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## DIEL VERTICAL MIGRATION BY JUVENILE SOCKEYE SALMON: EMPIRICAL EVIDENCE FOR THE ANTIPREDATION WINDOW

MARK D. SCHEUERELL<sup>1</sup> AND DANIEL E. SCHINDLER

*Department of Zoology, University of Washington, P.O. Box 351800, Seattle, Washington 98195-1800 USA*

**Abstract.** Diel vertical migration (DVM) is a widespread phenomenon in aquatic organisms, yet the adaptive significance of this behavior is still unclear. In particular, diel vertical migration by juvenile sockeye salmon (*Oncorhynchus nerka*) has received considerable attention. We studied how changes in the light environment affect juvenile sockeye DVM in Alaskan lakes through changes in foraging rates and predation risk. Using hydroacoustics to track temporal changes in fish distribution, we found clear patterns of DVM and a strong, significant correlation between the mean depth of the sockeye and the amount of light at the lake surface. However, we could not detect diel changes in the depth distribution of fish large enough to be sockeye predators. Given a lack of diel vertical migration in the zooplankton community, it appears that juvenile sockeye were not simply tracking their food supply. Calculations of the in situ light experienced by individual juvenile sockeye suggested that they migrate to maintain a constant light environment. This light environment allowed the sockeye to exploit an antipredation window whereby they could forage on zooplankton while reducing the odds of visual detection by their predators. Furthermore, this antipredation window was continuous in early summer, but was split into two discrete time periods during the crepuscular hours in late summer. These data support the hypothesis that changes in habitat use by juvenile sockeye salmon reflect a dynamic strategy to minimize the ratio of predation risk to foraging gain that changes dramatically over the course of diel cycles in pelagic ecosystems.

**Key words:** antipredation window; diel vertical migration; feeding rate vs. predation risk; foraging gain; kokanee; light environment; *Oncorhynchus nerka*; predation risk; sockeye salmon.

### INTRODUCTION

Diel vertical migration (DVM) is a common behavioral phenomenon among many aquatic taxa (Stich and Lampert 1981, Levy 1987, Wurtsbaugh and Neverman 1988). Among freshwater fishes, DVM by juvenile sockeye and kokanee salmon (*Oncorhynchus nerka*) has received considerable attention (e.g., Narver 1970, Levy 1987, 1990b, Steinhart and Wurtsbaugh 1999). While residing in the pelagic zone of their nursery lakes, juvenile sockeye typically occupy much deeper waters during the day than they do at night, with migrations often covering tens of meters (Levy 1987, Clark and Levy 1988, Levy 1990b). The ecological explanation for the evolution of this behavior remains elusive, but three general hypotheses have been proposed to account for the adaptive significance of DVM:

bioenergetic efficiency, foraging opportunity, and predator avoidance (Brett 1971, Eggers 1978, Levy 1987, Clark and Levy 1988, Levy 1990b, Bevelhimer and Adams 1993, Steinhart and Wurtsbaugh 1999).

The bioenergetic-efficiency hypothesis is based on vertical differences in temperature within the lake and proposes that juvenile sockeye select temperatures to maximize their growth rate (Brett 1971, Biette and Geen 1980, Bevelhimer and Adams 1993). Because sockeye salmon are visually foraging planktivores (Eggers 1977), they often feed on zooplankton in the warmer surface waters that have enough light for prey detection (Doble and Eggers 1978, Eggers 1978). Sockeye then presumably migrate to colder, deeper waters to decrease metabolic costs while not feeding (Bevelhimer and Adams 1993). The foraging-opportunity hypothesis suggests that fish track their prey in space and time to maximize foraging and subsequent growth rates (Narver 1970, Levy 1990a, b). Finally, the predator-avoidance hypothesis predicts that juvenile sockeye move vertically in the water column in response to piscivores. In this case, the juvenile sockeye migrate up in the water column once light levels have dimin-

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<sup>1</sup> Present address: School of Aquatic and Fishery Sciences, University of Washington, P.O. Box 355020, Seattle, Washington 98195-5020 USA.  
E-mail: scheuer1@u.washington.edu

ished enough to reduce detection by visually feeding piscivores (Eggers 1978, Levy 1987, Clark and Levy 1988).

In all likelihood, a combination of these three hypotheses controls changes in the timing and amplitude of the juvenile sockeye DVM (Clark and Levy 1988, Bevelhimer and Adams 1993, Steinhart and Wurtsbaugh 1999). Certainly we expect daily or seasonal changes in the depth distributions of light, temperature, zooplankton, and piscivores. These temporal and spatial fluctuations in the abiotic and biotic environments should alter the relative response of juvenile sockeye to certain stimuli over the growing season (Clark and Levy 1988, Bevelhimer and Adams 1993). However, given the visual foraging nature of both juvenile sockeye and their predators, the interaction between light and the distribution of both predators and prey on sockeye DVM has yet to be considered. A frequently cited behavioral model suggests that the timing of DVM should occur at the intermediate light levels during crepuscular periods (Clark and Levy 1988). During these times, referred to as the "antipredation window," the light levels allow for a visual range that minimizes the ratio of predation risk to feeding rate ( $\mu:f$ ) for the juvenile salmon. Thus far, empirical evidence for the antipredation window is lacking. Here we evaluated changes in the timing and amplitude of juvenile sockeye DVM caused by seasonal changes in the light environment with concomitant changes in the vertical distribution of their zooplankton prey and predators. We hypothesized that sockeye would change their migratory behavior to match changes in the light environment, allowing them to exploit the antipredation window (Clark and Levy 1988).

#### METHODS AND MATERIALS

We examined the influence of light, predators, and zooplankton prey on the spatial distribution of juvenile sockeye salmon in three lakes within the Wood River system in southwestern Alaska (59°50' N, 158°40' W). During the summer of 2000 we surveyed Lake Kulik on 8–9 July and 25–26 August, Lake Nerka on 3–4 July and 1–2 September, and Little Togiak Lake on 11–12 July. Our surveys ran from pre-dusk through dawn with an additional 1–2 h sampling period during midday. We used a 200 kHz BioSonics DT4000 split-beam echosounder (BioSonics, Seattle, Washington, USA) to measure changes in the spatial distribution of both juvenile sockeye salmon and their predators (details in Appendix A). We classified all targets less than -46 dB as juvenile sockeye and all fish greater than -37 dB as predators, which corresponded to fish lengths of <100 mm and >282 mm, respectively (Burczynski and Johnson 1986). Although the hydroacoustics cannot distinguish the species of fish, juvenile sockeye salmon constitute >75% of the pelagic fish abundance in the Wood River lakes (Rogers 1961, Pella 1964, Burgner et al. 1969; University of Washington Alaska Salmon

Program, unpublished data), and therefore the hydroacoustics provide a reasonable estimate of juvenile sockeye salmon density and depth distribution.

We calculated a maximum-likelihood estimate of the weighted mean fish depth for juvenile sockeye based on targets grouped into five-minute intervals (see Appendix A). These mean depths were based on an average of  $46 \pm 2.4$  (mean  $\pm 1$  SE) individual fish per five-minute sampling interval. For each lake and month combination ( $n = 5$  lake-date combinations), we grouped all of the predators together before calculating their depth distribution. We based this decision on the observation that the predators were  $\sim 200$  times less dense than the juvenile sockeye in July and  $\sim 30$  times less dense in August and September, which resulted in very small sample sizes for calculating summary statistics over the same interval as the juvenile sockeye.

The in situ light level ( $L_{i,t}$ ) experienced by fish  $i$  at time  $t$  was predicted as

$$L_{i,t} = L_{0,t} \exp(-Kz_{i,t}) \quad (1)$$

using the measured extinction coefficient  $K$ , fish depth  $z_{i,t}$ , and incident light level  $L_{0,t}$ . We measured  $L_{0,t}$  (400–700 nm wavelengths) with a LI-COR model 192SA light sensor (LI-COR, Lincoln, Nebraska). Light levels were recorded to a LI-COR model 1400 data logger and averaged over a 5-min interval. We calculated  $K$  on each sampling occasion by measuring the light intensity within the water column at 1-m intervals down to 25 m and fitting a least-squares regression through the standard equation for exponential light extinction (equivalent to Eq. 1). We then computed weighted means of  $L_{i,t}$  over 1-h intervals for juvenile sockeye salmon and their predators.

To assess day-night changes in the vertical distribution of zooplankton, we sampled Lake Kulik on 12 July 2001 at 0200 and 1400 hours and Lake Nerka on 29 August 2001 at 0100 and 1400 hours (all times throughout refer to Alaska Daylight Time). We collected duplicate samples from six discrete depths (1, 10, 20, 30, 40, and 50 m) with a 28.8-L Schindler-Patalas trap (Wildlife Supply Company, Buffalo, New York, USA) fitted with an 80- $\mu$ m mesh sock and plankton bucket. Zooplankton taxa consisted of *Daphnia longiremis*, *Eubosmina longispina*, *Holopedium gibberum*, *Cyclops columbianus*, *Diaptomus gracilis*, *D. pribilofensis*, and *Eurytemora yukonensis*. However, we lumped all species together for our analyses due to similar patterns in their vertical distribution and the wide diet breadth of juvenile sockeye. Furthermore, we did not include any copepod nauplii in our foraging rate calculations.

To evaluate the antipredation window and the optimal timing of juvenile sockeye diel vertical migration (DVM), we calculated the ratio of predation risk to foraging gain ( $\mu:f$ ) over time. For these analyses we combined all of our data from all of the lakes in July and again in August/September. We estimated potential

foraging rates ( $f$ ) of juvenile sockeye salmon as a function of reactive distance according to the model and parameter values of Clark and Levy (1988)

$$f_{i,t} = \frac{\pi(r_{i,t} + b)^2 v \rho}{1 + h\pi(r_{i,t} + b)^2 v \rho} \quad (2)$$

where  $r_{i,t}$  is the reactive distance of an individual juvenile sockeye salmon  $i$  at a given time  $t$ ,  $b$  is the radius of an individual zooplankton ( $=5 \times 10^{-4}$  m),  $v$  is the average fish swimming speed ( $=0.05$  m/s),  $\rho$  is the density of zooplankton, and  $h$  is the average attack and handling time ( $=1.8$  s). We modeled the reactive distance ( $r$ ) of juvenile sockeye as a function of the in situ light level based on the experimental work of Henderson and Northcote (1985) for juvenile Dolly Varden (*Salvelinus malma*) and cutthroat trout (*Salmo clarki clarki*). We combined their data for both species because there appears to be no difference in the ocular structure (Ali and Wagner 1980), retinomotor response (Ali 1975), or the pigment composition (Ali and Wagner 1975) among fishes in the genera *Oncorhynchus* and *Salvelinus*. We generated the following saturating relationship for  $r_{i,t}$  (measured in meters):

$$r_{i,t} = \begin{cases} 0 & \text{for } \log_{10}(L_{i,t}) \leq -3.60 \\ 0.0553 \log_{10}(L_{i,t}) + 0.199 & \text{for } -3.60 < \log_{10}(L_{i,t}) \leq 0.377 \\ 0.022 & \text{for } \log_{10}(L_{i,t}) > 0.377 \end{cases} \quad (3)$$

where  $L_{i,t}$  is the in situ light level (in watts per square meter) from Eq. 1.

Predation risk for juvenile sockeye ( $\mu$ ) was modeled as a product of the predator-encounter probability ( $P$ ) and the predator's reactive distance ( $R$ ). The probability of an individual sockeye  $i$  encountering a predator at depth  $z$  and time  $t$  equals the probability density function (pdf) of the predator depth distribution times the predator temporal density ( $\rho$ ) such that

$$p_{i,t} = \exp\left[-\frac{(z_i - m)^2}{2s^2}\right] \rho. \quad (4)$$

Here,  $z_i$  is the depth of an individual juvenile sockeye, while  $m$  is the mean ( $=19.7$  m) and  $s^2$  is the variance ( $=7.17$  m<sup>2</sup>) of the predator depths grouped across lakes on each sampling occasion ( $n = 51$  observed predators in July;  $n = 450$  observed predators in August). The predator temporal density ( $\rho$ ) equals the average number of predators observed per second over the course of the hydroacoustic surveys ( $n = 0.0015$  predators/s in July;  $n = 0.017$  predators/s in August). We also assumed that the vertical distribution of predators did not change over a diel cycle due to the lack of any observable vertical migration in their behavior (see *Results*).

The dominant predators of juvenile sockeye in the Wood River lake system are arctic char (*Salvelinus alpinus*) and Dolly Varden (*S. malma*) (Burgner et al.

1969, Ruggerone and Rogers 1984, Burgner 1991). We calculated their reactive distance using a model for closely related lake trout (*S. namaycush*) (Beauchamp et al. 1999, Vogel and Beauchamp 1999), where reactive distance ( $R$ , in meters) of a predator to an individual sockeye  $i$  at time  $t$  is a saturating function described by

$$R_{i,t} = \begin{cases} 1.906L_{i,t}^{0.4747} & \text{for } L_{i,t} < 0.0757 \\ 1.012 & \text{for } L_{i,t} \geq 0.0757 \end{cases} \quad (5)$$

and the in situ light level ( $L_{i,t}$ ) is taken from Eq. 1 (measured in watts per square meter). We assumed turbidity to be negligible in their model given the high water transparency in these lakes (extinction coefficients ( $K$ ) ranged from  $-0.18$  to  $-0.21$ /m; Secchi depths ranged from 10.5 to 12.5 m). Relative predation risk for an individual juvenile sockeye ( $\mu_{i,t}$ ) then becomes

$$\mu_{i,t} = P_{i,t} R_{i,t} \quad (6)$$

Finally, we computed the ratio of predation risk to foraging gain ( $\mu:f$ ) averaged over 5-min intervals.

## RESULTS

We observed clear diel vertical migrations of (DVM) juvenile sockeye salmon in all of the lakes (Fig. 1). During early July, sockeye began their upward migration around 2200 hours from their daytime depth near 75 m. They then reached their average nighttime depth of  $\sim 15$  m around 0230 hours where they remained for  $\sim 1$  h before migrating back down, again reaching their daytime depth around 0730 hours. During late August when night duration is substantially longer juvenile sockeye began their upward migration earlier and reached shallower depths than in July (Fig. 1). Juvenile sockeye began their upward migration around 2000 hours, reaching their average nighttime minimum depth between 7–10 m around 2300 hours, where they remained  $\sim 5$  h longer than in July. They began their downward migration around 0530 hours and reached a daytime depth near 75 m around 0900 hours. The mean daytime depth of the juvenile sockeye was  $66.2 \pm 0.278$  m (mean  $\pm 1$  SE) ( $n = 1629$  individuals) across all sampling dates and lakes. Some of the juvenile sockeye might have migrated below the 80-m threshold we imposed, but it is unlikely that they moved to the lake slope and schooled up given the pelagic nature of our survey transects.

We found a strong positive relationship between the amount of incident light at the lake surface and the depth of the juvenile sockeye salmon during the crepuscular periods and night (Table 1). As the light level increased, the mean depth of the juvenile sockeye also increased. In lakes Kulik and Nerka, the slope of the regression line through the data points was steeper in July than in late August (Kulik:  $t = 3.00$ ,  $df = 139$ ,  $P = 0.0016$ ) and early September (Nerka:  $t = 3.81$ ,  $df = 117$ ,

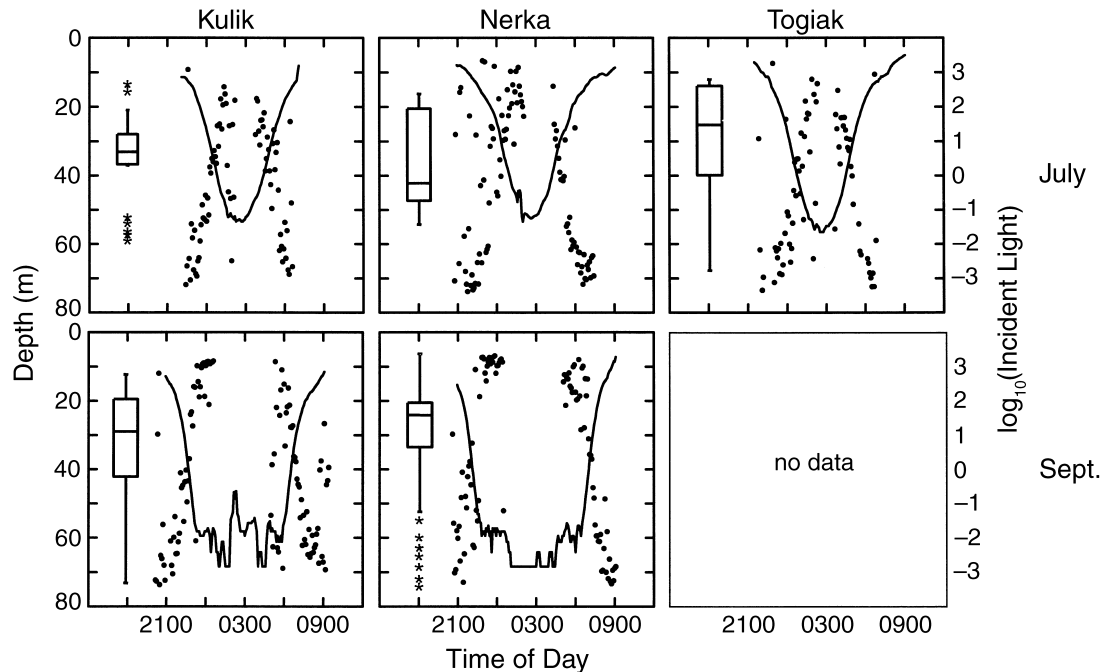


FIG. 1. Depth distribution of piscivorous fishes (box-and-whisker plot) combined with time series of the mean depth of juvenile sockeye (black dots) and the log of light intensity (measured as watts per square meter) at the lake surface (solid line) for Kulik, Nerka, and Little Togiak lakes, in July and September (2000). Each data point for the depth of juvenile sockeye represents an average over a 5-min interval. See *Methods* for details. Stars above or below the predator box-and-whisker plots denote observations outside the inner fence.

$P = 0.00011$ ), indicating a stronger response of juvenile sockeye to the same unit change in light level earlier in the year. Moonlight during the July sampling was negligible due to high cloud cover and was sporadic during the September sampling as evidenced by the small spikes in the incident light profile between 0200 and 0400 hours.

During the juvenile sockeye DVM, the light levels at the lake surface changed by 4–5 orders of magnitude (Fig. 1). However, the in situ light intensity experienced by juvenile sockeye during their migration changed by only 1–2 orders of magnitude (Fig. 2). During the juvenile sockeye migration in July, the mean in situ light level began near  $0.42 \text{ W/m}^2$  at 2100 hours. By 0100 hours it had decreased to  $\sim 4.2 \times 10^{-3} \text{ W/m}^2$  and remained near this level through the remainder of the night and into the following morning during their

downward migration. During late August and early September however, the mean in situ light level began at  $8.3 \times 10^{-3} \text{ W/m}^2$ , fell to  $7.6 \times 10^{-4} \text{ W/m}^2$  by 0100 hours, and then increased to near  $8.4 \times 10^{-3} \text{ W/m}^2$  again by the end of the migration at 0900 hours (Fig. 2).

The vertical limits of the distribution of predators across all sampling dates varied between 10 and 75 m, but these fish were generally found between 20 and 40 m (Fig. 1). This depth distribution remained relatively constant over the diel period, as linear regression of predator depth as a function of the  $\log_{10}$  of incident light explained <10% of the variation in predator depth. Furthermore, we only found significant, but very weak, relationships in August (Kulik:  $R^2 = 0.017$ ,  $F = 4.04$ ,  $P = 0.046$ ) and September (Nerka:  $R^2 = 0.088$ ,  $F = 27.4$ ,  $P < 0.0001$ ).

TABLE 1. Regression results for the relationship between the weighted depth of juvenile sockeye salmon and the  $\log_{10}$  of the incident light hitting the lake surface.

Lake	Month	$n^\dagger$	$R^2$	Intercept (1 SE)	Slope (1 SE)	$F$	$P$
Nerka	July	90	0.77	-9.07 (3.34)	15.4 (0.890)	298.6	<0.0001
	Sept.	89	0.93	10.0 (1.05)	11.7 (0.366)	1021	<0.0001
Kulik	July	75	0.82	4.34 (2.23)	12.8 (0.687)	346.1	<0.0001
	Aug.	87	0.87	17.7 (1.22)	10.4 (0.422)	602.7	<0.0001

$^\dagger$  The number of data points in the regression analyses (i.e., the number of 5-min mean depth estimates—the data points in Fig. 1).

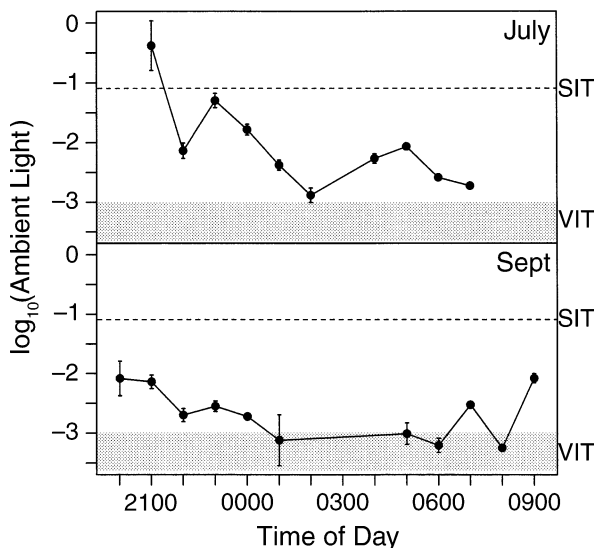


FIG. 2. Time series of hourly averages of the ambient (in situ) light levels for juvenile sockeye salmon in July and September. Error bars (some obscured by data points) represent 95% confidence intervals. For comparison, the horizontal dashed line at  $-1.1$  indicates the saturation irradiance threshold (SIT) for the detection of juvenile salmonid prey by adult lake trout (Vogel and Beauchamp 1999), and the shaded region between  $-3.0$  and  $-3.7$  indicates the range of lower light thresholds (visual irradiance threshold, VIT) for zooplankton prey detection by juvenile salmonids (Henderson and Northcote 1985).

The ratio of predation risk to foraging gain ( $\mu:f$ ) demonstrated substantial changes over the course of DVM by juvenile sockeye (Fig. 3). In July,  $\mu:f$  was minimized for one continuous 6-h period from 0000–0600 hours. However, later in the summer, this antipredation window was split into two discrete periods. The ratio of  $\mu:f$  was minimized for roughly one hour from 2200–2300 hours and again from ~0700–0800 hours. In both early and late summer, inspection of the mean incident light function (Fig. 3) indicated that the antipredation window was bounded by surface light levels of 100 and 0.01  $W/m^2$ .

We found no significant difference between the day and night vertical distributions of zooplankton in lakes Nerka and Kulik (Kolmogorov-Smirnov two-sample test, maximum difference = 0.5,  $P > 0.10$ ; Appendix B). Temperature–depth profiles for the three lakes showed a thermocline between 8 and 15 m and generally constant temperatures around 4–6°C below 30 m (Appendix C).

DISCUSSION

We found strong patterns of diel vertical migration (DVM) by juvenile sockeye salmon in all three of our study lakes, in both early and late summer (Fig. 1). This behavioral phenomenon has been reported for other populations of *Oncorhynchus nerka* throughout their range in North America (Narver 1970, Clark and Levy

1988, Beauchamp et al. 1997). In general, the explanations for this behavior focus on the sensory mechanisms of the fish, especially those pertaining to temperature and light (Levy 1987, 1990b).

The bioenergetic-efficiency explanation for DVM centers around water temperature, whereby the fish are thought to migrate to shallow, warm water to feed on zooplankton and then retreat to deeper, cool water where they remain while digesting their prey and minimizing the energy required for maintenance (Brett 1971, Bevelhimer and Adams 1993, Stockwell and Johnson 1997). However, the temperature environment alone rarely accounts for changes in the observed vertical distribution of juvenile sockeye (Beauchamp et al. 1997, Steinhart and Wurtsbaugh 1999). In our case, we generally observed juvenile sockeye below 60 m during the day, but the thermocline was generally between 8 and 15 m. If the fish were merely tracking cooler temperatures during the day to maximize bioenergetic efficiency, it is unclear why they should go so deep when the temperature was a constant 4–6°C below 30 m (Appendix C). Furthermore, the energy costs associated with the hydrostatic effects on the swim bladder during vertical migration of this amplitude would likely diminish any metabolic advantage associated with migration (Levy 1987).

The light environment within lakes can affect the vertical distribution of pelagic fishes (Luecke and Wurtsbaugh 1993, Appenzeller and Leggett 1995) including juvenile sockeye salmon (Levy 1987, 1990b). Juvenile sockeye salmon are visual foragers (Eggers 1977) and they largely feed on zooplankton during their residence in lakes (Doble and Eggers 1978). Given the

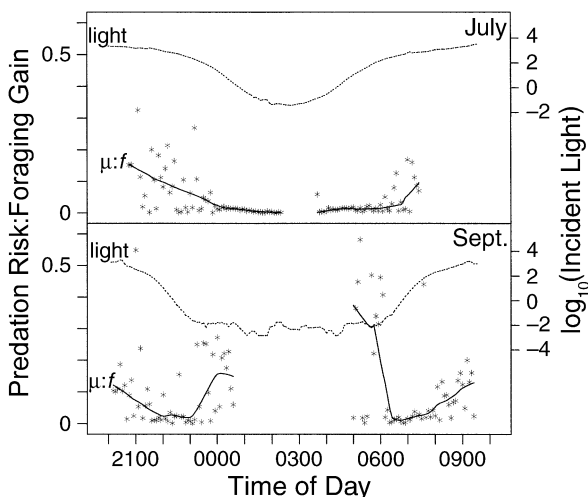


FIG. 3. Time series of the ratio of predation risk to foraging gain ( $\mu:f$ ) for juvenile sockeye salmon in July and August (2000). The asterisks represent the mean  $\mu:f$  from 5-min sampling intervals. The solid lines are local area regression (LOWESS) estimates through the observed data to aid in visualization. The dashed line is the mean incident light (measured as watts per square meter) across all lakes.

generally positive relationship between body size and survival (Miller et al. 1988, Koenings et al. 1993), juvenile fish may attempt to maximize their foraging opportunities and hence growth rate. If so, DVM by juvenile sockeye may reflect an attempt to maximize their spatial and temporal overlap with populations of vertically migrating zooplankton (Levy 1987, 1990a, b, Stockwell and Johnson 1999). However, we found no significant difference in the zooplankton depth distributions between night and day (Kolmogorov-Smirnov two-sample test, maximum difference = 0.5,  $P > 0.10$ ; Appendix B), suggesting that juvenile sockeye were not simply tracking vertical movements of their prey. Indeed, Levy (1990a) cites the general lack of spatial overlap between juvenile sockeye and their zooplankton prey as evidence against the foraging-efficiency hypothesis.

The vertical distribution of predators can also affect the timing and amplitude of DVM by juvenile sockeye salmon (Levy 1987, 1990b, Clark and Levy 1988, Bevelhimer and Adams 1993). Most of the pelagic predators of juvenile sockeye salmon are also visual foragers, occupying relatively shallow depths throughout the day and night (Beauchamp et al. 1999, this study). The predator-avoidance hypothesis suggests that fish should seek out isolums where the visual foraging ability of the predators is greatly diminished (Eggers 1978, Clark and Levy 1988, Levy 1990b). In Lake Washington, Eggers (1978) found that during dusk, the isolume at  $7.3 \times 10^{-4}$  W/m<sup>2</sup> separated individual juvenile sockeye from schools, a common defense against predators (Brock and Riffenburgh 1960). In our case we found that juvenile sockeye appeared to track light levels in the range of  $10^{-2}$  to  $10^{-4}$  W/m<sup>2</sup> throughout the course of their migration (Fig. 2). It is conceivable that their in situ light levels could have decreased somewhat during the middle of the night when we did not sample, as juvenile sockeye have been observed to decrease their nighttime depth slightly following their initial ascent at dusk (Narver 1970). We saw some evidence of this during our July surveys (Fig. 1).

Juvenile sockeye salmon should select isolums that allow them to forage effectively while simultaneously reducing the probability of detection by predators. The light level at which a fish's reactive distance, and hence foraging rate, goes to zero is called the "visual irradiance threshold" (VIT) (Henderson and Northcote 1985). Henderson and Northcote (1985) found that the VIT for juvenile cutthroat trout and Dolly Varden feeding on zooplankton prey was  $1.08 \times 10^{-3}$  and  $2.53 \times 10^{-4}$  W/m<sup>2</sup>, respectively. If we assume similar visual acuity for juvenile sockeye salmon, we see that in early July the juvenile sockeye were always found above the range of VIT's and could theoretically forage on zooplankton (Fig. 2). However, in late summer the juvenile sockeye were near or below the same threshold, suggesting that predator avoidance may have been more

important than foraging during that time. The saturation irradiance threshold (SIT) is the minimum irradiance that maximizes a predator's reactive distance, below which the predator's reactive distance declines dramatically (Henderson and Northcote 1985, Beauchamp et al. 1999, Vogel and Beauchamp 1999). For adult lake trout feeding on salmonid prey, Vogel and Beauchamp (1999) estimated SIT to be  $7.59 \times 10^{-2}$  W/m<sup>2</sup>. We found that the juvenile sockeye occupied depths with light levels below the SIT for lake trout (Fig. 2), suggesting that the juvenile sockeye migrated to avoid predators. We acknowledge that the actual VIT for juvenile sockeye and SIT for Dolly Varden predators may not match the surrogates we chose, but they should provide a good approximation given the general similarities in vision among the salmonids (Ali 1975, Ali and Wagner 1975, 1980).

Clark and Levy's (1988) dynamic-optimization model predicts that juvenile sockeye will balance their predation risk and foraging gain based on their present state and an ultimate goal. Assuming that the juvenile sockeye are attempting to reach a minimum size threshold before the winter or by the time they migrate to the ocean (Koenings et al. 1993), they might be willing to accept more predation risk in favor of better foraging opportunities in the early summer. We found that, on average, juvenile sockeye selected a darker environment in late August than in early July (Fig. 2). This could have resulted from the increased predation risk caused by the greater number of predators that we observed later in the summer—a reflection of the mid-summer movement of salmonid predators out of river mouths and into the pelagia of lakes (Ruggerone and Rogers 1984). These seasonal differences in light response and in situ light levels reflect a dynamic change in habitat utilization by the juvenile sockeye during their first year of life.

Clark and Levy (1988) hypothesized that juvenile sockeye migrate to select light levels sufficient enough to detect their prey while minimizing the detection ability of their predators, thus allowing them to exploit an "antipredation window." Furthermore, their dynamic-optimization model predicts that this antipredation window will occur around the crepuscular periods when light levels change most rapidly. Interestingly, in July we found a single antipredation window when  $\mu:f$  (the ratio of predation risk to feeding rate) was very low for approximately six hours that encompassed both crepuscular periods (Fig. 3). Due to the relatively high latitude of our study lakes, light levels in early July were apparently high enough to facilitate foraging throughout the evening hours (Fig. 2), which led to low  $\mu:f$  values. Later in the summer however, when nights were nearly an order of magnitude darker, the ratio of  $\mu:f$  was lowest during two distinct time periods (Fig. 3). In this case, these two antipredation windows were ~1 h long and coincided with the times when the incident light was changing most rapidly. As the evening

progressed, the light levels became insufficient for foraging and the ratio of  $\mu:f$  increased until dawn when light levels rose again and foraging rates increased relative to predation risk. The minimization of  $\mu:f$  (sensu Gilliam and Fraser 1987) has also been hypothesized to drive habitat choice in a variety of other terrestrial organisms including birds and reptiles (Cooper 2000, Carrascal et al. 2001). Indeed, our results provide strong evidence in support of Clark and Levy's (1988) prediction that DVM by juvenile sockeye salmon reflects a strategy of balancing the conflicting demands of minimizing predation risk while maximizing growth rate.

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#### APPENDIX A

Details of the hydroacoustic methodology are available in ESA's Electronic Data Archive: *Ecological Archives* E084-042-A1.

#### APPENDIX B

Zooplankton vertical distributions for Lakes Kulik and Nerka (southwestern Alaska) are available in ESA's Electronic Data Archive: *Ecological Archives* E084-042-A2.

#### APPENDIX C

Temperature–depth profiles for Lakes Kulik, Nerka, and Little Togiak are available in ESA's Electronic Data Archive: *Ecological Archives* E084-042-A3.