A Bioenergetics Analysis of Diel Vertical Migration by Kokanee Salmon, *Oncorhynchus nerka*

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Diel vertical migration of fishes is probably a result of the combined effects of several selective forces, including predator avoidance, foraging efficiency, and bioenergetic efficiency. We considered both foraging efficiency and energetic efficiency as a combined effect which we called growth maximization. The importance of growth maximization as a selective force was evaluated with a bioenergetics-based model to estimate growth rates of various migration scenarios of kokanee salmon, *Oncorhynchus nerka*. Environmental parameters (temperature and zooplankton distributions) in the model were obtained from a North Carolina reservoir with an established population of kokanee. The simulations demonstrated that vertical migrations can be energetically advantageous when kokanee and their prey are thermally segregated and that ontogenetic and seasonal differences in the optimal migration strategy should be expected. The general rule for vertical migration as determined from the simulations is to feed where net energy intake is maximized and then reside when not feeding where energetic costs are minimized and food is digested to the point that consumption during the next feeding period is not limited by the amount of undigested food remaining in the stomach. Data obtained from vertical gill nets and hydroacoustics were compared with model predictions.

La migration verticale nycthémérale des poissons résulte probablement des effets combinés de plusieurs forces, notamment l'évitement des prédateurs, l'efficacité de la recherche de nourriture et l'efficacité bioénergétique. Nous considérons l'efficacité de la recherche de nourriture et l'efficacité énergétique comme un effet combiné que nous appelons maximisation de la croissance. On a évalué l'importance de cet effet comme force de sélection à l'aide d'un modèle fondé sur la bioénergie afin d'estimer le taux de croissance dans le cadre de différents scénarios de migration du kokani, *Oncorhynchus nerka*. Les paramètres environnementaux (température et répartitions du zooplancton) du modèle provenaient d'un réservoir de la Caroline du Nord où s'est établie une population de kokani. Les simulations ont montré que des migrations verticales peuvent être intéressantes sur le plan énergétique lorsque le kokani et ses proies ne vivent pas dans les mêmes zones thermiques et qu'on devrait s'attendre à des différences ontogénétiques et saisonnières dans la stratégie de migration optimale. La règle générale d'une migration verticale établie à partir des simulations consiste à s'alimenter lorsqu'il y a maximisation de l'apport énergétique net puis, en période de non alimentation, à se tenir à un endroit où les dépenses énergétiques sont réduites au minimum et que la digestion des aliments est telle que la consommation pendant la période d'alimentation suivante n'est pas limitée par la quantité d'aliment non digéré demeurant dans l'estomac. Les données obtenues par les filets maillants verticaux et des données hydroacoustiques ont été comparées aux prévisions du modèle.

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The various hypotheses proposed to explain the adaptive significance of diel vertical migration of fish can for the most part be grouped into two categories: (1) those relating to maximization of growth (i.e., net energy assimilation) and (2) those relating to the minimization of the probability of premature mortality. The first category includes (i) maximizing food intake rate, either by feeding where prey densities are highest (Janssen and Brandt 1980; Munk et al. 1989) or by stimulating digestion via temperature selection (Wurtsbaugh and Neverman 1988), and (ii) maximizing assimilation efficiency by minimizing energetic costs (Brett 1971a). The second category includes (i) spatial and/or temporal avoidance of predators (Eggers 1978; Clark and Levy 1988) and (ii) avoidance of prolonged exposure to potentially stressful environmental conditions (e.g., high temperature or low dissolved oxygen (DO); Neill and Magnuson 1974; Olla et al. 1985). These selective forces are not independent of each other, and given the expected seasonal and ontogenetic variation in the relative importance of these forces, it is unreasonable to expect that any one can adequately explain the complex migration patterns of even a single species. Levy (1990a) suggested that vertical migration by juvenile sockeye salmon, *Oncorhynchus nerka*, may be a three-way compromise between foraging, predator

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avoidance, and metabolic efficiency. Although it is difficult to evaluate the adaptive value of these selective forces concurrently because of the difficulty in defining a common currency (McNamara and Houston 1986), evaluation of one of these individually can contribute toward understanding this rather complex phenomena.

Studies mentioned above evaluated individual components of growth such as energetic cost minimization, assimilation efficiency, or food consumption rate, but we chose to consider the cumulative response, which is growth itself. The growth maximization hypothesis as discussed here is actually just a broadened definition of Brett's (1971a) bioenergetics hypothesis and proposes that vertical migration through a range of temperatures can serve to maximize net energy assimilation by a combination of maximizing food consumption and minimizing metabolic costs. According to this hypothesis, the environmental conditions that would favor such movements are a spatial separation between optimal food densities and optimal thermal habitat. Under such conditions, a fish could reside at preferred temperatures where food is scarce (thus minimizing metabolic costs), reside where food is abundant but temperature is physiologically unfavorable (thus maximizing food consumption), reside where neither condition is optimal, or move between two (or more) depths taking advantage of the benefits of both (all).

Our primary objective was to evaluate the theoretical validity of the growth maximization hypothesis. To do this, we developed a detailed bioenergetics model which simulates the food consumption and growth of kokanee salmon (the nonanadromous freshwater variety of *O. nerka*) under various vertical migration scenarios. This analysis is similar to that performed by Swift (1976) on the vertical migration of *Chaoborus* larvae. We attempted to evaluate predictions of the model against the results of gillnet sampling and hydroacoustic surveys.

Input parameters for the model (temperature profiles and zooplankton densities and distributions) were derived from data collected from Nantahala Lake (western North Carolina) from 1985 to 1988. Nantahala Lake has an established population of kokanee and a seasonal spatial heterogeneity of temperature and food. It 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 adult kokanee (Northcote and Lorz 1966; Schneidervin and Hubert 1987), are concentrated in the upper portion of the water column where temperatures are typically greater than 15°C, the physiological optimum of this species (Brett 1971a).

Diel vertical migration of juvenile sockeye salmon (the anadromous variety of this species) has been documented and extensively studied by several investigators (Narver 1970; Brett 1971a; Eggers 1978; Levy 1987, 1990a, 1990b). 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. Northcote et al. (1964) observed vertical migration in adult kokanee, but little has been reported on juvenile kokanee. The general migration pattern observed for this species is an ascent to near the surface at dusk, followed by a partial descent during the night, a second ascent to the surface before dawn, and then a return to depths of 30–50 m where they reside during the day. Exceptions to this general pattern were reported by Northcote et al. (1964) and Levy (1990b).

In order to focus on growth maximization as a contributing factor to vertical migration, we attempted to minimize the influence of predator avoidance in this study by developing the model for 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, *Micropterus salmoides*, walleye, *Stizostedion vitreum*, and channel catfish, *Ictalurus punctatus*) would regularly consume fish larger than 250 mm. To minimize the influence of migratory behavior related to spawning, which occurs around the second week of October in this population, most of the sampling was performed from May to August.

Methods

Lake Description

Nantahala Lake (Macon County, North Carolina), located in the southern Appalachian Mountains at an elevation of 918 m, was impounded in 1942 principally for hydroelectric generation. Total surface area is 6.5 km^2, maximum depth is 69 m, and average depth is 26 m. Nantahala Lake is mesooligotrophic 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 low rainfall, drawdown can exceed 35 m.

Kokanee were stocked in Nantahala Lake for 2 or 3 yr in the early 1960s, and the population is presently self-supporting. Fall spawning migrations occur in the relatively pristine Nantahala River and its tributaries.

Field Data Collection

Temperature and DO profiles were determined with a Hydrolab Surveyor II at least once during each sampling trip. Secchi depths were also determined, and light penetration (PAR) was quantified with a photometer (Li-Cor model LI-188B) on a few occasions.

Zooplankton were collected by 1- to 2-min horizontal tows with a Clarke-Bumpus zooplankton sampler (10-cm diameter, 153-μm mesh) at five to seven depths between 3 and 27 m. These samples were collected in the same area where kokanee were captured. Samples were normally collected during midday (10:00–15:00) and on one occasion at night. Samples were preserved in 10% formalin for later identification and enumeration. Zooplankton larger than 1 mm (the size most likely to be consumed by adult kokanee as determined from stomach samples) were counted and identified to genus.

Six vertical gill nets (4.6 m wide × 30.5 m long; Horak and Tanner 1964) were used to collect kokanee and determine their depth distribution on 10 occasions (26 total nights) from May 1985 to June 1988. A different mesh size was used on each net (1.9, 2.5, 3.2, 3.8, 4.4, and 5.1 cm square measure). Nets were usually placed where maximum depths were 27–30 m so that the nets fished the entire water column. Because daytime sets proved mostly ineffective for all species, 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 stomachs were pumped (Seaburg 1957) and the contents preserved in 10% formalin. The fish 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 usually noted for nontarget species as well. Upon return to the laboratory, the kokanee were weighed, measured,

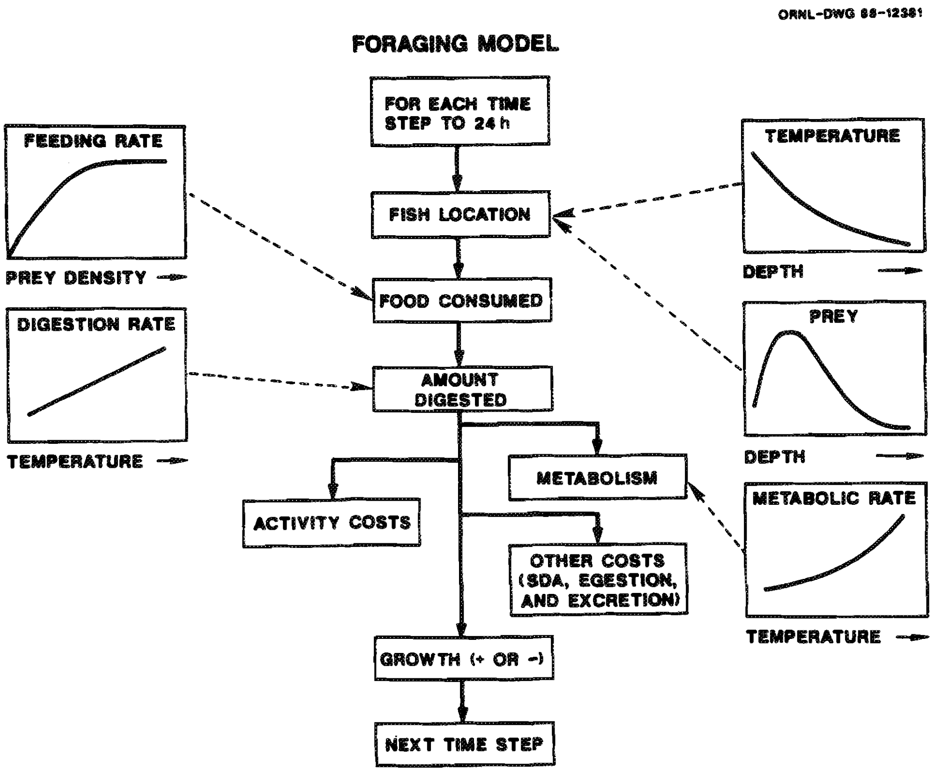

FIG. 1. Flow chart of bioenergetics model used to predict growth resulting from various vertical migration strategies of kokanee salmon.

and sexed.

Hydroacoustic surveys were conducted on 28–29 July 1987 and 7–8 June 1988 to estimate the distribution and vertical migration patterns of kokanee. A dual-beam/echo integration system was used for acoustic data acquisition and processing (Thorne 1983). This system consisted of the following equipment: 120-kHz, 10 × 25° BioSonics dual-beam transducer installed in a towed body, echo sounder with dual receivers, digital echo integrator, dual-beam processor, thermal chart recorder, microcomputer, and videocasette recorder.

Preliminary surveys were performed to determine the general location of highest kokanee concentration. Once an area with sufficient densities was located, 30-min surveys (six in 1987 and nine in 1988) were then conducted during a 24-h period. Each survey consisted of shore-to-shore transects in a zigzag pattern. The 1987 and 1988 surveys were in two different areas of the lake.

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 (millimetres) with Love's (1971) equation. Simultaneous gillnet data were also used to estimate the size of kokanee being tracked by hydroacoustics. The data were analyzed in 2-m depth intervals beginning at 2 m. Because the volume of water being sampled by this technique is conical, a correction was applied to the data so that the estimate of the number of targets marked in each depth interval represented an equal volume of water sampled.

Bioenergetics Model

Basic model operation

The bioenergetics model is based on a mass balance equation which accounts for energy from consumed food as it is partitioned among various energetic costs and the growth of an organism. Although 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

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

where G = specific growth rate (grams per gram per day), 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 more accurately reflect the time scale on which changes in thermal exposure and feeding occur as a result of vertical migration.

Figure 1 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 array (i.e., a vertical profile of prey densities and temperature), the weight of the fish, the depths between which vertical migration occurs, the time spent at each depth, and the time of active feeding. 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 to less than the maximum rate when the stomach fullness was near capacity due to prior

TABLE 1. Equations used in the bioenergetics model for kokanee salmon. The sources of the original data and/or equations upon which these derivations were based include (1) Hyatt (1980), (2) Brett (1971b), (3) Dumont et al. (1975), (4) Richman (1958), (5) Hewett and Johnson (1987), (6) Elliott and Persson (1978), (7) Brett and Higgs (1970), (8) Brett and Glass (1973), (9) Brett and Groves (1979), and (10) Elliott and Davison (1975).

Parameter	Source
Consumption (C)	
C (prey/h) = $(Z / (0.0138 \cdot Z + 11.5)) \cdot 60$	1
Stomach capacity of 100-g kokanee = $0.04 \cdot W$	2
Stomach capacity of 500- and 1000-g kokanee = $0.022 \cdot W$	2
Daphnia wet weight (mg) = $0.052 \cdot L_d^{3.012}$	3
Daphnia dry weight (mg) = $1.23 \times 10^{-10} \cdot (L_d \cdot 1000)^{2.61}$	3
Daphnia caloric content: 1 g wet weight = 586 cal	4
Kokanee caloric content: 1 g wet weight = $1362 + 0.736 \cdot W$ cal	5
Digestion (D)	
$D = W_{(0)} + C \cdot t - (W_{(0)} \cdot \exp(-rt)) + C/r \cdot (1 - \exp(-rt)))$	6
Digestion coefficient: $r = 0.0154 - 0.0140 \cdot T$	7
Egestion (F)	
$F = 0.455 \cdot T^{-0.222} \cdot D$	5
Excretion (U)	
$U = 0.0233 \cdot T^{0.580} \cdot A$	5
Respiration (R)	
Total respiration:	
$R = \exp[\ln(R_{(\mathrm{std})}) + ((\ln(R_{(\mathrm{act})}) - \ln(R_{(\mathrm{std})})) \cdot S/\mathrm{MSS})] + \mathrm{SDA}$	8
Maximum sustainable swimming speed (cm/s):	8
$\mathrm{MSS} = \exp(0.909 + 0.632 \cdot \ln(L) - 0.00901 \cdot T + 0.00349 \cdot T^2 - 0.000128 \cdot T^3)$	
Standard respiration (mg $O_2 \cdot g^{-1} \cdot h^{-1}$):	8
$R_{(\mathrm{std})} = \exp(-2.47 + 0.882 \cdot \ln(W) + 0.00126 \cdot T + 0.00286 \cdot T^2)$	
Active respiration (mg $O_2 \cdot g^{-1} \cdot h^{-1}$):	8
$R_{(\mathrm{act})} = \exp(-1.19 + 0.986 \cdot \ln(W) + 0.111 \cdot T - 0.00294 \cdot T^2)$	
Heat increment: $\mathrm{SDA} = 0.14 \cdot C$	9
Oxycalorific conversion factor: 3.24 mg O_2 = 1 cal	10
where	Range
Z = zooplankton density (no. /m^3)	0–7358
W = kokanee wet weight (g)	100–1000
L_d = *Daphnia* length (mm)	2.25
$W_{(0)}$ = weight (g) of food in the stomach at beginning of each time step	—
t = length of model time step (h)	0.5
T = temperature (°C)	5–25
S = swimming speed (cm/s)	0–20

feeding, but stomach fullness was not used as a trigger to terminate or initiate feeding. The amount of food consumed was added to the amount of undigested food remaining in the stomach (if any) from the previous time step. 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 plus 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, we 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. Equation (1) thus becomes

$$(2) \quad G = D - (R + F + U).$$

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

$$(3) \quad A = D - F.$$

Of this assimilated energy, 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

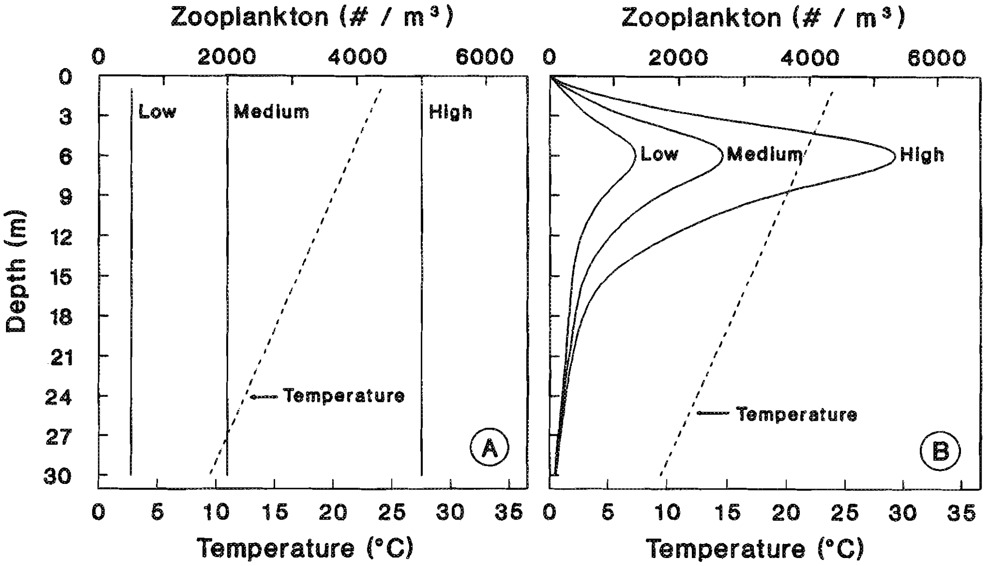

FIG. 2. (A) Uniform and (B) unimodal prey density distributions used in the bioenergetics model. Three levels of zooplankton densities (high, medium, and low) are represented by solid lines with temperature indicated by a broken line.

change in weight (either 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. A summary of the equations and values used in the model is found in Table 1. For a more detailed description of the components and format of the model, see Bevelhimer (1990).

The model continued 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 (grams per day). The simulation was repeated using the final stomach content value of the first 24-h 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 to achieve this steady state. A steady-state situation (equal initial and final stomach contents) would occur naturally if the 24-h feeding pattern of kokanee and the food density 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 diel cycle. The results of the final steady-state simulation were those used in the analysis. The data derived from the simulations were daily estimates of consumption rate, energetic costs, growth, and gross conversion efficiency (kilocalories growth per kilocalorie 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. The depths between which vertical migration occurred could be entered manually (one at a time) or automatically with spreadsheet macros. Once the initial conditions (prey/temperature array, migration depths and times, fish weight, and feeding status) were entered, the calculations and iterations were performed automatically.

Model simulations

Simulations were designed to evaluate the behavior of the model or to test possible patterns of diel vertical migration. Various scenarios were established through the choice of the prey/temperature array and the migration pattern of the kokanee. The 13 prey/temperature arrays used in the model included six hypothetical arrays, six empirical arrays constructed from field data, and one projected array based on field data. The six hypothetical arrays were used to evaluate the basic behavior of the model and included high, medium, and low densities of prey distributed uniformly throughout the water column (Fig. 2A) and high, medium, and low densities of prey in an unimodal distribution with peak prey density at 6 m (Fig. 2B). For the six hypothetical arrays, the temperature stratification was represented as a linear decrease from 24.5°C at the surface to 9.5°C at 30 m; these arrays will be identified by their prey distribution (e.g., uniform-medium or unimodal-high). The arrays with the unimodal prey distribution are similar to natural situations in which the heterogeneity in the prey and temperature distributions produces the foraging dilemma discussed in the introduction. The six empirical arrays consisted of sampling data from June 1985 to June 1988 and were used to evaluate migration strategies under natural prey densities and temperature stratification; these arrays will be identified by their date of collection. The projected array included an estimated nighttime distribution of zooplankton based on the measured nighttime distribution on a different date.

Initial simulations were run without any vertical migration of the 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 hypothetical prey/temperature arrays.

A typical simulation was run with a combination of two depths, one when 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 modeled at 3 m when feeding would be at either 3, 6, 9, . . ., or 30 m when not feeding, and so on for all possible feeding depths. Simulations were

TABLE 2. Variables used in simulations of the vertical migration of kokanee salmon. The conditions of the standard simulation are underlined.

Variable	Range of values
Fish size	100, <u>500</u>, or 1000 g
Feeding duration	8, 10, <u>12</u>, or 16 h/d
Feeding swim speed	<u>20</u> or 30 cm/s
Feeding pattern	<u>Diurnal</u> or nocturnal

normally limited to a maximum depth of 30 m, which was near the maximum depth of the reservoir in the upper half of the reservoir where kokanee were normally captured and water quality measurements were made. For each prey/temperature array, a series of up to 55 simulations was performed to determine the optimal migration strategy for a fish of a given size with a particular temporal feeding pattern.

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 array. Kokanee size, feeding duration, swimming speed, and feeding pattern were varied one at a time in other simulations to evaluate their respective effects on the predictions of the optimal migration strategy. The feeding pattern was usually diurnal, but a nocturnal pattern was also simulated. Table 2 summarizes those variables that were manipulated in the simulations. Simulations with the six empirical arrays were the same as the standard simulation except for the substitution of one of the empirical arrays for the hypothetical array.

The results of the modeling exercise were compared with the migration patterns observed during the hydroacoustic surveys. To facilitate this comparison, simulations using the prey/temperature array collected during the 1988 hydroacoustic survey were modified to reflect the observed kokanee behavior during the survey. These modifications included a smaller kokanee size (100 g) and a different feeding pattern (nocturnal instead of diurnal) with the projected nighttime zooplankton distribution. The projected nighttime zooplankton distribution was estimated using the same distribution shape as that observed during night sampling in June 1985 and then scaling it to the peak daytime density. Feeding at night by kokanee has been documented (Northcote and Lorz 1966), and feeding by sockeye at light levels less than bright moonlight (0.032 lx) has also been observed (Brett and Groot 1963).

Results

Temperature data from six dates were used in the model (Fig. 3). The temperature profile of Nantahala Lake can generally be characterized as gradually decreasing from the surface downward, usually with no distinct thermocline. 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. DO concentrations exceeded 7.0 ppm throughout the vertical profiles on four of the six dates. On the other two dates (July 1987 and October 1985), DO was <7.0 ppm below 9 and 24 m deep, respectively. The majority of the kokanee captured on these two dates were at depths where DO < 7.0, suggesting that even though there is evidence that Pacific salmon avoid DO < 7.0 ppm (Birtwell and Kruzynski 1989), these levels do not appear to be absolutely limiting. Secchi depths were normally in the 3- to 5-m range. Light profiles of the water column indicated that at midday the intensity at 30 m is approximately 1.1 lx. Brett and Groot (1963) found that juvenile salmon could feed at maximum rates at this intensity or higher, suggesting that light should not be a limiting factor on feeding to a depth of at least 30 m during midday. They also reported that at total darkness ($<1.1 \times 10^{-4}$ lx) the salmon did not feed even at high prey densities.

For vertical profiles of zooplankton densities (Fig. 3), linear interpolation provided values at depths that were not sampled on the six dates. Values at the surface and 30 m were projected to be zero to provide a complete profile of the prey density for the model simulations. *Daphnia* sp. accounted for nearly 95% of the larger zooplankton (>1 mm) in the lake with *Leptodora*, chironomid larvae and pupae, *Chaoborus*, *Holopedium* sp., and copepods making up smaller proportions of this size class of zooplankton. Large zooplankton were generally more abundant in late spring and early summer than in late summer and fall. Smaller zooplankton (<1 mm) consisted mainly of copepods, *Daphnia* sp., and *Bosmina* sp., but were not quantified.

Kokanee (180–550 mm total length, 51–1459 g wet weight) were captured over a wide range of depths (5–29 m) and temperatures (7–22°C) during the study. However, most (87%) were captured in an 8°C range (7.5–15.5°C) with a mode at 12°C (Fig. 4). The precise time of entanglement (i.e., late evening, during the night, or early morning) is unknown, although entanglement during the night was observed on one occasion when nets were checked throughout the night. Seasonal changes in kokanee distributions reflected the seasonal changes in the thermal profile of the lake. As the summer progressed and water temperatures warmed, they were captured at increasingly greater depths. Kokanee were captured at temperatures up to 22°C which indicates that some occasionally move into water that is much warmer than their preferred temperature range. No obvious size- or sex-related differences in depth or temperature of capture were noticed.

Species other than kokanee (rainbow trout, *Oncorhynchus mykiss*, channel catfish, walleye, black crappie, *Pomoxis nigromaculatus*, white crappie, *Pomoxis annularis*, rock bass, *Ambloplites rupestris*, redbreast sunfish, *Lepomis auritus*, and white sucker, *Catostomus commersoni*) composed approximately 50–65% of the total catch. Except for rainbow trout, which were captured at 16–20°C (Fig. 4), little overlap in depth/temperature distribution occurred between kokanee and the other species.

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. Large *Daphnia* (mean size approximately 2.25 mm) accounted for at least 95% of items in 55 of the 58 stomachs with identifiable prey.

Results of an intensive 24-h hydroacoustic survey indicated that adult kokanee were possibly undergoing limited vertical migrations in late July 1987 (Fig. 5A). Rainbow trout and kokanee were captured in gill nets at depths of 0–21 and 16–26 m, respectively, during this sampling trip. Given the depth and temperature range differences between these two species, the high temperatures (>25°C) in the upper 5 m, and general knowledge of the habitat preferences (particularly thermal) of the other species in the system, the following assumptions were made during the interpretation of the hydroacoustics output. Fish in the upper 8 m of the water column were assumed to be primarily channel catfish, rainbow trout, or other species, but not kokanee; fish from 8–20 m could conceivably have been rainbow trout or

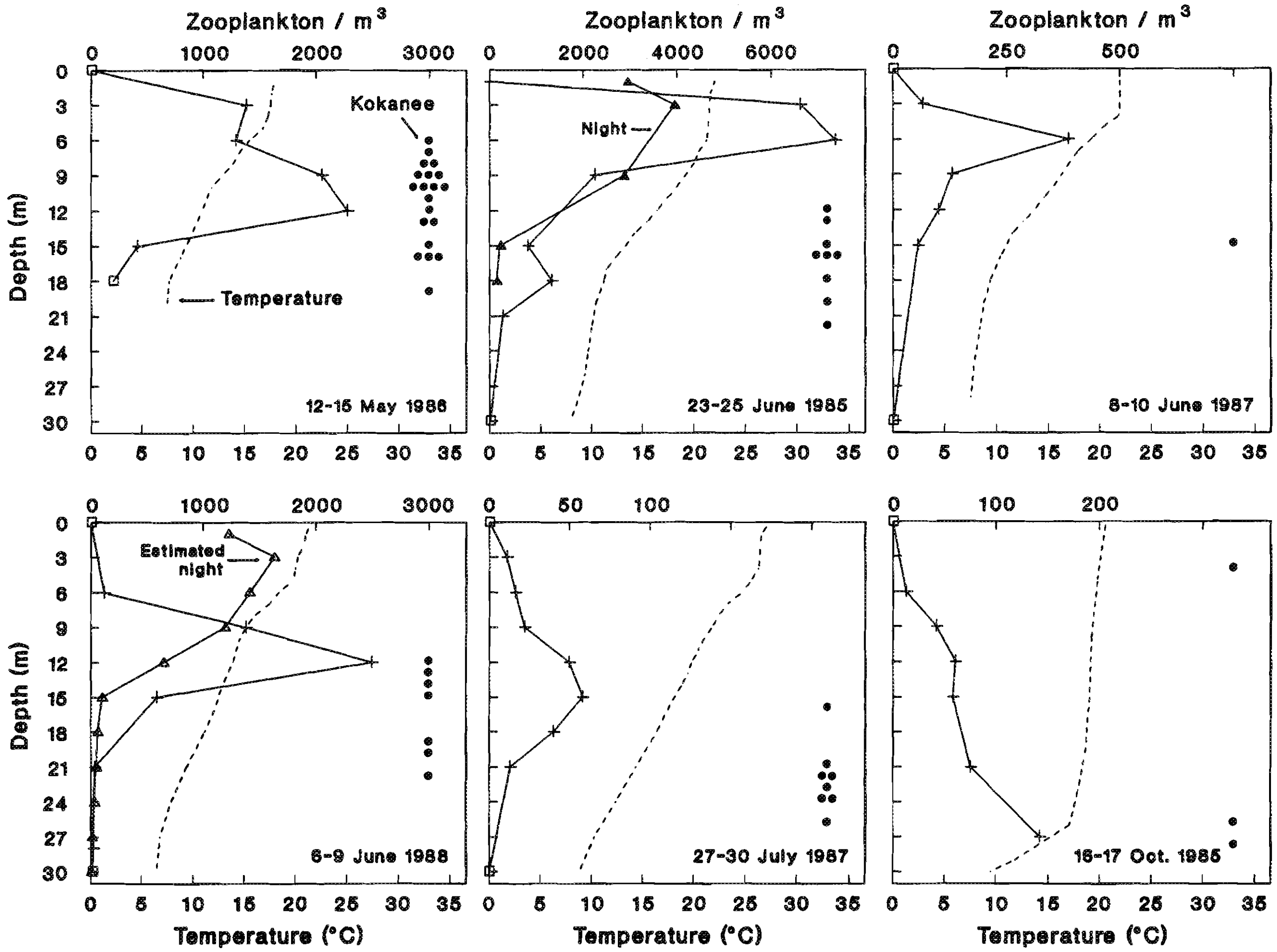

FIG. 3. Vertical profiles of zooplankton >1 mm (solid lines) and temperature (broken lines) measured in Nantahala Lake on six occasions. Plus signs represent measured densities from horizontal zooplankton tows, and open squares represent projected densities for use in the bioenergetics model when actual values were not available. All zooplankton profiles represent daytime distributions except for two nighttime distributions, one observed (solid triangles) and one projected (open triangles). Solid circles indicate the depths of individual kokanee salmon captured in gill nets on the same sampling trip.

kokanee; and fish from 20–36 m were most likely kokanee. Given these species-specific differences in depth distribution, the hydroacoustic survey results were interpreted as follows. At dawn (sample start time 05:58), kokanee were most likely between 20 and 32 m, but some may also be at 8–16 m. By midday (13:10) through late afternoon (17:10), they might be anywhere from 8 to 24 m. At dusk (20:25), kokanee were most likely between 14 and 24 m. After dark, the kokanee appear to move deeper to 20–32 m by 22:00 and 22–32 m by 23:55. Although it is impossible to tell what individuals are doing, the population as a whole appears to be between 8 and 24 m during the day (zooplankton densities were highest at 11–18 m, see Fig. 3) and between 20 and 32 m during the night. The kokanee appear to be distributed over a 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 may be an indication of the degree of precision (or lack thereof) with which vertical position is selected. This also suggests a fair amount of individual variation and/or asynchrony in the timing of movements.

In June 1988, reconnaissance surveys prior to the intensive 24-h survey were unable to locate any fish resembling adult kokanee, and no adult kokanee were captured in the nets at this time. A concentration of small fish (presumably juvenile kokanee) were located at depths >40 m during afternoon reconnaissance surveys. In addition, juvenile kokanee (179–197 mm) were captured in the nets. Unlike the previous year when surface temperatures during the hydroacoustic survey exceeded 25°C, the temperature at 1 m was only 21°C; therefore, fish marked in the upper few metres of the water column were not ruled out as kokanee. The results of this survey (Fig. 5B) were interpreted as follows. Although the targets from 2–10 m could be several species, the fish at 42–50 m in the afternoon (14:35) are almost certainly kokanee. Only three fish were marked from 10–42 m at this time. At dusk (20:50), these kokanee had left the deepest water and moved to shallower than 30 m. Throughout the night (21:25, 22:05, and 00:05), most targets were at 2–24 m with a few from 24–50 m. The overnight gillnet sets during this same sampling trip support this observation — juvenile kokanee were captured at 13–22 m. At dawn (05:40), most of the fish were observed at 24–42 m. After sunrise (06:30), most were at 30–42 m, and by late morning (10:55) the concentration of fish at 42–50 m was reestablished. Given this interpretation, the kokanee are migrating from 42–50 m to at least 24 m (an average

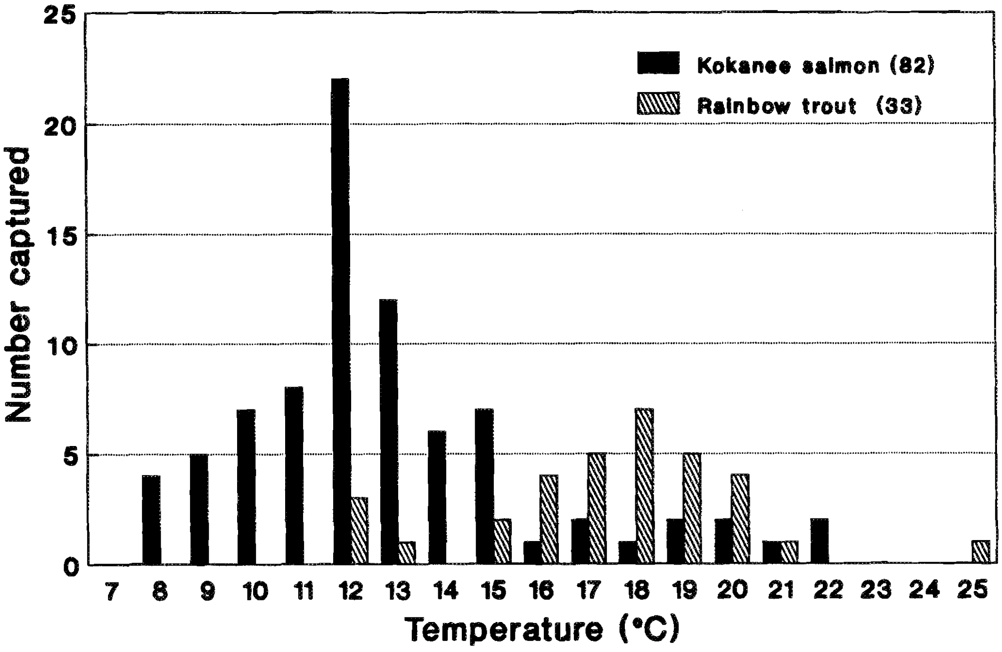

FIG. 4. Temperature distributions of 82 kokanee salmon (180–550 mm) and 33 rainbow trout (277–518 mm) captured in gill nets during 10 sampling trips from 1985 to 1988 in Nantahala Lake.

migration of 22 m) and possibly as far up as the surface (>40-m migration). The conspicuous absence of large numbers of fish at the 2- to 6-m range during the dawn (05:40 and 06:29) and dusk (20:48) surveys is difficult to explain. This could possibly be a result of offshore-inshore migrations by species other than kokanee or movements to the top 2 m where targets are not detected by this hydroacoustic technique.

Model Simulations

In simulations with the uniform–high array (Fig. 2A) and no vertical migration, growth for a 500-g kokanee was optimal at 18 m (15.5°C) (Fig. 6A). Growth was lower at depths <18 m due to increased metabolic rates associated with higher temperatures. At depths >18 m, growth was inhibited because food consumption was limited by slower digestion rates associated with colder temperatures. That is, because prey were abundant and feeding rate was high, the stomach was filled in a few hours, after which time 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). With the uniform–medium array, the effect of the digestion rate/stomach capacity interaction was only important at 27 and 30 m because of a decrease in the feeding rate, and the depth of optimal growth was therefore deeper (24 m, 12.5°C) than when food was more abundant. With the uniform–low array, the limitations on food consumption by digestion rate and stomach capacity were not important, and optimal growth was achieved at 30 m (9.5°C) where metabolic costs were minimal.

In simulations with the unimodal prey distributions (see Fig. 2B) and no vertical migration, the resulting growth-at-depth (Fig. 6B) was more reflective of the prey distribution than simulations with the uniform prey distributions. With the unimodal–high array, 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°C). The increased food consumption at 6 m as compared with 9 m was offset by an even greater total energetic cost at 6 m due to warmer temperatures. In addition, the difference in daily consumption of fish between 6 and 9 m was 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 28%. With the unimodal–medium and unimodal–low arrays the depth of maximum growth was 6 m. At lower levels of food availability and consumption, stomach capacity does not have the same limiting effects as at higher prey densities; therefore, the growth-at-depth relationship more closely reflects the prey distribution.

When diel vertical migration was included in the model, standard simulations with the unimodal–high array generated growth rates ranging from –0.51 to 3.28 g/d (Fig. 7). The most obvious result of these simulations is that there is a definite advantage to some type of vertical migration given this prey/temperature array. Although 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 to 9 m and then moving to 15–30 m when not feeding. Since the greatest growth occurred with a nonfeeding depth of 30 m, migration to a greater depth with cooler temperature would probably produce greater growth until digestion rates became slow enough to inhibit the quantity of food that could be consumed in future feedings.

Because differences among the top five or 10 most productive migration strategies were 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 produced the highest growth.

The effect of prey density was evaluated with the three hypothetical levels of unimodal prey distributions (Fig. 2B). A fourth level was created by doubling the consumption rate at the

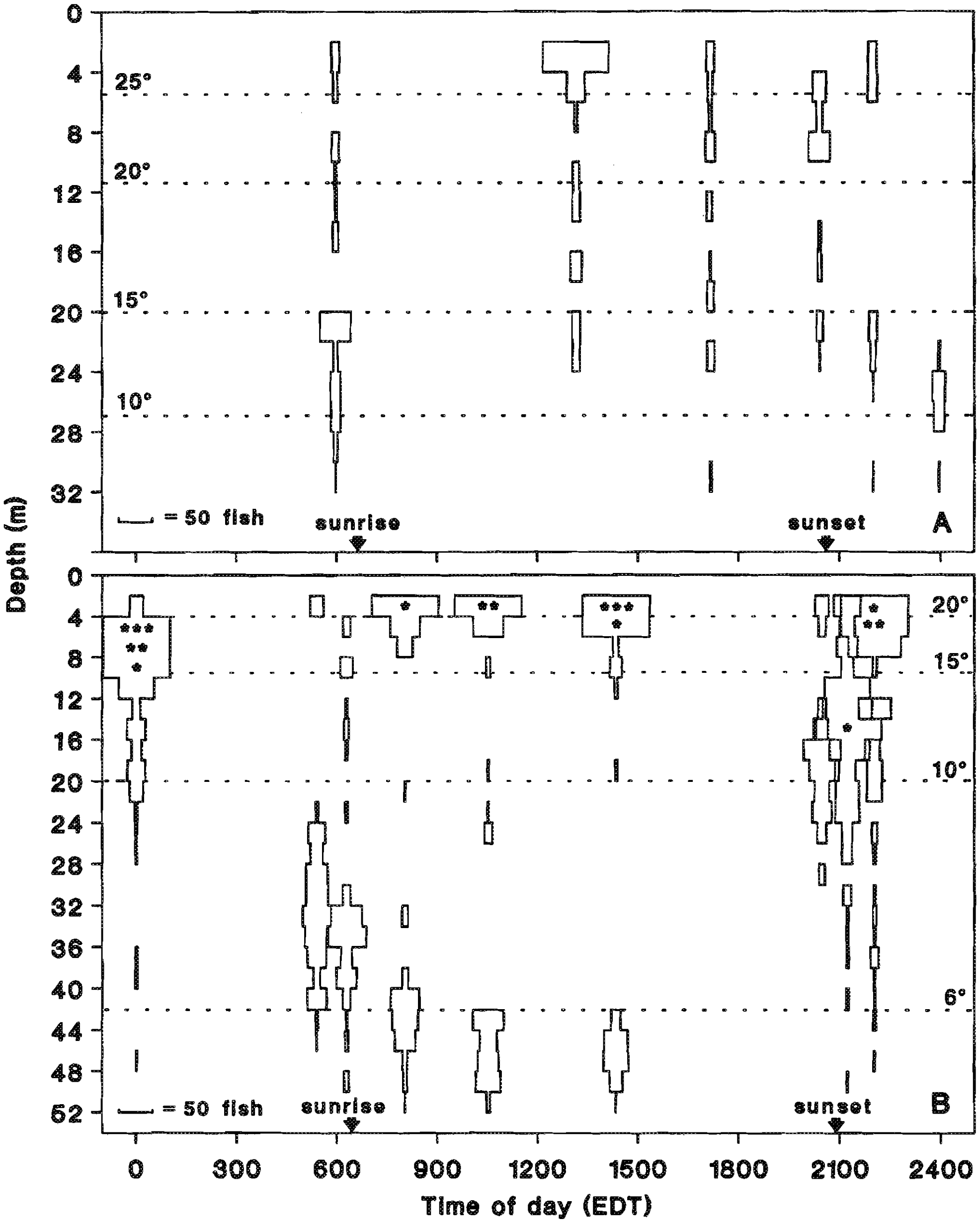

FIG. 5. Number of fish located (represented by the width of each block) at each 2-m depth interval during hydroacoustic surveys on (A) 28–29 July 1987 and (B) 7–8 June 1988. Intervals that exceeded 100 fish are marked with asterisks: *101–150, **151–200, and ***201–250 fish, respectively. The fish counted were those registering a target strength of –24 to –38 dB (comparable to adult-sized kokanee) and –39 to –59 dB (comparable to juvenile-sized kokanee) in 1987 and 1988, respectively. Horizontal dotted lines indicate temperatures.

high level. The results indicate that, generally, the best strategy is to move to where the food is most abundant to feed and then to the coolest water when not feeding (Fig. 8A) as long as the water is not so cold as to slow digestion to the point that subsequent feeding bouts are limited by leftover food in the stomach. The differences in growth were as expected — higher levels of prey resulted in greater growth. The advantages of migration as indicated by a comparison of the resulting growth versus the growth achieved when not migrating are most important in the simulation with low prey density and least important with the highest density (Fig. 8A).

The effect of the amount of time spent feeding each day was evaluated at foraging durations of 4, 8, 12, and 16 h/d with the standard setup. At 4 h/d, feeding at either 6 or 9 m was most productive (Fig. 8B). However, as feeding time increased, feeding at 6 m alone 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 most important at the shorter feeding durations (Fig. 8B).

The effect of fish size on optimal strategy was evaluated for fish of 100, 500, and 1000 g with other variables at the standard values. These results suggest that as size increases, the upper limits of migration should be slightly deeper (Fig. 8C). This pattern was largely influenced by weight-specific differences in

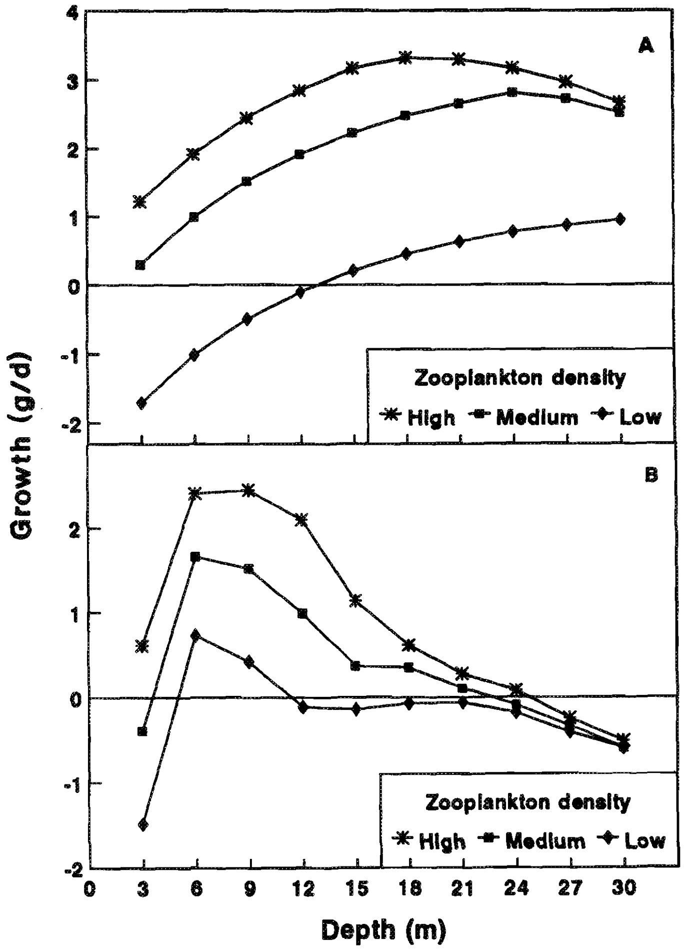

FIG. 6. Results of model simulations of growth at three prey densities with (A) uniform and (B) unimodal vertical distributions when no vertical migration of kokanee was simulated.

metabolic rate and stomach capacity. The advantages of migration are small for the 100-g fish, but become markedly more important as size increases (Fig. 8C).

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 to 30 cm/s. An additional simulation was performed to allow for an increase in consumption of the same magnitude (50%) as the increase in swimming speed, assuming that search volume and thus consumption increases proportionally to swimming speed. With changes in swimming speed alone, the basic migration strategy remained the same, but growth was lower at the higher swimming speed because of increased metabolic costs. Increasing consumption along with swimming speed resulted in the same general migration patterns being most productive. Growth in this instance (with increased speed and consumption) was greater than when the fish was at the "normal" swimming speed and rate of consumption.

The standard simulation was also performed with the six empirical prey/temperature arrays to evaluate seasonal variation in optimal migration strategy (Fig. 8D). The model predicted that under spring (May 1986) conditions, vertical migration would be limited or nonexistent and confined to the middle of the water column. With late spring and early summer (June 1985, 1987, 1988) conditions, the importance of vertical migration (as indicated by the resulting growth) increased, and the predicted range of migrations might be as great as 24 m. For midsummer (July 1987) and fall (October 1985) conditions, the model predicted that vertical migrations were of little value and that kokanee would select fairly deep locations.

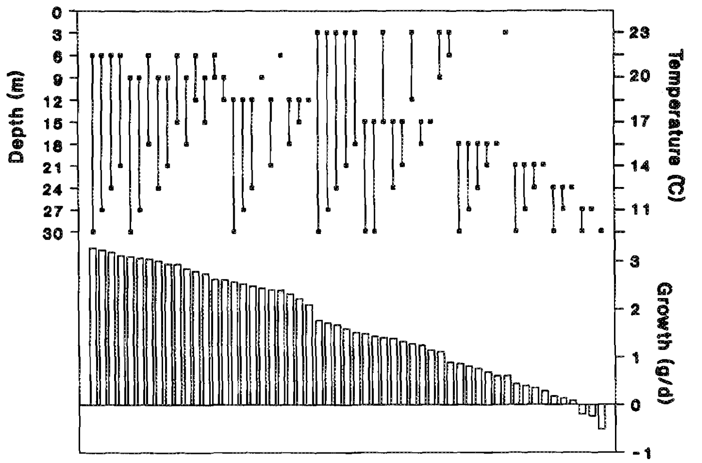

FIG. 7. Results of standard model simulation. Top half of graph indicates the combination of depths between which vertical migration occurred (no movement is indicated by a single point). Each histogram at the bottom indicates the growth resulting from the migration pattern directly above.

The modified June 1988 simulations (100-g kokanee feeding at night) predicted that ascending to 3 m to feed and descending to 9–21 m when not feeding was the most energetically efficient. The model predicts higher growth and different optimal migration patterns when feeding at night than during the day (Fig. 9).

Discussion

In general, predictions of the bioenergetics model are consistent with the expected growth dynamics of salmonids as evidenced by consumption rates that were about 4.5% body weight per day, growth rates about 1% body weight per day, and gross conversion efficiency of about 35%. All of these are within the ranges expected for this size of fish when feeding at a high ration (Brett 1979).

The modeling results demonstrate that when the preferred temperature and optimum prey density are spatially separated, vertical migration can result in greater growth compared with no migration. Because of the interaction of factors such as feeding rate, stomach evacuation rate, stomach capacity, and respiration rate, the most productive location for feeding is not always the one with the greatest food density. Likewise, the most productive location for resting is not always that where metabolic costs are minimized. In addition the combination of depths that produces the highest growth rate is usually not the same as the combination that produces the highest conversion efficiency. Greater growth can sometimes be achieved by processing more food at a lower efficiency than by processing less food at maximum efficiency.

Levy (1990a) minimized the importance of the energetic benefits of vertical migration based on the assumption that such benefits would only be realized when a substantial temperature difference existed between selected vertical positions. He concluded that the mean difference of 4°C that he observed would result in only minor growth differences. In fact, based on the

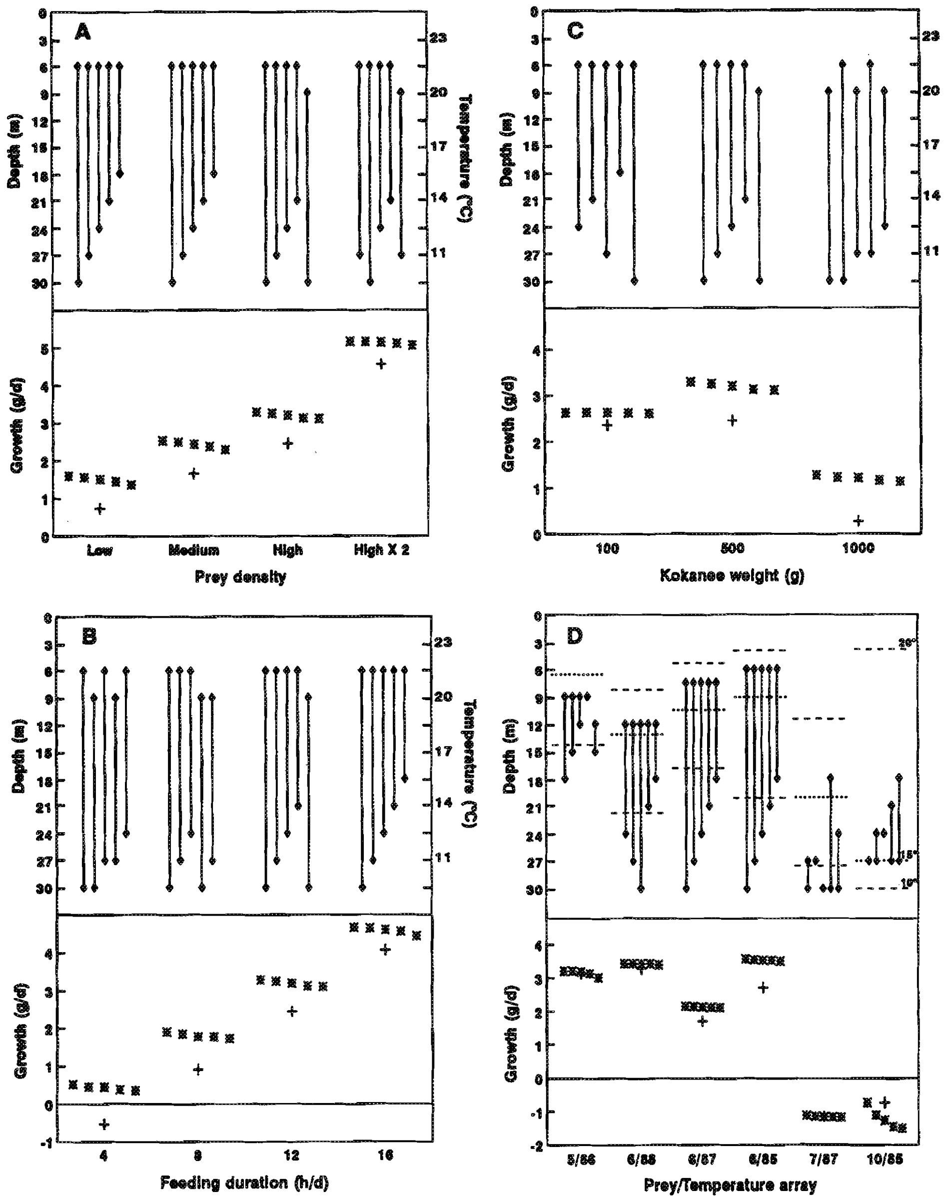

FIG. 8. Five migration patterns (upper panels) which resulted in the highest simulated growth (lower panels, in descending order left to right) for (A) each of four treatments of prey density, (B) each of four treatments of feeding duration, (C) each of three treatments of fish weight, and (D) each of six actual prey/temperature arrays from May 1986, June 1985, June 1987, June 1988, July 1987, and October 1985. In Fig. 8D, the 20°C depth is indicated by the top broken line, the 15°C depth by the dotted line, and the 10°C depth by the bottom broken line. Growth from each migration pattern indicated in the upper panels is indicated with an asterisk. Growth of the highest ranking nonmigration pattern (plus sign) is also included for comparison regardless of its overall rank.

results of the standard simulation (see Fig. 7), a difference of 4.5°C (21.5–17.0°C) from the feeding depth (6 m) to the nonfeeding depth (15 m) resulted in a 21% increase in growth rate over the nonmigration alternative of staying at 6 m. A more substantial temperature difference (9°C from 6 to 24 m) during vertical migration resulted in a 33% increase in growth rate over not migrating. Even a 21% difference in growth could have a substantial impact on size-dependent processes such as predation mortality, egg production, and mate selection.

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 because 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.

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 swim bladder to remain at the same depth. Alexander (1972) estimated the additional cost of swimming activity needed to compensate for negative buoyancy by a shallow-acclimated fish that migrates to deeper water as approximately 25 $cm^3\ O_2 \cdot kg^{-1} \cdot h^{-1}$ (36 $mg\ O_2 \cdot kg^{-1} \cdot h^{-1}$) while at the lower depth. 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, vertical migration is still a more productive strategy than not migrating at all. Alexander (1972) also estimated the cost of swim bladder inflation for buoyancy compensation as approximately 10 times less costly than active compensation. Although compensation via swim-bladder 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 (or any other species) are not available. Even Alexander (1972) stated 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 relative to prey density. This assumption had some effect on the predictions of vertical migration strategy, but is more critical to accurate predictions of growth. Information regarding differences in maximum feeding rate due to size for particulate-feeding fish is scarce. 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 assumption is reasonable, considering that 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.

Sensitivity analyses were performed on several variables in the model to determine their relative importance to model predictions. Changes in the swimming speed within the ranges tested 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 have differed.

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 where a combination of high food concentration and high digestion rate results in the maximum food consumption rate, 6 m).

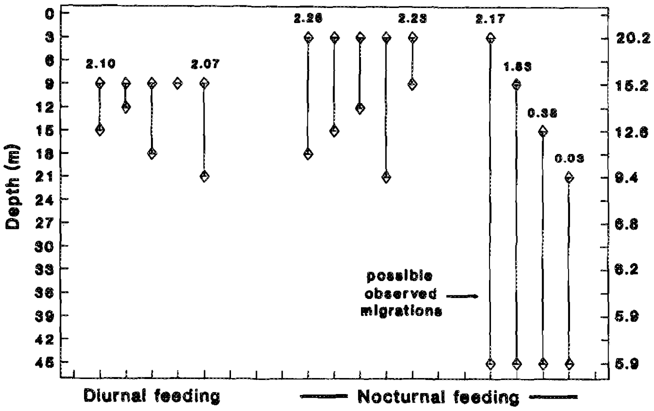

FIG. 9. Five migration patterns which resulted in the highest simulated growth (in descending order left to right) for 100-g kokanee with observed daytime (left side) and hypothetical nighttime (middle) prey distributions for June 1988. On the right are four possible migration patterns resulting from simulations (using the hypothetical nighttime prey distribution) as suggested by the hydroacoustics data. Corresponding growth (g/d) is included above some migration patterns.

Similar changes were predicted when fish size was varied. Because the prey consumption/prey density relationship was 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 not feeding.

When simulations were performed with actual prey/temperature distributions, a seasonal variation in migration strategy was predicted. In spring when water temperatures in the upper half of the water column were still relatively cool (<20°C) and a significant thermal stratification had not yet developed, migrations of 0–9 m were predicted. As temperatures warmed and thermal stratification progressed in late spring and early summer, the benefits of vertical migration were greater and the range of migrations encompassed most of the water column. And by late summer and early fall when prey densities were greatly reduced, the benefits of vertical migration disappeared. Narver (1970) observed similar seasonal shifts in the magnitude of vertical migrations. Unfortunately, no information regarding migration patterns could be obtained from our net data, since the precise time of capture of individual fish could not be determined. However, the locations of kokanee captured in the nets (see Fig. 3) rarely exceeded the range of occurrence predicted by the model (Fig. 8D) for each of the six dates.

Comparisons of the simulations for July 1987 and June 1988 with the results of the hydroacoustic surveys performed on those dates are difficult because of the uncertainty in the interpretation of the hydroacoustics results. With the July 1987 data, the model predicted that kokanee should undergo only limited migrations or none at all due to low prey densities and warm temperatures in the upper half of the water column (see Fig. 8D). Such patterns are not ruled out by the hydroacoustics results, but are not supported either.

An evaluation of the 1988 hydroacoustic survey with the simulation results raises two questions. First, what are the energetic differences between diurnal and nocturnal feeding? The resulting growth of the nocturnal simulations was slightly greater than that of the diurnal simulations (Fig. 9) even though the peak prey density was less during the night than during the day. Of course, this assumes that they can feed at the same rate during the night as 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 versus 3 m at night) was limited by the cooler temperatures (6°C less than at 3 m). Second, how does the observed migration pattern compare with the predictions of the model? The top five migration patterns predicted by the modified June 1988 simulations (Fig. 9) do not match the pattern observed during the hydroacoustic survey. The model predicted feeding at 3 m, which is not necessarily ruled out by the survey results, but also cannot be confirmed. The lower limits of migration predicted by the top five simulations were 9–21 m, which is much shallower than the observed lower limits of 42–50 m. However, the decrease in simulated growth associated with descending to the observed depths (i.e., migrating from 3 to 42–50 m) compared with the top ranked migration pattern (i.e., 3–18 m) is minimal — only a 4% decrease in growth. If the extent of the kokanee's upward migration is only 21 m, the predicted growth is 0.03 g/d — a 99% decrease from the optimal and not nearly enough to achieve normal growth. Although predator avoidance is a reasonable explanation for juvenile kokanee to feed at night and to descend to great depths during the day, these results suggest that there can be energetic advantages associated with nocturnal feeding as well.

We have demonstrated that bioenergetic differences among various vertical migration scenarios under a variety of conditions affect the growth advantage of a particular behavior. Whether vertical migration results in an energetic advantage depends on the size of forager, seasonal and daily variation in temperature profiles and prey distributions, consumption limitations, etc. Because of the variety of factors involved, vertical migration may vary widely among species and systems. In addition, vertical migration need not always be between areas of optimal thermal conditions and warmer than optimal conditions to be energetically advantageous. Energetic benefits may also be realized from migrating in and out of colder than optimal conditions (Wurtsbaugh and Neverman 1988). Lastly, growth maximization (or energetic efficiency) is not the only factor driving vertical migration. However, even when another factor (such as avoidance of predators) is of key importance, it seems reasonable to expect that energetic considerations still influence the vertical migration that is exhibited within the constraints of the primary factor. Ultimately, a complete understanding of vertical migration may necessitate a multifactor approach with individual factors receiving different value depending on seasonal and ontogenetic considerations.

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