
Ration	1,4	0.95	0.59	0.00
Time	1,4 (3,12)	1.25	3.32	19.04**
Day	2,8	3.55*	2.03	3.26*
Fish	4,8 (4,24)	118.13**	82.91**	116.70**
Ration*Time	1,4 (3,12)	0.63	1.90	1.13
Ration*Day	2,8	0.01	0.93	0.20
Ration*Time*Day	2,8 (6,24)	0.45	0.30	0.88

Table III-5. Mean percent time spent at each of seven positions (standard errors in parenthesis) during the ration experiments. Percent time at warm end (PCW) is the sum of time at positions 5, 6, and 7. Means with an asterisk (*) are significantly different (α=0.1) from the expected values given a random choice of position (14.3 for individual positions and 42.9 for PCW).

	Tank Position							
	1	2	3	4	5	6	7	PCW
High Ration	4.4* (2.4)	7.6* (2.3)	19.5 (5.3)	16.0 (3.0)	27.6* (5.1)	20.1 (5.6)	4.7* (1.6)	52.4 (9.4)
Low Ration	12.3 (5.4)	24.2* (5.0)	11.7 (2.0)	12.1 (2.6)	21.3 (5.2)	14.4 (5.0)	4.0* (1.3)	39.8 (9.1)
Com-bined	8.3 (3.0)	15.9 (3.1)	15.6 (2.9)	14.0 (2.0)	24.5 (3.6)	17.3 (3.7)	4.4 (1.0)	46.1 (6.5)

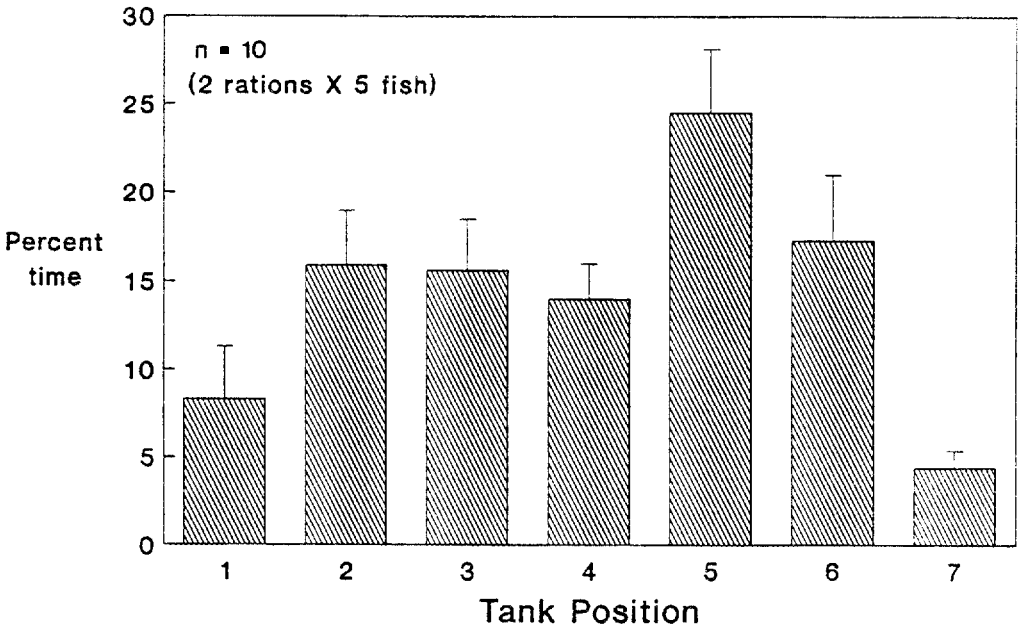

Figure III-10. Percent time spent by smallmouth bass at each of seven positions in thermal gradient tank for two ration treatments pooled. The temperature gradient within the tank was 21-28°C from position 1 to 7. Each bar represents the mean (+1 S.E.) for five fish over six days (2 treatments of 3 d each).

Table III-6. Results of Student-Newman-Keuls multiple comparisons test of differences among activity (m/h) means for four blocks of time in the ration experiment (n=5). Means connected by a dashed line are not significantly different (α=0.1).

Morning 0600-1059 h	Mid-day 1100-1559 h	Afternoon 1600-2059 h	Night 2100-0559 h
60.5	49.9	38.6	16.6
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Food availability

Although the smallmouth bass spent a majority of their time in the cooler "preferred" temperatures during all feeding treatments, the time spent at the warm end of the tank increased from day 1 to day 3 after food was presented and decreased from day 3 to day 4 when the fish was fed to satiation (Figure III-11 and Table III-7). This treatment effect was significant for the MeanP measure and nearly so for the PCW measure (P=0.12, Table III-8). A t-test used to make a single comparison between the maintenance and satiation treatments (days 3 and 4) found a significant difference for both MeanP and PCW (P=0.01 for both). A significant difference among fish was found for both measures position selection.

Significant treatment and time of day effects were evident for the activity measure (Table III-8 and Figure III-12). The multiple comparisons test showed that activity was less when the bass were fed to satiation than when fed a maintenance ration (Table III-9) and that the fish were most active during the feeding hours in the morning and least active at night (Table III-10).

Cover

Significant effects of cover and fish were found in the cover experiments for both measurements of position (Table III-11). (Note: One of the six fish remained next to the screen at one end of the tank for more than 99% of the experiment; this was considered abnormal behavior and this fish was not included in the analysis.) The positions with cover were highly preferred regardless of the cover position within the tank (Figure III-13 and Table III-12). The

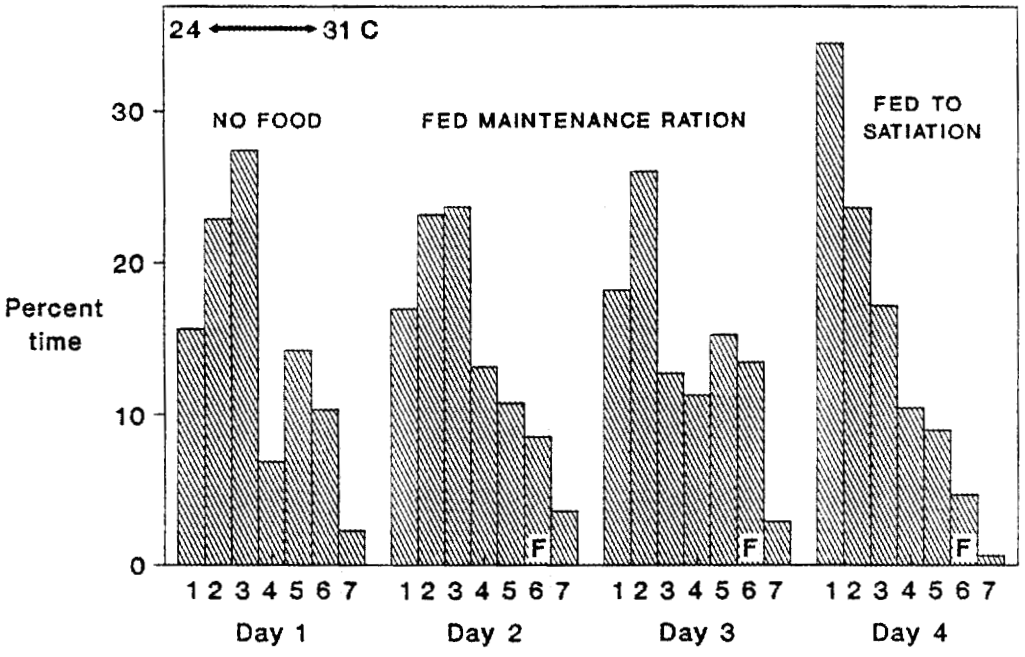

Figure III-11. Percent time spent by smallmouth bass at each of seven positions in thermal gradient tank during four days of food availability experiment. Temperature gradient within the tank was 24-31°C from positions 1 to 7. Position of food presentation is indicated by "F".

Table III-7. Mean percent time spent at each of seven positions (standard errors in parenthesis) during food availability experiments. Percent time at warm end (PCW) is the sum of time at positions 5, 6, and 7. No food was presented on day 1, maintenance ration was offered on days 2 and 3, and fish were fed to satiation on day 4. Means with an asterisk (*) are significantly different (α=0.1) from the expected values given a random choice of position (14.3 for individual positions and 42.9 for PCW).

	Tank Position							
Day	1	2	3	4	5	6	7	PCW
1	15.7	23.0	27.4	6.9*	14.4	10.4	2.3*	27.0
	(11.3)	(8.2)	(8.5)	(1.6)	(5.4)	(5.3)	(1.1)	(11.1)
2	17.0	23.2	23.7*	13.2	10.8	8.6*	3.6*	22.9*
	(6.2)	(5.8)	(4.5)	(4.2)	(2.6)	(2.9)	(1.6)	(5.5)
3	18.2	26.0	12.8	11.3	15.3	13.5	2.9*	31.7*
	(6.8)	(7.2)	(3.2)	(3.0)	(3.8)	(4.6)	(1.3)	(5.5)
4	34.5	23.6	17.2	10.5	9.0	4.7*	0.6*	14.2*
	(11.4)	(9.2)	(5.4)	(5.8)	(4.2)	(1.8)	(0.1)	(4.3)

Table III-8. Results of ANOVA for the food availability experiment. Asterisks symbolize statistical significance (* significant at α=0.10; ** significant at α=0.05). The time variable for mean position (MeanP) and percent time at the warm end (PCW) consisted of two blocks of time while for Activity it consisted of four blocks of time. The degrees of freedom in parentheses are those for the analysis of activity.

Source of variation	Degrees of freedom	F ratio		
		MeanP	PCW	Activity
Treatment	2,14	2.94*	2.46	2.90*
Time	1,7 (3,21)	0.00	0.00	23.84**
Fish	7,14 (7,42)	4.93**	4.01**	8.03**
Trtmnt*Time	2,14 (6,42)	0.46	0.38	2.24*

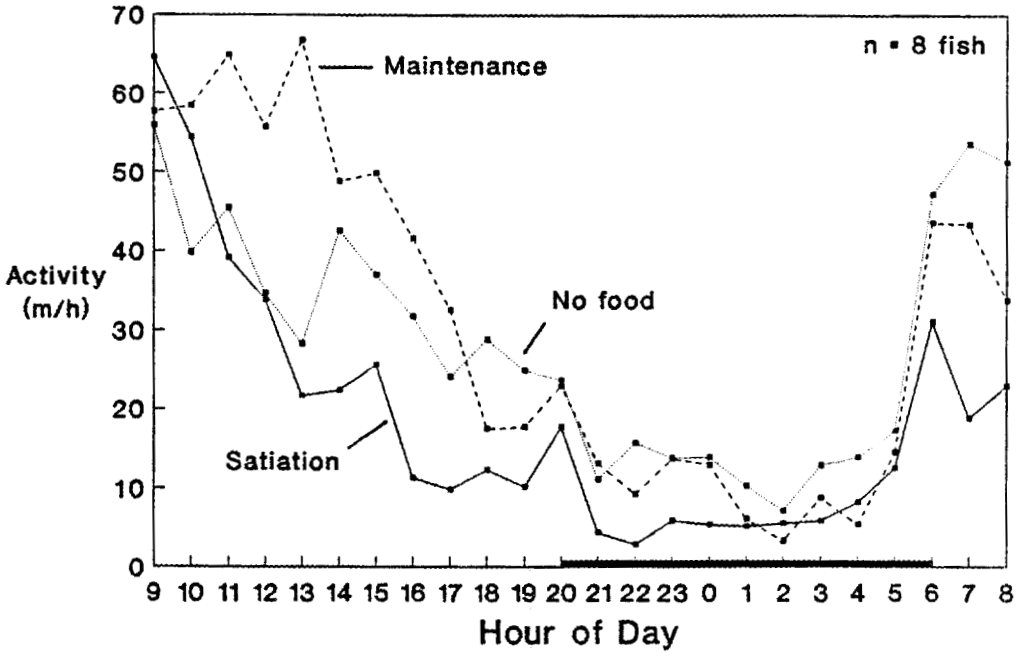

Figure III-12. Mean hourly activity (m/h) of eight smallmouth bass in food availability experiment for three treatments (Day 1 -- no food, Day 3 -- maintenance diet, and Day 4 -- fed to satiation). Dark hours indicated by bar on X-axis.

Table III-9. Results of Student-Newman-Keuls multiple comparisons test of differences among mean position selected (MeanP), percent time at warm end (PCW), and activity for three treatments in food availability experiment (n=8). Means connected by a dashed line are not significantly different (α=0.1).

	Maintenance	No food	Satiation
MeanP	3.3	3.2	2.5
PCW	0.32	0.26	0.14
Activity (m/h)	53	48	34

Table III-10. Results of Student-Newman-Keuls multiple comparisons test of differences among activity (m/h) means for four blocks of time in food availability experiment (n=8). Means connected by a dashed line are not significantly different (α=0.1).

Morning 0900-1259 h	Early AM 0600-0859 h	Afternoon 1300-1959 h	Night 2000-0559 h
72.0	50.0	41.2	15.5

Table III-11. Results of ANOVA for the cover experiment. Asterisks symbolize statistical significance (* significant at α=0.10; ** significant at α=0.05). The time variable for mean position (MeanP) and percent time at the warm end (PCW) consisted of two blocks of time while for Activity it consisted of four blocks of time. The degrees of freedom in parentheses are those for the analysis of activity.

Source of variation	Degrees of freedom	F ratio		
		MeanP	PCW	Activity
Cover	4,16	3.49*	6.71**	6.37**
Time	1,4 (3,12)	3.82	0.22	5.91**
Fish	4,16 (4,48)	13.10**	4.26**	15.39**
Cover*Time	4,16 (12,48)	0.71	0.41	1.68

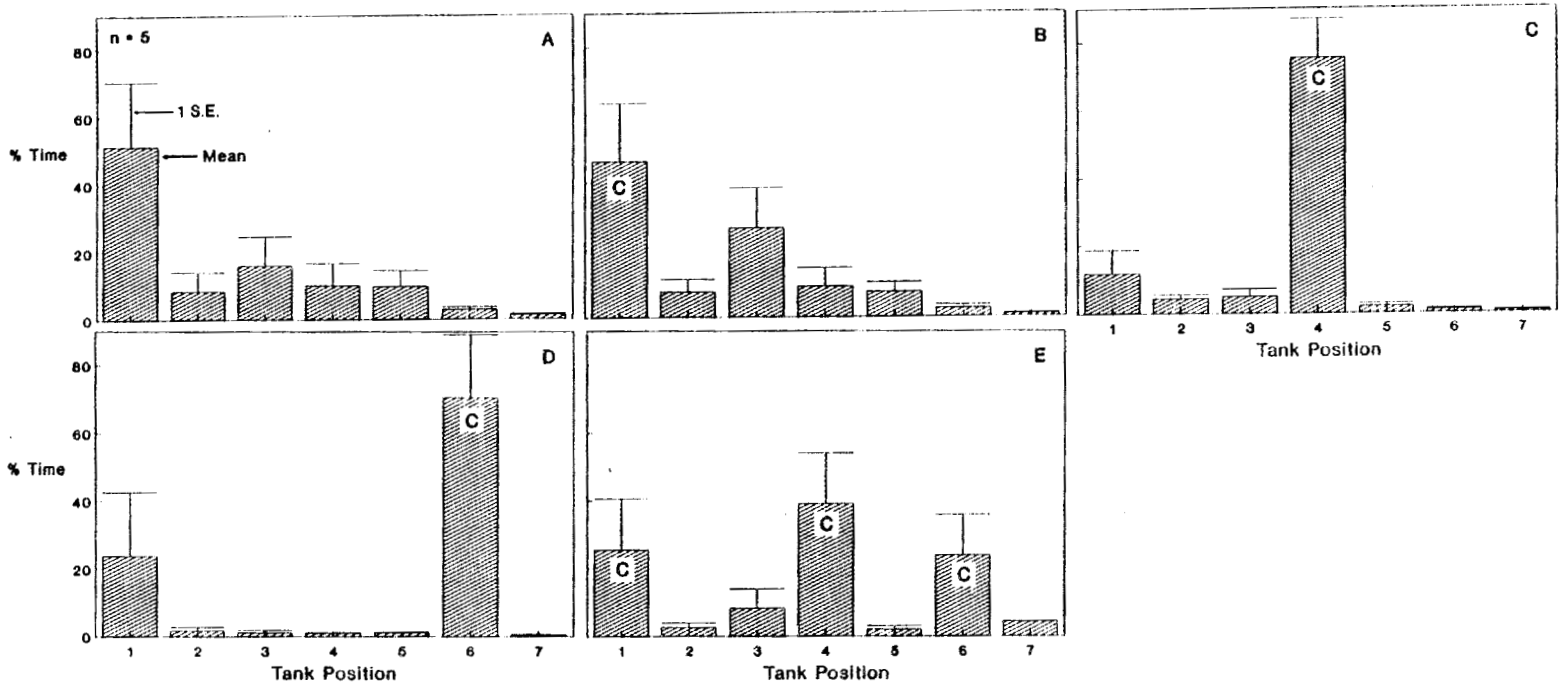

Figure III-13. Percent time spent by smallmouth bass at each of seven positions in thermal gradient tank during five 1-d treatments of cover experiment. Temperature gradient within the tank was 24-31°C from positions 1 to 7. Position of cover is indicated by "C".

Table III-12. Mean percent time spent at each of seven positions (standard errors in parenthesis) during cover experiments. Percent time at warm end (PCW) is the sum of time at positions 5, 6, and 7. Means with an asterisk (*) are significantly different (α=0.1) from the expected values given a random choice of position (14.3 for individual positions and 42.9 for PCW).

	Tank Position							
Cover	1	2	3	4	5	6	7	PCW
none	51.4	8.5	16.1	10.1	9.8	2.9*	1.3*	14.0*
	(19.1)	(5.6)	(8.6)	(6.5)	(4.7)	(0.8)	(0.5)	(5.4)
1	46.3	7.6	26.4	9.1	7.4*	2.4*	0.8*	10.6*
	(17.1)	(3.7)	(11.8)	(5.4)	(2.9)	(1.1)	(0.4)	(4.0)
4	11.8	4.4*	5.0*	75.3*	2.0*	1.0*	0.5*	3.5*
	(7.1)	(1.2)	(2.3)	(11.5)	(0.9)	(0.4)	(0.3)	(1.4)
6	23.8	1.7*	1.2*	1.0*	1.1*	70.7*	0.5*	72.3
	(18.8)	(1.1)	(0.8)	(0.3)	(0.3)	(18.3)	(0.2)	(18.6)
all	25.5	2.6*	8.3	39.2	2.1*	23.9	0.4*	26.5
	(15.1)	(1.4)	(5.7)	(14.8)	(0.9)	(11.9)	(0.2)	(12.9)

time spent in warmer water was significantly increased when cover was in position 6 compared to when cover was in position 1 or when cover was absent (SNK test, Table III-13). In fact, the warm end of the tank was avoided as shown by t-test comparisons to the expected (43% of the time), except when a cover was in position 6 (Table III-12). There was no difference in the amount of time spent at cover among the three single cover experiments (ANOVA, p=0.24, 2 d.f.) (Figure III-13b-d). There was also no difference in the amount of time spent at positions 1, 4, and 6 when covers were placed in all three positions at once (ANOVA, p=0.79, 2 d.f.) (Figure III-13e).

Cover, fish, and time of day were significant effects for the level of activity in the cover experiments (Table III-11). Activity was significantly reduced with cover in position 6 as opposed to when cover was absent or in position 1 or 4 (Table III-12 and Figure III-14). Activity at night was less than during the other three time periods (Table III-14).

DISCUSSION

Telemetry Study

Results of the telemetry study were similar to those reported by other investigators. Munther (1970), Emery (1973), Helfman (1981), and Gerber and Haynes (1988) also found that bass were rarely active at night. Gerber and Haynes (1988) found that smallmouth bass activity was highest at mid-day which is consistent with this study; however, Emery (1973) observed a crepuscular pattern of activity.

Table III-13. Results of Student-Newman-Keuls multiple comparisons test of differences among mean position selected (MeanP), percent time at warm end (PCW), and activity for five treatments in the cover experiment (n=5). Means connected by a dashed line are not significantly different (α=0.1).

	Cover placement				
	1	none	4	all	6
MeanP	2.33	2.34	3.60	3.68	4.69
PCW	0.03	0.10	0.14	0.27	0.73
Activity	26.0	29.5	22.7	15.5	10.8

Table III-14. Results of Student-Newman-Keuls multiple comparisons test of differences among activity (m/h) means for four blocks of time in cover experiment (n=5). Means connected by a dashed line are not significantly different (α=0.1).

Morning 0600-0859 h	Mid-day 1000-1459 h	Afternoon 1500-1959 h	Night 2000-0559 h
28.2	22.6	21.9	10.9

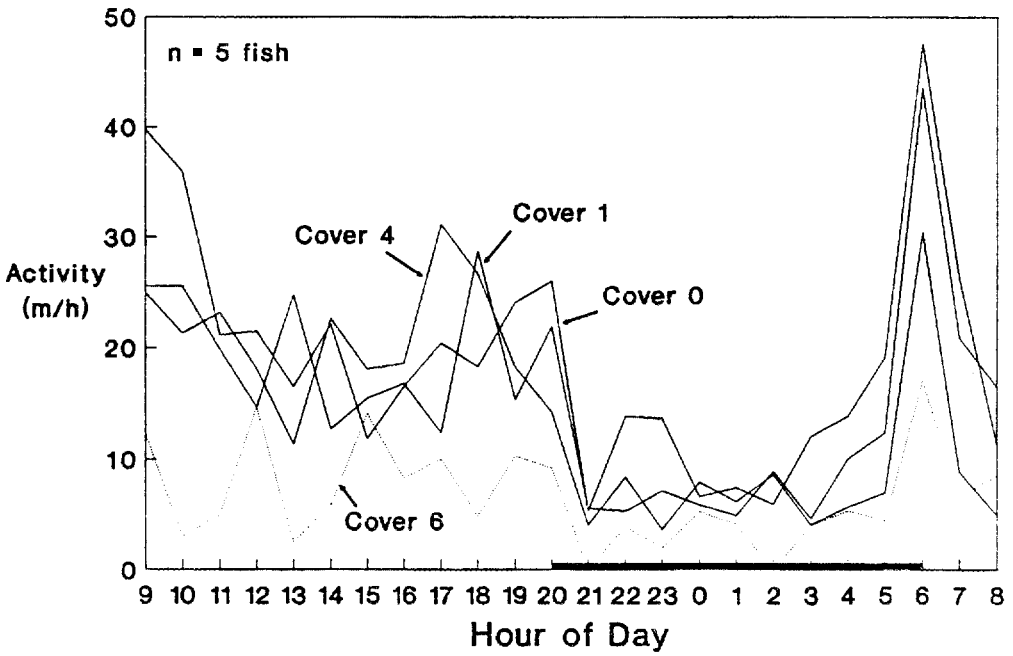

Figure III-14. Mean hourly activity (m/h) of five smallmouth bass in cover experiment for four treatments. Dark hours indicated by bar on X-axis.

Mean daily movement was estimated at 1243 m/d in this study compared to 984 m/d estimated by Todd and Rabeni (1989) in a stream study.

The use of home ranges by smallmouth bass was noted by several investigators (Hubert and Lackey 1980) and was evident in Melton Hill bass as well where the range of activity was generally linear along the shoreline. The mean linear range of activity for the tagged bass during the course of the study was 1258 m, though most of their daily ranges were much smaller. Hubert and Lackey (1980) report that smallmouth bass in another southeastern reservoir also maintained linear residence areas.

Many studies have measured the principal habitat variables associated with tracked bass. Maximum temperatures encountered by smallmouth bass in other Tennessee studies were 30°C (Peterson and Myhr 1977) and 31.5°C (Hubert and Lackey 1980). Gerber and Haines (1989) reported that tagged smallmouth bass in Lake Ontario selected water of 20-22°C when available and avoided water greater than 25°C. The variety of temperatures used and avoided by smallmouth bass suggest that the preferred temperatures may indeed be in the low 20's°C, but higher temperatures will also be used depending on the circumstances and the relative importance of other interacting habitat variables.

The use of cover is the one behavior that is reported by nearly every field study on smallmouth bass (Emery 1973; Peterson and Myhr 1977; Hubert and Lackey 1980; Todd and Rabeni 1989). These studies include a variety of ecosystems, including large lakes, reservoirs, and rivers, located throughout the natural geographic range of

smallmouth bass. The fact that the use of cover is reported by so many investigators, and is strongly implicated here, underscores the importance of this variable to habitat selection.

Gradient Tank Experiments

In the laboratory, experiments performed under conditions of uniform temperature demonstrated that no apparent features of the tank attracted or repelled fish from a particular position. Thus, the disproportionate selection or avoidance of any position in the rest of the experiments could be attributed to one or more of the controlled treatment variables (temperature, ration, food availability, or cover).

Ration level was expected to effect temperature selection and activity. Stuntz and Magnuson (1976) and Mac (1985), for example, found that the selected temperatures of bluegill and lake charr, respectively, decreased as rations decreased. Javaid and Anderson (1967) found that the selected temperatures of brook trout and rainbow trout decreased when starved, but increased for Atlantic salmon when starved. Several hypotheses can be proposed to explain these conflicting results. For example, should starved fish move to the coldest temperatures available to minimize energetic costs under low food availability or should they risk increased metabolic demands by searching available habitats for an uncertain food reward? Should a well-fed fish move to that temperature which allows for reduced metabolic costs while digesting and assimilating or, since it has ample energy reserves, should it behave without regard to energy

conservation? Unfortunately, none of these questions could be answered in this study. No differences in position selection or activity could be attributed to the two ration treatments. The lack of a significant ration effect could be a result of how the treatments were administered. First, the lengths of the treatments (7 d) might not have been long enough to affect the smallmouth's behavior. Secondly, since the fish on the high ration were not fed 24 h prior to being placed in the tank or during the 24-h acclimation period, they may have been of a similar physiological state of hunger as those fish that were held without food for 8 d (7 d of treatment plus 1 d of acclimation).

Smallmouth bass fed a maintenance diet reacted to the presentation of food at the warm end of the tank by spending slightly more time there than did fish that were not presented food at all. That this difference is not significant may be attributed to the lack of a strong preference for the cold end of the tank when no food was presented on day 1. In the cover experiment fish presented with the same "control" condition (i.e., no cover and no food) showed a strong preference for the cold end of the tank (Figure III-13a). Perhaps with a greater sample size the results of day 1 of the food availability experiment would have shown a stronger preference for the cold end of the tank resulting in a greater difference between the "no food" and "maintenance" treatments. The fact that the presence of food can motivate fish to spend more time at a temperature that is energetically sub-optimal is not surprising. In laboratory experiments, rainbow trout (Munson et al. 1980) and yellow

perch (Neill and Magnuson 1974) both moved into debilitating temperatures to feed. These results are consistent with the findings of my telemetry study where bass occupied the shallow, warmer water where their prey was most concentrated.

Fish fed to satiation, however, spent significantly less time at positions of high food availability and where energetic costs were high in favor of a position where the temperature was cooler and thus conducive to more efficient growth. In addition, energy was conserved by reducing activity when satiated. Translating these results to the field, one might expect to see offshore and/or vertical migrations to cooler temperatures when a bass is satiated. An explanation for the lack of observation of such migrations in Melton Hill Reservoir might be that the smallmouth bass in this system are seldom satiated. Unfortunately, prey abundance data and consumption estimates are not available for Melton Hill smallmouth bass.

Daily activity patterns measured in gradient tank experiments were consistent with field observations in that activity was significantly reduced during the night. Activity was greatest during the times of food presentation. Activity patterns may have been slightly different had the light to dark transition been more gradual instead of abruptly switching from dark to light.

Cover appeared to be the variable that had the strongest influence on position selection. The use of cover was apparently of greater importance than the energetic value of the habitats based on thermal quality. The assumption that the differences in energetic

costs associated with positions 1, 4, and 6 (a 6°C range) are great enough to affect position selection might be in error. In fact, the use of cover was the same regardless of the cover placement in the tank for both the individual cover treatments (cover at position 1, 4, or 6) and the multiple cover treatment (cover at positions 1, 4, and 6). That there was not significant preference for the cover at position 1 in the multiple cover treatment is difficult to explain in light of the results of the no cover treatment where a significant selection for the cold end of the tank was evident. On the other hand, the differences in activity associated with the use of cover at the various positions support the assumption that differences in energetic costs associated with the three cover positions do exist. This is illustrated in the relationship between mean position (MeanP) and activity. As MeanP (a measure of thermal exposure) increases, the level of activity decreases (Figure III-15). A linear regression analysis of these data (MeanP versus activity) found a significant relationship ($P=0.02$, $R^2=0.20$, $n=25$). Apparently, the disadvantage of incurring higher metabolic costs (increased basal metabolism), can be partially offset by a reduction in activity. Peterson and Myhr (1977) report that smallmouth bass activity decreased in the summer when surface temperatures exceeded 24°C as compared to when temperatures were between 11 and 24°C. Hubert and Lackey (1980) also reported that movement was greater in the spring and fall than in the summer.

The affinity for cover by black basses (Micropterus sp.) is well documented, but is generally more associated with largemouth bass

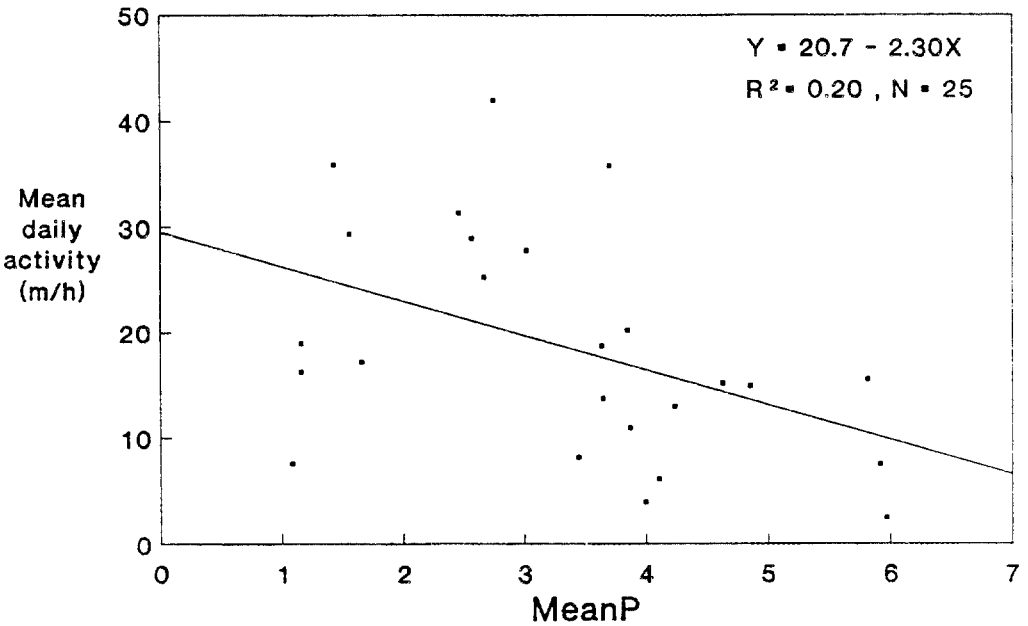

Figure III-15. Daily activity (m/h) of smallmouth bass plotted against mean position in thermal gradient tank for 25 observations (five fish on five days each) during the cover experiment.

than smallmouth bass. Various types of cover have been shown to be attractive to smallmouth bass in both laboratory experiments (Haines and Butler 1969; Sechnick et al. 1986) and field observations (Emery 1973; Peterson and Myhr 1977; Hubert and Lackey 1980). The results of my cover experiment support the field observations and provide a satisfactory explanation for the choice of nearshore habitats by bass monitored with telemetry. This finding raises the question as to why adult smallmouth bass have such a high affinity for cover. Since no dark/light difference in the use of cover was evident in the laboratory experiments it is doubtful that cover preference is due to light avoidance. For young smallmouth bass, appropriate cover serves as protection from larger predators, but adult smallmouth bass have very few natural predators. A reasonable explanation is that those young smallmouth bass that survived to adulthood must have successfully avoided predators and therefore probably used cover to a greater degree than those that were victims of predation. This behavior, although of less importance to adult smallmouth bass, may be highly ingrained and still quite evident throughout adulthood.

Another reasonable explanation of this affinity for cover by adults is found in the importance of cover in nest site selection by male smallmouth bass (Coble 1975; Neves 1975; Vogele and Rainwater 1975). Dominant males may defend prime spawning sites throughout the year by maintaining residency in the general area of those sites in lieu of other habitat variables (i.e., temperature) that may be less than optimal for growth.

One other possible advantage of cover to an adult smallmouth

bass is the added effectiveness that a good hiding place lends to an ambush predator. The higher metabolic costs incurred in a warmer environment may be offset by the reduction in activity of an ambush foraging mode as opposed to an actively searching mode.

Observational studies performed in the field provide data on the ultimate choice of habitat by an organism given the choice of available habitats. However, it may not be appropriate to attribute habitat use to a preference for some associated habitat variable. My laboratory experiments demonstrated the relative importance of some of the factors involved in habitat selection. As observed in the field and supported by laboratory data, cover appears to be a major factor influencing habitat choice by smallmouth bass. The laboratory experiments also demonstrated that food availability and hunger level affect habitat selection and ultimately thermal exposure. In reality, with even more factors involved, habitat selection may become a complicated process that involves balancing the value of several interacting variables.

Because adverse habitat modifications are becoming more frequent and severe in the aquatic environment, identification of optimal habitat requirements of fish and the primary factors that control these requirements is essential. As management decisions are considered to enhance habitats or the prey base, it is imperative that the problem be correctly identified as to which feature of the environment is limiting the success of the target species.

CHAPTER IV

SUMMARY AND DISCUSSION

KOKANEE SALMON STUDY

The majority of kokanee salmon captured in vertical gill nets were at 10-15°C regardless of depth suggesting a strong thermal preference. However, some fish were captured in water as warm as 22°C suggesting either a wide variation in preferred temperature or, more likely, occasional movements into warm water. In summer, large zooplankton were concentrated in warmer and more shallow water than the majority of the kokanee, suggesting that kokanee found in warm water (16-22°C) were there to feed.

A bioenergetics model was constructed to determine if an energetic advantage could be achieved by migrating vertically on a daily basis to feed. The model results indicated that under many temperature/prey distributions diel vertical migration is more productive than remaining at a single depth. The most productive migration strategies cannot be explained by simple rules, such as always feed at the depths of greatest food density or always rest at the lowest temperature available. The model results are based on an interaction of several important features, such as feeding rate, stomach capacity, digestion rate, and metabolic rate. The model also predicted that the greatest growth is often not achieved at the same combination of depths as is the greatest gross conversion efficiency. Greater growth can sometimes be achieved by processing more food at a lower efficiency than by processing less food at maximum efficiency.

The model also predicted seasonal changes in migration patterns that reflect seasonal variations in prey and temperature.

Hydroacoustic surveys were performed on two occasions to test the predictions of the model given the temperature/prey distributions that were evident at those times. During the first survey, adult kokanee displayed only a limited vertical migration, located about 6-8 m higher in the water column during the day than at night. Limited migrations were also predicted by the model at this time because of the small difference between prey densities at the preferred temperature range and those at higher temperatures. The second survey discovered vertical migrations of 40 m or more for juvenile kokanee only (large kokanee were not located during this survey). In this case the juvenile kokanee were near the surface during the night and deep during the day. This type of migration pattern for this species has been attributed to predator avoidance (Clark and Levy 1988). Within the constraints of only feeding at night to avoid predators, the depths chosen during the night by kokanee in Nantahala Lake compared favorably to model predictions based on energetic efficiency. Model results suggested that there might even be an energetic advantage to feeding at night instead of at day because the prey are concentrated near the surface where the high temperature allows more food to be processed due to increased digestion rates.

The research presented in this study is only a beginning interpretation of the factors involved in the diel migrations of kokanee salmon. These results have also provided insight into what

types of additional information would be useful for future research. For example, more seasonal information on diets and food availability is needed. In Nantahala Lake, zooplankton densities and kokanee diets were determined during the times of high Daphnia abundance, but more information on possible alternative prey during times of low Daphnia densities would be helpful. Another feature of the zooplankton population that was not detected, but possibly present, was the occurrence of a patchy distributional pattern. Data on zooplankton patchiness plus information on the ability of kokanee to exploit these patches would be useful. More information on the movement patterns of kokanee also needs to be determined. The hydroacoustic surveys indicated that diel vertical migrations of kokanee were indeed evident in Nantahala Lake, but more of these surveys need to be performed for better understanding of seasonal and ontogenetic differences in migration strategies. The method used to track smallmouth bass (ultrasonic telemetry) should also work quite well with the kokanee if they could be captured and handled in a way that minimizes stress. Actual observation with SCUBA could also be useful (Hyatt 1980).

The bioenergetics model also has areas that need refinement. Egestion, excretion, and heat increment (SDA) are not as well defined for O. nerka as are other processes, such as respiration and digestion. However, sophisticated error analysis has shown that the exact parameterization of these processes are relatively unimportant in the final predictions of bioenergetics models (Bartell et al. 1986). If it were available, information on changes in feeding rate

with size, swimming speed, and light intensity would be a significant contribution to the model. Large kokanee may be able to exploit low zooplankton densities better than small kokanee by maintaining a higher swimming speed while feeding. Better information on the metabolic costs of buoyancy compensation associated with vertical migration could also improve model predictions. The magnitude of vertical migrations may be limited by a fish's ability to deal with sudden changes in hydrostatic pressure (Blaxter 1980).

A more substantial addition to the model would be to include the effects of predation pressure on the kokanee. This can be done by including different probabilities of predation for the different habitats. The problem comes in defining some "common currency" with which to compare the costs and benefits of two factors as different as growth and predator avoidance. The effect of a 10% difference in growth on the lifetime reproductive fitness of a fish can be calculated, but it is more difficult to calculate the effect of a 10% difference in the probability of predation in the same terms. Mangel and Clark (1986) and McNamara and Houston (1986) presented models for the analysis of behavioral decisions that included both food acquisition and predator avoidance. Clark and Levy (1988) used the approach of Mangel and Clark (1986) to analyze the vertical migration of juvenile sockeye salmon with regards to feeding and predation; however, they failed to account for the temperature-related physiological differences at different depths. With proper consideration of the energetics of vertical migration, these models

might be useful for analyzing the combined strategies of growth maximization and predation minimization.

SMALLMOUTH BASS STUDY

The ultrasonic telemetry used to track individual smallmouth bass movements revealed no evidence of diel migration of smallmouth between shallow inshore areas and deep offshore areas during the summer. Activity, represented mainly by horizontal movements along the shore, was greater at day than at night. When not active, smallmouth bass often resided near obvious physical structure, such as overhanging bushes, fallen trees, and boulders.

To better understand the relationships among temperature, food availability, and physical cover, a series of laboratory experiments were conducted in a thermal gradient tank. Feeding to satiation resulted in the bass spending more time in cold water than when they were fed only a maintenance diet. This behavior resulted in more efficient digestion of the food captured in warm water. When cover was present in the tank, the smallmouth seemed to ignore energetic considerations in favor of residing near the cover regardless of the temperature. However, compensation for higher metabolic costs at the high temperatures was partly achieved through reduced activity during those trials when the smallmouth chose to reside at the cover at the warm end of the tank.

The density and distribution of smallmouth bass prey (small fish and crayfish), which are more difficult to determine than for kokanee prey (zooplankton), is important information that is missing in the

smallmouth study. Hydroacoustic methods could be useful for determining the prey densities of small fish, while SCUBA techniques would be useful to measure crayfish availability.

More information on the movement patterns of smallmouth bass is also needed. The use of hydroacoustics for determining smallmouth bass movements is probably not as feasible as for kokanee due to the inefficiency of this method in shallow water and the difficulty in differentiating smallmouth bass from many other fish of similar size in the nearshore area. More telemetry work with a greater number of fish and over a greater part of the year would provide the necessary information. Underwater observations of smallmouth bass with SCUBA have also been shown effective (Emery 1973; Helfman 1981).

The laboratory experiments can be expanded to include other important habitat variables, such as light and presence of predators. A larger variety of combinations of variables could be tested to achieve a better understanding of the relative importance of these different variables in habitat selection. Combinations of more than two variables could also be tested, for example, contrasting food availability at preferred temperatures versus cover at some extreme temperature.

PISCIVORE VERSUS PLANKTIVORE MIGRATION STRATEGIES

One purpose of performing this study with two different species was to compare the differences in diel migration patterns of two species of different foraging types. The kokanee salmon feeds on thousands of small prey items per day while the smallmouth bass feeds

on only a few relatively large items per day. The data collected during this study do not provide enough information to make generalizations about the differences between these two species, but based on the knowledge that was gained, reasonable speculations can be made.

The most obvious difference in the foraging behavior of these two predators is a result of differences in the distribution patterns of the prey. The prey of smallmouth should be encountered on a less regular (i.e., more random) basis than are the prey of kokanee (zooplankton), resulting in less regular diel migration patterns if the migration is based primarily on feeding. For example, in populations that display a crepuscular feeding/movement pattern, individuals that are satiated during one feeding bout may not return for the second.

These types of foraging differences would need to be included in a bioenergetics model for smallmouth bass similar to that of the kokanee. Prey size and encounter rate should be modeled as random functions. The migration strategies would therefore be highly dependent on the probability of prey encounter.

DISCUSSION OF INTEGRATED APPROACH

Using an approach that integrated field observations, laboratory experimentation, and simulation modeling provided more insight into the phenomena of diel habitat shifts than could have been obtained from a single approach. The field observations provided the base information on the behavior of each species. The laboratory study

teased apart the relative importance of various habitat variables which provided possible explanations for the field observations. The model simulations provided insight into the underlying mechanisms of the field observations and also provided predictions that could be tested with further field observations.

With this integrated approach I have shown that the growth maximization strategy can be an important factor in habitat selection, but that the effects of other strategies must be considered as well. The bioenergetics model demonstrated that diel habitat shifts of kokanee can be energetically advantageous, especially when prey is unevenly distributed and temperature is highly stratified. When tested against the results of the hydroacoustic surveys, the model demonstrated general agreement with the observed kokanee migration patterns. The effect of selection strategies other than growth maximization was evident in the migration pattern of the juvenile kokanee as determined by hydroacoustics. Within the constraints of predator avoidance, the migration patterns of the juvenile kokanee were still energetically sound.

The preference for cover by smallmouth bass in both the field and the laboratory seemed to overshadow any consideration for energetic efficiency. The influence of the growth maximization strategy was evident in satiated smallmouth bass who preferred the cold water habitats after feeding in the laboratory experiments. With this series of observations, experiments, and simulations, I

have demonstrated the importance of considering a combination of factors in the analysis of diel habitat shifts.

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APPENDIX A

NANTAHALA LAKE SAMPLING

Table A-1. Nantahala Lake sampling schedule with locations on vertical gill net sets and horizontal zooplankton tows. Locations are indicated by the station numbers as in Figure II-2.

Date	Net nights	Location of nets	Location of zooplankton tows
		1985	
5/15 - 5/17	12	25	14, 25
6/19 - 6/22	18	25, W1	W2
10/15 - 10/17	12	2, 14, 25, W1	14
		1986	
5/12 - 5/15	18	25, W1	25, W1
6/23 - 6/25	8	W1	
9/29 - 10/1	12	14, 22, 24, W1	12
		1987	
4/13 - 4/15	12	22, 26, W4	25
6/8 - 6/10	12	24, 25, W1	25
7/26 - 7/30	24	25, 26, W1	25
		1988	
6/6 - 6/9	18	3, 25, W1	2

Table A-2. Information collected from kokanee salmon captured in vertical gill nets in Nantahala Lake.

ID #	Date yymmdd	Mesh (in)	Depth (m)	Temp (C)	L (mm)	Wt (g)	Sex	Gonad (g)	Liver (g)	Viscera (g)
0001	840911	---	29	14.2	399	756	M	10.6	4.8	12.1
6753	850517	1.75	21	8.9	366	620	F	4.8	6.1	27.0
6743	850517	1	16	10.0	208	100	I	---	1.5	29.3
6748	850517	1.5	14	10.7	360	562	M	---	5.2	19.6
6752	850517	1.75	14	10.7	291	362	F	---	4.2	16.0
6747	850517	1.5	12	11.8	331	442	F	1.2	4.5	7.3
6750	850517	1.75	11	12.4	370	620	F	4.4	5.4	1.6
6751	850517	1.75	11	12.4	386	784	M	---	5.5	22.8
6745	850517	1.5	11	12.4	421	870	F	7.8	7.9	25.5
6746	850517	1.5	11	12.4	405	827	F	8.9	10.8	23.9
6742	850517	1	11	12.4	389	754	M	---	6.0	3.5
6744	850517	1.5	10	13.4	388	769	F	6.6	7.8	12.6
6741	850517	1	9	14.3	213	95	I	---	1.1	---
6749	850517	1.75	8	15.1	387	753	F	4.0	6.9	---
8200	850620	1.5	18	10.8	416	795	F	23.6	10.2	22.9
8202	850620	1.25	12	16.1	366	610	F	2.3	4.7	8.8
8212	850621	1	22	10.0	211	104	I	---	1.6	25.0
8210	850621	2	20	10.4	421	902	F	33.1	12.3	16.1
8209	850621	2	16	12.4	454	1102	M	---	8.0	22.7
8205	850621	1.5	16	12.4	431	908	M	---	8.8	51.4
8208	850621	2	15	13.4	482	1276	M	12.4	12.4	11.7
8218	850622	2	16	12.4	418	894	M	---	7.7	20.3
8217	850622	2	13	15.4	438	978	M	---	8.6	10.6
6898	851017	1	28	13.4	239	140	I	---	1.9	---
6895	851017	1.25	25.5	17.2	265	196	I	---	1.8	3.2
6851	851017	1	3.5	19.6	505	1140	M	11.6	10.8	15.4
6875	860513	1.5	19	7.7	331	452	I	---	5.1	7.2
6870	860513	1.5	16	8.5	342	550	F	3.7	6.5	19.4
6878	860513	1.5	16	8.5	376	665	M	1.2	7.5	7.8
6864	860513	1.75	10	11.8	405	761	M	3.2	6.4	12.6
7043	860513	1.25	9.5	12.3	355	511	F	3.8	4.9	23.3
6800	860513	1.25	8	13.9	342	493	M	1.0	4.9	---
7000	860513	1.75	6	15.5	359	589	F	4.2	6.1	5.1
7080	860514	1.5	16	8.8	365	534	F	3.0	5.5	21.8
7075	860514	1.75	15	9.3	364	556	M	1.6	5.3	30.7
7011	860514	1.75	13	10.4	328	441	F	2.3	5.1	18.9
6859	860514	0.75	13	10.4	183	56	I	---	0.7	21.0
6854	860514	0.75	9.5	12.3	195	70	I	---	0.7	26.1
6889	860514	1.5	9	12.9	367	637	M	2.2	6.5	17.7
6861	860514	1.75	9	12.9	437	983	M	neglig	9.5	21.5
7039	860514	0.75	8.5	13.4	198	67	I	---	0.7	22.2

Table A-2 (Continued).

ID #	Date yymmdd	Mesh (in)	Depth (m)	Temp (C)	L (mm)	Wt (g)	Sex	Gonad (g)	Liver (g)	Viscera (g)
7084	860514	1.5	7	14.6	412	759	M	1.9	6.5	12.3
7083	860515	1.75	12.5	10.7	354	518	M	2.3	4.8	24.1
7034	860515	1.5	11.5	11.2	350	511	F	3.4	4.6	5.8
7036	860515	1.75	10.5	11.6	344	495	F	3.6	4.8	16.9
7033	860515	2	10	11.8	361	570	F	6.2	6.5	6.8
7013	860624	1.5	14	12.4	382	680	F	18.0	9.3	3.4
7040	860624	1.5	14	12.4	367	543	I	---	5.9	22.9
7088	860624	1.75	13.5	13.4	400	650	M	3.5	6.1	28.7
7008	860624	2	13	14.3	402	556	-	---	---	14.6
7002	860624	1.75	12	15.5	380	599	M	2.0	5.1	---
7037	860624	2	12	15.5	480	1132	M	---	6.7	10.3
7009	860624	2	9	18.6	402	592	M	---	---	16.2
7004	860624	2	8	19.4	393	700	F	17.0	7.4	10.1
7085	860624	2	5	22.1	430	994	M	11.9	10.3	9.7
7073	860625	2	15	10.6	387	682	F	14.2	6.6	29.9
7081	860625	1.5	14	12.4	365	540	F	6.3	4.2	26.4
7010	860625	1.5	14	12.4	359	462	-	---	3.7	31.2
7045	860625	1.75	13.5	13.4	357	522	M	---	---	14.9
6894	860625	1.75	12	15.5	394	712	F	16.3	5.8	5.4
7014	860625	1.75	9.5	18.2	387	622	F	---	---	7.7
7065	860625	1.5	6	21.1	387	600	M	7.6	6.3	12.3
7020	861001	1.75	12	8.4	472	918	M	7.5	8.4	5.5
7028	861001	1.75	11	8.8	520	1342	M	12.3	12.4	21.8
7024	861001	1.75	5	20.4	444	832	M	11.7	7.1	11.2
7021	861001	2	2	21.8	551	1459	M	16.4	14.8	17.4
7051	870609	2	15	11.0	419	948	M	9.1	2.3	17.8
7449	870727	1.5	22	12.9	357	491	F	18.4	6.7	22.8
7019	870727	2	16	16.8	490	1252	M	26.5	12.2	4.3
7048	870728	1.5	24	11.6	361	566	F	20.1	6.6	18.1
7016	870728	2	21.5	13.2	410	788	M	18.7	5.9	20.4
7067	870728	2	21	13.6	507	1380	F	68.5	17.0	19.2
8280	870729	2	25.5	10.7	454	1013	M	1.3	8.7	33.4
7018	870729	1.75	23.5	11.9	500	1396	M	23.8	13.6	33.5
7697	870729	1.5	23.5	11.9	312	310	F	1.4	3.5	22.0
7614	880607	0.75	13	13.5	185	54.8	I	---	0.8	2.9
7654	880607	0.75	20.5	9.6	197	74.4	I	---	0.7	3.3
7618	880608	0.75	12.5	13.7	191	57.4	I	---	0.6	2.7
7636	880608	0.75	13.5	13.3	182	50.5	I	---	0.6	2.2
7655	880608	0.75	15	12.4	190	61	I	---	0.7	3.2
7191	880608	0.75	19	10.4	186	51.3	I	---	0.5	2.2
7657	880608	0.75	22	8.8	179	51	I	---	0.5	2.4

Table A-3. Zooplankton greater than 1 mm in length sorted by genus that were sampled with Clark-Bumpus horizontal sampler in Nantahala Lake. D=*Daphnia* sp., H=*Holopedium* sp., L=*Leptodora* sp., and others are those that comprised less than 1% of total numbers and include CH=*Chaoborus* sp., CL=*Chironomid* sp. larvae, CP=*Chironomid* sp. pupae, and CO=copepods.

Date	Station.	Depth (m)	Zooplankton >1 mm D	H	L	Others	Volume (cu. m)
04-15-87	25	3	76	726	11	1 CH	1797
	25	6	52	854	4		1721
	25	9	0	408	1		1746
	25	9	7	313	1		1778
	25	12	2	79	0		1518
	25	15	2	65	0	1 CL, few CO	1537
05-13-86	25	3	3684	141	24		1588
	25	6	2551	2	20	112 CO	1549
	25	9	3132	0	4	13 CO	1530
05-14-86	25	3	2388	197	10	10 CO	1676
	25	6	1150	12	15	24 CO	1651
	25	6	1894	17	12	24 CO	1657
	25	12	3509	0	0		1543
	25	15	604	0	0		1441
05-16-85	25	3	505	14	2		1937
	25	6	2760	33	13		1594
	14	3	8093	0	17		1797
05-17-85	14	6	1487	16	17		1664
	25	9	1650	8	26		1454
06-09-87	25	3	60	53	39		1524
	25	4.5	275	51	13		1480
	25	6	808	145	14		1448
	25	6	363	176	19	2 CH	1429
	25	6	423	136	12	1 CH	1353
	25	7.5	1708	16	34	3 CH	1359
	25	7.5	3166	0	67		2413
	25	7.5	2562	0	34		2413
	25	9	181	2	4		1429
	25	12	141	3	0	1 CH	1422
	25	15	77	1	0	2 CH, 1 CL	1467

Table A-3 (continued).

Date	Station.	Depth (m)	Zooplankton >1 mm D	H	L	Others	Volume (cu. m)
06-09-88	3	6	118	256	103		1791
	3	9	2068	41	69		1562
	3	9	1882	0	33		1372
	3	12	3213	0	44	2 CH	1308
	3	15	732	0	5		1245
	3	21	39	1	0		1041
	3	28	33	1	0		1245
06-20-85	W2	3	12160	0	78		1848
	W2	6	12689	0	66		1734
	W2	9	5421	0	40		1594
	W2	15	1075	0	12		1334
06-21-85	W2	1	10	0	0		1676
	W2	9	3480	0	46		1549
	W2	9	2632	0	20		1372
	W2	18	1923	0	5		1321
	W2	18	1551	0	2		1283
	W2	21	343	0	1		1194
06-21-85 Night	W2	1	5223	0	8	1 CH	1778
	W2	3	6618	0	16		1676
	W2	9	4218	0	47		1473
	W2	15	270	0	1		1238
	W2	18	194	0	0	1 CL	1334
07-29-87	25	3	3	3	18		1835
	25	9	14	2	19	1 CL	1530
	25	12	51	1	12	4 CH	1334
	25	15	79	2	0	5 CH	1461
	25	18	28	0	1	11 CH, 2CP	1486
	25	18	55	0	0	10 CH	1245
	25	21	9	0	0		1549
	25	21	22	0	2	6 CH	1467
09-30-86	14	3	0	0	67		1810
	14	6	0	0	36		1448
	14	6	0	1	32	3 CH	1264
	14	9	0	0	5	2 CH	1346
	14	12	0	0	1	6 CH, few CO	1327
	14	15	0	0	0	few CO	1080

Table A-3 (continued).

Date	Station.	Depth (m)	Zooplankton >1 mm D	H	L	Others	Volume (cu. m)
10-16-85	14	3	12	34	9		1708
	14	6	54	18	15		1657
	14	9	83	1	0		1372
	14	12	83	4	0		1429
	14	18	107	0	1		1448
	14	24	213	0	0	1 CH	1505
Totals			110016	3833	1227	283	
Proportion			0.95	0.03	0.01	<0.01	

APPENDIX B

COMPONENTS OF BIOENERGETICS MODEL

A. Lotus 1-2-3 spreadsheet model:

The main body of the spreadsheet model is illustrated in Figure B-1. Parts of the spreadsheet that are not shown here include parameters for some of bioenergetics equations, the 12 prey/temperature databases, and the macros required for automatic operation of the spreadsheet. Initial inputs were made at the top of the spreadsheet. These inputs included fish weight, prey/temperature database, depths where fish was located during 24 h period, whether the fish was feeding or not (0 = no, 1 = yes), and the time spent at each depth. In the example in Figure B-1, the model simulated migration by a fish that spent the first 720 min (12 h) at 30 m of depth when not feeding then moving to 6 m of depth for the remaining 720 min to feed. Once the initial inputs were made, the bioenergetics calculations were performed automatically in the lower half of the spreadsheet. The spreadsheet is organized in 48 rows that represent 30-min time steps for 24 h as indicated in the first column. The second through fourth columns indicate the depth, feeding mode, and temperature during each time step. All the cells in the fifth through thirteenth columns contain equations that correspond to other cells in the spreadsheet, such as temperature or feeding mode. The components of the bioenergetics model were calculated from left to right with a final estimate of growth for each time step in the last column. The program calculated growth for each time step in chronological order from the top of the spreadsheet to the bottom. The ending stomach content (twelfth column) at the completion of the calculations for a time step was carried over as the initial stomach content (sixth column) for the next time step. This continued to the last time step. The ending stomach content of the last time step was then used as the initial stomach content for the first time step if they were not already equal. The spreadsheet was recalculated in this manner until the initial and final stomach contents were equal. Normally, only three or four such iterations were required to reach the steady state.

B. Consumption equation:

Feeding rates (number/min) at three densities of *Daphnia* sp. were determined experimentally for kokanee by Hyatt (1980). The following equation was the best fit to the values from Figure 23 of Hyatt (1980):

$$C = Z / (0.0138 \cdot Z + 11.5) \qquad \text{(B.1)}$$

where C is consumption rate (number of *Daphnia* per min) and Z is zooplankton density (number per m^3). With this equation feeding rates could be estimated at any prey density (Figure B-2).

TimeStep	L(cm)	W(g)	Database #:	Model:
30	36.9	500	5	KOK30

Time Period	1	2	3	4	5	6
Depth	30	6				
Feeding	0	1				
Minutes	720	720				

Time Int. (min)	Depth (m)	Feeding? 0/1	Temp (C)	Consump. (g Dap)	Init. StomCon (g Dap)	Amount Proc. (Kcal)	Egest. (Kcal)	Excret. & SDA (Kcal)	Resp. (Kcal)	Growth (Kcal)	Ending StomCon (g Dap)	Growth (g Kok)
Totals				28.42	4.04	16.65	3.43	3.61	3.94	5.68	4.04	3.28
30	30	0	9.5	0	4.041	0.135	0.033	0.023	0.032	0.048	3.810	0.05
60	30	0	9.5	0	3.810	0.128	0.031	0.022	0.032	0.043	3.592	0.09
90	30	0	9.5	0	3.592	0.120	0.029	0.021	0.032	0.039	3.387	0.13
120	30	0	9.5	0	3.387	0.113	0.027	0.019	0.032	0.035	3.193	0.16
150	30	0	9.5	0	3.193	0.107	0.026	0.018	0.032	0.031	3.011	0.19
180	30	0	9.5	0	3.011	0.101	0.024	0.017	0.032	0.027	2.839	0.22
210	30	0	9.5	0	2.839	0.095	0.023	0.016	0.032	0.024	2.677	0.25
240	30	0	9.5	0	2.677	0.090	0.022	0.015	0.032	0.021	2.524	0.27
270	30	0	9.5	0	2.524	0.085	0.020	0.014	0.032	0.018	2.379	0.28
300	30	0	9.5	0	2.379	0.080	0.019	0.014	0.032	0.015	2.243	0.30
330	30	0	9.5	0	2.243	0.075	0.018	0.013	0.032	0.012	2.115	0.31
360	30	0	9.5	0	2.115	0.071	0.017	0.012	0.032	0.010	1.994	0.32
390	30	0	9.5	0	1.994	0.067	0.016	0.011	0.032	0.007	1.880	0.33
420	30	0	9.5	0	1.880	0.063	0.015	0.011	0.032	0.005	1.773	0.33
450	30	0	9.5	0	1.773	0.059	0.014	0.010	0.032	0.003	1.672	0.34
480	30	0	9.5	0	1.672	0.056	0.014	0.010	0.032	0.001	1.576	0.34
510	30	0	9.5	0	1.576	0.053	0.013	0.009	0.032	-0.001	1.486	0.34
540	30	0	9.5	0	1.486	0.050	0.012	0.009	0.032	-0.003	1.401	0.33
570	30	0	9.5	0	1.401	0.047	0.011	0.008	0.032	-0.004	1.321	0.33
600	30	0	9.5	0	1.321	0.044	0.011	0.008	0.032	-0.006	1.245	0.32
630	30	0	9.5	0	1.245	0.042	0.010	0.007	0.032	-0.007	1.174	0.32
660	30	0	9.5	0	1.174	0.039	0.010	0.007	0.032	-0.009	1.107	0.31
690	30	0	9.5	0	1.107	0.037	0.009	0.006	0.032	-0.010	1.044	0.30
720	30	0	9.5	0	1.044	0.035	-0.008	0.006	0.032	-0.011	0.984	0.29
750	6	1	21.5	1.18421	2.168	0.447	0.090	0.099	0.132	0.126	1.405	0.41
780	6	1	21.5	1.18421	2.589	0.480	0.097	0.107	0.132	0.145	1.770	0.56
810	6	1	21.5	1.18421	2.954	0.509	0.103	0.113	0.132	0.161	2.086	0.72
840	6	1	21.5	1.18421	3.270	0.533	0.108	0.118	0.132	0.175	2.360	0.89
870	6	1	21.5	1.18421	3.544	0.555	0.112	0.123	0.132	0.187	2.597	1.08
900	6	1	21.5	1.18421	3.781	0.573	0.116	0.127	0.132	0.198	2.803	1.28
930	6	1	21.5	1.18421	3.987	0.589	0.119	0.131	0.132	0.207	2.982	1.48
960	6	1	21.5	1.18421	4.166	0.603	0.122	0.134	0.132	0.215	3.136	1.70
990	6	1	21.5	1.18421	4.320	0.615	0.124	0.137	0.132	0.222	3.270	1.92
1020	6	1	21.5	1.18421	4.455	0.626	0.126	0.139	0.132	0.228	3.387	2.15
1050	6	1	21.5	1.18421	4.571	0.635	0.128	0.141	0.132	0.234	3.487	2.38
1080	6	1	21.5	1.18421	4.672	0.643	0.130	0.143	0.132	0.238	3.575	2.62
1110	6	1	21.5	1.18421	4.759	0.650	0.131	0.144	0.132	0.242	3.650	2.86
1140	6	1	21.5	1.18421	4.835	0.655	0.132	0.145	0.132	0.246	3.716	3.11
1170	6	1	21.5	1.18421	4.900	0.661	0.133	0.147	0.132	0.248	3.773	3.36
1200	6	1	21.5	1.18421	4.957	0.665	0.134	0.148	0.132	0.251	3.822	3.61
1230	6	1	21.5	1.18421	5.006	0.669	0.135	0.148	0.132	0.253	3.865	3.86
1260	6	1	21.5	1.18421	5.049	0.672	0.136	0.149	0.132	0.255	3.902	4.12
1290	6	1	21.5	1.18421	5.086	0.675	0.136	0.150	0.132	0.257	3.934	4.38
1320	6	1	21.5	1.18421	5.118	0.678	0.137	0.150	0.132	0.258	3.962	4.63
1350	6	1	21.5	1.18421	5.146	0.680	0.137	0.151	0.132	0.260	3.986	4.89
1380	6	1	21.5	1.18421	5.170	0.682	0.137	0.151	0.132	0.261	4.007	5.15
1410	6	1	21.5	1.18421	5.191	0.683	0.138	0.152	0.132	0.262	4.025	5.42
1440	6	1	21.5	1.18421	5.209	0.685	0.138	0.152	0.132	0.262	4.041	5.68

Figure B-1. Sample of spreadsheet output from bioenergetics model of vertical migration.

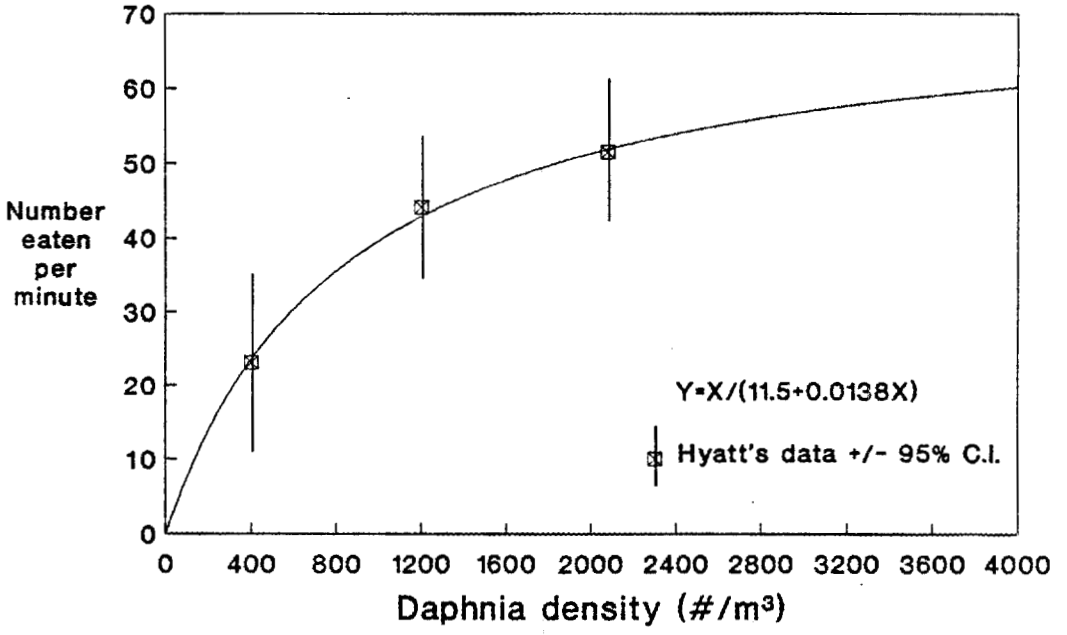

Figure B-2. Feeding rate curve determined from laboratory data on consumption rates (Daphnia/min) of kokanee salmon at various densities of Daphnia as determined by Hyatt (1980).

C. Digestion equations:

Brett and Higgs (1970) determined that digestion of sockeye salmon was exponential. When not feeding, digestion can be described by the following equation:

(B.2) $$W_t = W_0 \cdot \exp(-rt)$$

where W_t is the amount of food in the stomach at time t, W_0 is the initial stomach content, r is the digestion coefficient, and t is time. The digestion coefficient, r, is temperature dependent and can be calculated by solving for r in equation B.2 if the time to some particular state of digestion is known:

(B.3) $$r = -\ln(W_t/W_0) \ / \ t$$

Brett and Higgs (1970) determined digestion times for four levels of digestion at five temperatures as shown in the following table:

	Time (h) to digestion of:			
Temp.(°C)	50%	75%	90%	99%
3.1	25.6	45.5	74.0	147.0
5.5	12.0	23.7	39.5	79.4
9.9	6.0	11.6	19.2	37.8
14.9	3.35 6.75	11.3	22.6	
20.1	2.66 5.34	8.82 17.7		

The values in the above table were used to estimate r for each temperature/stage of digestion combination with equation B.3. These values are in the following table:

	r at digestion level:				
Temp.(°C)	50%	75%	90%	99%	Mean
3.1	0.027	0.030	0.031	0.031	0.030
5.5	0.058	0.058	0.058	0.058	0.058
9.9	0.116	0.120	0.120	0.122	0.119
14.9	0.207	0.205	0.204	0.204	0.205
20.1	0.261	0.260	0.261	0.260	0.260

Theoretically, r should be the same at any level of digestion for a particular temperature. A linear regression model was used to develop the following equation to estimate r at any temperature (T):

$$r = -0.0154 + 0.0140 \cdot T \tag{B.4}$$

D. Respiration equations:

Brett (1970) provides three equations, one at each of three temperatures (5.3, 15, and 20°C), to describe standard respiration rates for sockeye salmon as a function of fish weight. These equations are of the following form:

$$R_{(std)} = a \cdot W^b \tag{B.5}$$

where W is weight (g). These equations were used to generate estimates of $R_{(std)}$ at the three temperatures for 11 different weights (50-1000 g). A linear regression analysis (SAS) was used to generate a single weight- and temperature-dependent equation from the 33 values. This curve-fitting exercise resulted in the following equation:

$$R_{(std)} = \exp(-2.77 + 0.882 \cdot \ln(W) + 0.00126 \cdot T + 0.00286 \cdot T^2) \tag{B.6}$$

where W is weight (g) and T is temperature.

The same analysis was done for active respiration, $R_{(act)}$. Brett's (1970) three equations for $R_{(act)}$, which were the same model as used for $R_{(std)}$, were used to generate a single equation for $R_{(act)}$ which would be useful at all temperatures:

$$R_{(act)} = \exp(-1.191 + 0.986 \cdot \ln(W) + 0.111 \cdot T - 0.00294 \cdot T^2) \tag{B.7}$$

where W is weight (g) and T is temperature.

Brett (1970) measured $R_{(act)}$ at the fish's maximum sustainable swimming speed, MSS, (i.e., the maximum speed at which swimming could be maintained for 1 h). Brett developed weight-dependent curves for MSS at five temperatures (2, 5, 10, 15, and 20°C). In order to have one equation for all temperatures, I used MSS estimates from Brett's equations for 11 different weights as with the respiration equations to generate the following equation by linear regression:

$$MSS = \exp(0.909 + 0.632 \cdot \ln(L) - 0.00901 \cdot T + 0.00349 \cdot T^2 - 0.000128 \cdot T^3) \tag{B.8}$$

where L is length (cm) and T is temperature.

Brett proposes a graphical method by which $R_{(std)}$, $R_{(act)}$, and MSS can be used to estimate the respiration rate, R, at any swimming speed. For the purpose of this study the graphical method was converted to the following algebraic method:

(B.9) $R = \exp[\ln(R_{(std)})+((\ln(R_{(act)})-\ln(R_{(std)}))\cdot S/MSS)]$

where S is the swimming speed (cm/sec). Values from this equation were compared to those estimates from Brett's equations to demonstrate its accuracy (Figure B-3).

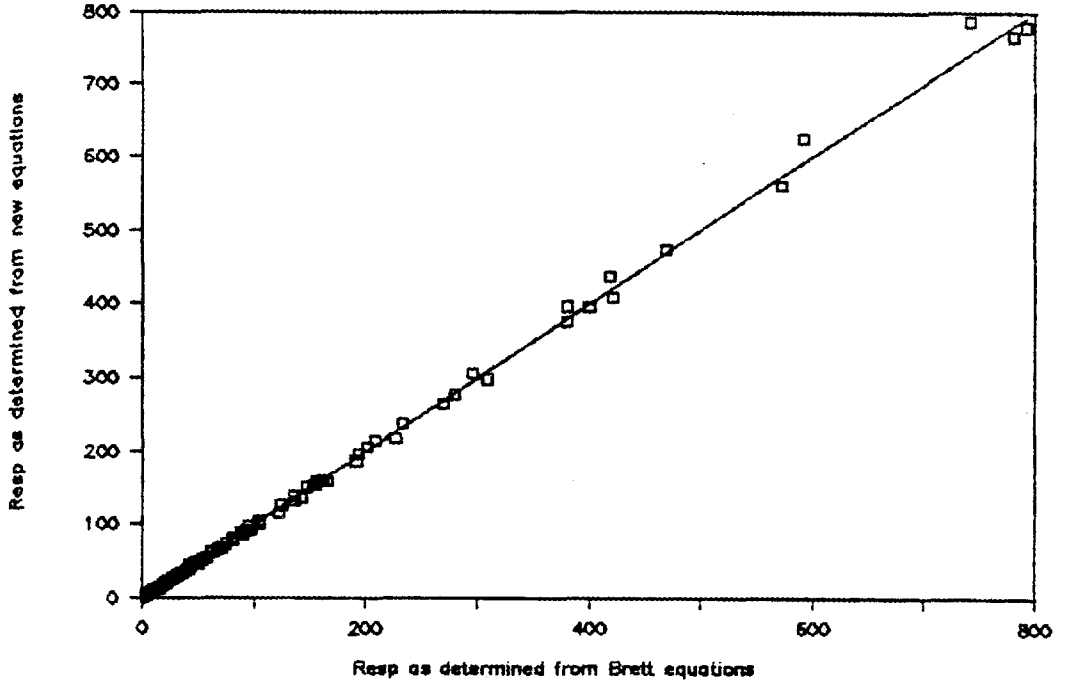

Figure B-3. Plot of respiration (mg O_2/h) estimates from equation A.9 versus estimates from separate equations from Brett (1970) for sockeye salmon of five different weights at three different temperatures and several swimming speeds (n=127).

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