

Habitat Selection by Lacustrine Rainbow Trout within Gradients of Temperature, Oxygen, and Food Availability

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Abstract. Rainbow trout (*Oncorhynchus mykiss* [Walbaum]) in Castle Lake, California were concentrated at certain depths during day and evening hours. A fish bioenergetics simulation model based on vertical gradients of temperature, oxygen concentration, and food availability indicated that rainbow trout selected habitats that maximized growth rate. In 1 of the 2 years of study, a strong pattern of diel vertical migration of rainbow trout was evident and was associated with vertical migrations of daphnids in the lake. The simulation model correctly predicted the occurrence and magnitude of fish migration. During the day some trout resided at depths with little potential for feeding and growth but close to regions of high food availability and low oxygen concentrations. Hydroacoustic sampling from stationary platforms suggested that fish briefly descended into anoxic layers to feed on abundant zooplankton.

Introduction

Attempts to understand habitat relationships among fishes follow two general approaches. One is a microhabitat preference approach in which physical, chemical or biological parameters are correlated with the selection of habitat by fishes (Binns and Eisermann 1979; Moyle and Vondracek 1985; Rudstam and Magnuson 1985). This allows ranking of diverse habitats according to fish preference (Hickes et al. 1991), but it neither provides predictions of how given habitats support a species (Bowlby and Roff 1986; Orth 1987) nor effectively integrates small-scale measurements into larger-scale habitats that fish operate within.

In the second approach, measuring fitness correlates of organisms living in different habitats has been emphasized. Werner and Gilliam (1984) and Fraser and Cerri (1982) developed and tested models that allowed fish to choose habitat types based on relative fitness. These models successfully described habitat choices of fishes under field conditions (Gilliam and Fraser 1987; Werner and Hall 1988). This approach has two advantages over the microhabitat preference approach. First, performance of the fish can be assessed in each habitat, and second, habitats are assessed over the larger

rate will maximize survival and thus enhance fitness. Ware (1982) argues that for most fish species, surplus power (instantaneous growth rate) is a good analog of fitness. Many researchers use growth rate or mortality risk, or both, as an index of fitness (Houde 1989). A second problem with the fitness approach is the difficulty in extrapolating measures of growth rate or mortality risk to new study sites without initiating new investigations.

We argue that a hybrid of these two approaches would be a more effective means of understanding habitat selection by fishes. Hughes (1992) and Hill and Grossman (1993) correlate microhabitat variables with fitness characteristics of stream fishes occupying different habitats. They estimated potential energy gain under different microhabitat conditions and argue that fitness of fish should correlate with energy gain (Ware 1982; Magnhagen and Kvarnemo 1989). These correlations between microhabitat variables and potential energy gain are transferable to other study sites.

We followed a similar approach in examining habitat selection by rainbow trout (*Oncorhynchus mykiss* [Walbaum]) along vertical gradients of temperature, oxygen, and food availability in Castle Lake, California. Our objective was to determine if rainbow trout select habitats with environmental characteristics that maximize their potential growth rate. Potential growth rate was the predicted growth rate determined from a bioenergetics and foraging model with dependent variables of zooplankton food availability, temperature, and oxygen concentration. Our approach is similar to that recommended by Brandt et al. (1992) in their analyses of spatially explicit growth rate potential. We estimated vertical distribution of fish with hydroacoustic methods and compared the distribution of fish to potential growth rate derived from the bioenergetics model. Our study occurred in Sept. 1989 and 1990, when thermal stratification of Castle Lake was greatest and zooplankton comprised a substantial portion of the diet of rainbow trout.

Study Area

Castle Lake is a small (20 ha), deep (32 m maximum), mesotrophic lake located in the Siskiyou Mountains of northern California (elevation 1657 m). A central sampling station, located over the deepest portion of the lake, was used to collect temperature, oxygen, zooplankton, fish in vertical gillnets and stationary hydroacoustic information. Summer Secchi transparency ranged from 7 to 12 m and epilimnetic chlorophyll *a* concentration ranged from 1 to 5 $\mu\text{g l}^{-1}$. Macrozooplankton were dominated by *Daphnia rosea*, *D. middendorffiana*, *Holopedium gibberum*, *Diacyclops thomasi*, and *Diaptomus novamexicanus* (Elser and Goldman 1991).

Rainbow trout have been annually stocked into Castle Lake since the mid-1950s and during this study were the numerically dominant fish captured in gill nets. Brook char (*Salvelinus fontinalis* [Mitchill]) and golden shiners (*Notemigonus crysoleucas* [Mitchill]) were also present in the lake.

Piscivory on rainbow trout was apparently very low during the study period. Examination of over 600 stomachs of brook char and rainbow trout collected during 1989–1991 failed to reveal a single occurrence of a salmonid prey. No piscivorous birds resided at the lake. An osprey, whose nest was ~4 mi from the lake, was occasionally seen fishing. Anglers likely exert the greatest mortality on rainbow trout in Castle Lake.

Methods

POTENTIAL GROWTH RATE

Potential growth rate of rainbow trout was calculated using a bioenergetics simulation model. The model was a variation of the generalized salmonid model of Hewett and Johnson (1987) except that respiration rate was decreased by 8% (Weiser 1985). The model was run for a 100-g rainbow trout occupying each of seven depth strata in the lake. Simulations conducted with different sizes of rainbow trout changed only the magnitude of potential growth rate, not the relative rankings of the depth strata. Inputs to the model were temperature, oxygen, and biomass of daphnids >1.0 mm in length. This length criterion was used because stomach samples from rainbow trout indicated that only the daphnids >1.0 mm were consumed by these fishes. Copepods and smaller cladocerans were not consumed. Potential growth was assumed to be minimal in habitats where oxygen concentrations were below 3 mg l⁻¹ (Cech et al. 1990).

The energetics model incorporates a mass balance approach where the amount of energy ingested daily by an individual fish is partitioned into costs of respiration, specific dynamic action, egestion, and excretion. After these costs have been subtracted, the remaining ingested energy results in positive growth. If energetic costs exceed ingested energy, growth is negative. Temperature, mass of the fish, and amount of food consumed influence the energetic costs according to the equations in Hewett and Johnson (1987).

The amount of food ingested is based on the density of daphnids present in each depth stratum according to a relationship established for rainbow trout preying on daphnids in both Utah reservoirs (Tabor 1990) and in large limnocorrals (Teuscher 1993) (Fig. 1). For this feeding rate analysis, we measured the growth rate of rainbow trout exposed to different levels of daphnid food resources (Table 1). We used the energetics model to estimate the proportion of maximum consumption (p-max) realized by rainbow trout in these field conditions. Then the relationship between daphnid biomass and p-max was examined and a least squares curvilinear regression was used to define this relationship (Fig. 1). From these studies we correlated observed growth of rainbow trout with measured biomass of daphnids. Temperature and body size effects on fish growth were corrected for use with the bioenergetics model (Hewett and Johnson 1987). This correlation between daphnid availability and rainbow trout growth (Fig. 1) allowed us to predict growth of rainbow trout in Castle Lake given information on daphnid availability and temperature.

TEMPERATURE AND OXYGEN

Temperature and oxygen concentrations were measured with a YSI oxygen/temperature meter at the central sampling station. Measurements were taken every meter from a depth of 32 m to the surface at ~1200 on 8 Sept. 1989 and on 5 Sept. 1990.

ZOOPLANKTON SAMPLING

Zooplankton were collected from the central sampling station in the lake with a 12.5-l Schindler trap equipped with a 64- μ m mesh net on 11 Sept. 1989 and 5 Sept. 1990. Three samples were collected

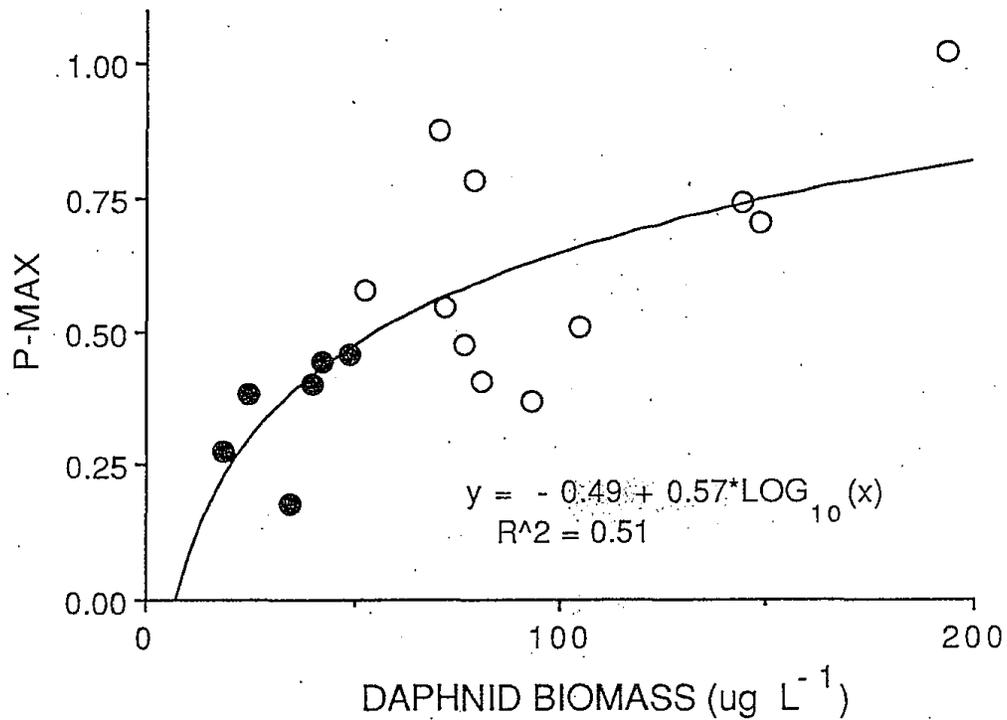


Figure 1. Relationship between the proportion of maximum consumption (p-max) observed for rainbow trout and density of daphnid food resources. O = bioenergetics simulations of rainbow trout growth in East Canyon Reservoir, Utah (Tabor 1990); ● = bioenergetics simulations of rainbow trout growth in mesocosm enclosures in Flaming Gorge Reservoir, Utah (Teuscher 1993).

Table 1. Mean daphnid biomass, rainbow trout growth rate, and proportion of maximum consumption (P-max) exhibited by rainbow trout in limnocorral experiments (Teuscher 1993). Number of rainbow trout in each corral and number used to calculate mean growth rate are presented. Initial weight of rainbow trout ranged from 4.44 to 7.76 g.

Number	Mean daphnid biomass µg l ⁻¹	Trout growth % d ⁻¹	P-max
2	42.0	1.8	0.445
2	24.2	.3	0.381
4	48.5	.1	0.455
4	39.4	.6	0.400
8	18.3	.65	0.277
8	34.3	0.056	0.175

and pooled from each of seven depths: 0–5, 5–10, 10–15, 15–20, 20–25, 25–30, and 30–32 m. Zooplankton samples were collected between 1300 and 1400 h and at 2100–2200 (Pacific Daylight Time), and preserved with a 5% formalin solution saturated with sucrose.

Daphnids were enumerated under a dissecting microscope at 24X magnification. Examination of post-abdominal claws from selected individuals indicated that ~90% of the daphnids were *D. rosea*, with *D. middendorffiana* representing the other 10%. The length of the first 20 individuals from each depth was measured, and biomass of daphnids was calculated from the mean length of daphnids in the sample and the length-weight regression for *D. rosea* (Downing and Rigler 1984).

HYDROACOUSTIC SAMPLING

Mobile hydroacoustic surveys were used in early September of each year (11–12 Sept. 1989 and 5–6 Sept. 1990) to assess the abundance and spatial distribution of fish in Castle Lake. Each hydroacoustic survey consisted of six cross-lake transects covering a distance of 3.2 km. Surveys were done twice during the day (1300–1500 h) and twice during dusk (1900–2100 h). Acoustic surveys were then repeated on a subsequent date, providing four estimates of fish density during the day and four estimates during dusk. Acoustic samples were collected with a BioSonics model 105 echosounder equipped with a 420-kHz dual beam (6x15°) transducer that allowed us to estimate fish sizes. We sampled at a rate of 2 pings s⁻¹ traveling at a boat speed of 4–6 m s⁻¹.

In addition to the moving acoustic surveys, acoustic data were also collected from a stationary platform near the middle of the lake. Data were collected in 20-min blocks from the stationary platform at ~1200 and 2100. Acoustic data were recorded directly into computer files as digitized echoes, as well as on Betamax videotape, and on a paper chart used to generate an echogram.

Acoustic data were analyzed by counting echoes with dual-beam information processed with a BioSonics ESP Dual Beam Processor (Model 281) and software. Only single fish targets within 4° of the acoustic beam axis were used to calculate fish target strength and to obtain fish density estimates. Single fish targets with dual beam target strengths ranging from -51 to -35 decibels (db), representing fish of 5–40 cm TL (Love 1971), were used. This size range included all lengths of rainbow trout and eliminated age-0 golden shiners, which were present in the surface waters at dusk.

FISH SAMPLING

In addition to acoustic sampling, bottom-set gillnets were set in early September of both years. Catches from these nets allowed us to estimate the relative abundance of rainbow trout and brook char in the lake, and to partition acoustic targets to each species (Burczynski et al. 1987). A stratified random design was used for placing a bottom net within each of the four areas within the lake. Each net was 30 m long, 2 m high and composed of five mesh sizes (19, 25, 32, 39 and 54 mm stretch). Nets were set at night between 1930 and 0700 for 4–5 consecutive nights in early September of each year. All fish were removed from gillnets, measured (standard length to the nearest mm), weighed (wet weight to the nearest 0.1 g) and sexed.

A series of six vertical gillnets (3 m wide by 32 m long) was set near the central sampling station 4–9 Sept. 1990. The top of each net floated at the surface and the bottom reached the sediments. Each net consisted of single-mesh monofilament with stretch mesh sizes of 19, 25, 32, 39, 54, and 69 mm.

Nets were set and pulled at sunrise and sunset and the species, length, mass, and depth of each fish captured was recorded. Catch in the vertical gillnets provided information on distribution and diet of fish occupying the pelagic region of the lake.

DIETS OF FISH

The stomach of each fish captured in gillnets was preserved in 10% formalin and later examined for diet contents under a dissecting microscope at 22X magnification. Stomach contents were separated into four prey types (daphnids, other zooplankton, aquatic insects, and other prey). The wet weight of each prey type was measured on a Sartorius electronic balance (± 0.001 g). The proportion by weight of each prey type was calculated for each stomach.

Results

TEMPERATURE AND OXYGEN

Temperature and oxygen conditions were similar in both years (Fig. 2). Epilimnion temperatures exceeded 18°C , a preferred temperature for rainbow trout (Hicks et al. 1991), and hypolimnetic temperatures ranged from 4°C to 5°C . A metalimnetic oxygen maximum was apparent in each year. Oxygen concentrations fell below 3 mg l^{-1} at 25-30 m and likely limited occupation of this stratum by rainbow trout. Anoxic conditions occurred below 30 m in both years.

ZOOPLANKTON SAMPLING

Daphnid biomass differed significantly between years (Fig. 3, Mann-Whitney U test, $U_{14,14} = 143$, $p < 0.01$), with a strong pattern of diel vertical migration being apparent in 1989. During the day the highest daphnid biomass occurred at 30-32 m. At dusk these zooplankters moved up in the water column such that the highest daphnid biomass occurred in the metalimnion. In 1990 the overall abundance of daphnid biomass was reduced and no vertical migration was apparent (Fig. 3).

HYDROACOUSTIC SAMPLING

The density of fish estimated with hydroacoustic surveys did not vary between years. Three-way ANOVA (year X depth X time of day) indicated that overall fish density was not significantly different between years ($F_{1,72} = 1.24$, $p > 0.05$), but there were highly significant effects of time of day ($F_{1,72} = 18.7$, $p < 0.01$) and depth ($F_{5,72} = 14.4$, $p < 0.01$). Fish density was greater during the day, indicating that some fish at dusk had settled too close to the bottom to be detected by hydroacoustic gear. Fish density was consistently greater in the metalimnion (Figs. 4 and 5). A significant depth X time interaction ($F_{5,72} = 8.05$, $p < 0.01$) indicated that fish were undergoing diel vertical migration, especially in 1989 (Fig. 4).

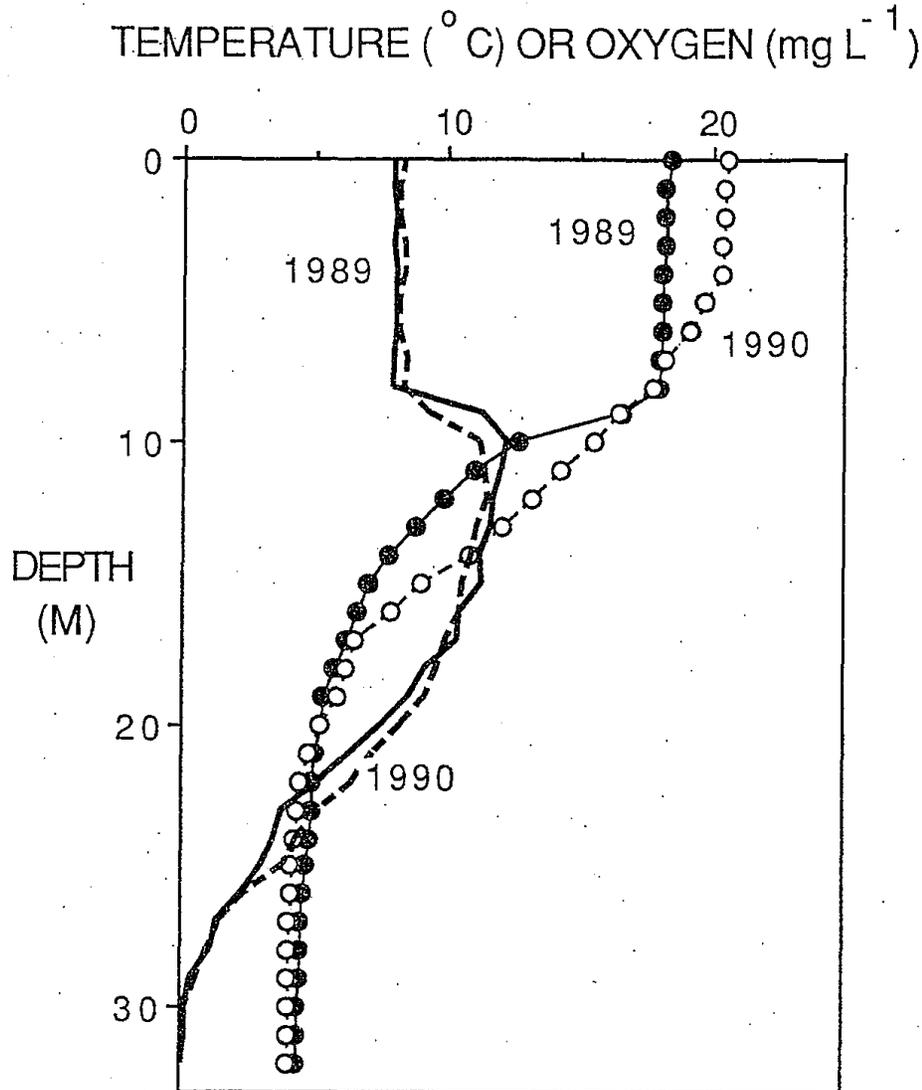


Figure 2. Temperature (circles) and oxygen (lines) conditions at different depths in Castle Lake on 8 Sept. 1989 (● and —), and 5 Sept. 1990 (○ and ---).

Rainbow trout and brook char were the only fish caught in gillnets. Rainbow trout comprised 54% of the catch in bottom-set gillnets (67 rainbow trout and 58 brook char, both years combined). Vertical gillnet catches indicated that rainbow trout occupied the pelagic regions of the lake more frequently than did brook char (Table 2), since 90% of fish caught in vertical gillnets were rainbow trout.

DIETS OF FISH

Daphnids comprised an important diet item for both rainbow trout and brook char in late summer of 1989 and 1990 (Table 3). Daphnids accounted for 25% and 29% of the diet of rainbow trout caught

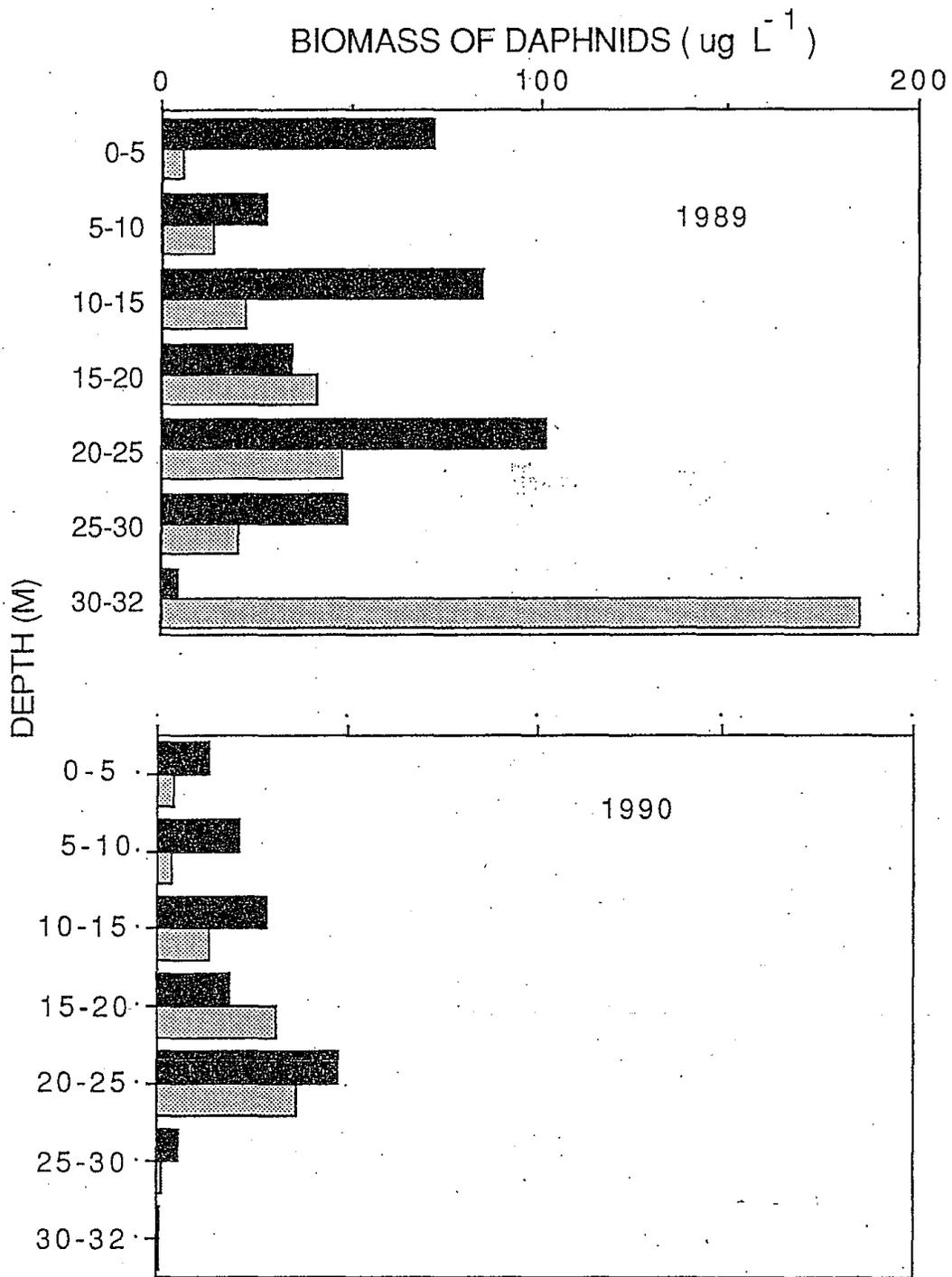


Figure 3. Biomass of daphnids longer than 1 mm in different depth strata of Castle Lake on 11 Sept. 1989 and 5 Sept. 1990. Stippled bars represent samples collected at 1300–1400 h, and dark bars represent samples collected at 2100–2200 h.

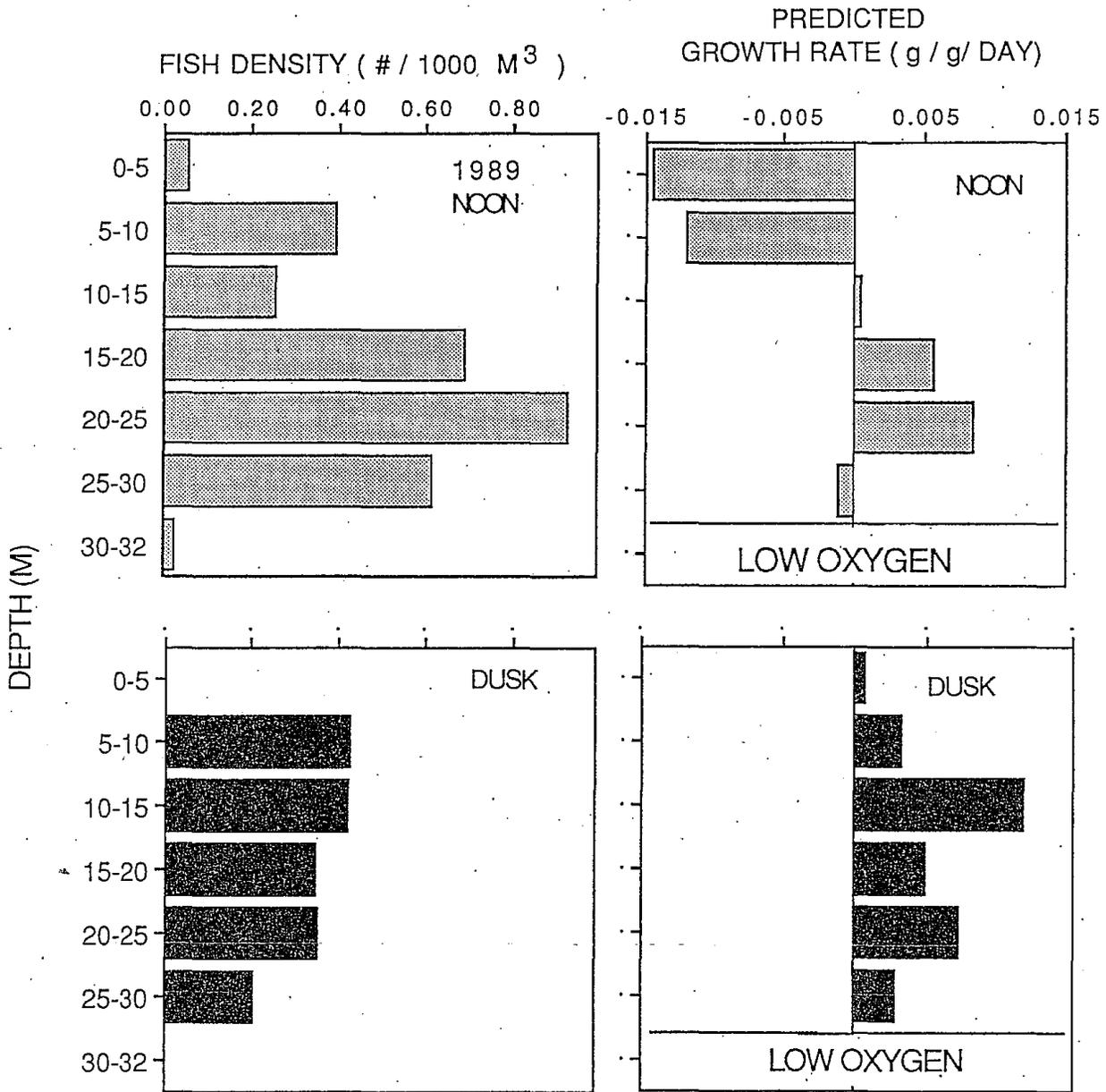


Figure 4. Fish density (left graphs) in different depth strata of Castle Lake during the day (top) and dusk (bottom) periods in 1989 estimated with mobile hydroacoustic samples. Each histogram is a mean of four samples collected on two consecutive days. Potential growth rate (right graphs) of rainbow trout in each depth stratum of Castle Lake during day (top) and dusk (bottom) periods in 1989 (estimated from bioenergetics simulations using zooplankton biomass and temperature as inputs).

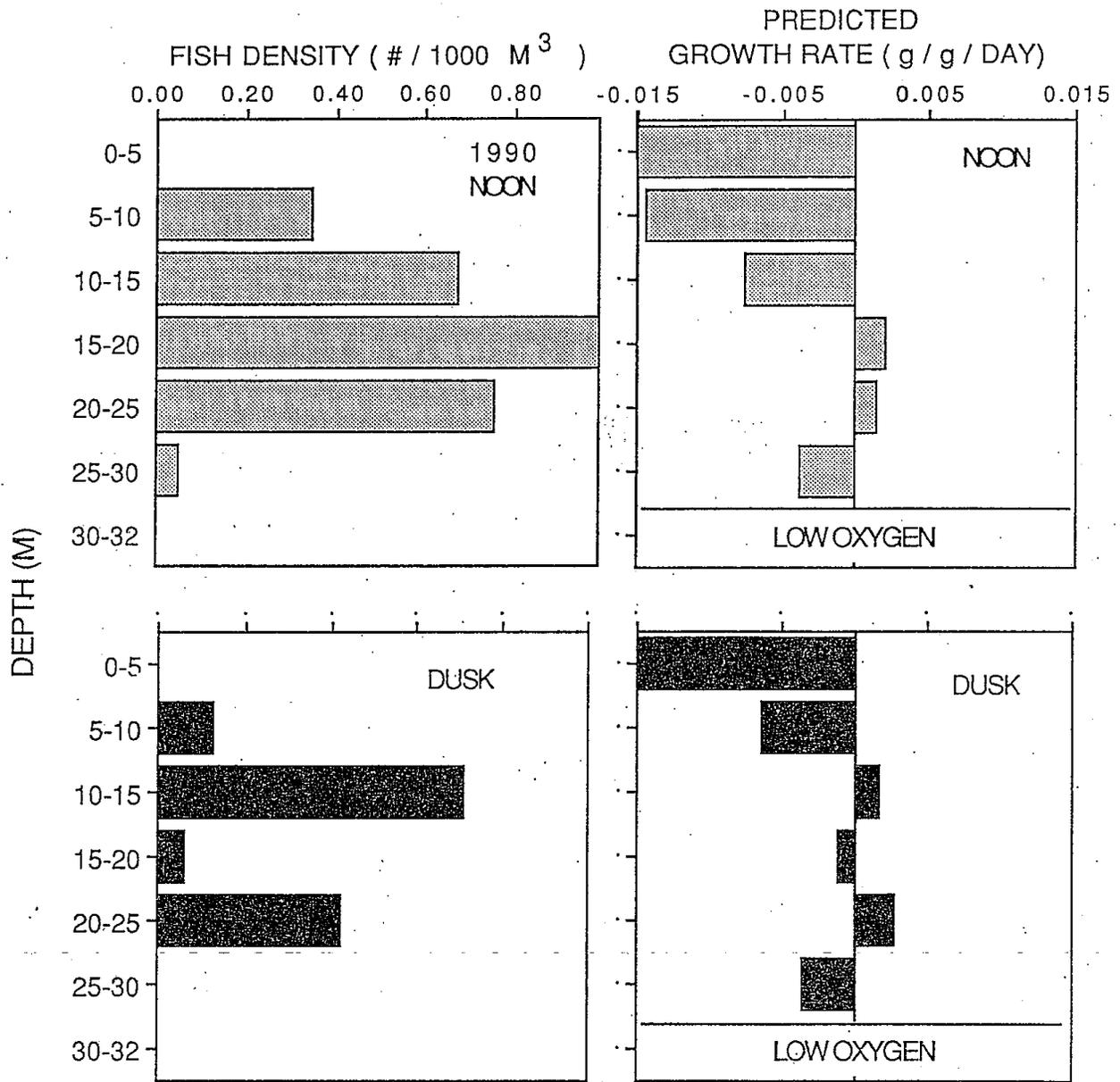


Figure 5. Fish density (left graphs) in different depth strata of Castle Lake during the day (top) and dusk (bottom) periods in 1990 estimated with mobile hydroacoustic samples. Each histogram is a mean of four samples collected on two consecutive days. Potential growth rate (right graphs) of rainbow trout in each depth stratum of Castle Lake during day (top) and dusk (bottom) periods in 1990 (estimated from bioenergetics simulations using zooplankton biomass and temperature as inputs).

Table 2. Catch of rainbow trout and brook char in vertical gillnets 4–9 September 1990. Day sample catches are from 0600 to 2000; night samples from 2000 to 0600.

Depth (m)	Day		Night	
	Rainbow	Brook	Rainbow	Brook
0–5	0	0	0	0
5–10	1	0	1	0
10–15	0	0	2	1
15–20	2	0	2	0
20–25	1	0	0	0
25–30	0	0	0	0
30–32	0	0	0	0

Table 3. Diet proportions by weight for rainbow trout and brook char caught in bottom-set and vertical gillnets in early September 1989 and 1990. Number of stomachs examined are in parentheses. Other zooplankton are mainly *Holopedium gibberum* and copepods. Other prey include terrestrial insects and molluscs.

		Prey type			
		Daphnids	Other zooplankton	Aquatic insects	Other prey
<u>1989</u>					
Bottom-set					
	Rainbow (40)	0.25	0.02	0.46	0.27
	Brook (31)	0.29	0.00	0.62	0.09
<u>1990</u>					
Bottom-set					
	Rainbow (27)	0.29	0.03	0.50	0.18
	Brook (27)	0.30	0.00	0.59	0.11
<u>Vertical</u>					
	Rainbow (9)	0.52	0.08	0.30	0.10
	Brook (1)	0.32	0.00	0.49	0.19

in bottom set gillnets in 1989 and 1990, respectively. Rainbow trout captured in vertical gillnets consumed a greater proportion of daphnids (52%) than those caught in bottom set gillnets. Aquatic insects and unidentified prey accounted for most of the remaining prey of rainbow trout. Diets of brook char consisted mostly of aquatic insects and daphnids.

POTENTIAL GROWTH RATE

Potential growth of rainbow trout predicted from bioenergetics models varied by depth stratum (Figs. 4 and 5). In 1989 potential growth rate was negative in the epilimnion and generally positive in the deeper portions of the lake during the day (Fig. 4). At night, potential growth rate of rainbow trout

was greatest at 10–15 m, corresponding to reasonably high concentrations of daphnids and water temperatures of 7–13°C.

In 1989, densities of fish in different depth strata during the day appeared to correspond to predicted potential growth rate. The highest densities of fish were recorded in the 15- to 25-m strata, where two of the three positive growth potentials were estimated (Fig. 4). A high biomass of daphnids was measured in at 30–32 m, but low oxygen concentration likely restricted fish from permanently occupying these zones. Stationary hydroacoustic sampling indicated that fish were making brief foraging forays into this region to feed on abundant daphnids. Paper chart recordings of this acoustic data show fish targets residing around 26 m, making descents down to 30 m, and then returning to the 26-m region (Fig. 6). The presence of these diving fish may be the reason why fish densities were relatively high at 25–30 m, where growth potential was low.

At dusk in 1989 both daphnids and fish moved up in the water column. The bioenergetics model indicated that potential growth for rainbow trout was greatest at 10–15 m. Fish densities were high in this stratum but were slightly greater at 5–10 m (Fig. 4).

For 1990 the bioenergetics model indicated that overall growth potential for rainbow trout was reduced compared with 1989 (Fig. 5). During both day and dusk periods, potential growth was positive only in the lower portions of the metalimnion. This reduction occurred because of declines in the abundance of large daphnids (Fig. 3). As in 1989, the abundance of fish targets in 1990 was greatest in depth strata where potential growth was positive. The growth rate potential was similar during day and dusk periods, and fish showed no pattern of diel vertical migration.

The potential growth rate model was a good predictor of habitat use by rainbow trout in this study. Spearman's rank correlation test indicated that potential growth rate and fish target density were strongly correlated during both day and dusk periods in 1989 and 1990. Assuming that depth strata with $<3 \text{ mg l}^{-1} \text{ O}_2$ provided the lowest potential growth, Spearman's ($r_n = 7$) yielded day and dusk correlations of 0.982 and 0.958, and 0.982 and 0.964 for 1989 and 1990, respectively. Each of these values is significant ($p < 0.05$).

Discussion

The potential growth rate model for rainbow trout suggested that conditions for trout growth were highly variable during late summer periods in Castle Lake. The model indicated that trout occupying surface waters during the day would lose 1.5% of their body weight each day, whereas regions in the metalimnion at dusk exhibited potential growth rates $>1\% \text{ d}^{-1}$. This variation in predicted growth potential was due to vertical changes in temperature, oxygen, and zooplankton food resources. The potential growth rate of trout corresponded closely with their vertical distribution in the lake. In 1989 the simulation model indicated that rainbow trout growth would be greatest in the hypolimnion during the day while hydroacoustic sampling indicated that fish density was greatest in the 15- to 30-m strata. The model predicted that rainbow trout should move into metalimnetic strata at dusk to feed on vertically migrating zooplankton, and acoustic sampling verified this prediction in that fish targets moved up into the 5- to 15-m strata after sunset.

In 1990 vertical migration of zooplankton was not observed and the growth rate potential was similar under day and dusk conditions. Acoustic sampling indicated that fish targets remained in the 10- to 25-m strata during day and dusk periods, corresponding closely with the strata that exhibited

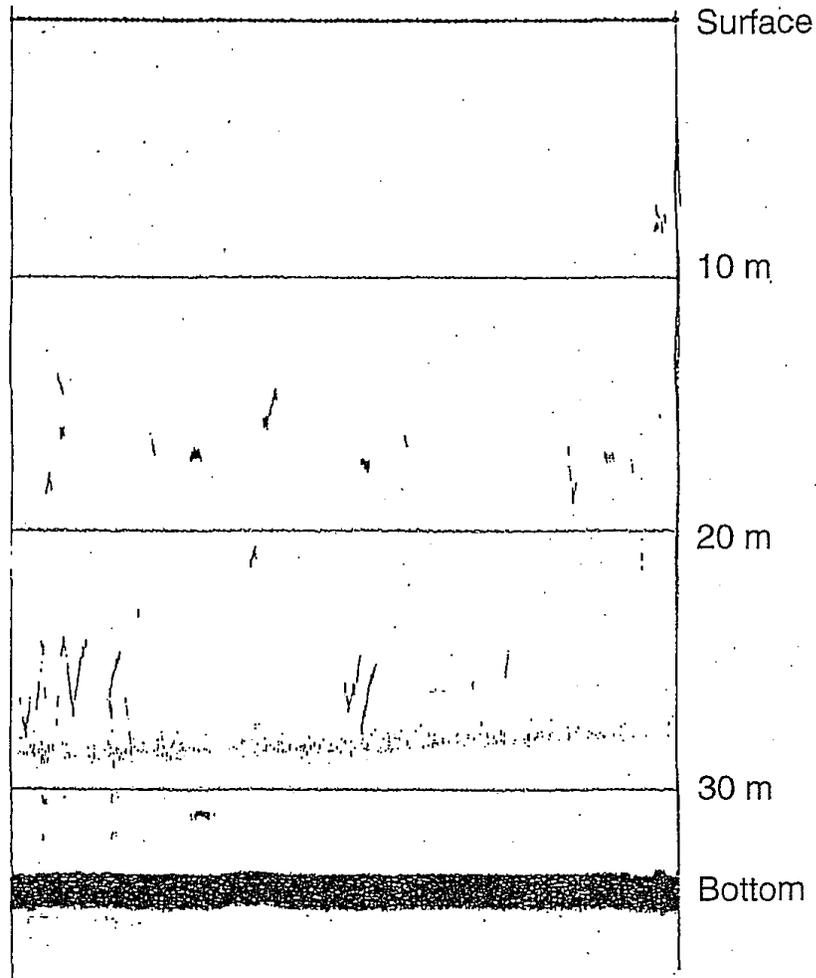


Figure 6. Paper chart of stationary hydroacoustic recordings 1435–1442 h on 12 September 1989. The transducer was located ~1 m below the surface. Time moves from left to right on the figure. The wide vertical bar represents the sediments at ~33 m below the transducer. A faint scattering layer is present 29 m below the transducer corresponding to a layer of very high zooplankton concentrations. Several fish targets are located between 15 and 20 m, and several are located around 26 m and make descents (V-shaped tracings) into the stratum of high zooplankton abundance.

a positive growth potential. In both 1989 and 1990, fish densities were greatest in depth strata exhibiting the highest growth potential.

Hydroacoustic sampling of fish can bias distributional patterns (Luecke and Wurtsbaugh 1993a). In the Castle Lake surveys, we were not able to sample fish targets within 2 m of the surface and 1 m of the bottom of the lake. In addition to these limitations, the survey boat likely disturbed fish near the surface. Our acoustic methodology thus underestimated fish density in surface and near-bottom strata. Although the degree of this underestimation is not known, rainbow trout or brook char were not caught in vertical gillnets in the top or bottom strata of the lake, suggesting that any bias in the acoustic data was not severe.

The potential growth rate model was specific to rainbow trout, but bottom-set gillnet catches indicated that rainbow trout and brook char were about equally abundant in Castle Lake during the

study period. We contend that catches in vertical gillnets, while small in number, provide a good representation of the relative abundance of rainbow trout and brook char in the pelagic region. The similar size distribution of rainbow trout and brook char suggests that vulnerability to gillnets would be similar for both species. For these reasons, we conclude that the majority of the acoustic targets were rainbow trout. Given the close taxonomic relationship of brook char and rainbow trout, brook char should respond to environmental gradients of daphnids, temperature, and oxygen in a manner similar to rainbow trout. The inclusion of brook char in our fish distribution does not greatly weaken our conclusions.

In the potential growth model, it is assumed that rainbow trout fed entirely on daphnids, yet analysis of stomachs indicated that daphnids composed only 25–50% of the diet. Our objective was to determine whether potential growth rate corresponded with the distribution of pelagic fish in Castle Lake. Given that the diets of rainbow trout caught in vertical gillnets in the pelagic region contained higher proportions of daphnids than rainbow trout caught in bottom gillnets, it appears that pelagic rainbow trout were actively seeking and foraging on daphnids. The hydroacoustic surveys coupled with the potential growth rate model provide a reasonable description and mechanism of the vertical distribution of pelagic rainbow trout.

In Castle Lake, determination of potential growth rates appears sufficient to understand habitat selection of pelagic rainbow trout. In our approach we ignored alternative food resources and potential predators. Inclusion of information about the abundance of benthic and terrestrially derived prey in the simulation model would likely have improved predictions of rainbow trout habitat use. Unfortunately, we know of no information relating insect food abundance to salmonid growth in lakes, however, Tabor (1990) reports that rainbow trout appear to ignore benthic prey if the densities of large daphnids exceed 5 individuals l^{-1} . This density corresponds to $\sim 50 \mu g l^{-1}$, a biomass that typically produced slightly positive growth rates in our simulations.

Piscivorous fish or birds were not important in determining rainbow trout distributions during our study but could be crucial in other studies (Bowby and Roff 1986). Few large rainbow trout or brook char were captured during our study. Only 2% of salmonids captured in gillnets from 1898 to 1991 exceeded 300 mm TL, and these fish fed almost exclusively on benthic invertebrates (C. Luecke, unpubl. data).

The approach followed in this study of using bioenergetics relationships to construct habitat use models can be applied to a variety of organisms (Morrison et al. 1992), including stream salmonids (Hughes 1992) and stream cyprinids (Hill and Grossman 1993). Clark and Levy (1989) extend this approach and use both potential growth rate and predation risk to predict the vertical distribution of sockeye salmon in lakes. Levy (1990) presents information suggesting that sockeye salmon vertical distribution corresponds to abundance and degree of migration exhibited by zooplankton populations. His results closely conform to the predictions of potential growth rates and patterns of fish distribution we report for Castle Lake in 1989 and 1990.

One advantage of using an energetics approach is that the simulations can predict absolute growth rates in different habitats and time periods. This approach would particularly lend itself to problems in conservation biology, where determining the potential for a species to thrive is paramount. For instance, we presently know that the population of endangered Snake River sockeye salmon (*Oncorhynchus nerka* [Walbaum]) is declining (Nehlsen et al. 1991). Although mortality of smolts passing through reservoirs on the Columbia River is the likely reason for the decline of this stock, nutrient enhancement of the rearing lake environment is being considered as a means of improving survival of the smolts (Luecke and Wurtsbaugh 1993b). Estimating potential growth of juvenile sockeye

salmon using a bioenergetics approach could be useful in evaluating options for whole-lake nutrient additions.

Metapopulation models, involving population sources and sinks, are widely used in conservation biology (Gilpin and Hanski 1991). Estimating potential growth rates of different habitats or regions could better define sources and sinks. As fish habitats become more fragmented (Minckley and Deacon 1991), identification and preservation of habitats capable of high fish production will become essential. Potential growth rate models, like that used for rainbow trout in Castle Lake, would be helpful in understanding source/sink population dynamics and prioritizing habitat preservation efforts.

The ability to estimate potential growth rates of fishes in different habitats during different time periods would also benefit fisheries managers. Questions of habitat preservation, rehabilitation, and mitigation could be addressed using models of potential growth rate. Estimating potential growth rate may provide a better means of integrating the physical, chemical, and biological factors inherent in any habitat evaluation (Orth 1987), and likely provides a better estimate of the habitat value to the fishes in question (Hughes 1992).

Presently the advantages of this approach are negated by the paucity of data relating prey resources to growth of stream and lake fishes. Future research needs to be focused on the relationships between food quantity and quality, and growth of fishes under the varying physical regimes that characterize lake and stream habitats.

Acknowledgments

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