ARCTIC CHAR PREDATION ON SOCKEYE SALMON SMOLTS AT LITTLE TOGIAK RIVER, ALASKA[1]

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ABSTRACT

Observations of Arctic char feeding on migrating sockeye salmon smolts at Little Togiak River, Alaska, indicate a Type II functional response where the number of smolts consumed increased with smolt abundance. The number of smolts migrating was usually low (<20,000 smolts/24 hours) and the corresponding consumption of smolts averaged 0.8 smolts/char per 24 hours. When large smolt migrations occurred (>80,000 smolts/24 hours), char consumption of smolts generally increased to 5.6 smolts/char per 24 hours. In addition to smolt abundance, smaller smolts and longer char were correlated with an increase in the number of smolts consumed. Estimates of percent smolt mortality, based on two hypothetical char numerical responses to varying smolt abundances, indicate that smolts were migrating at densities most susceptible to predation.

A comparison of length of smolts consumed by char with those in the migration shows that char consumed larger than average smolts when their stomachs were not full and smaller than average smolts when char approached stomach fullness. This may be explained by the migration of larger smolts during the feeding period of char and the possibility of char feeding less effectively when approaching fullness. Although major hatchery releases often exceed 100,000 smolts per day, these data suggest that hatchery-released smolts may be less susceptible to predation in small rivers when released during the night in large numbers (>20,000 smolts/24 hours).

The relationship between predation on juvenile salmon and relevant biological and environmental factors is important to the understanding of salmon population dynamics. Development of these relationships may be useful for establishment of "optimal" escapement levels and for maximum production from salmon enhancement projects. A few investigations have related predation rates to juvenile salmon abundance and have reported up to 85% juvenile mortality (Neave 1953; Hunter 1959; Parker 1968; Peterman and Gatto 1978). Other investigations have examined the effect of biological or environmental variables such as juvenile salmon size (Parker 1971), predator size (Ricker 1941; Hunter 1959; Rogers et al. 1972), infection by parasites (Burke 1978), river velocity and turbidity (Ginetz and Larkin 1976), thermal stress (Sylvester 1972; Coutant 1973), or several variables independent of juvenile salmon density (Fresh et al. 1980). No investigation has analyzed predation while concurrently assessing the partial effect of prey density along with the partial effect of biological and environmental factors.

This investigation represents a 5-yr study of predation by Arctic char, *Salvelinus alpinus*, on emigrating sockeye salmon, *Oncorhynchus nerka*, smolts at Little Togiak River, Alaska (Fig. 1). Predator-prey interaction appears to be especially refined in this river. With the onset of the smolt emigration each spring, char migrate to the interconnecting rivers in the lake system where migrating smolts are most vulnerable (McBride 1979). After the smolt migration ends, char return to their spawning streams in the fall. The objectives of this investigation, which were tested during this brief period of predator-prey interaction, were 1) to empirically model the daily functional response of char (i.e., the relationship between smolt abundance and number of smolts consumed/char per 24-h period (Fig. 2)) while concurrently measuring the effect of biological and environmental variables; 2) to estimate percent smolt mortality in relation to smolt abundance; and 3) to test for disproportional consumption of large or small smolts by char that differ in stomach fullness and fork length.

Numerous biological and environmental variables are likely to influence char predation on salmon smolts. The variables concurrently tested in the functional response model were 1) the number of migrating smolts during the 24-h period prior to sampling the char; 2) the number of migrating smolts during the 24-48 h period prior to sampling; 3) smolt weight; 4) char length; 5)

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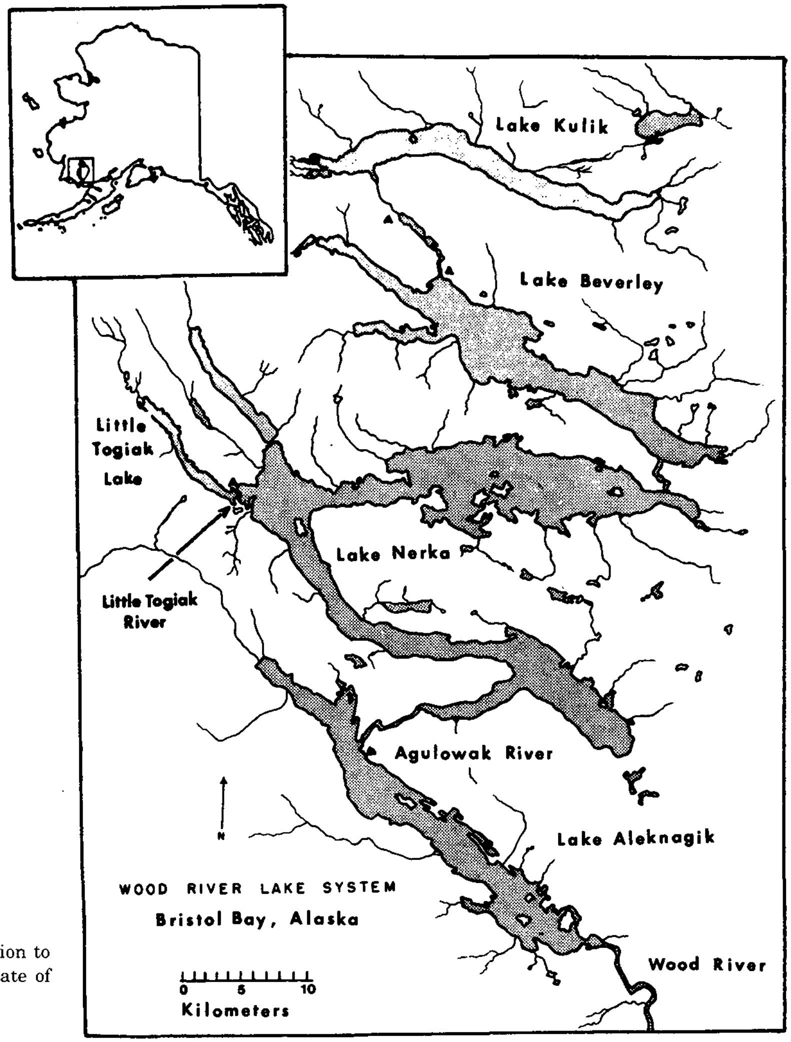

FIGURE 1.—Little Togiak River in relation to the Wood River lake system and the State of Alaska.

number of smolts migrating during the daylight; 6) percent of migration during the daylight; 7) presence of adult sockeye in the river; 8) days after ice-out; 9) river temperature; 10) river depth; 11) light intensity at dusk; and 12) incident solar radiation.

METHODS

Description of Study Site

Little Togiak River is a small nonturbid river located in the Wood River lakes system, Alaska (Fig. 1). River length is about 200 m as it flows from the smaller Little Togiak Lake to the larger Lake Nerka. River width is about 20 m and average depth ranges from about 2 m during spring high water to <1 m during midsummer.

Collection of Char Samples

Arctic char were collected from Little Togiak River from 1976 to 1980. Each year the sampling season began soon after ice breakup (about 7 June) and terminated at the end of the smolt migration near the end of July. About 10 char were collected daily during the morning and/or the evening (shortly before and after the peak smolt migration), and their stomach contents were analyzed within 1 h after capture. Information on the size of smolts consumed and on the population size of char at Little Togiak River was collected only in 1980.

Char were collected by fishing with unbaited

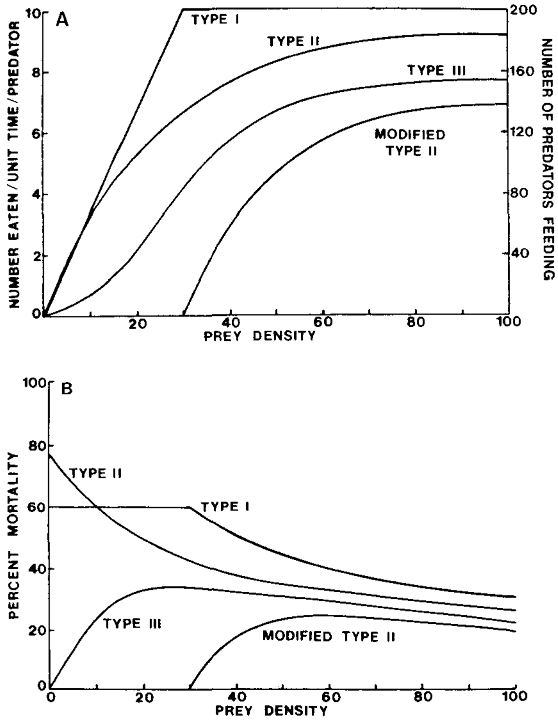

FIGURE 2.—Shapes of different types of hypothetical functional (left ordinate) and numerical responses (right ordinate) (A) and percent mortality curves (B) (redrawn from Holling 1959; Peterman and Gatto 1978).

lures from 1976 to 1979. In 1980, the primary method of char capture was a variable mesh size (5.1, 6.4, 7.6, and 10.2 cm stretch measure), monofilament gill net set across the river and allowed to drift downstream for 15 min. Nonparametic statistical analysis of 99 char caught by hook and line or gill net on the same day indicated no significant difference in char consumption of smolts estimated by each method (Mann-Whitney U-test: $0.10 < P < 0.20$). The collected char were anesthetized with tricaine methane sulfonate (MS-222), then their stomach contents were flushed out by a stomach pump. Examination of stomach contents from sacrificed char showed that about 90% of the smolts were removed by the pump. Before returning the char to the river, we measured the fork length and placed a numbered Dennison flag-type tag just below the dorsal fin. Stomach fullness was estimated visually and categorized as either full or less full.

Consumed Smolt Analysis

Smolts consumed by char were counted and measured after standardizing their length in 10% Formalin[3] for at least 24 h (Burgner 1962). The consumed smolts were measured by one of three methods and converted to fork length using one of the following regression equations (Ruggerone 1981):

1) Fork length (mm) = 0.44 + 1.09 (standard length); $r^2 = 0.99$;
2) Fork length (mm) = 3.70 + 1.37 (pectoral fin to hypural bone plate); $r^2 = 0.98$.

The preferred method of measurement was fork length; the next preferred method was standard length. When neither of these methods was adequate, the length from the pectoral fin insertion to the hypural bone plate was measured. Preserved fork length measurements were multiplied by a factor of 1.042 to convert back to "live" fork lengths (Rogers 1964).

Collection and Enumeration of Migrating Smolts

Migrating smolts were collected and enumerated with a winged-fyke net placed in an area of intermediate, but substantial water flow. Smolts trapped in the "live box" were counted and set free every 4 h during the day (0800-2200 h) and continuously during the major migration period (2200-0200 h). Daily smolt abundance was estimated by multiplying the fyke net counts by a river width factor. Previous experimentation with two fyke nets indicated an even distribution of smolts across the river. At least one sample containing 30 or more smolts was collected each night for length measurements, and when a substantial number of smolts migrated during the day, an additional sample was collected. Samples to determine a length-weight relationship were collected about every 10 d. Fork lengths were measured to the nearest mm and weights to the nearest 0.01 g.

Environmental Data Collection

The water temperature of Little Togiak River was measured to the nearest 0.1°C several times each day. To account for smolt density in the water column, we measured the water level of Lake Nerka as an approximation of the relative water depth in Little Togiak River. The water level was

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

measured continuously with a lake level recorder and calibrated every 2 wk with benchmark measurements in Lake Nerka. To measure the effect of light on the feeding success of char, we measured incident solar radiation continuously with a pyrheliometer. As a qualitative measure of light intensity after sunset, we used a scale from 0 to 4 where 0 represented clear skies with relatively high light intensity and 4 represented low overcast skies with relatively low light intensity.

Data Analysis Procedures

Functional Response of Char

To determine the functional response of char and the effects of other variables on the number of consumed smolts, we grouped the data into 24-h periods with 1200 h as the first hour of the day. The number of smolts consumed per 24 h by an individual char was calculated by the following equation:

$$N = S \left(\frac{24}{D} \right),$$

where N = number of smolts consumed/char per 24 h
S = number of smolts observed in a char stomach
D = digestion time.

Average digestion time (h) was determined from data collected by Meacham and Clark (1979) and calculated by the following curvilinear equation (Fänge and Grove 1979):

$$\ln D = 4.892 - 0.143\,(T),$$

where D = digestion time
T = temperature (°C).

The functional response model based on multiple regression analysis was developed with the SPSS nonlinear program utilizing Marquardt's method of least squares estimation (Marquardt 1963). Residual and partial residual analysis were used to determine which independent variables should be added and the shape of their partial effect curve (Larsen and McCleary 1972; Draper and Smith 1981). This method allows for analysis of each new variable while including the effect of previous variables.

Percent Smolt Mortality

The average number of smolts consumed per char, as described by the functional response, may not represent the entire char population. Char may migrate to the river to feed, then return to the nearby lake environment for several days. Evidence for this behavior stems from gill net catches of char along the nearby lake shore and several underwater observations of relatively few char in the river during midday. Because the numerical response of char is not known, 2% mortality curves were developed from two hypothetical responses. The first percent-mortality curve was based on the assumption that the entire char population of 1,100 fish (Ruggerone 1981) fed each day (Type I numerical response; Fig. 2A). The second curve was based on the assumption that char immigrate to the feeding area in response to smolt abundance, thus a Type II numerical response was assumed (Fig. 2A).

Char Consumption of Smolts by Length

A two-factor analysis of variance with replication (Zar 1974) was used to test for random consumption of smolts by char. We divided the char data into three time periods containing two levels of char stomach fullness (full or less full) and three sublevels of char length (295-445 mm; 446-470 mm; 471-502 mm). To concurrently compare the length of smolts consumed by char with those smolt lengths available in the migration, we calculated the difference between average length of smolts consumed and average length of smolts available. This difference was utilized in each level of analysis.

RESULTS

Char Functional Response

Nonlinear regression analysis indicated that 4 of the 12 variables tested affect the number of smolts consumed/char per 24 h. The most important of these variables was the number of smolts migrating during the previous day's migration (approximate partial F, $P < 0.01$). The next important variable was the average weight of migrating smolts ($P < 0.01$), then the number of smolts migrating during the day of capture ($P < 0.01$), and finally char length ($P \leqslant 0.08$). The amount of variability explained by all four variables was 59% and the standard deviation was ± 0.8 smolts consumed/char per 24 h. Other variables such as the number of smolts migrating during the daylight, the percent of smolts migrating during the daylight, the presence of adult sockeye, days after ice-out, river temperature, incident solar radiation, light intensity during the evening as a function of cloud cover, and river depth as a function of lake level did not add any new information.

The model describing char consumption of smolts has the following form:

$$N = a + b(1 - e^{-cP}) + de^{-W} + f(1 - e^{-gC}) + hL^{3.02}$$

where a, b, c, d, f, g, h = empirical constants
N = number of smolts consumed/char per 24 h
P = number of smolts during previous migration
W = smolt weight
C = number of smolts during day of capture migration
L = char length.

A graphical interpretation of the empirically derived model is shown in Figure 3. Confidence intervals about each curve are difficult to interpret because they do not consider the concurrent value of other parameters (Draper and Smith 1981) and are not shown. Instead, a plot of smolts consumed by char versus the number of smolts migrating in the previous day's migration demonstrates the initial variability and the basis for the model (Fig. 4). The average predicted consumption rate was 0.8 smolts/char per 24 h and the maximum was 5.6 smolts/char per 24 h. These predictions were similar to the observed average and maximum consumption rates of 0.8 and 6.0 smolts/char per 24 h.

The functional response of char was best described as a Type II response and was separated into two curves: consumption of smolts versus smolt abundance during the day of char capture and consumption of smolts versus smolt abundance during the previous day (Fig. 3A). Two curves were needed because most char digestion times were longer than 24 h. Thus, the predicted number of smolts consumed/char per 24 h was an average based on 2 successive days of feeding. The maximum partial effect of smolt abundance on the char consumption rate was about 3.7 smolts/char per 24 h when other variables were held at their mean values.

Smaller smolts and larger char were associated with increased consumption rates by char. Consumption of smolts increased exponentially with

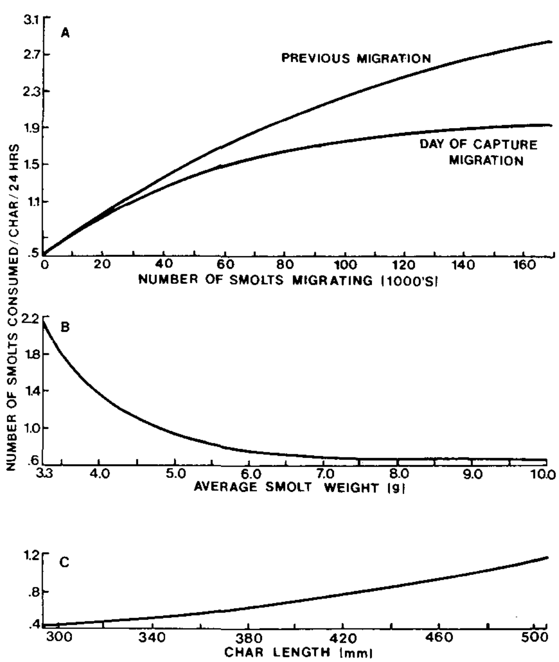

FIGURE 3.—The partial effect of the previous day's migration, the day of capture migration (A), average smolt weight (B), and Arctic char fork length (C) on the number of smolts consumed/char per 24 h. Smolt consumption was calculated by setting the alternate variables to their mean value.

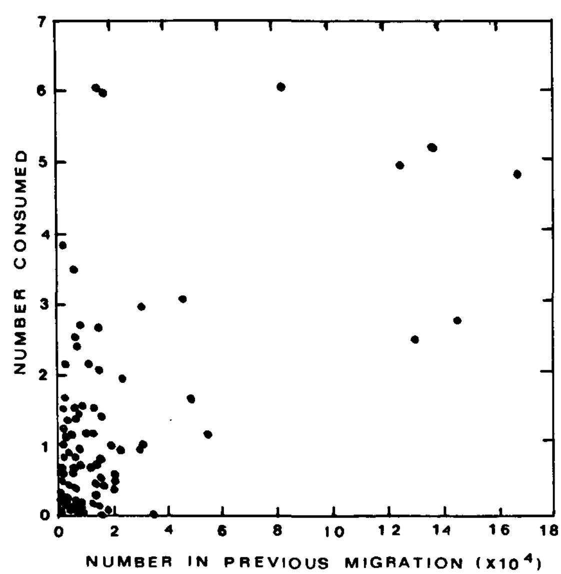

FIGURE 4.—Smolt consumption/Arctic char per 24 h in comparison with smolt abundance during the previous day's migration.

lighter smolts and increased curvilinearly with longer char (Fig. 3B, C). The maximum increase in char consumption of smolts due to changes in smolt weight and char length was about 1.4 and 0.8 smolts/char per 24 h, respectively.

The predicting power of this model is weak at high consumption rates by char. This problem arises from increasing residual variability as the predicted value increases. Increasing residual variability is usually corrected by using a weighting factor; however, when applied, the only data points carrying weight were those near the origin and any relationship between the variables was lost. Linear models were attempted, but did not approach the fit of the nonlinear model. Thus, at high rates of consumption by char, the model is best used for descriptive purposes.

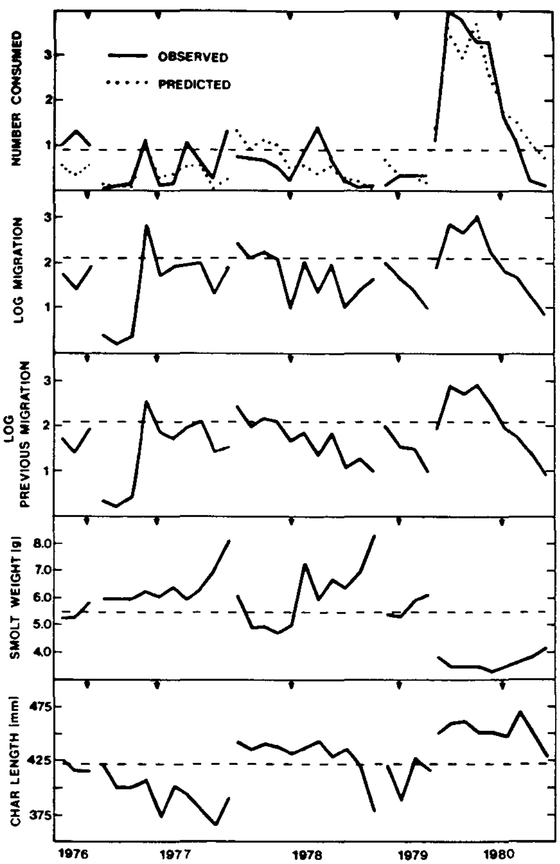

FIGURE 5.—Comparison of observed and predicted smolt consumption/Arctic char per 24 h with smolt abundance, average smolt weight, and char length during each sampling year. Data grouped into 3- to 5-d sampling periods. Dash line indicates mean value for all years. Log smolt abundance calculated from hundreds of smolts migrating. Arrows indicate entry of adult sockeye salmon in to Little Togiak River.

Comparison of consumption rates by char between years demonstrates the large variability that may be explained by smolt abundance, smolt weight, and char length (Fig. 5). During 1980 there were more than three times the number of migrating smolts, the weight of smolts was 30-50% less, and length of char was 24-68 mm greater than in any of the previous years. The combined effects of these variables resulted in a relatively large number of consumed smolts per char, which was also predicted by the model.

Percent Smolt Mortality

Two different percent smolt mortality curve types were produced from the two hypothetical numerical responses (number feeding) and the estimated consumption rates of char. A Type II curve (Fig. 2B) exhibiting an inverse relationship between percent smolt mortality and smolt abundance was produced from the assumption that all 1,100 char fed each day (Fig. 6A). Smolt mortality ranged from 0 to 100% when the number of migrating smolts was $<$ 6,750 smolts/24 h and $<$15% when the number of migrating smolts exceeded 20,000 smolts/24 h. A Type III percent mortality curve was produced from the assumption that the number of char feeding varied with smolt abundance (Fig. 6B). Although variability exists, percent mortality increased at low smolt abundances ($<$20,000 smolts/24 h), then decreased after char became overwhelmed and/or satiated[4] by smolts.

Char Consumption of Smolts by Length

The comparison of mean lengths of smolt consumed by char with mean length in the migration indicates that less full char consumed larger than average smolts ($\bar{d}$ = 1.7-2.9 mm, α = 0.05; Fig. 7). Char with full stomachs consumed smolts that were not different than the average length in the migration ($\bar{d} = -0.1$-0.6 mm, $\alpha = 0.05$). The length of char did not have a significant effect on the length of smolt consumed.

The comparison of length of smolts consumed in each stomach fullness category with the length

[4]During days of large smolt migrations, the number of smolts observed in individual char ranged from 0 to 45 smolts (not corrected by digestion period). Because of this variability in consumption, it is difficult to determine whether the char were overwhelmed by smolt abundance or satiated. This observed variability in consumption may be due to individual char migrating from the local lake area to the river at different times, thereby causing variable feeding durations.

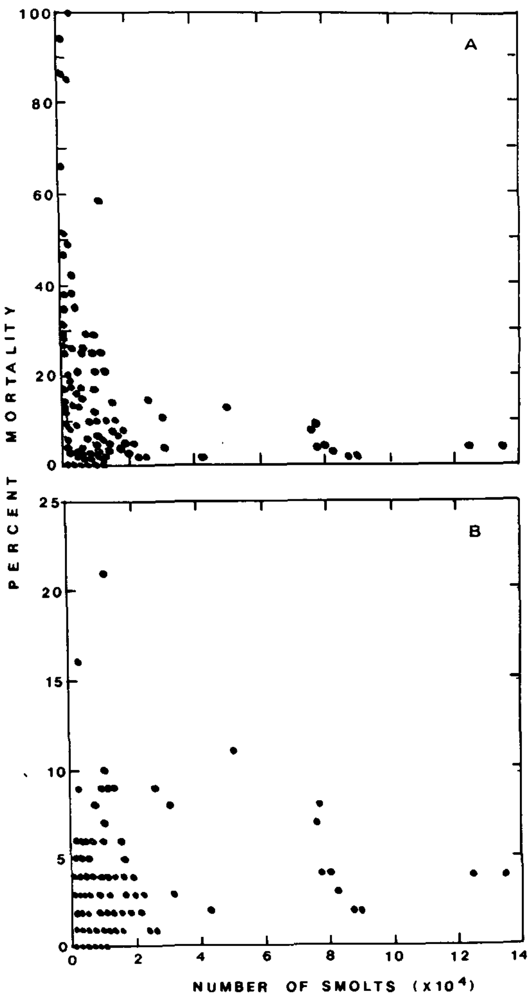

FIGURE 6.—Percent mortality at various levels of smolt abundance. (A) Entire population of 1,100 Arctic char fed each day; (B) number of feeding char equaled 1,100 $(1 - e^{-0.00004M})$, where M = number of migrating smolts.

distribution of smolts in the migration indicates the vulnerability of the smallest and largest smolts (Fig. 7). The large peaks represent age I smolts and the smaller peaks to the right are age II smolts. In each of the three time periods, the distribution of smolts from full char was consistently broader than the distribution of smolts in the migration, indicating that smolts average in length have a greater probability of escaping predation. The length distribution of smolts consumed by less full char was also broader than the distribution of smolts in the migration, but was skewed to the right. Thus, a greater proportion of age II smolts was consumed by less full char and to a lesser extent by full char than proportionately available in the migration.

When smolts consumed by full and less full char were combined, the average consumed smolt length was significantly larger than the average length from the migration ($\bar{d}$ = 0.1-1.1 mm, α = 0.05); however, the length distribution of the consumed smolts was similar to the smolt length distribution from the full char. This was due to the large proportion of smolts consumed by full char.

DISCUSSION

Char Functional Response

The functional response of char at Little Togiak River was similar to those reported for other salmon predators in one aspect (Ricker 1941; Cameron 1958; Hunter 1959; MacDonald *in* Foerster 1968). Because smolt abundance was usually low, char normally operated at the low end

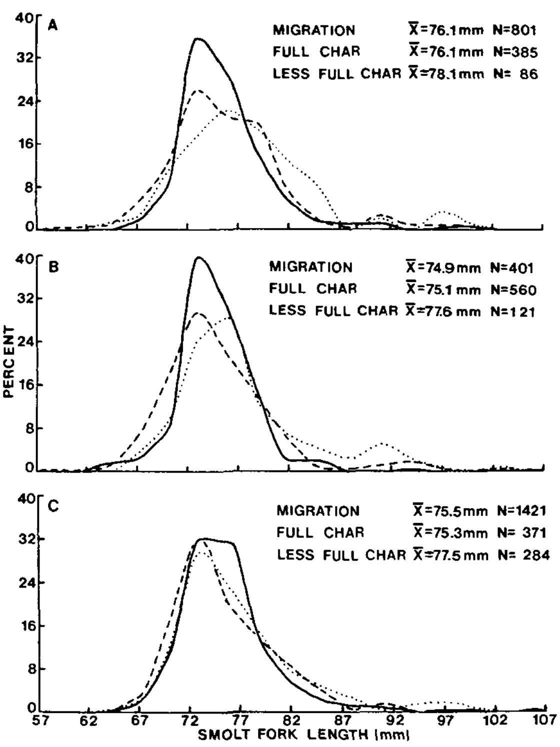

FIGURE 7.—Length distribution of smolts in the migration and in Arctic char stomachs according to stomach fullness. Solid line refers to smolts in the migration, dash line refers to smolts from full char, and dotted line refers to smolts from less full char. Sampling period from 9 to 16 June (A), 16 to 20 June (B), and 20 June to 17 July (C).

of their functional response where smolts could potentially be more vulnerable. Contrary to results of Ricker (1941) and Cameron (1958), consumption rates by char were proportional to smolt abundance and smolts did not find refuge at low migration numbers. On occasion (primarily in 1980) smolt abundance was great and consumption rates of char were disproportionately low, a response observed by Neave (1953). Thus, char at Little Togiak River exhibited a Type II functional response where vulnerability of smolts to predation may be greater at lower migration densities. This increased vulnerability ultimately depends on the numerical response of char to smolt abundance.

The inclusion of smolt weight and char length in the functional response multiple regression model further described important variables that influence char predation, as well as reducing within- and between-year variability. The exponential increase in consumption rates by char during migrations of smaller smolts is probably due to more smolts needed to decrease feeding activity and a greater ease in capturing small smolts. Because juvenile salmon growth is density dependent (i.e., smaller smolts at greater densities; Rogers 1968), increased consumption during migrations of smaller smolts may act to cancel the proportionately lower consumption rates of char at greater smolt abundances. Thus, it is important to test concurrently the effect of smolt weight and smolt density when describing the functional response of char.

The relationship of char length to consumption of smolts by char was best described by the allometric conversion (Moriarty 1977) of char length to char weight. According to regression analysis, the significance of char weight (as converted from char length) is questionable; however, char length was included in the model because it seems reasonable that a larger predator would require more food and may be able to capture mobile prey easier than a smaller predator. Rogers et al. (1972) reported larger char consumed more smolts than smaller char.

The average number of smolts consumed per char, as predicted by the model, was 0.8 smolts/24 h, and the maximum was 5.6 smolts/24 h. These values were corrected for smolt weight and char length. The low average of consumed smolts reflects the low number of smolts that generally migrate. The predicted maximum of 5.6 smolts/char corresponds quite well with the observed maximum of 6.0 smolts/char per 24 h. These estimates are lower than the average and maximum consumption rates by char at the Agulowak River (3.4, 8.4 smolts/char per 24 h, respectively) calculated from weekly estimates (Meacham and Clark 1979). This difference between the two rivers may be explained, in part, by the larger char size (Moriarty 1977) and the probable extension of the daily migration period at the Agulowak River, which is a large river that intercepts smolts from several lakes in the Wood River system.

Percent Smolt Mortality

The shape of a percent-mortality curve can provide valuable information on the stability characteristics of a salmon population (Peterman 1977) and provide information to a hatchery manager planning to release smolts. For example, percent smolt mortality could vary as in a Type III or modified Type II curve where smolt mortality increases up to a certain threshold density of smolts before decreasing. In this example, a hatchery manager should release smolts at densities greater than the threshold density.

Results from this investigation indicate the char numerical response (number feeding) may influence the type of percent-mortality curve. If the char numerical response is constant, then percent mortality will decrease as more smolts migrate. However, if the numerical response of char varies with smolt abundance, as we suspect, then percent mortality may increase with more smolts up to a threshold density. Beyond this threshold density, percent mortality decreases. The importance of the percent-mortality curve is to indicate the smolt density at which mortality is minimized. Smolts at Little Togiak River experience less risk of predation at daily migration abundances of about 20,000 smolts or greater. However, migration densities of this magnitude were rare.

Char Consumption of Smolts by Length

Char with less full stomachs contained smolts that were, on average, significantly larger than those in full char and those in the migration. A plausible explanation for the greater average smolt length in less full char than full char involves the effect of hunger on feeding behavior. Char containing only a few smolts may be hungry and aggressive (Ware 1972), which may induce a high success rate when feeding on the larger, more mobile smolts. When char approached stomach fullness, their hunger and aggressiveness may have been lower, thereby reducing their success rate when attacking the larger smolts in the migration.

The larger smolts in less full char as compared with average smolt length in the migration may be due to the relationship between light intensity, migrating smolt size, and decreased feeding activity by char during the darkest portion of the night. Smolts migrating at night were significantly shorter than those migrating during the day (Ruggerone 1981; Burgner 1962; Aspinwall 1963). Feeding activity of char was observed to decrease substantially during the darkest 1-2 h of the night (often char would leap from the water while feeding). Also, hook and line fishing with lures was notably less effective during darkness. Therefore, the difference in average length of smolts consumed by less full char and those in the migration resulted from a decrease in smolt consumption when smolts in the migration were smaller. These results indicate that predation may be reduced by releasing hatchery salmon during the night.

The difference between smolt length in all char and length in the migration was relatively small. In part, this was due to the large proportion of smolts observed in full char, which was related to high smolt abundance. Because fewer char will reach stomach fullness during years of fewer smolts, the difference between length of smolts consumed and length in the migration is likely to be greater.

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