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of Juvenile Sockeye Salmon,
Oncorhynchus nerka,
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Larry Peltz
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ABSTRACT

Hugh Smith Lake consistently produces small sockeye salmon smolts (2-3 g) regardless of numbers of parent-year spawners and benefits of lake enrichment. The narrow range in smolt sizes suggested temperature-inhibited growth during rearing. To evaluate this hypothesis, the locations of in-lake rearing relative to temperature regimes from May to November were determined using six hydroacoustic surveys. Each diel survey consisted of 12 transects equally spaced at 2-hour intervals over a 24-hour period. During the daylight hours from late May to late August, juvenile sockeye salmon were located at a depth of 20-30 m and in temperatures <5°C. During darkness the sockeye salmon fry reached their upper limit at 5-15 m in temperatures from <5°C to 14.4°C. During November, the rearing juveniles continued the diel migration pattern established earlier, even though the lake was isothermal.

The age-1 sockeye salmon smolt weights predicted on the basis of changes in mean rearing temperature (MRT) are nearly identical to observed age-1 smolt weights for 3 out of 5 years. MRT also explained nearly two-thirds of the variation in age-1 smolt weight with less than one-third being explained by the number of age-1 smolts ($P=.025$; f-test), and none by zooplankton biomass. Thus, the small size of Hugh Smith Lake sockeye salmon smolts reflects suboptimal rearing temperatures and is in large part independent of both juvenile density and zooplankton biomass.

KEY WORDS: sockeye salmon, *Oncorhynchus nerka*, smolt, diel migration, depth distribution, growth.

INTRODUCTION

Two major extrinsic factors influencing the freshwater growth of juvenile sockeye salmon are the physical one of temperature (Goodlad et al. 1974; Koenings and Burkett 1987a, 1987b) and the biotic one of competition for food (Weatherley and Rogers 1978; Kyle et al. 1988). A result of severe competition for food during rearing is a small smolt (2-3 g), a condition reversible by lake enrichment as documented by Nelson (1958), Hyatt and Stockner (1985), and Koenings and Burkett (1987b). Briefly, the addition of inorganic nutrients to the epilimnion of a lake should increase the food supply (zooplankton) for lake rearing sockeye salmon fry. If food is limiting growth and survival, a larger forage base results in either increased smolt size, a greater freshwater survival, or an increase in the overall density of juveniles the lake is capable of rearing.

Brett et al. (1969), Shelbourn et al. (1973), and Biette and Geen (1980a) have found optimal temperatures for sockeye salmon growth under various regimes of food supply, and that low temperatures can inhibit growth even under food-satiated conditions. Sockeye salmon juveniles, including those at Hugh Smith Lake, undergo diel vertical migration (DVM) ascending to visually feed in warmer surfacial strata while descending to digest stomach contents in cooler lower strata. Small fish are particularly affected by low temperatures and thus the transfer of McLaren's hypothesis (1963) concerning the physiological advantages of vertical migration from zooplankton to rearing scuplin (*Cottus extensus*) (Wurtsbaugh and Neverman 1988) and sockeye salmon (Narver 1970; Levy 1987).

The epilimnion of Hugh Smith Lake was enriched with nitrogen and phosphorus during July-September of 1980 through 1984 because sockeye salmon smolts were very small (2-3 g). Even though smolts produced after enrichment were generally larger, the maximum difference between pre- and post-fertilization age-1 smolt weight was 0.8 g; and ~15-fold differences in smolt numbers produced <15% change in weight. Since these changes are not consistent with density-dependent growth, research was initiated in 1984 to determine the vertical distribution of sockeye salmon juveniles relative to in-lake rearing temperatures and the effect of temperature on the size of sockeye salmon smolts from Hugh Smith Lake.

Study Site Description

Hugh Smith Lake (55°06' N, 130°40' W) is located on mainland southeast Alaska just below the City of Ketchikan (Figure 1). Sockeye Creek (Alaska Department of Fish and Game [ADF&G] stream identification code 101-30-75), the outlet stream, drains into Boca de Quadra and covers the distance (from the lake to mean high tide) of ~50 m with an elevation drop of only 4 m. The creek is 25 m wide at the lake outlet, discharges range from 1.4 m^3/second to greater than 28.0 m^3/second, and the water level at the lake outlet fluctuates within a 2-m range. Hugh Smith Lake has a surface area of 309 ha and ~381 cm of precipitation are received annually over a 49.27-km^2 watershed.

MATERIALS AND METHODS

Diel Vertical Migration (DVM) Patterns

Hydroacoustic surveys using a Simrad EYM echosounder® were conducted to determine the diel vertical distribution of sockeye salmon fry. Six diel surveys were conducted between late May and early November. Prior to each 24-hour survey, an area of high

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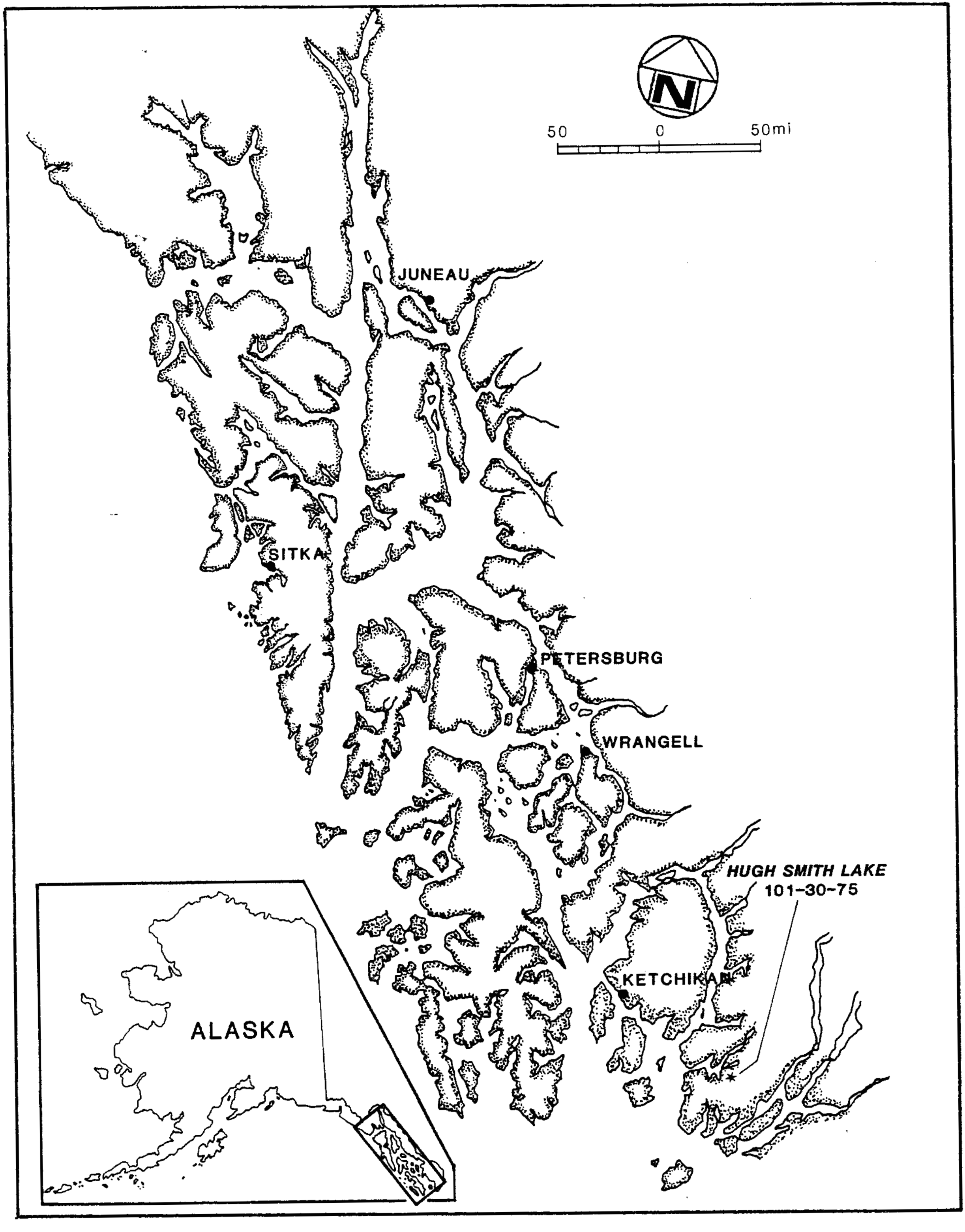


Figure 1. Map of Southeast Alaska showing the location of Hugh Smith Lake relative to the city of Ketchikan.

fish density was located using the echosounder. Each diel survey (12 transects) consisted of running a transect with the echosounder across this area at 2-hour intervals over a 24-hour period. The 25-26 May survey began at 1600 and ended at 1400, while the five remaining surveys started at 1400 and ended at 1200. The paper readout from the echosounder was used to determine the upper and lower limits of sockeye salmon fry distribution at each 2-hour interval during a 24-hour period.

Mean Rearing Temperature (MRT)

At the beginning and end of each diel hydroacoustic survey, temperature profiles were taken using a Kemmerer® bottle with a mercury-filled thermometer mounted inside. The two temperatures at each depth were averaged to obtain a 24-hour mean. A mean rearing temperature (MRT) was calculated for a 24-hour period using the midpoint depth of the sockeye salmon distribution for each time interval and the temperature at that depth.

Theoretical Growth Calculation

Theoretical juvenile sockeye salmon growth was calculated using a growth model developed by Iwama and Tautz (1981):

$$W_t = (W_o^{.33} + G_s\ t)^3$$

Where:

W_t = final weight (g)
W_o = initial weight (g)
G_s = average water temperature/1,000 (°C)
t = time reared (d)

Although this model is designed for hatchery use, it was chosen because of its simplicity and the ability to use existing data to obtain predicted weights.

The following assumptions, based on data collected from 1980 to 1985, were made to enable use of the model:

1) Sockeye salmon alevins emerge from the gravel and move into the lake in late May as a 0.2-g fry.

2) Sockeye salmon juveniles grow from June to October with food rations being 100% of the desired amount.

3) Sockeye salmon pre-smolts are on a maintenance or submaintenance diet from November to April.

4) Sockeye salmon pre-smolts are on a maintenance to above maintenance diet during the subsequent April to mid-May period; i.e., weight lost during the winter is recovered.

5) Age-1 sockeye salmon smolts leave the lake during mid to late May.

Temperature data from the 1980-1984 rearing years were used to predict smolt weights. Temperatures during daylight hours were computed at a depth of 20 m and nighttime temperatures were computed at 10 m.

Zooplankton Biomass

Zooplankton were sampled six to eight times over the rearing period of sockeye salmon juveniles using a 0.5-m-diameter, 153-u-mesh net. Replicated vertical hauls were made from 50 m to the surface at each of two limnetic stations. Zooplankters from each haul were preserved in separate bottles containing 10% buffered formalin, and counted, identified, and body sizes determined after Koenings et al. (1987). Wet size versus dry weight regressions, previously determined for each species, were used to estimate biomass from the mean sizes and weights found for each sampling period. The seasonal mean was then determined for each species which were summed to give the overall seasonal-mean biomass within the lake (Koenings et al. 1987).

Sockeye Salmon Smolt Evaluation

We first attempted an estimate of the total smolt outmigration in 1980, but the original location of the fence allowed an undetermined number of smolts to elude capture. The location of the fence was changed in 1981, and a total count of the smolts was obtained in each successive year.

Sockeye salmon smolts in 1981-1985 were enumerated using a fence that extended from top to bottom of Sockeye Creek and across the entire width of the stream. The fence consisted of a wooden frame covered with 0.6-cm plastic netting. All outmigrating smolts were identified daily as to species (without subsampling), while scale samples and length-weight measurements were obtained daily from subsamples taken without known bias. Sample sizes varied as 15 smolts were sampled at capture rates of less than 100 sockeye salmon per day, while 30 were sampled at capture rates greater or equal to 100 per day.

Smolts were anesthetized with MS-222®, weighed to the nearest 0.1 g using a digital electronic balance, sized to the nearest 1 mm (fork-length), and sampled for scales using glass slides. Freshwater ages were determined using a microfiche projector to magnify the scale smears.

RESULTS

Diel Vertical Migration (DVM) Patterns

Results of the DVM surveys are presented in Figures 2A through 2F. The diel patterns were nearly identical in the first four surveys (Figures 2A through 2D). During the daylight hours the sockeye salmon fry were found at 20-30 m in water less than 5°C. As sunset approached, the fish migrated up in the water column. During darkness, the sockeye salmon fry were found at 5-15 m in temperatures from less than 5°C to 14.4°C. As sunrise approached, the sockeye salmon fry moved back down to depths between 20-30 m. This DVM pattern is similar to that previously described by Narver (1970). During the October and November surveys (Figures 2E and 2F), there was only a slight deviation from the crepuscular pattern described earlier. That is, the descent to deeper waters after surficial feeding occurred several hours prior to sunrise rather than just before or at sunrise. More importantly, the DVM pattern established when the lake was thermally stratified continued in the November survey even though the lake was isothermal (Figure 2F).

Mean Rearing Temperature (MRT)

The 24-hour MRT for each survey is presented in Table 1. The daily MRT appeared to be constant at 5.1°C from late May to late July. By late August the MRT had increased to 6.8°C and it appeared to have stayed at this level into early October when it was 6.9°C. In early November the MRT had dropped to 5.0°C. Expanding this data over a 5-month growing season enables calculation of a predicted weight. Since the MRT from late May to late July was 5.1°C, this temperature was used in the June and July calculations. The MRT increased from 5.1°C to 6.8°C between late July to late August, so 6.8°C was used as the MRT for August to avoid any data interpolation. Little change was noted in the

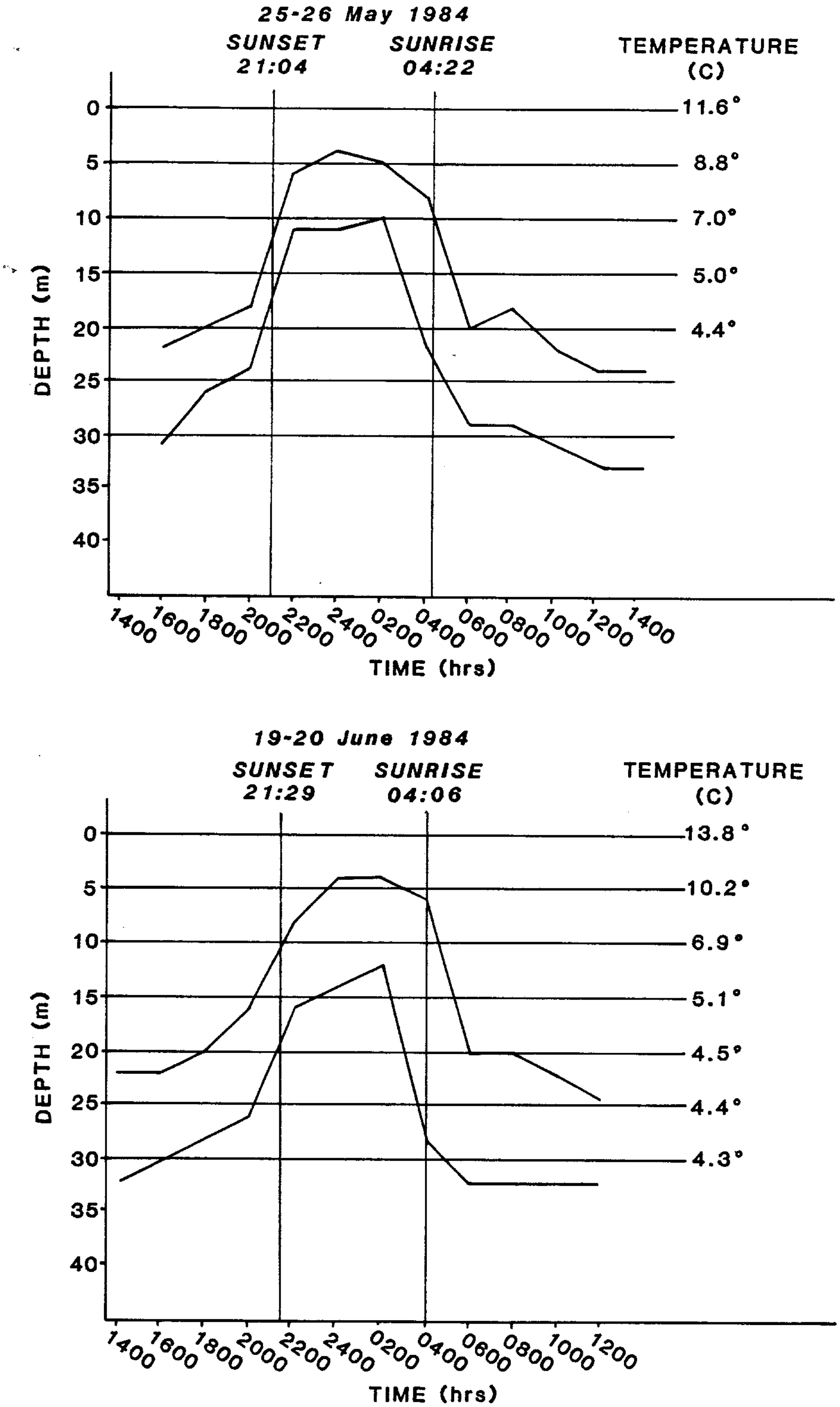
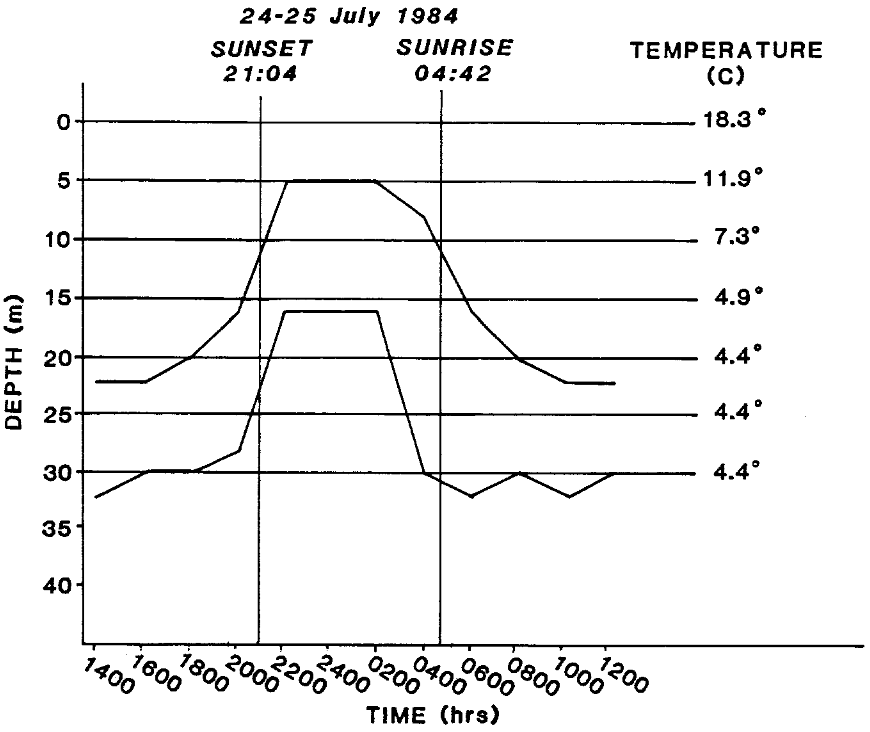
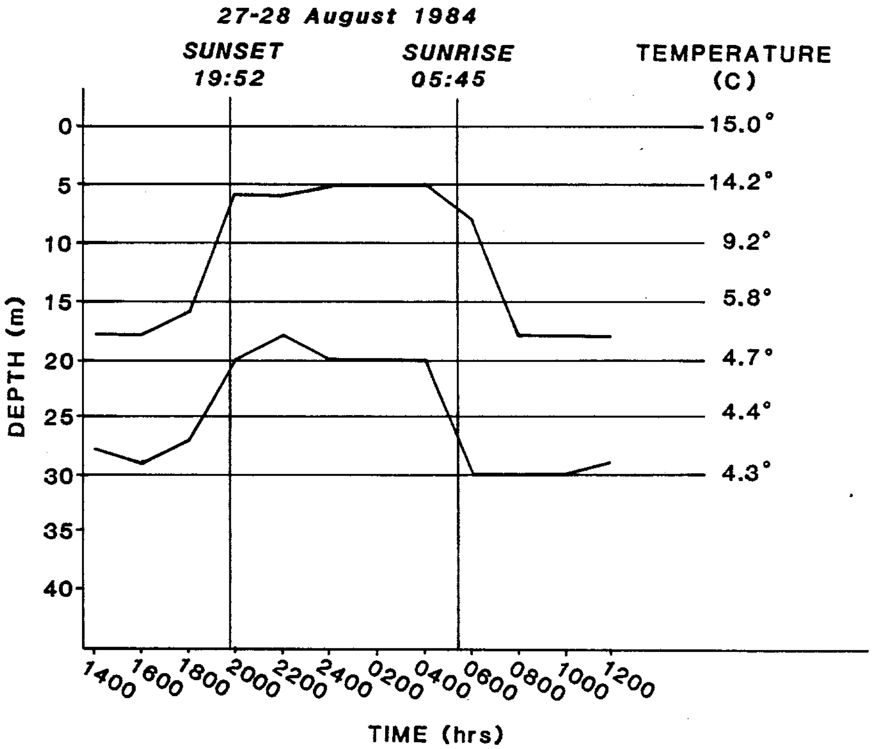


Figure 2. The upper and lower limits of the distribution of Hugh Smith Lake juvenile sockeye salmon during 1984 showing the timing and extent of diel vertical migration (DVM) on (A) 25-26 May, (B) 19-20 June, (C) 24-25 July, (D) 27-28 August, (E) 8-9 October, and (F) on 2-3 November.





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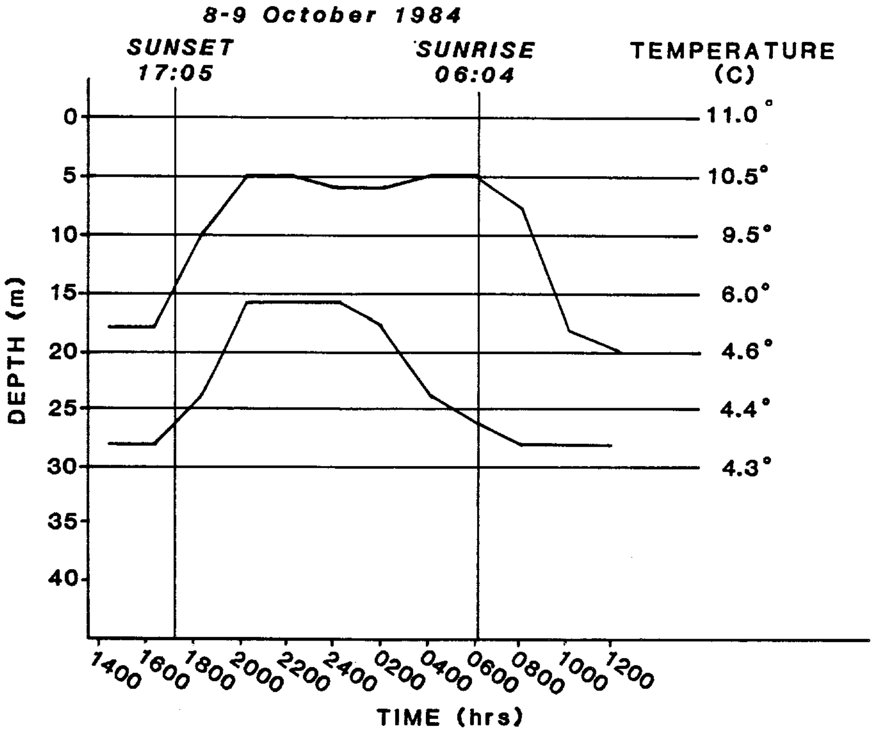

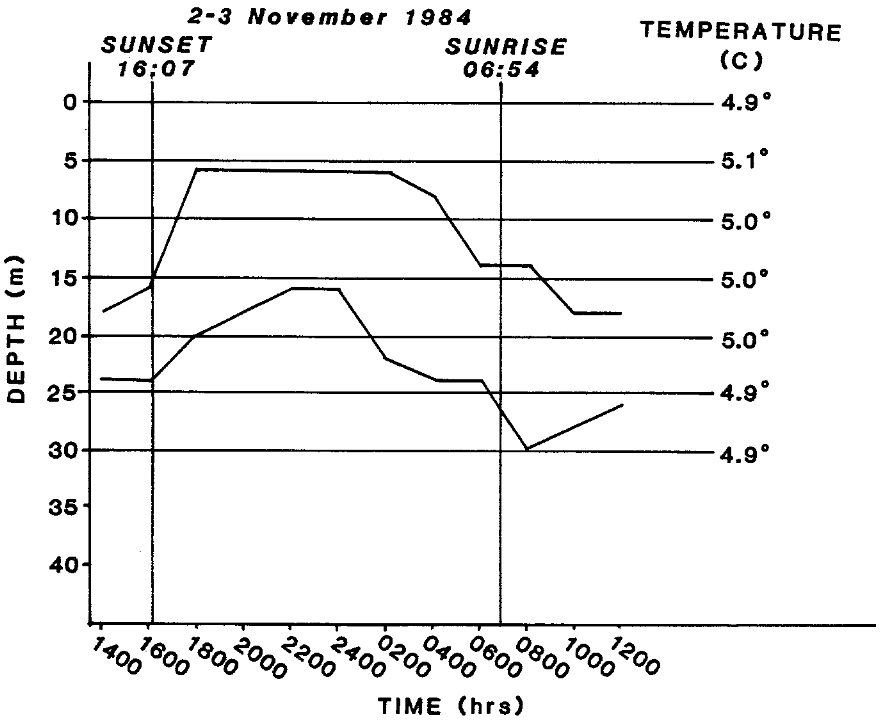

Figure 2 continued.

Table 1. The mean rearing temperature (MRT) of sockeye salmon juveniles in Hugh Smith Lake during 1984 determined from diel vertical migration patterns.

Date	Depth (m)	Lake water temperature (C)	Duration of residence (hrs)	Acquired temperature units	MRT
May 25-26	>20	4.4	16	70.4	
	15	5.0	2	10.0	5.1
	8	7.0	6	42.0	
June 19-20	>20	4.4	16	70.4	
	15	5.1	2	10.2	5.1
	10	6.9	6	41.4	
July 24-25	>20	4.4	18	79.2	5.1
	10	7.3	6	43.8	
August 27-28	>20	4.4	12	52.8	6.8
	10	9.2	12	110.4	
October 8-9	>20	4.6	10	46.0	
	15	6.0	4	24.0	6.9
	10	9.5	10	95.0	
November 2-3	10-20	5.0 (isothermal)	24	120.0	5.0

MRT between late August and early October; consequently, 6.8°C was used as the MRT for September. Even though the MRT decreased from 6.9°C to 5.0°C between early October and early November, 6.9°C was used to once again avoid data interpolation (Table 2).

Numbers of Sockeye Salmon Smolts Relative to Mean Weights

The number of age-1 smolts ranged from a high of 298,653 in 1984 to a low of 20,987 counted out in 1985 (Table 3). Thus, over the five years, the number of age-1 smolts varied by nearly 15-fold.

The size of age-1 sockeye salmon smolts in 1980 (prior to fertilization) was 2.73 g; and post-fertilization (1981-1985) mean weights ranged between 2.68 g and 3.57 g (Table 3). The weight of the age-1 smolts prior to fertilization was less than the weights of age-1 smolts produced after fertilization on four out of the five years. The relationship (Table 4) between observed age-1 smolt weight and the number of smolts is positive, but the slope was not different from zero (r=.55; p-.34; t-test). Moreover, the change in smolt weights was not proportional to the change in the number of smolts. For example, in 1984 the mean weight of 298,653 age-1 smolts equaled 3.57 g, while the mean weight of 20,987 age-1 smolts in 1985 was reduced by only 15%.

The number of age-2 smolts could have an effect on the numbers and weight of age-1 smolts through competition for the same forage. During the years of 1981 and 1985, the numbers of age-2 smolts ranged between 18,536 and 103,629 (Table 3) and were always less than or equal to the number of age-1 smolts. Age-2 smolt numbers were negatively ($r=-.34$; $r_s=-.56$) related to the weight of age-1 smolts, although the amount of variation (12%) explained by the regression was low (Table 4). In addition, zooplankton biomass explained 77% of the variation in the number of age-2 smolts ($r_s=+0.67$). This positive relationship suggests that a greater number of age-2 smolts was related to higher levels of zooplankton biomass.

Table 2. Example calculation for predicting the weight of Hugh Smith Lake sockeye smolt in 1984, based upon the assumption of food satiation and in-lake rearing temperatures, using the sockeye growth model of Iwama and Tautz (1981).

Model:

$W_t = (W_o^{0.33} + G_s \times t)^3$
W_t = final weight (g)
W_o = initial weight (g)
G_s = T/1000 T = average water temperature (C)
t = days

Data:

Month	Days (t)		Mean water temperatures (C)		Temperature units (C x t)
June	30	x	5.1	=	153.0
July	31	x	5.1	=	158.1
August	31	x	6.8	=	210.8
September	30	x	6.8	=	204.0
October	31	x	6.9	=	213.9
Total	153 days				939.8 units

$T = 939.8 \text{ units}/153 \text{ days} = 6.142 \text{ C}$

and

Results:

$W_t = [(0.2)^{0.33} + 0.006142\ (153)]^3$
$W_t = (0.5879 + 0.9398)^3$
$W_t = (1.5277)^3$
$W_t = 3.57 \text{ g}$

Table 3. Observed sockeye salmon smolt weights and numbers in years (Y), and the mean rearing temperature (MRT) and zooplankton biomass found in Hugh Smith Lake in years (Y-1).

	Sockeye smolts			Seasonal means for rearing year (Y-1)	
Year (Y)	Age 1. (No.)	Age 2. (No.)	Age 1. mean weight (g)	Rearing temperature (C)	Zooplankton biomass (mg/m^2)
1980	--	--	2.73	--	--
1981	215,228	103,629	2.88	5.32	1,266
1982	53,789	36,536	2.68	5.28	393
1983	45,315	31,703	3.19	6.11	595
1984	298,653	31,716	3.57	6.12	843
1985	20,987	18,536	3.05	6.14	366

Table 4. Correlation matrix for smolt population characteristics and physical factors at Hugh Smith Lake: shown above the dashed line are the parametric correlation co-efficients (r) while those below are the non-parametric Spearman's Rho (r_s).

	Smolts			Seasonal mean	
	Age 1. (No.)	Age 2. (No.)	Age 1. weight (g)	Rearing temperature (C)	Zooplankton biomass
Age 1. smolts (No.)	--	+0.45	+0.54	+0.19	+0.77
Age 2. smolts (No.)	+0.56	--	-0.34	-0.23	+0.88*
Age 1. smolt weight (g)	+0.20	-0.56	--	+0.78	+0.16
Rearing temperature (C)	-0.30	-0.87	+0.70	--	+0.14
Zooplankton biomass	+0.80	+0.67	+0.20	-0.30	--

*Significant at 0.05 level for a one-tailed test ($r \geq 0.80$).
**Significant at 0.05 level for a one-tailed test ($r_s \geq 0.90$).

Theoretical Versus Observed Smolt Weights

In the example calculation (*See* Table 2), the predicted age-1 smolt weight (SW) of 3.57 g compares favorably to an observed mean of 3.05 g in May 1985 (Table 5). Since data gaps existed in computing the August and October MRTs, they may be inflated, causing the predicted weight to be larger than the observed weight. By assuming consistent DVM patterns from year to year, temperature regimes from 1980-1984 were used to predict smolt weights for those rearing years. The predicted weights ranged from 2.72 g to 3.54 g, while observed weights ranged from 2.68 g to 3.57 g (Table 5). Predicted weights are nearly identical to observed weights for three of the five years, and the accuracy ranged from -0.8% to 17.0% of observed weights. When age-1 smolt numbers exceeded 200,000 and total smolts were above 300,000, the weights of age-1 smolts were less than those observed. In contrast, in the remaining three years when the age-1 smolt numbers were at or below 50,000, the predicted weights exceeded the observed weights (Table 5). Finally, the relationship of MRT to observed age-1 smolt weight ($SW = -0.372 + 0.595\ MRT$) was not significant ($r=.78$; $p=.11$; t-test), although the slope was positive (*See* Table 4).

Zooplankton Biomass Relative to Age-1 Smolt Weight

During the rearing years of 1980 through 1984, the zooplankton biomass ranged from 1,266 to 366 mg/m^2 with the highest biomass occurring in the prefertilization period (*See* Table 3). In both the parametric and nonparametric regressions, the zooplankton biomass appeared to be more related to the number of age-1 and -2 smolts rather than to the weight of the age-1 smolts (*See* Table 4). That is, zooplankton biomass explained from 59% to 77% of the variation in the numbers of age-1 or -2 smolts, respectively, but <3% of the variation ($r_s=+.20$) in age-1 smolt weight.

Table 5. Comparisons between sockeye smolt weights predicted from the growth model of Iwama and Tautz (1981) and observed smolt weights at Hugh Smith Lake from 1981 to 1985.

Year	Predicted smolt weights (g)	Observed smolt weights (g)	Accuracy of prediction (%)
1981	2.76	2.88	-4.2
1982	2.72	2.68	+1.5
1983	3.54	3.19	+11.0
1984	3.54	3.57	-0.8
1985	3.57	3.05	+17.0

Rearing Temperatures and Smolt Numbers Relative to Age-1 Smolt Weights

Smolt numbers (SN) and MRT individually did not explain enough of the variation in smolt weight (SW) to be statistically significant; i.e., $P \geq .05$. However, both variables together ($SW = -0.696 + 0.616\ MRT + 1.6 \times 10^{-6}\ SN$) explained 98% of the variation in smolt weights ($P=.025$; f-test). That is, nearly two-thirds of the variation in age-1 smolt weights was explained by MRT compared to less than one-third by smolt numbers and none by zooplankton biomass.

DISCUSSION

The assumptions made in using the growth model of Iwama and Tautz (1981) represent the life history of Hugh Smith Lake sockeye salmon juveniles under typical climatological conditions. Yearly variation in weather may cause changes in the growth assumptions; e.g., entrance of juveniles from the inlet stream to the lake may be delayed by a late spring. Despite such possible fluctuations, the weights of Hugh Smith sockeye salmon smolts varied little from year to year (*See* Table 5). This lack of change may reflect MRTs derived from sockeye salmon fry spending most of their freshwater life in water consistently <5°C-7°C (*See* Table 2).

In addition to rearing in temperatures that seldom, if ever, approach that of optimum growth of 15°C (Brett et al. 1969), the findings of Shelbourn et al. (1973) suggest that the growth of newly emerged juveniles (~0.2 g) in Hugh Smith Lake may be particularly inhibited by low water temperatures. McLaren (1963) suggested that DVM may enable zooplankton to feed in warmer more surficial strata for a short time and then spend the remaining time digesting food in the cooler hypolimnion. Based on the findings of Clarke (1978) and Biette and Geen (1980a; 1980b), it appears that the hypothesis of the physiological advantage of DVM could be applied to juvenile sockeye salmon. Indeed, the DVM pattern of juvenile sockeye salmon at Hugh Smith Lake showed an apparent cold/warm water crepuscular cycle triggered by approaching sunrise and sunset (*See* Figures 2A-2E). However, the DVM pattern established when the lake was thermally stratified during May through October continued in November when the lake was isothermal (*See* Figure 2F). As the physiological benefit of DVM under isothermal conditions is questionable, DVM may persist as a learned behavior in response to changing light regimes.

If DVM is physiologically driven, then the MRTs of sockeye salmon must, in turn, be derived from the DVM patterns. Clearly deriving MRTs from surficial temperatures (Rounsefell 1958) are erroneous (Koenings and Burkett 1987a). Goodlad et al. (1974) related rearing temperatures to sockeye salmon growth by considering mean temperatures from a range of depths thought to be representative of sockeye salmon residence during the May to October period (i.e., MRT). Even at this level of resolution the growth of Chilko Lake sockeye salmon appeared to be closely related to temperature. Goodlad et al. (1974) suggested that further refinement required a more detailed analysis involving DVM since a daily range of temperatures during both feeding and digestion would determine growth rates. Thus, we followed the DVM of juvenile sockeye salmon over a growth cycle and through the heating and cooling cycles of Hugh Smith Lake to refine estimates of MRT.

The MRTs at Hugh Smith are lower than the seasonal monthly average during the spring-early summer period because sockeye salmon descend to cold, deeper water during extended daylight. In contrast, the MRTs of the summer-fall months (August-November) are greater than the monthly average. As day-length shortens, the sockeye salmon juveniles spend more of the diel cycle in warmer surface strata (*See* Figures 2A-2F). Moreover, as fall progresses, warmer water is pushed deeper in the lake by wind mixing. Consequently, the fall period may be the time when a majority of growth occurs. Thus, the MRTs, as constructed from the diel patterns, can be related to the size of age-1 smolts. However, the number of age-1 smolts also entered into the multiple regression equation as a significant variable. It may be that a change in the number of juveniles spreads or contracts the distribution of the fish in the lake. In our analysis, we assumed a consistent pattern across all densities since we lacked yearly distributions. This may not be the case since MRTs consistently underpredicted smolt weights of the two largest outmigrations and overpredicted those of the three smaller outmigrations (*See* Tables 3 and 5).

We found that yearly changes in MRT could explain two-thirds of the annual variation of age-1 smolt weight (*See* Table 4), and the MRT itself useful in predicting the absolute value of smolt weights (*See* Table 5). This suggests that the determination of MRT over the rearing cycle of sockeye salmon juveniles can be used to assess limitations of growth based on competition for forage versus temperature; i.e., density-dependent versus density-independent freshwater growth as described by Koenings and Burkett (1987b).

Based on the approach presented here, it is unlikely that the size of Hugh Smith Lake sockeye salmon smolts could be increased beyond a small range. Other lakes in Alaska probably have small smolts whose size are inhibited by temperature, not food supply. In all likelihood, the uniformly small size (2-3 g) of sockeye salmon smolts produced from cold, glacial lakes in both Alaska (Koenings et al. 1986; Koenings and Burkett 1987) and Canada (Ruggles 1965) could be included within this classification. Thus, the use of juvenile growth rates or resultant smolt characteristics to construct density-dependent relationships (Johnson 1965; Brockson et al. 1970) should be exercised carefully when including systems like Chilko or Owikeno Lake (Canada) whose unfavorable temperature regimes (Goodlad et al. 1974; Ruggles 1965) and not food supply may limit sockeye salmon growth.

Recommendations

1. Future selection of candidate lakes for nutrient enrichment should include a detailed study of the rearing temperature regimes as well as relative estimates of rearing fish densities.

2. Lakes which have high juvenile sockeye salmon densities, small threshold-sized smolts, and a limiting food supply are prime candidates for lake enrichment in southern southeast Alaska.

ACKNOWLEDGMENTS

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