

Do Predators Influence the Distribution of Age-0 Kokanee in a Colorado Reservoir?

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Abstract.—Seasonal changes in reservoir conditions such as productivity, light, and temperature create spatiotemporal variation in habitat that may segregate or aggregate predators and prey, producing implications for the distribution, growth, and survival of fishes. We used hydroacoustics to document the diel vertical distribution of age-0 kokanee *Oncorhynchus nerka* relative to environmental gradients at Blue Mesa Reservoir, Colorado, during May–August of 2002. Temperature, light, and zooplankton density profiles were examined relative to foraging conditions for kokanee and their primary predator, lake trout *Salvelinus namaycush*. Age-0 kokanee displayed large diel vertical migrations in May despite the lack of an energetic advantage before reservoir stratification. Age-0 kokanee minimized near-surface foraging at this time, perhaps to avoid predation by visual predators, such as lake trout, in the well-lit surface waters. Strong reservoir stratification in midsummer appeared to provide a thermal refuge from lake trout that the kokanee exploited. By August vertical migrations were shallow and most kokanee remained in the epilimnion throughout the day. Although the energetic implications of the late-summer strategy are unclear, it appears that kokanee were responding to changes in their predator environment. A robust model for kokanee diel vertical migration across a range of systems should include a predator avoidance component.

In many lentic systems, vertical spatial structure is an important feature that can influence fish distribution through energetic constraints and predation risk. Seasonal changes in vertical gradients of prey density, light, and temperature create spatiotemporal variation in habitat that may segregate or aggregate predators and prey producing implications for distribution, growth, and survival of fishes (Magnuson et al. 1979; Goyke and Brandt 1993; Mason et al. 1995). Thus, environmental conditions can mediate predator–prey interactions and thereby influence aquatic community structure (Carpenter et al. 1985; DeVries and Stein 1992).

Diel migration is a behavior that evolved in response to the challenges of a spatially stratified environment. Sockeye salmon *Oncorhynchus nerka* and kokanee (the landlocked form) perform diel

vertical migrations (DVM) in both the marine and freshwater environment (Narver 1970; Levy 1987, 1990; Beauchamp et al. 1997; Stockwell and Johnson 1997). Diel vertical migration by juvenile sockeye salmon is well documented (Narver 1970; Brett 1971a; Eggers 1978; Levy 1987; Clark and Levy 1988; Scheuerell and Schindler 2003). However, fewer studies have investigated juvenile kokanee distributions (Finnel and Reed 1969; Beauchamp et al. 1997; Stockwell and Johnson 1999), and very little is known about age-0 kokanee migrations (Johnston 1990). The typical pattern for sockeye salmon and kokanee migrations is ascent to near-surface waters at dusk, remaining in shallow waters during the night, and descent at dawn to deep depths where they remain during daytime (Narver 1970). We will refer to this as “normal DVM.” Variations in this pattern involve depth, timing, number and duration of surface ascents (Northcote et al. 1964; Levy 1987). A “reverse DVM” has also been described, particularly in tur-

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bid waters, in which juveniles ascend close to the surface by day and descend into deep water at dusk (Finnel and Reed 1969; Levy 1987).

It has been suggested that DVM patterns change from system to system; they can also change temporally within systems due to fish response to changing environmental and ecological conditions such as light intensity, predator influence, and zooplankton productivity (Beauchamp et al. 1997; Stockwell and Johnson 1999). For vertical migrations to persist across systems there must be some ecological or evolutionary benefit to compensate for costs of migrating tens of meters and foregoing foraging opportunities in more productive surface waters (Levy 1990). Research on optimal foraging theory and predation risk for small fishes suggested that minimizing predator contact and maximizing growth are two antagonistic selective forces that may perpetuate the migration behavior (Mittlebach 1981; Werner et al. 1983). Such arguments have also been proposed for sockeye salmon and kokanee.

Hypotheses associated with DVM in fishes have generally focused on foraging opportunity (Jansen and Brandt 1980; Wurtsbaugh and Neverman 1988), energetics (Brett 1971a), or predator avoidance (Eggers 1978; Clark and Levy 1988). The foraging hypothesis posits that vertical migrations arise from fish following concentrations of vertically migrating prey so as to minimize search time and maximize capture rates. Brett (1971a) proposed that growth maximization could be achieved by feeding in the warmer surface waters, then vertically migrating through markedly different temperature zones, thus reducing daytime metabolic costs by thermoregulating in the cold hypolimnion. Energetics appears to be at least a partial explanation for DVM in kokanee (Bevelhimer and Adams 1993; Stockwell and Johnson 1999), but there is also evidence for predator avoidance as a migration determinant (Levy 1987; Paragamian and Bowles 1995; Stockwell and Johnson 1999). The predator avoidance theory suggests DVM as a strategy to avoid visual predators by minimizing time spent foraging near the surface where the possibility of being seen by visual feeding piscivores is high (Eggers 1978; Werner et al. 1983). A fourth, multifactor hypothesis called the "antipredation window" suggests that fish behavior is explained by a tradeoff between foraging opportunity and predation risk (Werner et al. 1983; Clark and Levy 1988; Scheuerell and Schindler 2003). The complexity of the processes involved makes these hypotheses extremely difficult to study in a lab-

oratory setting. Thus, field observations in ecosystems like Blue Mesa Reservoir, Colorado, are particularly useful for evaluating these hypotheses because they span a variety of limnological conditions in which to compare and contrast the importance of each ecological strategy within a single system where predation pressure is intense (Johnson and Martinez 2000; Johnson et al. 2002).

Compared with other sockeye salmon lakes, Blue Mesa Reservoir is an unusual system because it is located at relatively low latitude and has warm water temperatures and high secondary productivity, which support very high kokanee growth rates. Age-0 kokanee in Blue Mesa Reservoir are typically much larger (125 mm in August) than in many of the studies investigating age-0 sockeye salmon in more northern lakes where food may be more limited, such as British Columbia (53 mm in August; Narver 1970) and Idaho (30–80 mm in September; Beauchamp et al. 1997). It also has a somewhat novel, deep-water predator, lake trout *Salvelinus namaycush*, unlike some of the more coevolved systems having the northern pikeminnow *Ptychocheilus oregonensis* and cutthroat trout *Oncorhynchus clarki* as predators (Beauchamp et al. 1995).

The objectives of this study were to describe daily and seasonal changes in the vertical distribution of age-0 kokanee from the time they are stocked through their first summer and to thereby evaluate critical periods and areas for growth and predation risk. Because year-class strength is determined in the first year of life in many fishes, it is important to understand the age-0 distribution in relation to changing environmental conditions for growth and predation risk. We therefore wanted to assess age-0 distribution and habitat profitability based on time to satiation and predation risk. Summer encompasses a wide range of changing environmental conditions in terms of thermal stratification, food density, water clarity, and distribution of predators. The seasonal changes in reservoir conditions allow for evaluation of the relative importance of foraging efficiency, growth maximization, and predator avoidance in DVM.

Methods

Study site.—Blue Mesa Reservoir is a 3,700-ha, mesotrophic impoundment on the Gunnison River located near Gunnison, Colorado. The reservoir is the largest in Colorado and has a maximum depth of 101 m. Penstocks are located 50 m below the surface (at full pool; surface elevation 2,292 m ASL). Blue Mesa Reservoir holds a fish assem-

blage of kokanee, rainbow trout *Oncorhynchus mykiss*, lake trout, brown trout *Salmo trutta*, white sucker *Catostomus commersoni*, and longnose sucker *C. catostomus*. Yellow perch *Perca flavescens* were recently introduced illegally but their abundance was very low during our study. Kokanee, the predominant pelagic fish species, composed about 89% of all fish caught in 5 years of gillnetting (standardized, experimental vertical gill nets) from 1995 to 2002 (B. M. Johnson, unpublished data). Blue Mesa Reservoir supports a substantial kokanee fishery and has one of the most rapid kokanee growth rates in North America (Stockwell and Johnson 1997).

Limnological conditions.—Field data on temperature, dissolved oxygen, Secchi depths, and zooplankton densities were collected from two locations within the main basin of Blue Mesa Reservoir to (1) describe environmental conditions, (2) input into feeding rate models, and (3) determine lake trout habitat thresholds. Limnological data were collected within 1 week of the new moon each month to correspond with hydroacoustic surveys. Temperature and dissolved oxygen profiles were obtained using a YSI model 52 digital meter with a 60 m cable. Measurements were taken at 1-m intervals from depths of 0 to 20 m and at 5-m intervals from 20 to 55 m. The depth of the thermocline was identified each month as the point where the water temperature decreased by approximately 1°C per 1 m (Horne and Goldman 1994). Two Secchi depth measurements, made with a standard 200 mm white and black Secchi disk (Wetzel and Likens 1991), were the average of two replicate readings (m) taken on the shaded side of the boat.

We used an algorithm developed by Janiczeck and DeYoung (1987) to determine incident light intensity at Blue Mesa Reservoir throughout the day for each sampling date and then calculated ambient light intensity by depth via an extinction coefficient (η) derived from Idso and Gilbert (1974), namely,

$$\eta = 1.7z_{sd}^{-1}, \quad (1)$$

where z_{sd} is Secchi depth. Light intensity (I_z) at 1-m intervals (z) was calculated using the following relationship (Horne and Goldman 1994):

$$I_z = I_0 e^{-\eta z}, \quad (2)$$

where I_0 is the light intensity (lx) at the surface (0 m).

Zooplankton prey density was measured with

oblique tows using a Wildco Model 37-315 Clarke–Bumpus plankton sampler (Lind 1979) with a 130-mm-diameter opening and 153- μ m-mesh size. From early May to early August and within 2 d of the new moon, a single tow was made in each of four depth strata (0–5, 5–10, 10–15, and 15–30 m) at two midbasin locations. In Blue Mesa Reservoir, *Daphnia* (the primary food item for kokanee in Blue Mesa Reservoir; Stockwell et al. 1999) are found primarily in the upper 10 m of the water column (Stockwell and Johnson 1997) and do not exhibit diel vertical migrations (Johnson 1994; Johnson et al. 1995). Zooplankton samples were taken between 0730 and 1030 hours in 2002, except in August when sampling continued until 1500 hours; samples were preserved in 70% ethanol. Each sample was diluted and three replicate 1-mL aliquot subsamples were placed in a Sedgwick–Rafter counting cell, where all taxa were identified and enumerated (Lind 1979) under a compound microscope. Zooplankton densities were computed as number per liter for each depth stratum. Only densities of *D. pulex* (the predominant prey item found in kokanee stomachs; Stockwell et al. 1999) were used as inputs to feeding rate models.

Feeding rate and time to satiation.—We assumed that time to satiation was a better indicator of habitat profitability than feeding rate because time to satiation accounts for changes in body size due to growth and because energetic costs and exposure to predators are likely proportional to feeding duration. We used light dependent functional response models developed for juvenile kokanee by Koski and Johnson (2002) to estimate spatially-explicit feeding rates using measured light conditions and zooplankton density. Pacific salmon require ≥ 0.001 lx to feed (Ali 1959); thus, if ambient light was < 0.001 lx we assumed no feeding occurred. At light levels of 0.001–3.4 lx (Ali 1959; corresponding to light availability at the surface on a clear night) we used Koski and Johnson's (2002) low light model, that is,

$$N = 1.74 \cdot P, \quad (3)$$

where N is consumption rate (*Daphnia*/min), and P is prey density (*Daphnia*/L). The use of this model may allow for some overestimation of feeding rates at light levels between 0.001 lx and 0.1 lx (the light level tested by Koski and Johnson 2002) and underestimation of feeding rates for light between 0.1 lx and 3.4 lx. However, we feel that this model is the best estimation of age-0 ko-

kane feeding rates. Furthermore, because these light levels change very rapidly at the time and depths where these differences may occur we believe it would not significantly change our results. When ambient light exceeded 3.4 lx we applied their high light model,

$$N = (\beta_0 \cdot P) / (\beta_1 + P), \quad (4)$$

where β_0 is maximum consumption rate (163.6 *Daphnia*/min), and β_1 is prey density at which consumption rate reaches half its maximum (42.2 *Daphnia*/L). We used depth-specific feeding rates and stomach capacity (Brett 1971b) to compute time to satiation (feeding duration) in the manner of Koski and Johnson (2002). We were not able to measure zooplankton density below 30 m, so we assumed that densities were the same as in the 15–30-m stratum. Work elsewhere (Wissel and Ramcharan 2003) suggests that this is a conservative assumption for our work because *Daphnia* densities are likely to be even lower below 30 m than in the 15–30 m stratum.

Predation risk.—To assess predation risk we focused on lake trout. Based on size structure and abundance data (Johnson and Martinez 2000; Crockett 2004), lake trout was the primary piscivore. Salmonids (including kokanee) composed more than 75% of the diet of lake trout 425 mm or greater in total length (Johnson et al. 2002). Although vertical gill-net data indicate that brown trout were present in the pelagic zone, they were relatively small in size (mean length = 313 mm; B.M.J., unpublished data). Rainbow trout were only 3.2% of the total catch in vertical gill nets and were rarely piscivorous in Blue Mesa Reservoir (Johnson et al. 2002). Previous reservoirwide hydroacoustic surveys indicated that approximately 50% of the total fish biomass in Blue Mesa Reservoir was composed of fish greater than 425 mm (Johnson and Martinez 2000) and were almost exclusively lake trout, as indicated by horizontal and vertical experimental gill nets (Johnson et al. 1995; Crockett 2004). Consumption by piscivorous lake trout was estimated to exceed the annual production of kokanee in Blue Mesa Reservoir in some years (Johnson and Martinez 2000).

For predation to occur there must be a spatio-temporal overlap between predators (lake trout) and their prey (kokanee). Lake trout have a physiological optimum of about 10°C, and will thermoregulate to this temperature when possible (Martin and Olver 1980; Stewart et al. 1983; Madenjian and O'Connor 1999). Temperatures at

TABLE 1.—Summary of dates, times, and number of consecutive transects for diel periods of hydroacoustic sampling for kokanee at Blue Mesa Reservoir, Colorado, 2002.

Date	Time of day	Diel period	Number of transects
May 11	1121–1423	Day	6
May 12	0444–0755	Dawn	8
May 12	1821–2121	Dusk	6
May 12	2154–2352	Night	6
Total			26
Jun 5	0409–0704	Dawn	6
Jun 5	1302–1355	Day	2
Jun 5	1853–2145	Dusk	6
Jun 5–6	2228–050	Night	5
Total			19
Jul 9	0349–0659	Dawn	6
Jul 10	1204–1402	Day	4
Jul 10	1848–2219	Dusk	7
Jul 10–11	2243–0100	Night	6
Total			23
Aug 6	1143–1336	Day	5
Aug 6	1833–2135	Dusk	7
Aug 6–7	2223–026	Night	6
Aug 9	0430–0742	Dawn	6
Total			24

which lake trout in Blue Mesa Reservoir were captured in vertical gill nets during summers of 1994–1997 (B.M.J., unpublished data) averaged 9.5°C (SD = 2.1, $N = 59$), supporting this assumption of behavioral thermoregulation. Mazur and Beauchamp (2003) observed that lake trout predation rates at less than 0.3 lx increased four fold at 0.5–0.7 lx. We used these thresholds (0.5 lx and 10°C) and observed monthly temperature and light profiles to approximate the depths and times at which lake trout predation could occur. Regions of the reservoir where both temperature and light conditions were favorable for lake trout feeding were assumed to represent the highest predation risk to kokanee.

Fish distribution.—Age-0 kokanee were released from the Roaring Judy Hatchery on 12 April 2002 during the new moon; fish reached the reservoir approximately 24 h later. Kokanee vertical distribution was monitored during the new moons from May to August via hydroacoustic sampling (HTI Model 243 split-beam 200-kHz echosounder with 15° transducer). This sampling was conducted continuously along a 1-km transect, which was sampled four times over a 24-h diel period: mid-day, at least 1 h before and after sunset, night, and at least 1 h before and after sunrise (Table 1). Hydroacoustic surveys were not taken during 0800–1100 hours when other sampling was being performed, or during 1400–1800 hours when af-

TABLE 2.—Mean total lengths (TL) of age-0 kokanee in Blue Mesa Reservoir, Colorado, in 2002 (as estimated from growth curves) and their target strength (TS) equivalents (as computed from Love's 1971 equation). Bounds for TS range are approximately ± 3 decibels (dB).

Date	Mean TL (mm)	TS (dB)	Bounds for classifying age-0 fish			
			Target strength (dB)		Total length (mm)	
			Lower	Upper	Lower	Upper
May 11–12	68	-48.2	-51.2	-45.2	48	98
Jun 5–6	86	-46.2	-49.2	-43.2	60	123
Jul 9–10	107	-44.4	-47.4	-41.4	74	153
Aug 5–6	122	-43.3	-46.3	-40.3	85	176

ternoon winds made surveys impossible. The hydroacoustic gear was calibrated with a tungsten calibration sphere before data collection each month. Boat locations were recorded every 5 s via a global positioning system and were used to calculate transect lengths. Volumes sampled for each 5-s interval, as determined from the effective beam width that was acoustically sampled, bottom depth, and the distance traveled, were summed over each transect. Transect volumes were parsed into 1-m depth strata to investigate vertical distribution of kokanee. Their densities were determined by counting the individual tracked fish per strata across the transect, which we then divided by the effective volume of that strata, thus effectively weighting fish counts by volume sampled.

Fish echoes were discriminated from noise via a fish target-tracking algorithm in Echoscape. Target selection criteria (Hardiman 2003) were recommended by the manufacturer to suit Blue Mesa Reservoir depths and target sizes of interest and had been used in previous hydroacoustic surveys

of the reservoir (Johnson and Martinez 2000). We tested the sensitivity of the fish counts by varying the following target-tracking characters: echo selection criteria, ping gap, velocity, change in range, and expansion area, and reprocessing the data. We found that the number of fish counted varied by less than 6% (coefficient of variation) and the standard deviation on fish counts varied by less than 2% (Hardiman 2003), increasing our confidence in the nominal character set.

Echoes from age-0 kokanee were classified on the basis of target strength (TS) estimated from observed growth and Love's (1971) equation (Table 2). Age-0 growth was determined from measurements of fish ($N = 275$) just before release from the hatchery and from catches in horizontal gill nets (stretch mesh sizes 1.3, 1.9, and 2.5 cm). Because behavioral changes in fish aspect can cause wide variations in TS (Gunderson 1993), a range of ± 3 decibels was applied to the estimated TS of age-0 kokanee. This range corresponded to the average standard deviation of TS of individual fish in our dataset and was consistent with values reported in the literature (MacLennan and Simmonds 1992; Ehrenberg and Torkelson 1996; Ransom et al. 1999). To describe temporal patterns in vertical distribution of kokanee we computed median, 25th and 75th percentiles, and the range of depths occupied by kokanee during each sampling interval.

Results

Limnological Conditions

In May the reservoir was nearly isothermal (Figure 1) and zooplankton density was low. The entire water column was less than 10°C, slowly decreasing to about 5°C at 55 m. Zooplankton density was highest near the surface (3.4 *Daphnia*/L), and gradually decreased with depth. Water clarity during the summer of 2002 was least on May 15, when Secchi depth was 3.9 m, which limited the depths

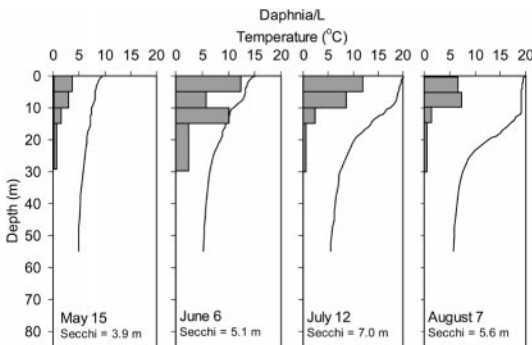


FIGURE 1.—Densities of *Daphnia* (bars) and temperature profiles (lines), as measured on one sample day per month (May to August 2002) during diel hydroacoustic surveys in Blue Mesa Reservoir, Colorado. Secchi depth is also provided for each month; dissolved oxygen (not shown) always exceeded 3.2 mg/L to a depth of 55 m.

to which light (0.001 lx or higher) penetrated for kokanee feeding to 40 m at midday. In June a thermocline occurred at 9 m, zooplankton densities were the greatest of any observed (13.3 *Daphnia*/L at the surface) throughout the summer, and Secchi depth increased to 5.1 m. The greater Secchi depth increased the depths for light (0.001 lx or higher) penetration to 55.5 m at midday. During sampling in July and August the reservoir was strongly stratified, the thermocline persisting at approximately 13 m in both months; a second thermocline formed in August at 20 m. Zooplankton densities were also relatively high in July (11.2 *Daphnia*/L at surface) and decreased in August (7.2 *Daphnia*/L at 5–10 m). Zooplankton density in the upper 10 m of the water column for July and August was substantially greater (>85% of total) than below 10 m (Figure 1). The reservoir was somewhat clearer during July (Secchi depth = 7.0 m) and August (5.6 m), which allowed for light (0.001 lx or higher) penetration to 60 m at midday. Dissolved oxygen exceeded 3.2 mg/L to a depth of 55 m for the entire study period.

Age-0 Distribution

Over the summer, we observed a behavioral change: a single, large DVM and deeper median depth distribution observed on May 11 and 12 gradually changed to multiple, smaller-amplitude migrations and shallower median daytime depths by August 6 and 7 (Figure 2). Age-0 kokanee occupied average daytime median depths of 67 m in May, 74 m in June, 29 m in July, and 19 m in August. During sampling in each month fish were least dispersed vertically at night and the median nighttime depth occupied varied: 21 m in May, 14 m in June, 21 m in July, and 23 m in August. Throughout the study, fish were never schooled to a point where distinguishing individual targets was not possible.

Depths of age-0 kokanee were greater during May, and they performed larger DVMs than later in the summer (Figure 2). The median depths of the cohort were always located where light was less than the 0.001 lx threshold for kokanee visual feeding (Figure 3). We also observed fish more dispersed throughout the water column in May during nonnight hours. Fish descended at around 0500 hours, spent the day at great depths (about 67 m), and ascended to about 25 m after nightfall, performing a single, normal migration per day (Figure 2).

In June, the age-0 kokanee depths continued to be distributed in deeper water during the day (Fig-

ure 2), but some bimodality was observed near 15 m (Figure 3). Fish were also observed scattered throughout the water column during the crepuscular hours, similar to May. During June, fish descended later in the morning (0600 hours) and ascended earlier in the evening (1900 hours) than during May observations (Figure 2). The fish appeared to perform a single DVM, as observed in May.

By July the cohort was much less dispersed in the water column during the crepuscular periods than in May and June (Figure 3), the median depths occurring between 15 and 20 m (Figure 2). Many fish still occupied the deeper depths during the day (Figure 3), but median daytime depths were shallower than those observed in May and June sampling. There appeared to be two diel vertical migrations of lower amplitude in July: fish ascended for an extended period in the morning, descended at midday, then ascended again to near the surface until about 2100 hours, and lastly descended to a nighttime depth of 20 m (Figures 2, 3).

In August, fish displayed the shallowest median diel distribution (Figure 2). Fish ascended near 0500 hours and occupied the upper 20 m throughout the day; very few fish were in the deeper depths throughout this diel cycle (Figure 3). The distribution pattern suggested multiple, smaller-amplitude diel migrations in the upper water column. Fish were aggregated near the thermocline during the night.

Fish Distribution Relative to Feeding Duration and Predation Risk

In May, zooplankton densities were low (Figure 1); however, time to satiation was similar to that in other months because fish were small with smaller stomach capacities. Age-0 kokanee were rarely observed near the surface in May, where time to satiation was least (<12 h; Figure 3). At the depths that light was available for feeding, fish were at 20–30 m, where time to satiation was greater than 12 h. The highest densities, however, were in areas where light was less than 0.001 lx and feeding was not possible. In May, kokanee were most vulnerable to lake trout predation near the surface and above 30 m (≥ 0.5 lx) because the entire water column was less than 10°C and light intensity was highest near the surface. The majority of age-0 kokanee during the day were located in areas with minimal light—that is, deep areas away from the high predation risk.

During June, zooplankton density was the highest measured for the summer, resulting in lower

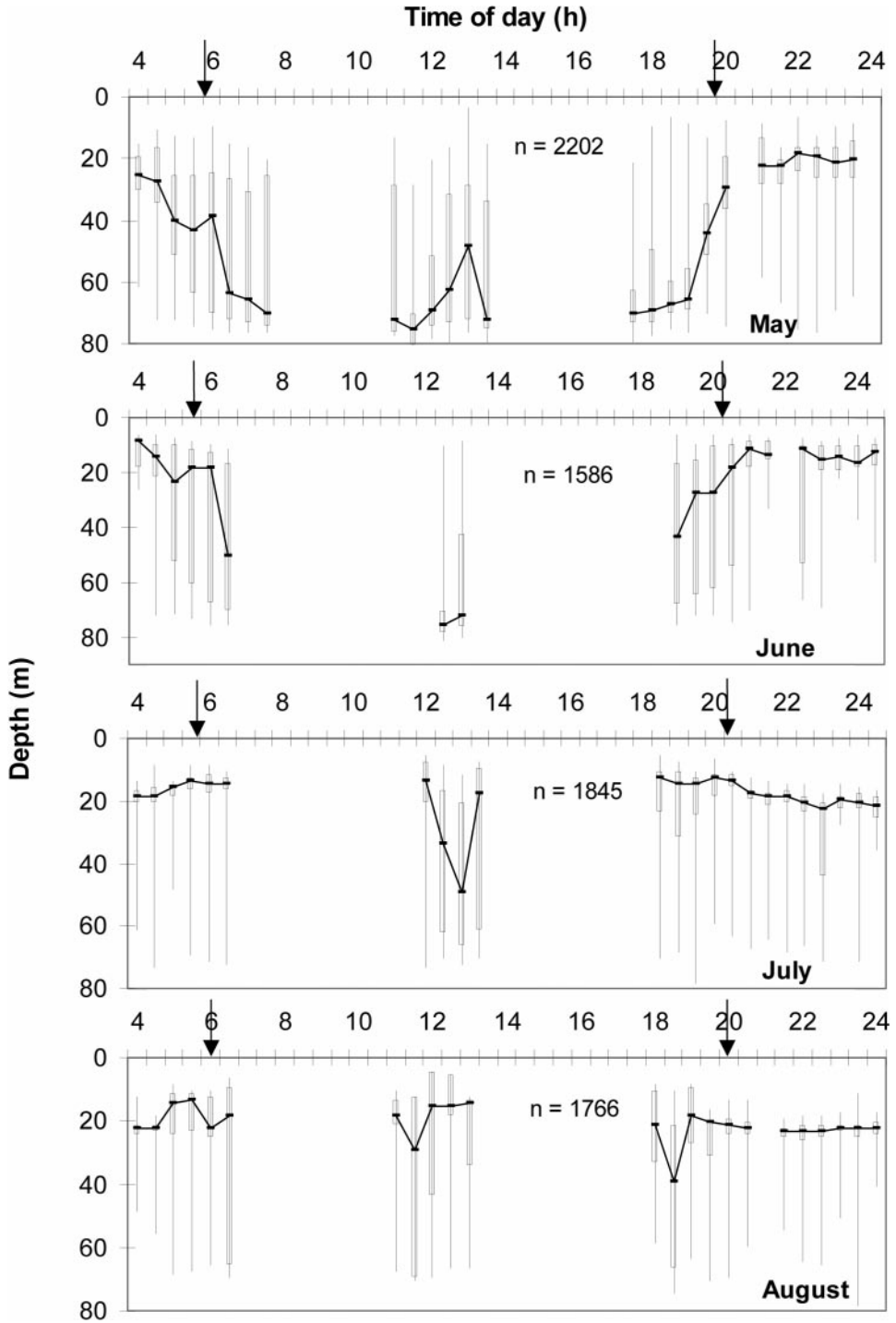


FIGURE 2.—Diel vertical distribution—shown as median (line connecting dashes), 25th and 75th percentiles (boxes), and range (vertical lines)—of age-0 kokanee targets in Blue Mesa Reservoir, Colorado, as recorded in hydroacoustic sampling performed during the new moon in May, June, July, and August 2002. Arrows indicate time of sunrise and sunset. The number of fish observed (*n*) has not been depth-corrected for differential sampling volumes.

time to satiation in the upper 15 m (Figure 3). Water clarity allowed sufficient light at dawn for kokanee to feed to a depth of 55 m, as it did at dusk. Age-0 kokanee were located in areas where satiation time was less than 12 h (typically above 10°C), especially during crepuscular periods. During June daylight hours, there was a bimodal distribution. Some age-0 kokanee were still located near areas with minimal satiation time, but median depths exceeded 70 m (Figure 2). In June the 10°C isotherm occurred around 15 m, and light from late dawn to early dusk was sufficient for predation on kokanee to a depth of 35 m. Some fish were observed in the high-predation risk areas, but their densities were lower than in other areas (Figure 3).

In July and August light levels were available for kokanee feeding from dawn to dusk and penetrated to about 60 m at midday. Calculated feeding rates were always highest in the upper 15 m, where time to satiation was less than 12 h (Figure 3). In July 10°C occurred deeper (about 20 m), and water was clearer (Secchi depth of 7 m), allowing for adequate light penetration for predation to 50 m. In August the 10°C isotherm occurred slightly deeper (about 22 m) than in July; however, light penetration was less, so lake trout predation could occur to about 40 m at midday. In July, during daylight hours when light intensity was adequate for kokanee feeding, fish occupied deeper areas (60–70 m) where time to satiation exceeded 12 h and predation risk was low, or they were in areas that exceeded 10°C (Figure 3). In August, however, they occupied areas where time to satiation was less than 12 h but predation risk at that time was low; that is, relatively few age-0 kokanee during daytime were found at the deep depths observed during the previous months. In July and August, age-0 kokanee were located near the thermocline (15–22 m; typically $\geq 10^\circ\text{C}$) during hours of darkness.

Discussion

Vertical distribution of age-0 kokanee changed greatly from May to August, indicating an influence of changing limnological conditions. Seasonal changes in temperature, light, and zooplankton densities altered age-0 kokanee foraging conditions and predation risk by lake trout. In May, age-0 kokanee were shallow at night and deep during the day, displaying large vertical migrations with a large amount of variation in distribution throughout the water column. At this time the reservoir was nearly isothermal, and zooplankton

productivity and resultant kokanee feeding rates were low (Hardiman 2003) and predation risk high. This behavior refutes the foraging hypothesis because fish are not orienting to greater densities of *Daphnia* in the upper water column. The lack of thermal stratification in May provides no bioenergetic advantage for performing vertical migrations to maximize growth. Other studies have also documented sockeye salmon vertical migrations occurring during isothermal conditions, such as in Lake Washington, Washington, in autumn (Woodey 1972) and in Stanley Lake, Idaho, in winter (Steinhart and Wurtsbaugh 1999). This indicates that other selective forces, such as foraging opportunity and predation pressure, must be influencing the migration behavior.

The opportunity for predation by lake trout in Blue Mesa Reservoir's well-lit surface waters in May may have limited near-surface foraging opportunities for age-0 kokanee to the brief periods of limited light intensity at dusk and dawn, as suggested by Clark and Levy (1988). Similar limnological conditions occurred in Alturas Lake, Idaho, in September (Beauchamp et al. 1997), where zooplankton densities were low and piscivore densities were high. There, juvenile sockeye salmon (≤ 180 mm) were nearly absent from the limnetic zone in daylight hours and were concentrated at colder intermediate depths (15–30 m) during crepuscular and nocturnal periods. Beauchamp et al. (1997) suggested that sockeye salmon consumed less and minimized metabolic costs in colder waters, optimizing growth efficiency and minimizing predation risk. The age-0 kokanee distribution in Blue Mesa Reservoir in May also best matched the antipredation window hypothesis. Age-0 kokanee were observed near the surface only during periods of limited light intensity.

Deep migrations at Blue Mesa Reservoir continued in June as the reservoir began to thermally stratify and zooplankton densities increased. Kokanee distribution in June was less variable throughout the water column than in May. They were concentrated at depths of higher zooplankton densities at crepuscular periods and at the thermocline during nocturnal periods, and they displayed a bimodal distribution during daylight periods. During daylight hours they were either oriented near high zooplankton densities (15–20 m) or very deep (70 m). Daily bimodal distribution patterns of juvenile sockeye salmon have also been observed periodically in Babine Lake (Narver 1970), Lake Washington (Beauchamp et al. 1999), and Great Central Lake (Barraclough and Robin-

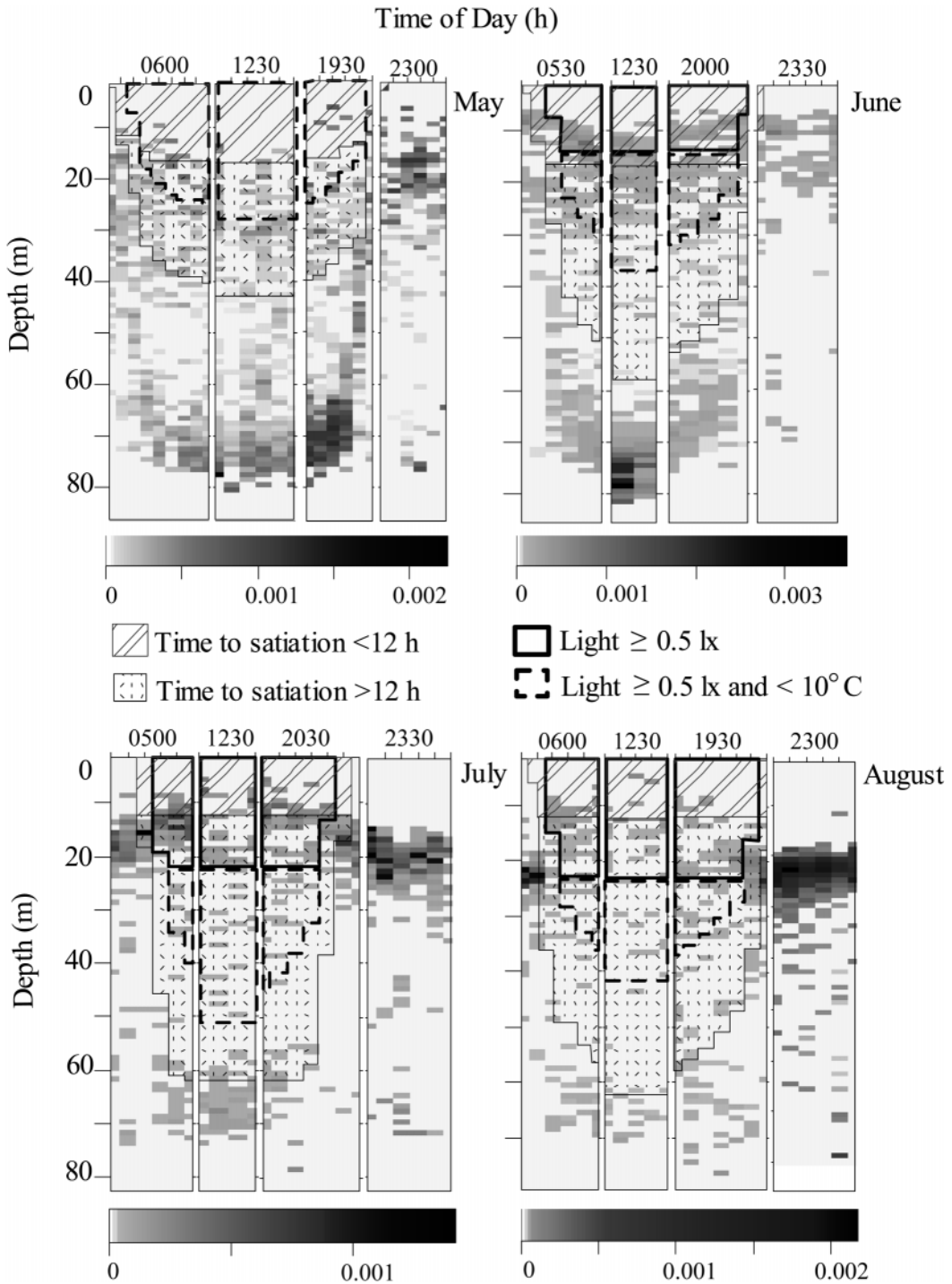


FIGURE 3.—Diel vertical distribution of age-0 kokanee target densities from hydroacoustic transects taken from May to August 2002 at Blue Mesa Reservoir, Colorado, showing regions where time to satiation was less than 12 h and more than 12 h, as estimated from kokanee size, densities of *Daphnia pulex*, water clarity, and a light-dependent functional response. Predation risk areas are indicated by regions where temperature was less than 10°C and light was 0.5 lx or greater (dashed outline) and areas available for lake trout feeding where light was 0.5 lx or greater (solid dark outline). Bar scales beneath panels are kokanee densities (fish/ m^3) within a 1-m stratum and

son 1972) and in previous research at Blue Mesa Reservoir (Stockwell and Johnson 1999). This depth segregation in juvenile sockeye salmon was the result of feeding by part of the population (Narver 1970; Woodey 1972). We speculated that the bimodal distribution observed at Blue Mesa Reservoir was also probably due to feeding by part of the cohort because the upper modal depth was associated with the higher zooplankton densities and shorter time to satiation. This distribution may represent two manifestations of the tradeoff between profitable foraging opportunities (where light is available and zooplankton abundance is high) and predation risk. Because we had limited ability to track lake trout distribution, we can only assess spatial overlap and degree of predation risk by inferring favorable lake trout habitat from their thermal and light preferences. However, hydroacoustics data and results from sonic telemetry tracking of lake trout (Crockett 2004) suggest that the onset of thermal stratification in June may provide refuge for kokanee in the water temperatures that may be too warm for lake trout.

By July and August the reservoir was strongly stratified yet maintained relatively high zooplankton abundance. Age-0 kokanee were less dispersed throughout the water column. Evidence of large DVM was less apparent, most fish orienting near the surface throughout the diel cycle. This behavior was similar to reverse migrations observed in kokanee and lake trout in Lake Granby, another Colorado reservoir where age-0 kokanee oriented near the surface during the day and were deeper at night (Finnel and Reed 1969).

In August, age-0 kokanee distribution in Blue Mesa Reservoir was markedly different than in May, suggesting a seasonal ontogeny in DVM similar to that observed for older age-classes in 1997 (Stockwell and Johnson 1999). Strong thermal stratification in late summer created a large surface volume that probably served as a refuge from lake trout predation. Although lake trout could make short feeding forays into the epilimnion, we never observed this behavior, and work with striped bass suggests that some piscivores do not avail themselves of high prey densities in shallow water if temperatures are above their preferred temperature (Coutant 1987; Young and Isely 2002).

This thermal refuge probably relieved the predation pressure in the surface waters, allowing age-0 kokanee to exploit high epilimnetic prey densities. Beauchamp et al. (1997) documented similar behavior in Stanley Lake, Idaho, where smaller fish (≤ 180 mm) were oriented towards the surface when zooplankton densities were high in the epilimnion (temperatures, 14–18°C) and piscivore densities were low. They observed that under favorable predator conditions (low predator density) sockeye salmon occupy shallower depths with warmer temperatures and high zooplankton densities and grow faster but less efficiently. It appears that age-0 kokanee in Blue Mesa Reservoir took advantage of the increased foraging opportunities in the warmer, surface waters in August in response to a decrease in epilimnetic predator density. However, some DVM persisted, fish periodically moving deeper even during daylight hours. Such behavior seems inconsistent with the hypothesis that predator avoidance is the sole driver of DVM in sockeye salmon.

Bevelhimer and Adams (1993) concluded, based on bioenergetic modeling, that DVM can be advantageous when kokanee and their prey are thermally segregated. Our investigation did not adequately assess the energetic benefits associated with observed migrations, our data neither adequately refuting nor entirely supporting the ecological advantage of increased bioenergetic efficiency through migrations. It is likely, however, to be only one of several factors influencing DVM at Blue Mesa Reservoir. The reverse migration behavior observed in August suggests that fish may not have exploited the energetic benefits associated with thermoregulation through migrations. This behavior diverges from other sockeye salmon systems with shallow water predators and may be attributed to the thermal refuge in Blue Mesa Reservoir that reduces seasonal overlap with predators. In Washington State's Lake Ozette (Beauchamp et al. 1995) and Lake Washington (Beauchamp et al. 1999) sockeye salmon were limited to feeding primarily during crepuscular periods to avoid spatial overlap with their primary predators, cutthroat trout and northern pikeminnow. This behavior was also observed in Lake Kulik and Lake Nerka in Alaska, particularly in September when

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are scaled for each month. Time of day is the median transect time for a series of transects conducted at about 1 h before and after sunrise (0400–0730 hours), 1 h before and after sunset (1830–2100 hours), midday (1130–1400 hours), and night (2200–0030 hours).

density of predators, arctic char *Salvelinus alpinus* and Dolly Varden *Salvelinus malma*, increased (Scheuerell and Schindler 2003).

In any system, including Blue Mesa Reservoir, DVM is likely to be the product of the combined effects of predator avoidance and energetics considerations. However, the relative importance of these drivers changes seasonally and from system to system (Bevelhimer and Adams 1993; Beauchamp et al. 1997; Stockwell and Johnson 1999). The changes in age-0 kokanee distribution in Blue Mesa Reservoir from deep DVM in May to shallow DVM in August suggest that age-0 kokanee (1) were not using DVM to maximize energetic efficiency but primarily to avoid predators, and (2) were responding to seasonal changes in their predator environment. Although more analysis of the energetics of DVM by age-0 kokanee in warm, productive systems such as Blue Mesa Reservoir is necessary, our observations point to the need to include predator avoidance in a robust model for sockeye salmon DVM behavior applicable over a range of systems exhibiting different thermal, food, light, and predator conditions.

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