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Diel Vertical Migration and Feeding of Underyearling Bear Lake Sculpin Cottus extensus (Pisces, Cottidae)

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THE DIEL VERTICAL MIGRATION AND FEEDING OF UNDERYEARLING BEAR LAKE SCULPIN *Cottus extensus* (PISCES, COTTIDAE)

by

Darcy Neverman

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Others I am indebted to are Steve Shope, Georg Blommer and Terry Shrader for their dedicated field and lab work. And, without the assistance of many fellow students the field work would never have been completed - my thanks to them.

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Darcy Neverman

TABLE OF CONTENTS

LIST OF TABLES

Table | Page

LIST OF FIGURES

ABSTRACT

Diel Vertical Migration and Feeding of Underyearling Bear Lake Sculpin Cottus extensus (Pisces, Cottidae).

by

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Utah State University, 1988

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Underyearling Bear Lake sculpin exhibit a diel pattern of vertical migration throughout the pelagic region of Bear Lake (Utah-Idaho) until they are approximately 22 mm standard length. Individuals move from the bottom of the lake (5° C) during the day into the water column (13 - 16° C) at night. The migration, however, is not related to feeding. Although the dominant copepod in the water column, Epischura nevadensis, do undergo a similar diel vertical migration, stomach analysis of juvenile sculpin captured by trawling shows that they do not feed in the water column. Instead, from July through October, their diet is dominated (70-93%) by benthic copepods and ostracods. Also, gut fullness of sculpin increases through the daylight period and decreases through the night, reaching minimum levels just before the dawn descent. Furthermore, feeding trials conducted in the laboratory show that juvenile sculpin feed most efficiently at light intensities found on the bottom (30- 60m) of Bear Lake during the day. Feeding rate coefficients increase markedly from

10^{13} photons·m^{-2}·s^{-1} until peaking at intermediate intensities of 10^{16} photons·m^{-2}·s^{-1} and then decline at higher light levels. Although they do not migrate to feed, the movement into the warmer water appears to increase the sculpin's digestion rate, thereby allowing continued feeding during the day. This supports the hypothesis that diel vertical migration in Bear Lake sculpin is a thermoregulatory strategy that increases growth rate.

(75 pages)

INTRODUCTION AND LITERATURE REVIEW

Many aquatic invertebrates and fish inhabit shallow strata of lakes and oceans at night but migrate to deeper layers for the day (e.g., Bainbridge 1961; Hutchinson 1967; Northcote 1967). These diel vertical migrations appear to be initiated by changes in light intensity (Blaxter 1974). However, the adaptive significance of this behavior has not been determined for many organisms.

Three hypotheses commonly suggested to explain this behavior in fish and zooplankton address the role diel vertical migration plays in an organism's foraging strategy:

(1) Predation risk. Animals migrate into food-rich surface layers at night to feed when risks of predation are low and retreat to deeper, darker strata during the day to avoid predators. This hypothesis has received considerable support from researchers interested in zooplankton migrations (Zaret and Suffern 1976; Wright et al. 1980; Stich and Lampert 1981; Gliwicz 1986) and has been suggested as a mechanism controlling fish migrations (Eggers 1978; Clark and Levy 1988).

(2) Bioenergetic hypothesis. McLaren (1963) and later Brett (1971) suggested that migrating animals, under food-limited conditions, may conserve energy by reducing their metabolic rates when they descend to the cold hypolimnion. Tests of this hypothesis, however, have been unsupportive (Lock and McLaren 1970; Swift 1976) or only partially supportive (Enright and Honegger 1977; Biette and Geen 1980).

(3) Prey tracking. A third hypothesis for diel vertical

migration is that predators are simply tracking the migrations of their prey. Begg (1976) and Janssen and Brandt (1979) provided evidence that some fish may migrate for this reason.

Many marine fish larvae exhibit diel vertical migrations, but relatively little work has been done to determine the adaptive value of these movements (Table 1). This is also the case for freshwater fish, for which only a few examples have been documented. Juvenile sockeye salmon begin diel vertical migrations one to two months after hatching (McDonald 1969). Vendace larvae (Coregonus albula), as well as young-of-the-year and adults, undergo diel vertical migrations in thermally stratified lakes in southern Sweden (Hamrin 1986). Larvae and adults of the dwarf pelagic sculpin (Cottus sp.) in Lake Washington also migrate, residing near the bottom (35 - 47m) during the day and nearer the surface (5 - 27m) at night (Ikusemiju 1967, 1975). Another cottid larva, Cottus asper, also shows a similar diel periodicity in two British Columbia lakes (Sinclair 1968).

I report on the diel vertical migration of another underyearling cottid (0^+ age class), the Bear Lake sculpin (Cottus extensus), an endemic species to Bear Lake. The sculpin are among the most abundant fish in the lake (W. Wurtsbaugh, Utah State University, pers. comm.) and are an important forage item for cutthroat trout (Salmo clarki) and lake trout (Salvalinus namaycush) (Nielson 1981).

Despite its importance, little is known about the life history of this species. It is known that adult sculpin spawn in rocky littoral

Table 1. Marine fish larvae known to undergo diel vertical migrations, and hypothesized reasons for their adaptive significance.

Specific name	Hypothesized adaptive significance tested*	Source
Engraulis mordax	SR	Brewer and Kleppel (1986)
Clupea harengus harengus	PT	Fortier and Leggett (1983)
Mallotus villosus	PT	Fortier and Leggett (1983)
Pomatomus saltatrix	-	Kendall and Naplin (1981)
Merluccius bilinearis	-	Kendall and Naplin (1981)
Citharichthys arctifrons	-	Kendall and Naplin (1981)
Peprilus triacanthus	-	Kendall and Naplin (1981)
Hippoglossina oblonga	-	Kendall and Naplin (1981)
Urophycis spp.	-	Kendall and Naplin (1981)
Auxis sp.	-	Kendall and Naplin (1981)
Etropus microstomus	-	Kendall and Naplin (1981)
Gilbertidia sigalutes	F, SR	Marliave (1986)
Limanda ferruginea	D*	Smith et al. (1977)
Clupea harengus	-	Seliverstov (1974)

SR = near shore retention, D = dispersal, PT = prey tracking, F = feeding.

regions and that the eggs hatch in May or early June. Also, the larval and underyearling stages of this fish are known to be pelagic for a portion of the day and are suspected to undergo a diel vertical migration.

The first objective of my study was to confirm and describe the diel vertical migration of underyearling Bear Lake sculpin. Then, I tested two of the previously mentioned hypotheses. First, is the diel vertical migration a foraging strategy in which the fish move into the water column at night to feed? If so, is feeding ability impaired at low light intensities? Secondly, if the movement is part of a foraging strategy, are the sculpin following a vertically migrating prey species? Finally, the research provides additional life history information on this little-studied species.

STUDY AREA AND METHODS

Bear Lake (Utah-Idaho) is a large, oligotrophic, tilt-block lake (Fig. 1). Marl substrates dominate the deeper portion of the lake, where my sampling was done. The precipitous eastern shore is rocky, whereas the western shore grades gradually from rock and sand in shallow water to marl sediments at a depth of about 23 m (Smart 1958). The lake is thermally stratified during the summer, with surface temperatures of 20-21°C and bottom temperatures of 4-5°C. Oxygen levels in the hypolimnion are normally above 5 mg/L, except in the deepest portion of the lake (E. Moreno, Utah State Univ., pers. comm.). Zooplankton abundance is low, with maximum total densities of 5 to 15 crustaceans·L^{-1} occurring in the metalimnion (Lentz 1986). Additional limnological characteristics are shown in Appendix G.

Diel variations in the distribution of underyearling sculpin and zooplankton

Underyearling sculpin - Diel changes in the vertical distribution and feeding activity of larval sculpin were determined by trawling over 24-h periods on five dates in 1985: 1-2 July, 30-31 July, 14-15 August, 27-28 August and 16-17 September. On two dates (18-19 July and 25-26 October 1985) I collected samples near midday and midnight in lieu of the full 24-h data set. Larval sculpin were sampled from benthic and pelagic environments at the 40-m contour during all diel-sampling efforts.

A sampling run consisted of one 20-min bottom trawl and three,

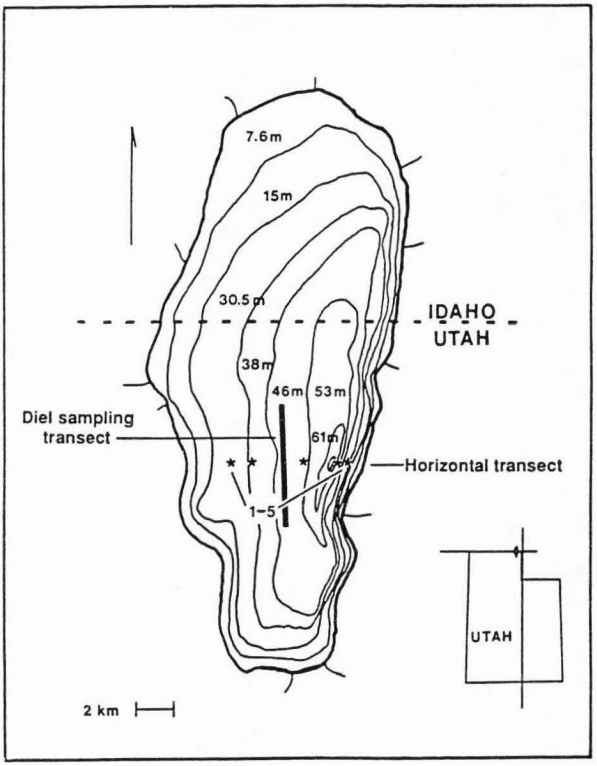

FIGURE 1: A bathymetric map of Bear Lake showing stations used to study diel vertical migration (diel sampling transect) and the horizontal distribution (Sta. 1-5) of underyearling Cottus extensus.

15-min mid-water trawls. One run was completed approximately every three hours. Fish were collected from the bottom with an otter trawl (2.9 m head rope, 3.6 m lead line, 0.6 cm height and 5.6 m length) pulled at ca. 1.0 m/s. The body of the trawl was constructed of 5.3-mm netting, and the final third was lined with 1.0-mm mesh net. Fish were collected from the water column with a 1 m^2 Tucker trawl (Hopkins et al. 1973) equipped with three, 1 mm^2 mesh nets that were opened and closed with a messenger-initiated release. Initially, each of the three nets was towed within one of three regions in the water column: epilimnion (2 - 9 m), metalimnion (9 - 20 m) and hypolimnion (20 - 30 m). To sample through a stratum (e.g., metalimnion) one net was pulled for 5 min at each of three depths (1-2 m apart) at a speed of approximately 1.5 m/s. After completing one strata, the sampling net was tripped, opening the next, and moved to the next strata (Fig. 2; Appendix A).

By mid-August, however, catches in all strata were declining; they were particularly low in the hypolimnion and epilimnion. Consequently, from late August on, all three open-water trawls were towed only in the metalimnion. In 1986 and 1987 additional metalimnetic Tucker trawling was done to determine how sculpin larvae were distributed in relation to temperature.

All fish captured during diel sampling efforts were anesthetized in MS-222 to prevent possible regurgitation of stomach contents and then preserved in 10% formaldehyde for subsequent measurements and gut analyses. Stomach contents of the preserved larvae were analyzed in the laboratory to determine their diet composition and feeding

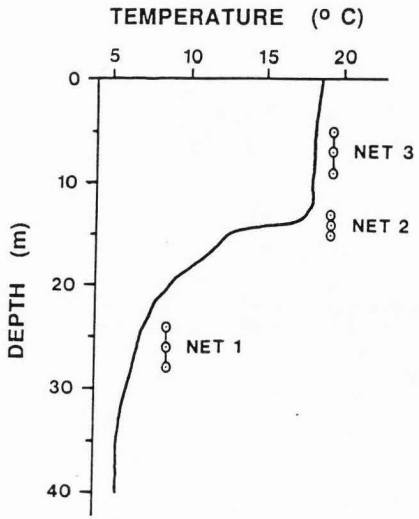

FIGURE 2: A mid-summer (14 August 1985) temperature profile from Bear Lake depicting where juvenile sculpin were sampled from the water column. Connected circles indicate the depths sampled by a single net of a Tucker trawl.

chronology. All prey items in the stomach were measured with an ocular micrometer, identified to the family level or lower, counted and weighed. The foregut contents from one subsample of ten fish or two subsamples of five fish from each trawl were pooled into one or two groups of pans, respectively. The food items were dried to a constant weight at 65°C (about 4 h) and weighed on a Cahn 29 microbalance to the nearest 0.5 μg.

I inferred the sculpin's feeding chronology from changes in gut fullness. Because stomach capacity increases with fish size, I expressed foregut weight as a percentage of fish weight. The diel cycle in stomach fullness was further standardized by dividing foregut weight from each time period by the maximum observed during the 24-h period.

The exact proportion of migrating versus nonmigrating fish could not be calculated because sampling efficiency of the otter trawl and the Tucker trawl differed. So, to help determine when the migration ceased I derived the following two indices.

$$A = \frac{\text{Daytime otter trawl CPUE}}{\text{Daytime + Nighttime otter trawl CPUE}}$$

$$B = \frac{\text{Nighttime Tucker trawl CPUE}}{\text{Nighttime Tucker CPUE + Nighttime otter trawl CPUE}}$$

(where CPUE = catch per unit effort)

Both indices are equal to 1.0 when no sculpin larvae are captured on the bottom at night (i.e., all 0^+ sculpin migrate into the water

column). A decrease in these indices indicates a decline in the percent of the population exhibiting diel vertical migration.

Each of the indices, however, is differentially sensitive to changes in CPUE. Index A is based only on changes in daytime versus nighttime otter trawl CPUE, whereas index B is based on the nighttime CPUE of otter and Tucker trawls. Daytime otter trawls captured many more fish than nighttime otter or Tucker trawls. Therefore, a large change in CPUE of nighttime otter trawls is necessary to be reflected by index A. Conversely, index B is very sensitive to a slight increase in the CPUE of nighttime otter trawls, a good indicator of cessation of diel vertical migration. Index B, however, is also sensitive to daily variability in Tucker trawl CPUE. Because Tucker trawl CPUE has high variability, it does not consistently reflect the status of the migratory behavior of the sculpin. Therefore, I felt that observing both indices was necessary to accurately assess the migratory status of the sculpin.

Zooplankton - I measured changes in zooplankton vertical distribution concurrently with diel sampling of larval sculpin. Duplicate daytime (1100 h - 1400 h) and nighttime (0130 h - 0330 h) samples were taken with a 50-L Schindler zooplankton trap (Redfield 1984). Eight discrete depths were sampled, two above, three in and three below the metalimnion. All crustacean zooplankton in each sample were counted.

Light and temperature profiles - Profiles of light and temperature were taken during each diel-sampling period. I measured intensity of photosynthetic active radiation (400 - 700 nm) from 0-

22 m between 1100 and 1400 h with a spherical collector of a Li-Cor 188B integrating radiometer. The vertical light extinction coefficients determined from these profiles were used to extrapolate intensities to the lake bottom under full sunlight and night sky conditions. The spectral composition and irradiance of full moonlight and starlight (Munz and McFarland 1977) were used to estimate light intensities in the water column at night.

Laboratory feeding trials

I investigated the effect different light levels have on the feeding rate of underyearling sculpin in the laboratory. A black, 40-L aquarium served as the experimental chamber. Fish were kept in 250-ml beakers inside this chamber. Water surrounding the beakers was kept at 10 - 11.5°C. Light intensity in the chamber was varied by screening a 40-w cool-white fluorescent bulb with 2 - 46 layers of window screens (Blaxter 1968, 1969; Dabrowski and Jewson 1984). The bulb was suspended 200 mm above the water's surface. At intensities below 6.0×10^{15} photons$\cdot m^{-2} \cdot s^{-2}$ (18 screens) I could not measure light levels, so I estimated it by extrapolating the relationship between screen number and light intensity.

Feeding trials were conducted with fish that had been captured by trawling and acclimated to laboratory conditions for a minimum of 15 days. I began experimental acclimatization by placing individual fish in 100 ml of lake water in a 250-ml beaker and holding them in the dark for 12 h at 6°C. Fish were measured by placing the beaker over a ruler and were then allowed to acclimate an additional 2 h under experimental conditions of light and temperature. I began each

experiment by adding 30 live Epischura nevadensis to each of seven beakers while lights were out. One control contained no fish. Lights were then turned on for a 15-min feeding period. The experiment was terminated by turning out the lights and immediately removing the fish with the aid of a low-intensity red light. I then killed and counted the remaining prey and determined the number eaten by difference. Instantaneous feeding rate coefficients (k) were calculated as:

$$k = \frac{-\ln(P_f / P_i)}{Xt}$$

Where: P_f = final number of prey in one beaker, P_i = initial number of prey (30), t = 0.25 h and X = number of predators$\cdot L^{-1}$ (Dodson 1975). This coefficient indicates the number of liters cleared of prey by a single fish in one hour. I performed this experiment one to six times at 15 light intensities, ranging from total darkness to the full intensity of the 40-w bulb diffused through two screens (3.5×10^{19} photons m^{-2} s^{-1}).

Horizontal variation in sculpin abundance

To see if underyearling sculpin displayed diel vertical migration throughout the pelagic zone I sampled the thermocline region at night on five dates and at five stations along an east-to-west transect across the lake (Fig. 1). I sampled each of the stations in a randomly selected order with the Tucker trawl. Replicates were obtained by sequential sampling with two nets pulled within the thermocline at each station in the same manner used for the diel sampling. Because they were not randomly assigned, these replicates

were actually "pseudoreplicates" (sensu Hurlbert 1984). If time allowed I took additional samples.

RESULTS

Diel vertical distribution of Bear Lake sculpin

Underyearling sculpin exhibited a pronounced diel vertical migration. This was confirmed by their absence in the bottom trawls at night, coupled with their appearance in the pelagic zone at this time (Fig. 3; Appendix B). They also exhibited this behavior in the laboratory, commonly swimming to the surface of their aquaria when it was dark. Fine-scale Tucker trawling indicated that fish in the metalimnion concentrated at temperatures between 13 and 16°C (Fig. 4).

There were significant differences in day vs. night CPUE of 0^+ sculpin for both Tucker trawls ($p < 0.0005$; RANDTEST, Green 1977) and otter trawls ($p < 0.0005$; RANDTEST). But, because night length changed from July to October (7 to 9.2 h), the migration pattern was not accurately represented by plotting pooled CPUE over time of day. Consequently, I standardized the night length by dividing the total hours in each night by 5. One of these segments (e.g., 1.2 h) served as the base unit of time for each corresponding day and allowed for an accurate presentation of data from all five diel-sampling periods (Fig. 3).

Diel vertical migration of the 0^+ sculpin persisted throughout the study (June - October), but by late summer only a small proportion of the juvenile fish were migrating into the water column. This decline was reflected by a drop in both indices of migration (Fig. 5).

As the proportion of migrating larval sculpin declined, the size of the migrators versus the non-migrators became distinctly different

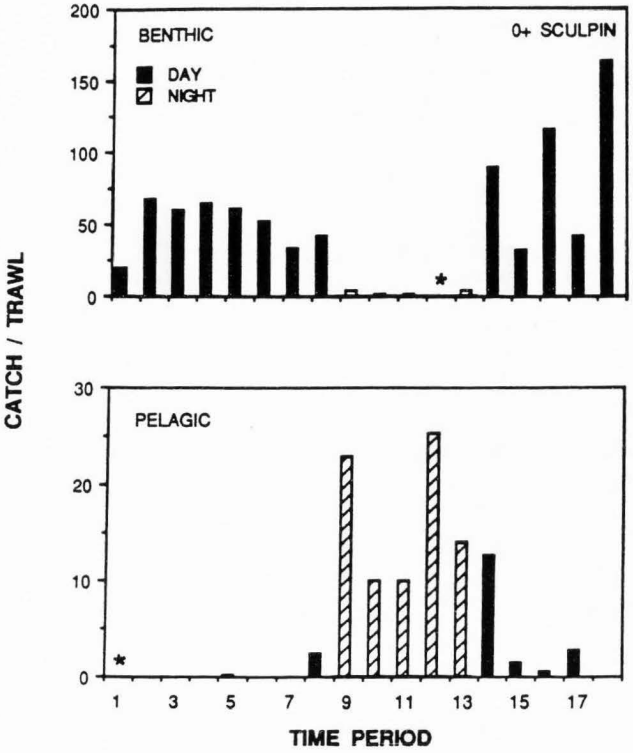

FIGURE 3: Relative abundance of 0^{+} Bear Lake sculpin over diel cycles captured in the benthic zone (top) or in the pelagic zone (below). Each day was divided into 18 standardized units of time to allow pooling of data (see text for explanation). * indicates that there were no trawls pulled during a time period.

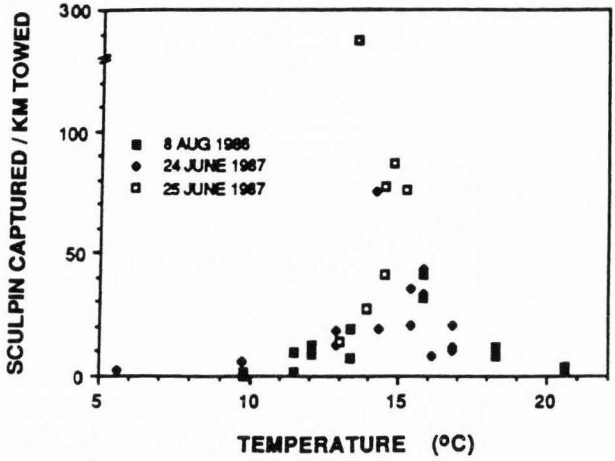

FIGURE 4: Nighttime catch of underyearling sculpin in the water column with respect to temperature. The fish were sampled with a $1m^2$ Tucker trawl between 2300 and 0500 hours.

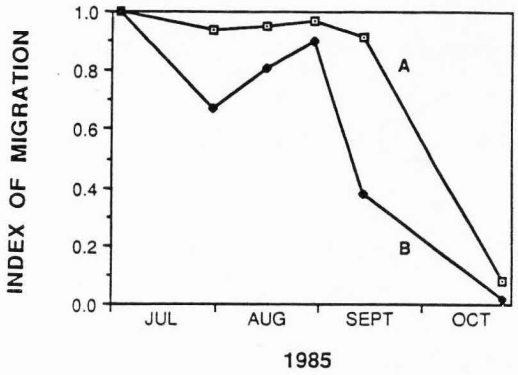

FIGURE 5: Indices of migration of underyearling Bear Lake sculpin throughout the study (see text for definitions). A relative increase in the number of juvenile sculpin captured on the bottom at night causes each index to decrease.

(Fig. 6). From June to August sample sizes of non-migrators were small and no consistent effect of fish size was noted. In September, however, underyearlings that moved into the water column at night were significantly smaller than those remaining on the bottom ($p < 0.0005$; RANDTEST). In October this difference was not significant ($p = 0.18$; RANDTEST), but statistical power was poor because only five fish were captured in the water column at night. The two largest fish that I captured in the water column were 22-mm standard length (SL).

Sculpin $\geq$ 1 year old did not migrate. The similarity in day vs. night otter trawl CPUE attests to this ($p = 0.3$; RANDTEST)(Fig.7). One exception was a migrating 22-mm SL fish captured on 1 July 1985.

Diet and feeding chronology

Juvenile sculpin fed on the bottom throughout the day but ceased feeding when they moved into the water column (Fig. 8). Gut fullness increased throughout the daylight hours and peaked during late twilight (Fig. 8; Appendix C). The sculpin's guts were often near bursting. Maximum fullness was usually found just before the juveniles left the bottom. Because the sampling intervals were too coarse, the maximum sometimes appeared in fish captured in the first nighttime Tucker trawls. Gut fullness decreased through the night with no addition of fresh prey items. This suggests that little or no feeding occurred in the water column. Feeding resumed and gut fullness increased when the larvae returned to the bottom in the morning.

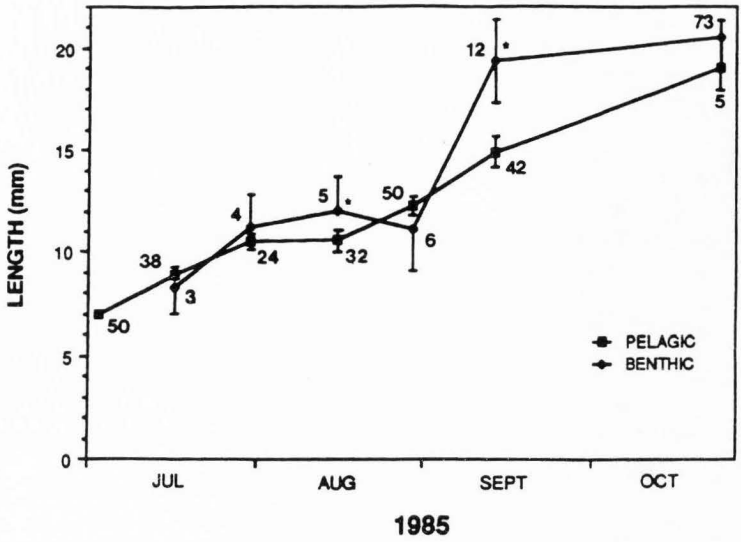

FIGURE 6: Standard lengths (X ± 95% CI) of underyearling sculpin captured at night in the pelagic and benthic zones of Bear Lake. Sample sizes are shown next to each point. * Indicates a significant size difference between the two groups ($p = 0.028$, 14 August; $p < 0.005$, 16 September).

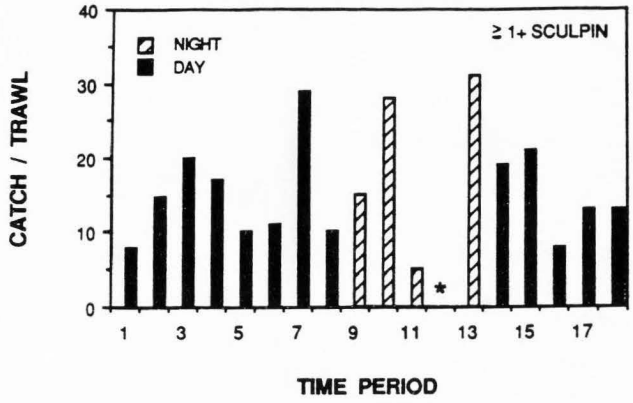

FIGURE 7: Mean catch per unit effort of 1^{+} Bear Lake sculpin captured in bentic trawls during 5 diel periods in 1985 (1-2 July; 30-31 July; 14-15 August; 27-28 August and 16-17 September). Each day was divided into 18 standardized units of time to allow pooling of data (see text for explanation). * indicates that there were no trawls pulled during a time period.

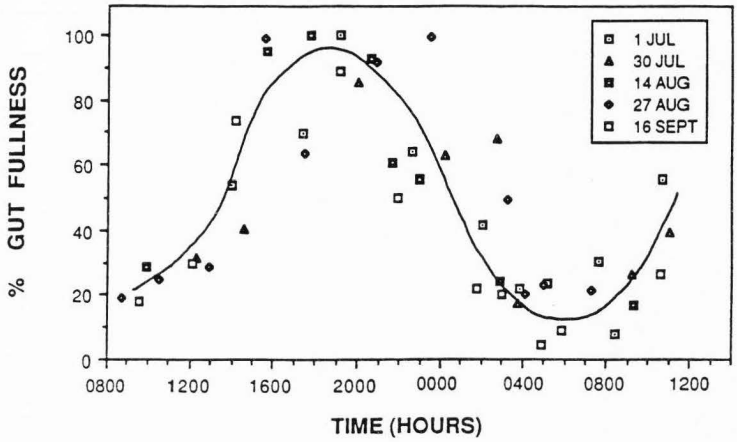

FIGURE 8: Gut fullness of underyearling sculpin over diel periods on five dates. Each point represents the mean percent fullness of 10 fish. Time is Mountain Daylight Savings Time. The curve is fitted by eye.

The diet composition of the juvenile sculpin also indicated that they fed primarily on the bottom. Epibenthic prey dominated the diet of larval sculpin (Fig. 9; Appendix C). From July through mid-August, cyclopoid copepods (Acanthocyclops vernalis) represented at least 40% of the diet. Although cyclopoid nauplii were captured in the water column, the copepodite and adult stages were only encountered in samples taken near the bottom (Appendix D). As the summer progressed, ostracods became increasingly important, representing 53% of the diet by weight in mid-August. Harpacticoid copepods were also eaten but formed an insignificant part of the diet (Appendix C). "Pelagic" prey (Epischura nevadiensis, Bosmina longirostris, Diaphanosoma sp. and Daphnia sp.), which could have been captured in either the pelagic or epibenthic environment, represented up to 4% of the diet.

Effect of light intensity on feeding

Nighttime light intensities in the lake were too low for larval sculpin to feed. Sculpin feeding rates peaked at intermediate irradiances similar to those found on the bottom during the day (Fig. 10 and 11; Appendix E). From complete darkness to approximately 6 x 10^{16} photons$\cdot m^{-2} \cdot s^{-1}$ the feeding rate coefficient (FRC) increased exponentially. Beyond this light level, FRC decreased linearly with increasing intensity ($p < 0.05$).

Horizontal variation in the distribution of larval sculpin

Underyearling sculpin underwent diel vertical migrations at all stations along the horizontal transect (Fig. 12), but there were spatial and temporal differences in the relative abundances of the

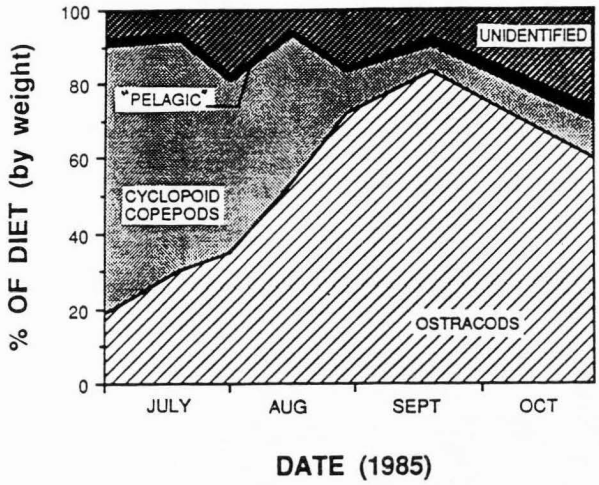

FIGURE 9: Temporal changes in the diet of underyearling Bear Lake sculpin from July 1 - October 1985. Fifty fish were sampled on each date except in October when only 30 fish were used. "Pelagic" indicates crustacean prey that could have been eaten in either the pelagic or benthic regions. "Unidentified" material was too digested for accurate taxonomic classification.

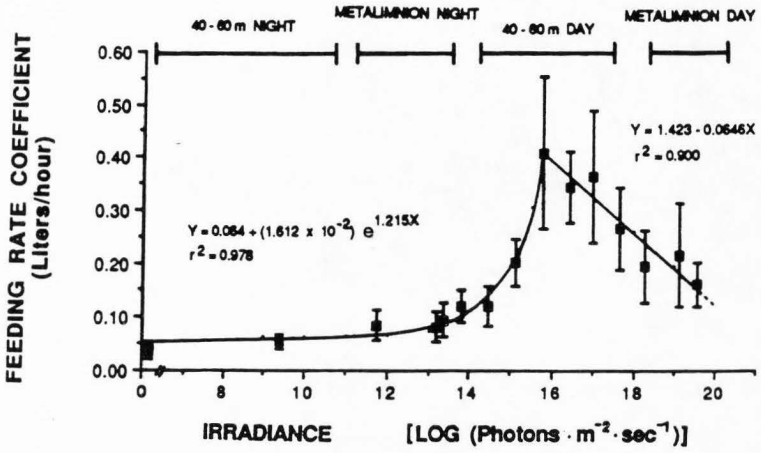

FIGURE 10: Feeding rate coefficients (X ± 95% CI) of juvenile sculpin in relation to light intensity. The least squares equations were fitted to the ascending and descending portions of the curve. The bars at the top of the figure indicate approximate light intensities throughout the day in different strata of the lake (See Fig. 11).

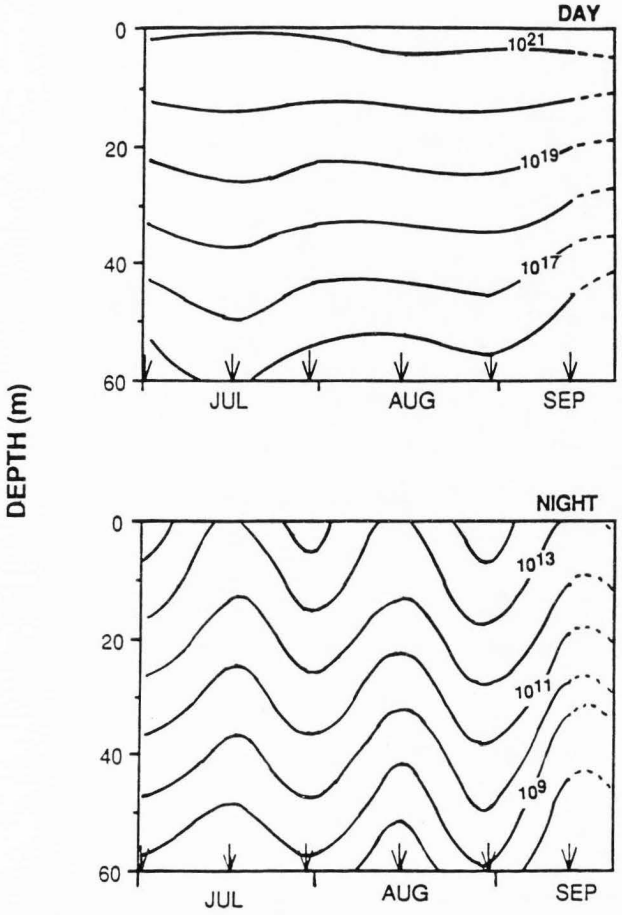

FIGURE 11: Isopleths of light intensity (photons·m^{-2}·sec^{-1}) in Bear Lake during the day and night through the summer of 1985. The cyclic changes in light intensities at night were caused by the lunar cycle. Arrows indicate dates when light penetration was measured.

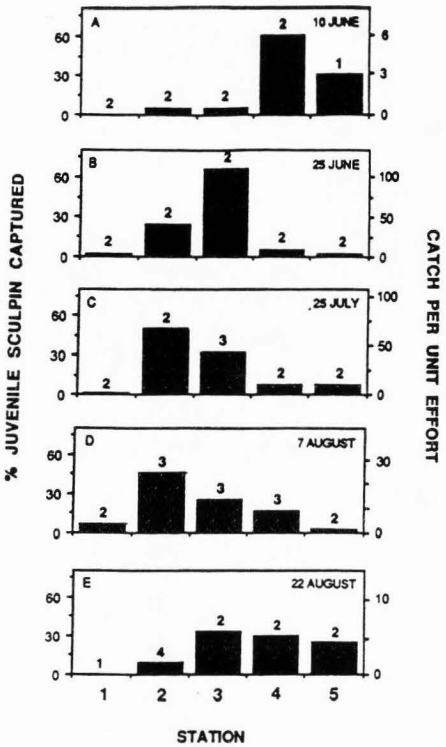

FIGURE 12 (A - E): The horizontal distribution of juvenile sculpin in Bear Lake along a west (station 1) to east (station 5) transect (see Fig. 1 for locations of stations). The number of Tucker trawls towed at each station is indicated above each bar. Mean CPUE (no./km) as well as the relative catch at each station is shown.

fish. In early June the 0^+ sculpin were more concentrated near the east shore of Bear Lake (Fig. 12 A). From late June on they appeared to disperse into offshore areas (Fig. 12 B-E).

Catches of sculpin juveniles in the water column at the westernmost and shallowest station (#1), however, were consistently low. Subsequent sampling with a bottom trawl in the littoral zone of the west shore (2 - 5 m) showed that the 0^+ sculpin there were abundant and that they did not migrate into the water column (W. Wurtsbaugh, personal communication). This may have been the case at station 1.

Another factor, which may have accounted for much of the variation in abundance between stations, was the presence of seiches. Although seiches, per se, have not been measured in Bear Lake, daily east-west variations in the thickness of the epilimnion of up to 8m, and commonly 2m, were measured subsequent to my study (E. Moreno, personal communication). Because all stations were sampled at a fixed depth, rather than at a fixed temperature, trawls at some stations may have missed the strata where the fish were concentrated. Consequently, the differences in CPUE may have reflected temperature differences instead of actual density differences between the stations.

Zooplankton vertical migration

Of the abundant crustacean zooplankton, only the copepod Epischura nevadensis exhibited a diel vertical migration similar to the sculpin's. However, only the larger instars migrated. Fifth and sixth instars were most concentrated near the bottom during the day and appeared to move to just below the thermocline at night for each

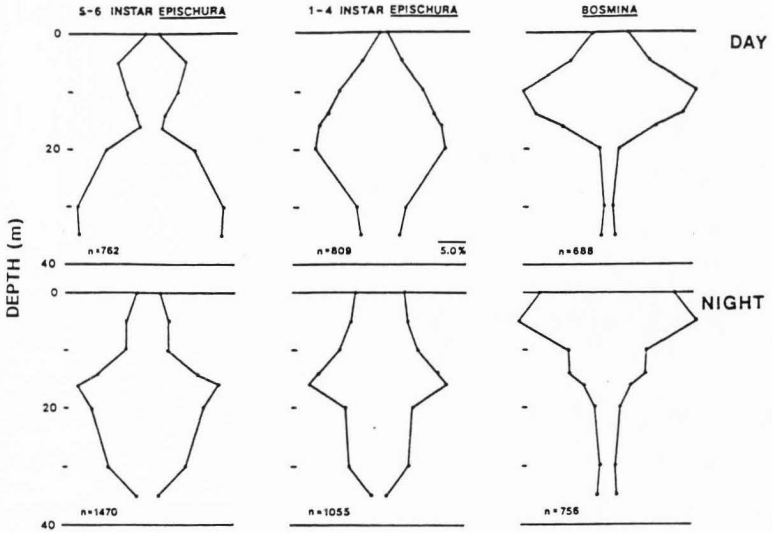

FIGURE 13: Vertical distribution of the dominant crustacean zooplankton in Bear Lake during the day (above) and night (below) on 14-15 August 1985. Values represent the percent captured at each depth. n = total number captured throughout the water column.

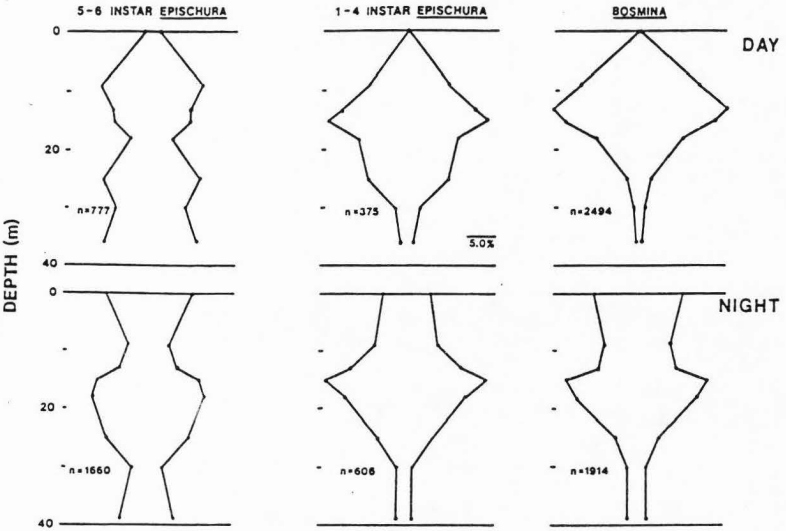

FIGURE 14: Vertical distribution of the dominant crustacean zooplankton in Bear Lake during the day (above) and night (below) on 27-28 August 1985. Values represent the percent captured at each depth. n = total number captured throughout the water column.

of two days (Figs. 13 and 14). Bosmina longirostris also exhibited a slight diel vertical migration by avoiding the surface (0 - 5 m) during the day and moving up at night (Figs. 13 and 14).

DISCUSSION

Although my results document diel vertical migration of sculpin, they were inconclusive as to the adaptive significance of this movement. Three observations refuted the hypothesis that underyearling sculpin migrate into the water column to feed. First, stomach fullness reached a peak before the fish ascended. Second, benthic prey (ostracods and benthic copepods) comprised from 70 to 93% of the gut contents (by weight). A maximum of 4.0% of their diet consisted of potentially pelagic prey items. Thirdly, the laboratory experiments demonstrated that juvenile sculpin fed visually, and that light intensities in the water column at night were inadequate for significant feeding activity (Fig. 11).

The visual daytime feeding exhibited by Bear Lake sculpin contrasts with the nighttime feeding of C. bairdi in Lake Michigan (Hoekstra and Janssen 1985). Cottus bairdi apparently uses non-visual sensory mechanisms to feed. Bear Lake sculpin clearly feed visually, as consumption rates increase rapidly with increases in light intensity up to intermediate levels of 10^{16} photons$\cdot m^{-2} \cdot s^{-1}$. The decline in feeding rates at still higher intensities is unusual and has not been reported for other fishes. The reason for the decline at high light levels is not clear.

The low feeding rates predicted at nighttime light levels would be further reduced by the very low densities of prey present in the water column. With a mean density of 5 crustacean prey$\cdot L^{-1}$ (Fig. 13 & 14) and a predicted FRC of 0.08 at nighttime metalimnetic light intensities (Fig. 11), I estimated that sculpin would only consume 0.4

prey·h^{-1}. Therefore, if sculpin fed in the water column for 8 h at night they would be able to consume only a small fraction of what they ate during the day on the bottom.

The hypothesis that the sculpin were tracking migrating prey was refuted by the field results. Although the migration of the late instar of the copepod E. nevadensis was synchronous with those of the underyearling sculpin (cf Fig. 3, 13 and 14), these copepods represented only 0.4 - 4.0% of the sculpin's diet and were not fed on by the juvenile sculpin at night.

Contradictory to my results, Lentz (1986) concludes that E. nevadensis does not undergo diel vertical migrations. He does not, however, differentiate early and late instar copepods, and this may confound his results (Zaret and Suffern 1976).

Overall, my results do not support the feeding hypothesis. This contrasts with current hypotheses on the adaptive significance of diel vertical migration that overwhelmingly cite foraging in food-rich surface waters as the driving mechanism behind these movements (Bainbridge 1961; McLaren 1963; Swift 1976; Zaret and Suffern 1976; Enright and Honegger 1977; Stich and Lampert 1981; Gliwicz 1986). Some other factor must therefore be responsible for the pattern observed in Bear Lake.

One possibility involves an energetic consequence of diel movement. By migrating into the warmer water column, individuals incur an elevated digestive rate. This increase, by allowing migrators to digest an entire meal overnight (Fig. 8), may result in a considerable increase in food consumption the next day.

This idea is supported by data on other vertebrates. After feeding, many reptiles show an increase in preferred ambient temperature (Regal 1966, McGinnis and Moore 1969, Gatten 1974, Schall 1977, Witten and Heatwole 1978). Regal (1966) and Gatten (1974) concluded that several species of reptiles facilitate digestion and increase the rate at which they assimilate energy by increasing their body temperature. The diel inshore migration of the fish Tilapia rendalli also appears to be a thermoregulatory strategy that increases the rate of consumption, leading to an increase in growth (Caulton 1978). Results from an energetic model by Caulton (1978) show that these fish have the greatest growth potential when experiencing a diel temperature flux of 12°C and will not grow when held at a constant high or low temperature. The migration is particularly evident in immature T. rendalli, those individuals investing, proportionately, the most energy into growth. Juvenile sculpin probably also invest a large portion of their energy intake into growth.

If diel vertical migration is a thermoregulatory strategy that increases growth, migrating sculpin would be expected to grow faster that non-migrators. This is supported by laboratory data. Sculpin held in temperatures cycled between 5 and 15°C grew three times faster than those reared at 5°C (Wurtsbaugh and Neverman 1988; Appendix H). Furthermore, juvenile sculpin held at 15°C digested a meal in 8 h, whereas several days were required for gut evacuation at hypolimnetic temperatures of 5°C. These results lend support to the hypothesis that migration into warm metalimnetic water increases the growth rate of Bear Lake sculpin.

In contrast, other researchers working with aquatic organisms suggest that fish and zooplankton migrate to cooler waters after feeding to reduce routine metabolic costs (McLaren 1963; Brett 1971). This hypothesis, however, does not necessarily conflict with the one I propose for sculpin. At the high feeding rates observed in Bear Lake sculpin, growth may be limited by the rate at which food is digested, and hence, assimilated. Consequently, the increase in metabolic rate at higher temperatures may be beneficial. If, however, food is limiting, and the rate at which it is digested does not limit food intake, it might be more advantageous for organisms to save energy by reducing their metabolic rates in cold hypolimnetic water (Giguere and Dill 1980). Nevertheless, tests of this energy-saving hypothesis have either been unsupportive (Lock and McLaren 1970; Swift 1976; Orcutt and Porter 1983; Stich and Lampert 1984) or have been inconclusive (Biette and Geen 1980).

If migration benefits 0^+ Bear Lake sculpin by increasing their growth rate, why does migratory behavior cease at the end of the summer? Juvenile sculpin apparently do not migrate after reaching 22 mm SL (Fig. 6). Perhaps the cost of migrating begins to exceed the benefit of an increased consumption rate. To answer this, respirometry work needs to be done to determine the energetic cost of migration to juvenile Bear Lake sculpin.

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APPENDICES

Appendix A. *Bear Lake temperature data*

Table 2. Temperatures at different depths in Bear Lake during each diel sampling period. A Mark V thermistor was used to measure temperatures from 1 - 30 July. A Hydrolab thermistor was used on subsequent dates. The depths in each strata sampled with the Tucker trawl are indicated by: [1]epilimnion, [2]metalimnion, [3]hypolimnion.

	DATE (1985)						
Depth (m)	1 Jy	18 Jy	30 Jy	14 Au	27 Au	16 Sp	25 Oct
0	18.7	21.5	20.0	18.5	20.6	16.8	10.4
1	17.8	21.3	20.0	18.4	19.6	16.6	10.4
2	17.6	21.3	20.0	18.3	19.2	16.5	10.4
3	17.5	21.2	-[1]	18.3	-	-	-
4	-	21.2[1]	20.0[1]	18.1	18.9	-	10.2
5	17.4[1]	21.2	-[1]	18.1[1]	-	-	-
6	-	21.0[1]	19.9	18.0	18.6	16.4	10.2
7	16.9[1]	20.9	19.9	18.0[1]	-	-	-
8	-	20.6	19.9	18.0	18.3	-	10.1
9	16.0	19.1[2]	19.8[2]	18.0[1]	-	-	-
10	15.9	16.1	17.0[2]	17.8	18.0	16.3	10.2
11	15.3	15.7	15.4[2]	17.8	-	-	-
12	13.8[2]	14.0[2]	14.0	18.0	17.6	16.2	10.2
13	9.5[2]	12.1	-	17.6[2]	17.3	-	-
14	8.6[2]	11.1[2]	-	16.5[2]	16.9[2]	16.2	9.9
15	7.4	8.9	-	12.5[2]	15.5[2]	-	-
16	6.7	8.3	-	12.0	12.5	16.0	9.8

Table 2 cont.

Depth (m)	DATE (1985) 1 Jy	18 Jy	30 Jy	14 Au	27 Au	16 Sp	25 Oct
17	6.2	7.9	-	10.7	11.0[2]	15.6[2]	-
18	5.8	6.9	-	10.5	9.2	14.9[2]	9.8[2]
19	5.7	6.4	-	9.4	8.5	14.0	-
20	5.5	6.1	9.0[3]	8.7	8.0	12.3[3]	9.7
21	-	-	-	-	7.5	10.8	-
22	5.1	5.3	-	8.0	7.0	9.7	9.1[2]
23	-[3]	-	-	-	-	8.5	-
24	4.9	4.5	-[3]	7.1[3]	6.2	8.2	8.6
25	-	-[3]	-	-	-	7.9	7.4
26	4.6[3]	4.4	-	6.8[3]	5.5	7.5	7.0[2]
27	4.4	-	-	-	-	6.7	-
28	-	-[3]	-[3]	6.5[3]	5.5	6.4	6.5
29	-	-	-	-	-	-	5.9
30	4.1[3]	-	6.0	5.9	5.4	5.7	5.7
31	-	-[3]	-	-	-	-	-
32	4.1	-	-	5.7	5.0	-	5.7
34	4.1	3.6	-	5.7	5.0	4.8	5.4
36	4.1	3.6	-	5.5	5.1	5.0	5.3
38	4.1	3.6	-	5.5	5.1	5.8	5.1
39	-	-	5.8	-	-	-	-
40	4.3	4.1	-	5.7	5.3	5.7	5.1

Appendix B. *Diel catch data*

Table 3. Number of fish captured in Tucker trawls and otter trawls during diel sampling periods in 1985. Tucker trawls were towed at 1.5m/s and otter trawls were pulled at 1.0m/s. Strata: H = hypolimnion; M = metalimnion; E = epilimnion; B = bottom. Dur = duration of trawl in minutes. Times are given in Daylight Mountain Time (July - September) and as Mountain Standard Time (October).

Time(Dur)	Strata	YOY sculpin	1+ sculpin	YOY cisco	1+ cisco	Other
			TUCKER TRAWLS (1-2 JULY)			
1545 (16)	H	0	0	0	0	0
1602 (16)	M	0	0	0	0	0
1627 (16)	E	1	0	0	0	0
1917 (15)	M	0	0	0	0	0
1940 (15)	E	0	0	0	0	0
2317 (18)	H	15	0	0	0	0
2335 (14)	M	6	0	0	0	0
2349 (15)	E	10	0	2	0	0
0235 (16)	H	27	0	1	0	0
0251 (15)	M	167	0	0	0	0
0317 (31)	E,M	49	0	0	0	0
0405 (32)	M,E	50	0	0	0	0
0448 (15)	E	15	0	0	0	0
0515 (31)	H,M	44	0	5	0	0
0924 (17)	H	11	0	0	0	0
0942 (15)	M	0	0	0	0	0

Table 3. cont.

Time(Dur)	Strata	YOY sculpin	1+ sculpin	YOY cisco	1+ cisco	Other
1009 (31)	E,M	0	0	0	0	0
1054 (17)	H	0	0	0	0	0
1111 (16)	M	0	0	0	0	0
		OTTER TRAWLS (1-2 JULY)				
1459 (20)	B	53	0	10	0	0
1819 (20)	B	37	0	4	0	0
2008 (20)	B	178	6	6	0	WF 2
2230 (20)	B	0	2	1	0	0
0145 (20)	B	0	1	0	0	0
0608 (20)	B	267	15	3	0	WF 1
0839 (20)	B	229	13	20	3	0
1141 (20)	B	164	21	0	4	0
		TUCKER TRAWLS (30-31 JULY)				
1401 (28)	H,M	1	0	0	0	0
1447 (15)	M	0	0	0	0	0
1503 (15)	E	0	0	0	0	0
1641 (15)	H	0	0	0	0	0
1659 (15)	M	0	0	0	0	0
1727 (15)	E	0	0	0	0	0
1955 (17)	H	0	0	0	0	0
2012 (15)	M	0	0	0	0	0
2027 (16)	E	0	0	0	0	0
0109 (17)	H	6	0	1	0	0

Table 3. cont.

Time(Dur)	Strata	YOY sculpin	1+ sculpin	YOY cisco	1+ cisco	Other
0126 (16)	M	4	0	2	0	0
0142 (15)	E	0	0	0	0	0
0430 (17)	E	0	0	0	0	0
0448 (15)	M	9	0	1	0	0
0503 (23)	H	2	0	0	0	0
0901 (17)	M	0	0	0	0	0
0919 (18)	E	0	0	0	0	0
0938 (15)	H	0	0	0	1	0
1055 (17)	M	0	0	0	0	0
1113 (16)	H	0	0	0	0	0
1129 (15)	M	0	0	0	0	0
		OTTER TRAWLS (30-31 JULY)				
1317 (20)	B	114	12	7	1	0
1536 (20)	B	21	1	12	0	0
2101 (20)	B	10	4	0	3	0
0017 (20)	B	1	24	0	12	WF 2
0342 (20)	B	3	21	0	0	LT 1
1010 (20)	B	10	2	2	0	0
1203 (20)	B	89	4	14	0	0
		TUCKER TRAWLS (14-15 AUGUST)				
1156 (18)	H	0	0	0	0	0
1215 (16)	M	0	0	0	0	0

Table 3. cont.

Time(Dur)	Strata	YOY sculpin	1+ sculpin	YOY cisco	1+ cisco	Other
1231 (16)	E	0	0	0	0	0
1732 (16)	H	0	0	0	0	0
1749 (15)	M	0	0	0	0	0
1804 (15)	E	0	0	0	0	0
2113 (17)	H	1	0	0	0	0
2131 (15)	M	6	0	0	0	0
2147 (15)	E	3	0	0	0	0
2339 (17)	H	1	0	0	0	0
2357 (16)	M	9	0	0	0	0
0013 (15)	E	4	0	0	0	0
0344 (16)	H	2	0	0	0	0
0401 (16)	M	18	0	2	0	0
0417 (15)	E	2	0	0	0	0
0556 (16)	H	1	0	0	0	0
0513 (16)	M	2	0	1	0	0
0529 (15)	E	1	0	0	0	0
0914 (17)	H	0	0	0	0	0
0932 (16)	M	0	0	0	0	0
0948 (15)	E	0	0	0	0	0
		OTTER TRAWLS (14-15 AUGUST)				
1056 (20)	B	20	8	0	0	0
1639 (20)	B	61	10	0	0	0
1842 (20)	B	33	20	0	1	0

Table 3. cont.

Time (Dur)	Strata	YOY sculpin	1+ sculpin	YOY cisco	1+ cisco	Other
2241 (20)	B	2	13	1	12	0
0145 (20)	B	1	6	0	4	0
0458 (20)	B	2	0	0	1	0
0826 (20)	B	3	2	0	0	0
1017 (20)	B	36	22	4	0	0
		TUCKER TRAWLS (27-28 AUGUST)				
1025 (16)	M	0	0	0	0	0
1041 (16)	M	0	0	0	0	0
1057 (15)	M	0	0	0	0	0
1523 (15)	M	0	0	0	0	0
1538 (15)	M	0	0	0	0	0
1553 (16)	M	0	0	0	0	0
1714 (15)	M	0	0	0	0	0
1728 (15)	M	0	0	0	0	0
1743 (16)	M	0	0	0	0	0
2130 (21)	M	39	0	1	0	0
2152 (22)	M	34	0	2	0	0
2214 (21)	M	25	0	1	0	0
2351 (16)	M	39	0	2	0	WF 1
0057 (18)	M	11	0	0	0	0
0304 (15)	M	23	0	5	0	0
0318 (15)	M	3	0	0	0	0

Table 3. cont.

Time(Dur)	Strata	YOY sculpin	1+ sculpin	YOY cisco	1+ cisco	Other
0333 (15)	M	20	0	0	2	0
0449 (15)	M	4	0	6	3	0
0504 (15)	M	15	0	3	2	0
0519 (15)	M	22	0	0	0	0
0907 (15)	M	0	0	0	0	0
0922 (15)	M	0	0	2	0	0
0937 (15)	M	1	0	0	0	0
		OTTER TRAWLS (27-28 AUGUST)				
0941 (20)	B	21	16	1	1	0
1134 (20)	B	72	27	4	6	US 2
1352 (20)	B	134	25	3	0	0
1631 (20)	B	97	16	2	1	0
1825 (20)	B	35	29	1	0	0
2057 (20)	B	1	7	0	15	0
2315 (20)	B	2	32	0	7	C 1
0413 (20)	B	4	25	0	17	WF 3
0602 (20)	B	15	20	0	3	0
0816 (20)	B	32	21	8	0	0
		TUCKER TRAWLS (16-17 SEPTEMBER)				
1403 (15)	M	0	0	0	0	0
1419 (15)	M	0	0	0	0	0
1435 (15)	M	0	0	0	0	0

Table 3. cont.

Time(Dur)	Strata	YOY sculpin	1+ sculpin	YOY cisco	1+ cisco	Other
1650 (15)	M	0	0	0	0	0
1706 (15)	M	0	0	0	0	0
1721 (15)	M	0	0	0	0	0
2030 (22)	M	3	0	0	1	0
2053 (15)	M	0	0	0	0	0
2108 (15)	M	0	0	0	0	0
2236 (16)	M	6	0	1	0	0
2252 (16)	M	2	0	0	0	0
2308 (15)	M	9	0	0	0	0
0238 (16)	M	1	0	0	1	0
0254 (16)	M	2	0	1	1	0
0310 (15)	M	0	0	0	0	0
0342 (15)	E	4	0	0	0	0
0357 (16)	E	7	0	0	0	0
0413 (15)	E	3	0	0	0	0
0531 (15)	M	4	0	1	0	WF 1
0546 (15)	M	0	0	0	3	0
0601 (15)	M	4	0	0	2	0
0739 (15)	M	0	0	0	0	0
0754 (16)	M	0	0	0	0	0
0810 (15)	M	0	0	0	0	0
1214 (15)	M	0	0	0	0	0
1229 (15)	M	0	0	0	0	0

Table 3. cont.

Time(Dur)	Strata	YOY sculpin	1+ sculpin	YOY cisco	1+ cisco	Other
1244 (15)	M	0	0	0	0	0
		OTTER TRAWLS (16-17 SEPTEMBER)				
1023 (20)	B	48	20	0	2	0
1256 (20)	B	49	42	0	0	0
1555 (20)	B	25	9	1	2	0
1955 (20)	B	23	21	0	0	0
2143 (20)	B	8	29	0	3	0
0158 (20)	B	4	7	0	8	0
0449 (20)	B	3	47	3	0	0
0643 (20)	B	92	22	0	5	0
1125 (20)	B	82	16	0	0	WF 1
		TUCKER TRAWLS (25-26 OCTOBER)				
2042 (15)	M	0	0	0	0	0
2304 (15)	M	0	0	0	0	0
2335 (15)	M	0	0	0	0	0
0247 (16)	M	1	0	0	0	0
0303 (16)	M	1	0	1	0	0
0320 (15)	M	0	0	0	0	0
0509 (19)	M	0	0	1	0	0
0528 (21)	M	1	0	0	0	0
0549 (15)	M	2	0	1	0	0
1301 (16)	M	0	0	0	0	0

Table 3. cont.

Time(Dur)	Strata	YOY sculpin	1+ sculpin	YOY cisco	1+ cisco	Other
1317 (16)	M	0	0	0	0	0
1333 (15)	M	0	0	0	0	0
		OTTER TRAWLS (25-26 OCTOBER)				
0020 (20)	B	38	54	0	0	0
0408 (20)	B	41	3	0	14	0
1405 (20)	B	2	10	5	1	0
1608 (20)	B	5	7	1	0	0

[1]1-2 July, Tucker trawl velocity = 1.25 m/s.
WF = whitefish, LT = lake trout, US = Utah sucker, C = carp.

Appendix C. *Stomach analysis data*

Table 4. Number and dry weight (mg) of food items in juvenile sculpin stomachs. n = number of fish in sample, SL = mean standard length, OST = ostracods, CYC = Cyclops sp. HARP = harpactacoid copepods, EPI=Epischura sp., CLAD = misc. cladocerans. ND = no data.

TIME (hrs)	n	SL	Ostracods No/wt	CYC No/wt	HARP[1]	EPI	CLAD & OTHER	TOTL[2] WT
				TUCKER TRAWLS (1-2 JULY)				
1627	1	6.8	0	0	0	0	0	0
2317	10	7.0	4/ 0.0159	28/ 0.0744	0	1[1]	0	0.0903
2335	6	6.6	0/ 0	21/ 0.0742	0	0	0	0.0866
2349	10	7.2	4/ 0.0359	39/ 0.1433	1	0	0	0.1915
0235	10	7.2	8/ 0.0544	15/ 0.0292	0	0	0	0.0878
0251	10	6.9	5/ 0.0516	10/ 0.0264	0	0	0	0.0808
0317	10	7.0	2/ 0.0399	18/ 0.0478	0	0	0	0.0973
0405	10	7.1	3/ 0.0122	14/ 0.0370	0	1[1]	0	0.0671
0448	10	7.4	4/ 0.0025	7/ 0.0152	0	0	0	0.0217
0515	10	7.2	4/ 0.0310	10/ 0.0252	0	0	0	0.0632
0924	10	7.1	0/ 0	9/ 0.0175	0	0	0	0.0175

Table 4. cont.

TIME (hrs)	n	SL	Ostracods No/wt	CYC No/wt	HARP[1]	EPI	CLAD & OTHER	TOTL[2] WT
			OTTER TRAWLS (1-2 JULY)					
1459	10	7.5	1/ 0.0095	34/ 0.1249	1	3[1]	0	0.1468
1819	10	7.4	10/ 0.0855	23/ 0.0903	1	0	0	0.1815
2008	10	7.6	7/ 0.0331	71/ 0.2398	0	1[1]	0	0.2870
0608	10	7.3	3/ 0.0280	9/ 0.0259	0	0	0	0.0585
0839	10	7.5	2/ 0.0252	16/ 0.0547	0	0	0	0.0824
1141	10	7.3	1/ 0.0024	39/ 0.1252	0	0	0	0.1377
			TUCKER TRAWLS (30-31 JULY)					
1401	1	8.0	0	0	0	0	0	0
0109	5	10.2	5/ 0.0528	67/ 0.2730	1	0	1[3]	0.3606
0126	5[4]	10.3	14/ 0.1389	38/ 0.1783	0	1[1]	0	0.3604
0430	3	10.0	3/ 0.0161	10/ 0.0229	0	0	0	0.0446
0448	5	10.8	5/ 0.1131	0	0	0	0	0.1478
0448	5[4]	10.7	4/ 0.0953	7/ 0.0153	0	0	0	0.1106
			OTTER TRAWLS (30-31 JULY)					
1317	5	11.3	4/ 0.0493	41/ 0.1499	0	0	0	0.2203

Table 4. cont.

TIME (hrs)	n	SL	Ostracods No/wt	CYC No/wt	HARP[1]	EPI	CLAD & OTHER	TOTL[2] WT
1317	5	10.4	8/ 0.0575	35/ 0.1468	0	0	0	0.2171
1536	5	10.1	4/ 0.0242	48/ 0.1924	0	1[1]	0	0.2610
1536	5	11.4	4/ 0.0173	54/ 0.2295	0	0	2[3]	0.2833
2101	5	10.8	24/ 0.1966	42/ 0.2648	0	2[1]	1[3]	0.6958
2101	5	11.8	31/ 0.4037	34/ 0.1762	0	0	1/ ND	0.6873
0017	1	10.5	3/ ND	10/ ND	0	0	0	ND
0342	3	11.5	14/ 0.2145	37/ 0.1450	0	0	0	0.3595
1010	5	11.0	5/ 0.0463	29/ 0.1375	0	0	0	0.2042
1010	5	10.7	5/ 0.0694	20/ 0.0902	0	0	0	0.1679
1203	5	10.4	3/ 0.0521	27/ 0.1366	0	0	2[3]	0.2112
1203	5	10.0	1/ 0.0173	35/ 0.1612	1	0	1/ .032	0.2255
			TUCKER TRAWLS (14-15 AUGUST)					
2131	7[4]	10.9	35/ 0.3730	134/ 0.6322	0	0	3/ ND	1.0828
2147	3	10.3	13/ 0.1762	33/ 0.1516	1	0	2/ ND	0.3431
2339	1	11.0	4/ 0.0377	3/ 0.0126	0	0	0	0.0503

Table 4. cont.

TIME (hrs)	n	SL	Ostracods No/wt	CYC No/wt	HARP[1]	EPI	CLAD & OTHER	TOTL[2] WT
2357	9	10.9	30/ 0.7519	42/ 0.1732	0	0	0	0.9367
0013	4	11.0	16/ 0.3048	30/ 0.1398	0	0	1/ ND	0.4772
0344	2	10.5	3/ 0.0571	3/ 0.0115	0	0	0	0.0686
0401	10	10.7	15/ 0.3186	2/ 0.0116	0	0	0	0.3468
0417	2	11.5	2	0	0	0	0	-
0613	4[4]	9.9	3/ 0.0382	1/ 0.0038	0	0	0	0.1050
			OTTER TRAWLS (14-15 AUGUST)					
1056	10	11.7	10/ 0.1331	62/ 0.3405	0	0	8	0.5984
1639	10	11.1	60/ 1.0111	100/ 0.5683	0	3[1]	2	1.6247
1842	10	10.9	44/ 0.6600	151/ 0.7864	0	2[1]	3	1.6002
2241	2	14.0	18/ 0.3135	28/ 0.1698	0	0	0	0.4940
0458	2	11.0	2	0	0	0	0	ND
0826	3	10.5	1	11	0	1	0	ND
1017	10	11.2	9/ 0.1251	28/ 0.1549	0	0	2	0.2979
			TUCKER TRAWLS (27-28 AUGUST)					
2130	10	13.3	102/ 2.4282	43/ 0.1892	0	4/ 0.0520	5[3]	3.8388
2152	10	12.1	84/ 1.6222	44/ 0.1870	2	4/ 0.0358	4[3]	2.0103

Table 4. cont.

TIME (hrs)	n	SL	Ostracods No/wt	CYC No/wt	HARP[1]	EPI	CLAD & OTHER	TOTL[2] WT
2214	10	12.9	99/ 2.5502	79/ 0.3728	5	9/ 0.0447	5/ ND	3.4343
2351	10	12.1	75/ ND	47/ 0.1452	0	3/ ND	3[3]	-
0015	10	11.3	63/ 1.7102	27/ 0.1196	1	2/ 0.009	5[3]	2.0831
0333	10	12.7	43/ 0.6732	45/ 0.1551	0	0	5/ ND	0.8788
0449	4	11.0	6/ 0.0717	10/ 0.0216	1	0	2/ ND	0.0984
0504	10	12.6	35/ 0.5464	15/ 0.0398	0	1[1]	0	0.6477
			OTTER TRAWLS (27-28 AUGUST)					
0941	10	13.4	22/ 0.6969	11/ 0.0558	0	0	1/ .039	0.7917
1134	10	13.0	16/ 0.3871	23/ 0.1311	0	0	3[1]	0.5182
1134	10	13.2	26/ 0.7235	28/ 0.2108	0	1[1]	2/ ND	1.1933
1352	10	13.0	34/ 0.8605	42/ 0.1490	0	0	1[3]	1.2545
1631	10	12.3	79/ 2.6527	56/ 0.2645	2	0	2/ ND	3.0978
1825	10 3.6828	13.5	71/ 2.0926	68/ 0.4825	0	2/ 0.057	9[3,5]	
2315	2	12.3	6/ 0.1182	4/ 0.0099	0	0	0	0.1303
0413	4	10.8	14/ 0.2398	30/ 0.1093	0	0	1/ ND	0.3631

Table 4. cont.

TIME (hrs)	n	SL	Ostracods No/wt	CYC No/wt	HARP[1]	EPI	CLAD & OTHER	TOTL[2] WT
0602	10	12.1	23/ 0.6030	5/ 0.0259	1	0	1/ ND	0.6289
0816	10	12.6	20/ 0.6173	15/ 0.0574	1	0	3[4,6]	0.7854
			TUCKER TRAWLS (16-17 SEPTEMBER)					
2030	3	13.0	25/ 0.3838	19/ 0.0670	0	1[2]	5/ ND	0.5487
2236	5	15.6	69/ 2.0880	32/ 0.0880	0	3/ 0.0333	2[7]	2.1909
2308	5[5]	15.7	57/ 1.6354	23/ 0.0945	0	0	3/ 0.0328	1.8613
2308	5	14.5	67/ 1.8185	7/ 0.0193	0	1/ 0.0018	0	1.9377
0254	3[5]	14.0	15/ 0.3487	1/ 0.0026	0	0	0	0.3802
0342	55	15.3	15/ 0.7667	0	0	0	0	0.7748
0357	5	15.3	9/ 0.4528	2/ 0.0072	1	0	3/ ND	0.4707
0357	4[5]	13.9	14/ 0.6121	0	0	0	0	0.6761
0531	5[5]	15.9	8/ 0.1878	0	0	0	0	0.2122
0601	3	16.2	0	0	0	0	0	0
			OTTER TRAWLS (16-17 SEPTEMBER)					
1023	5	15.3	24/ 0.6758	15/ 0.0674	1	2[2]	3/ ND	0.8191
1023	5	14.1	13/ 0.3477	17/ 0.0648	0	2[2]	3[4]	0.4805

Table 4. cont.

TIME (hrs)	n	SL	Ostracods No/wt	CYC No/wt	HARP[1]	EPI	CLAD & OTHER	TOTL[2] WT
1256	5	15.8	35/ 0.8976	46/ 0.1107	1	16/ 0.0871	13/ 0.0321	1.2255
1256	5	15.6	47/ 1.3042	25/ 0.0629	0	1[2]	2/ 0.0209	1.4458
1555	5	16.5	68/ 2.0947	67/ 0.2457	2	8/ 0.1667	8/ 0.0432	2.9072
1555	5	13.6	72/ 2.1581	30/ 0.1071	3	3/ 0.0232	7/ 0.0519	2.4505
1955	5	16.4	105/ 3.5564	62/ 0.1701	3	7/ 0.0385	9/ 0.0691	4.0529
1955	5	16.2	111/ 4.1362	92/ 0.3408	7	1/ 0.0079	7/ 0.0815	5.0275
2143	5	17.2	82/ 2.8294	26/ 0.0866	0	5/ 0.0257	2/ 0.0086	3.1886
0158	4	18.9	60/ 1.5271	4/ 0.0061	0	0	3/ ND	1.7968
0449	1	23.0	25/ 1.1144	2/ 0.0070	1	0	0	1.1813
0643	5	14.8	10/ 0.3978	7/ 0.0225	0	1/ 0.0017	1/ ND	0.4705
0643	5	15.3	5/ 0.1614	2/ 0.0009	0	0	0	0.1726
1125	5	14.6	29/ 0.7726	26/ 0.0615	0	3/ 0.0255	3[7]	0.8917
1125	5	15.6	39/ 1.0381	17/ 0.0552	0	2/ 0.0233	6[7]	1.1721
			TUCKER TRAWLS (25-26 OCTOBER)					
0247	2[5]	19.5	14/ 0.3552	9/ 0.0108	1	0	0	0.4374

Table 4. cont.

TIME (hrs)	n	SL	Ostracods No/wt	CYC No/wt	HARP[1]	EPI	CLAD & OTHER	TOTL[2] WT
0549	3[5]	18.7	15/ 0.4976	2/ 0.0089	0	0	0	0.6187
			OTTER TRAWLS (25-26 OCTOBER)					
0020	5	18.1	55/ 1.1535	102/ 0.2572	1 0.0640	4/	11[7]	2.0717
0020	5	19.3	55/ 1.3961	67/ 0.1888	0 0.0492	2/	5[7]	2.0483
0408	5	19.2	46/ 0.9975	65/ 0.1339	0	0 0.0373	4/	1.5652
0408	5	18.4	48/ 1.2836	72/ 0.1866	0	1[2] 0.0408	6/	2.1771
1608	5	18.3	65/ 1.0456	69/ 0.2984	18 0.2105	2/	20[7]	2.1954

[1]Weight included with cyclopoid copepods (CYC).
[2]The weight of unidentifiable organisms was included with the total.
[3]The weight of these organisms were included with the unidentifiable organisms.
[4]Gut contents of fish from a prior or subsequent trawl were added to increase the sample size.
[5]Two chironomids + miscellaneous cladocerans.
[6]Weight of these was combined with "EPI".

Appendix D. *Zooplankton vertical migration*

Table 5. Vertical distribution of crustacean zooplankton in the water column of Bear Lake during the day (1100hrs - 1400hrs) and night (0130hrs - 0330hrs). "AEpi" are V instar and adult Epischura nevadensis copepods. "BEpi" are I - IV instar copepidites of E. nevadensis. CD = Ceriodaphnia sp., C = Cyclops sp., D = Daphnia sp., O = ostracod, H = harpactacoid copepod. "No data" is represented by a "-".

Depth (m)	NUMBER/50 LITERS (day/night)						
	AEpi	BEpi	Epi Nauplii	Bosmina	Diaphan-osoma	Cyclopoid nauplii	Other
			1 - 2 JULY 1985				
0	9/505	1/15	3/83	0/7	0/0	0/0	0/0
0	83/389	0/36	19/201	0/1	0/0	0/0	0/0
5	215/470[1]	-	286/262	1/1	0/0	0/0	1D/0
5	115/264	46/88	342/331	1/1	0/0	0/0	0/0
10	254/49	58/13	107/65	5/1	0/0	0/0	0/0
10	210/195	47/35	74/93	1/2	0/0	0/0	0/0
12	269/263	34/23	85/79	0/0	0/0	0/0	0/0
12	197/241	24/39	106/80	3/1	0/0	0/0	0/0
17	205/128[1]	17/-	22/18	0/1	0/0	0/0	0/0
17	266/91	20/34	25/9	1/1	0/0	0/0	0/0
25	119/63	14/6	8/16	0/0	0/0	0/0	0/0
25	53/98	7/16	5/23	0/0	0/0	0/0	0/0
35	47/32	5/4	16/13	0/0	0/0	0/1	0/0
35	43/24	4/3	13/12	1/1	0/0	0/0	0/0
40	53/36	4/3	38/25	0/5	0/0	0/0	15C,1D/1C

Table 5. cont

Depth (m)	NUMBER/50 LITERS (day/night) AEpi	BEpi	Epi Nauplii	Bosmina	Diaphan-osoma	Cyclopoid nauplii	Other
40	6/22	1/0	5/30	0/0	0/0	0/0	2C/0
			14-15 AUGUST 1985				
0	25/35	7/62	10/22	9/126	0/10	0/0	0/1CD
0	8/81	11/115	2/54	74/230	1/22	2/0	0/0
5	82/111	58/84	37/47	60/243	46/31	0/0	0/0
5	110/113	50/121	26/66	130/228	64/26	0/0	0/0
10	57/111	119/148	96/59	231/137	61/	0/2	0/0
10	78/110	115/135	83/106	189/68	17/	0/0	0/0
14	34/252	162/207	182/288	170/97	30/2	0/4	0/6CD
14	37/274	139/225	163/380	186/101	7/1	1/6	0/2CD
16	29/429	205/297	408/297	125/42	6/8	0/0	0/2CD
16	32/307	138/206	325/269	100/83	5/6	3/1	0/1CD
20	137/261	216/100	192/88	25/26	5/1	4/0	0/0
20	109/322	144/140	174/131	21/42	8/2	1/0	1C/0
30	246/79	83/29	152/51	11/13	0/1	0/1	0/1C
30	154/340	58/185	219/142	13/27	2/3	2/1	1C/1C
35	181/57	56/19	1005/77	17/28	3/1	99/9	34C,26O,17H /0
35	204/57	56/36	1168/36	15/20	2/3	80/12	19C/0
			27 - 28 AUGUST 1985				
0	16/333	0/62	3/51	8/387	0/35	0/0	0/0
0	16/176	1/35	1/25	1/201	0/28	0/0	0/0
9	137/119	47/65	28/58	540/222	31/62	0/3	1CD/1CD

Table 5. cont.

Depth (m)	NUMBER/50 LITERS (day/night)						
	AEpi	BEpi	Epi Nauplii	Bosmina	Diaphan-osoma	Cyclopoid nauplii	Other
9	140/ -	53/ -	38/ -	503/ -	57/ -	5/ -	1CD/ -
13	89/157	69/124	54/109	876/363	38/33	18/3	1CD/0
13	125/177	101/106	156/174	640/158	27/29	10/9	1CD/0
15	99/298	100/168	133/197	659/468	16/35	13/14	2CD/3CD
15	111/ -	103/ -	- / -	661/ -	11/ -	9/ -	0/ -
18	38/301	56/137	239/233	352/414	3/5	11/3	0/1CD
18	73/359	71/108	216/123	407/388	3/6	22/0	1CD/1CD
25	138/242	65/55	254/222	97/148	2/5	1/0	0/1CD
25	128/ -	37/ -	254/ -	106/ -	0/ -	3/ -	0/0
30	101/72	15/11	80/44	44/53	2/3	1/2	1CD/0
30	89/105	15/19	84/48	44/68	0/9	2/4	0/0
36	125/161	8/17	165/82	27/60	0/3	35/3	2D,2C,7H/0
36	128/ -	8/ -	394/ -	23/ -	1/ -	131/-	1CD,1C,15H /0
			25 - 26 OCTOBER 1985				
0	176/ -	6/ -	2/ -	32/ -	2/ -	0/ -	0/ -
0	170/ -	3/ -	2/ -	52/ -	20 -	2/ -	0/ -
6	258/268	6/8	13/11	77/74	6/13	2/0	0/0
6	305/217	11/4	0/4	70/94	12/20	0/1	0/0
8	320/111	5/4	18/15	58/91	5/42	1/5	0/0
8	301/95	19/3	1/25	35/81	7/32	0/6	0/0
15	74/43	0/0	34/56	35/7	3/3	4/16	0/0
15	63/ -	1/ -	43/ -	26/ -	2/ -	14/ -	0/0

Table 5. cont.

Depth (m)	NUMBER/50 LITERS (day/night)						
	AEpi	BEpi	Epi Nauplii	Bosmina	Diaphan-osoma	Cyclopoid nauplii	Other
20	23/46	0/2	350/500	3/6	4/6	5/5	0/0
20	47/52	0/3	576/420	28/9	18/9	9/4	0/0
25	21/38	2/0	426/535	3/4	7/1	1/2	0/0
25	25/30	1/1	408/484	11/3	3/0	4/0	0/0
30	33/50	0/0	110/193	5/9	3/1	6/3	0/0
30	28/80	1/1	123/157	2/22	4/3	0/1	0/0
35	20/93[1]	2/ -	57/ -	2/ -	1/ -	5/53	1C/15C,5H
35	22/73[1]	1/ -	109/ -	7/ -	2/ -	7/54	0/6H

Appendix E. *Light attenuation data*

Table 6. Light attenuation (b) in Bear Lake expressed as a linear function ($C_2 = a + bC_1$). Where C_1 = depth in meters, and C_2 = ln(% light transmission).

Date (1985)	Depth Range (m)	Light Attenuation	r^2
1 July	0 - 11.5	$C_2 = 0.075 - 0.186C_1$	99.9
	11.5 - 27	$C_2 = 0.687 - 0.245C_1$	99.8
	0 - 27[a]	$C_2 = 0.274 - 0.225C_1$	99.6
18 July	0 - 12	$C_2 = 0.152 - 0.193C_1$	98.9
	12 - 27	$C_2 = 2.260 - 0.207C_1$	97.6
	0 - 27[a]	$C_2 = 0.152 - 0.193C_1$	98.9
30 July	0 - 17.5	$C_2 = -0.089 - 0.192C_1$	99.7
	17.5 - 27	$C_2 = 0.548 - 0.241C_1$	99.9
	0 - 17.5[a]	$C_2 = 0.138 - 1.220C_1$	99.5
14 Aug	0 - 19	$C_2 = 0.417 - 0.176C_1$	94.2
	19 - 26	$C_2 = 5.580 - 0.458C_1$	96.3
	0 - 26[a]	$C_2 = 0.856 - 0.240C_1$	92.8
27 Aug	0 - 21	$C_2 = 0.279 - 0.183C_1$	98.3
	21 - 26	$C_2 = 5.820 - 0.456C_1$	99.3
	0 - 26[a]	$C_2 = 0.530 - 0.220C_1$	95.8
16 Sept	0 - 18	$C_2 = 0.490 - 0.240C_1$	100.0
	18 - 27	$C_2 = 2.990 - 0.380C_1$	100.0
	0 - 27[a]	$C_2 = 0.739 - 0.275C_1$	98.7
25 Oct	0 - 26[a]	$C_2 = 0.281 - 0.262C_1$	99.9

[a]These equations were used to calculate light intensities at various depths for Figures 11 and 12.

Appendix F. *Sculpin growth*

Table 7. The mean standard length (SL), dry weight[1] and corresponding instantaneous daily growth rates (dry weight) of underyearling sculpin captured during 1985. Individuals were captured on the bottom during the day. Consequently, growth rates were indicative of the entire population (e.g. migratory and non-migratory.)

Date (1985)	Sample size	SL (mm)	Dry weight (mg)	Growth rate (%/day)
2 July	60	7.2	0.5	
				4.7
18 July	60	8.9	1.1	
				6.0
31 July	40	10.8	2.3	
				1.8
14 Aug	50	11.5	2.9	
				3.3
28 Aug	51	13.0	4.6	
				3.5
16 Sept	60	15.7	9.9	
				2.6
26 Oct	64	20.7	24.6	
Overall	-	-	-	3.3[2]

[1]weight was calculated from standard length using the regression: log(drywt) = -3.53 + 3.74(log SL), n = 30, r^2 = 0.987. Five fish from each date were taken from morning and early afternoon bottom trawls (excluding 18 July).

[2]From the following regression:
ln(drywt) = -0.55 + 0.033(day), n = 7, r^2 = 0.98.

Appendix G. *Limnological characteristics of Bear Lake*

Table 8. Limnological characteristics of Bear Lake.

Parameter	No. Samples	$\bar{X}$	Range	Year/mo.
Secchi Depth(m)	5	5.1	3.8 - 6.3	1985/Jul-Oct
Oxygen (mg/L)	70	8.1	3.8 - 12.2	1981/Apr-Dec[1]
pH	84	ND	8.4 - 8.8	1981/Apr-Dec[1]
Tot. Alkalinity (meq/L)	1.94	5.42	4.86 - 6.76	1981/Apr-Dec[1]
Chlorophyll *a* (mg/m^3)	24	0.92	.42 - 1.88[2]	1987/Jul-Sept
Max. Depth (m)	-	63	-	-
Mean Depth (m)	-	28	-	-
Surface area (km^2)	-	285	-	-
Altitude (m)	-	1807	-	-

ND = no data
[1]Data from Lamarra et al. (1983).
[2] Maximum concentrations are found in the metalimnion.

Appendix H. *Wurtsbaugh and Neverman (1988)*

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Post-feeding thermotaxis and daily vertical migration in a larval fish

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Many aquatic animals make daily vertical migrations, typically ascending into warm shallow strata for the night and descending to cooler, deeper layers of lakes or oceans for the day. Although some organisms may migrate to avoid predation[1-3] researchers have also suggested that daily migration is a thermoregulatory strategy allowing ectotherms to lower their metabolic rates in cold, deep waters, thus conserving energy[4,5]. Tests of this hypothesis, however, have been equivocal[6-8]. Here we suggest an alternative hypothesis: that fish ascend into warmer water after feeding to stimulate digestion, thereby allowing greater feeding and growth. We tested this hypothesis using the Bear Lake sculpin (*Cottus extensus*) which feeds on the bed of the lake during the day, and at night migrates into the water column where temperatures are 10 °C warmer. The warmer temperatures promoted digestion and allowed the fish to feed and grow three times faster than if they had remained in the cold hypolimnion. Thus, daily vertical migration in this species is an adaptation allowing them to exploit thermal gradients in their environment[9] to maximize energetic intake.

Our field study was conducted in Bear Lake, Utah-Idaho, USA (42°00′ N, 111°20′ W), a 520 km^2, oligotrophic system, with a maximum depth of 60 m. The lake is thermally stratified in the summer, with surface temperatures near 20 °C and bottom temperatures of 4–5 °C. We studied the movements of juvenile (6–30 mm standard length) sculpin during their first summer of life.

The juvenile fish had a pronounced daily vertical migration. During the daylight hours they were on the bottom where temperatures were 4–5 °C (Fig. 1*a*). At night, however, they moved into the water column, appearing at dusk and disappearing at dawn (Fig. 1*b*). When they moved into the water column the fish concentrated in the region of the thermocline (metalimnion) at temperatures between 13–16 °C (Fig. 2).

Although many organisms migrate into surface waters to feed[1-3], the sculpin did not consume prey when they were in the water column. Analysis of 330 sculpin collected throughout the summer demonstrated that they consumed primarily ostracods (59% by weight) and adult cyclopoid copepods (39%). These organisms were found only in the sediments or immediately above them (D. Neverman, unpublished data). Furthermore, the sculpin fed only during the day when they were on the bottom, and stomach filling peaked just before the dusk ascent (Fig. 3). During the night the fullness of the gut decreased monotonically, reaching a minimum at dawn as the fish returned to the bottom.

We reasoned that the fish moved to warmer strata to increase their digestion rate. We tested this in the laboratory by measuring gut clearance rates of satiated sculpin at two temperatures. At 5 °C the instantaneous digestion rate[10] was 3.2% per hour (±1.1; 95% confidence interval, CI), and only 22% of the meal was evacuated from the stomach during the 7.5 h digestion trial. At this rate, 50 hours would have been required for a fish to digest 80% of its meal. In contrast, at 15°C the digestion rate was 23.4% per hour (±0.9; 95% CI) and 80% of the meal was evacuated in 7.5 hours. This rate was nearly identical to actual digestion rates of wild fish (25–27% per hour) captured in the metalimnion (Fig. 3). Nocturnal migration into warmer water apparently allowed large meals to be digested rapidly before feeding began the following day.

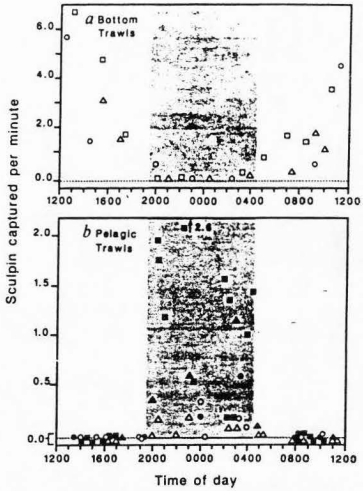

Fig. 1 Temporal changes in the catch rates of juvenile Bear Lake sculpin collected with trawls on the bottom of the lake (*a*), and in the water column (*b*). Closed symbols in *b* indicate captures in the metalimnion; open symbols indicate densities in the epilimnion and hypolimnion. Circles, 30–31 July 1985; triangles, 14–15 August 1985; squares, 27–28 August 1985. The shaded area denotes the time from evening to morning civil twilight (Mountain standard time) on 14 August. Fish were sampled at a site 5.5 km from shore where the mean depth was 40 m. We collected fish on the bottom with a 2.9-m otter trawl pulled at 1.0 m s^{-1}. In the water column they were sampled with a 1-m^2 opening-closing Tucker trawl pulled at 1.5 m s^{-1}. Although capture efficiencies during the day may have been lower than at night due to visual net avoidance, catch rates of adult sculpin in the otter trawl were not significantly different between day and night (*t*-test; $P = 0.338$). This indicates that changes in avoidance of this net were minimal during any 24-h period.

The rapid evacuation of the gut during the night also increased the feeding rate the following day. Sculpin that had digested their meals at 15 °C and were then fed at 5 °C made significantly more feeding attempts than fish kept continuously at 5 °C (Table 1; $P < 0.026$, paired *t*-test).

This increased feeding rate would be advantageous only if it provided sufficient energy to overcome the elevated respiratory costs of inhabiting warm water at night. To determine if a migration could increase the net energy gain of sculpin, we conducted a growth experiment in the laboratory. Fish were exposed to either a constant temperature of 5 °C (bottom temperatures), or a fluctuating regime of 5–15 °C that mimicked the actual temperatures encountered by migrating individuals. To simulate the actual feeding regime, fish were fed *ad libitum* only during the day.

Sculpin in the fluctuating temperature regime grew 300% faster than those reared at 5 °C. This difference was highly significant ($P < 0.0001$; Table 1). The growth experiment, however, may have over-estimated the net energy benefit of the migratory behaviour of wild sculpins, because fish in the laboratory did not have to swim to the metalimnion and maintain themselves in the water column each night. Swimming costs of small fish like sculpin have not been measured, but moderate

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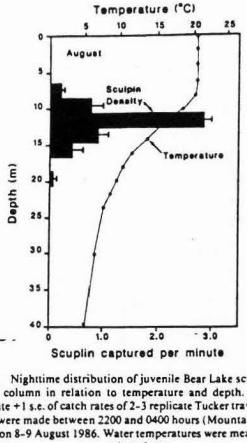

Fig. 2 Nighttime distribution of juvenile Bear Lake sculpin in the water column in relation to temperature and depth. Error bars indicate +1 s.e. of catch rates of 2-3 replicate Tucker trawls. Collections were made between 2200 and 0400 hours (Mountain standard time) on 8-9 August 1986. Water temperatures were measured with a thermistor.

Table 1 Effects of constant and fluctuating temperatures on feeding and growth rates (dry weight) of juvenile Bear Lake sculpin (*Cottus extensus*) reared in the laboratory

Temperature	Condition simulated	Feeding rate* at 5 °C (strikes per fish min^{-1})	Growth rate* (% per day)
5 °C	Hypolimnion	0.22 ± 0.08	0.74 ± 0.30
5-15 °C	Migratory	0.48 ± 0.15	2.15 ± 0.45

To quantify feeding rates in constant and fluctuating temperatures we first allowed groups of ten fish to digest a large meal of zooplankton overnight (7.5 h) at either 5 or 15 °C. Fish at 15 °C were then moved to 5 °C and allowed 1 h to acclimate. We then fed the sculpin live zooplankton and observed the number of feeding strikes made at prey during six 2-min periods over the following hour. To measure growth, fish with an estimated mean dry mass of 2.4 mg were anesthetized, measured, and randomly assigned to a temperature treatment (5 °C; or 5-15 °C, 16 h : 8 h), or killed to provide a subsample for determining the initial length-dry-weight relationship. In each treatment we reared 15 sculpin individually in 0.5-litre containers constructed of 300 and 1,000-μm nylon mesh on the sides and bottom, respectively. We placed these in glass, flow-through aquaria. To simulate natural conditions, fish were fed repletion rations of plankton only during the day. The diet was 75% *Ceriodaphnia* sp., 8% *Daphnia magna*, and 7% *Cyclops* spp., all between 300-500 μm. During the day all sculpin were kept at 5 °C. In the evening the cups were lifted from their tanks, rinsed to remove plankton, and placed into a zooplankton-free aquaria of the appropriate night time temperature. After eight hours we moved the fish again and allowed them one hour in their new aquaria before feeding. The temperature of the 5-15 °C treatment was tempered over 1-h periods when the fish were transferred. After 21 days, the fish were removed, dried and weighed on a microbalance. Other experimental protocol and growth calculations followed Wurtsbaugh and Cech[17].

* Means ±95% confidence intervals.

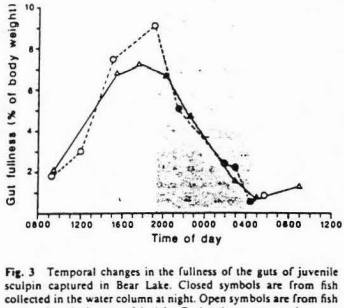

Fig. 3 Temporal changes in the fullness of the guts of juvenile sculpin captured in Bear Lake. Closed symbols are from fish collected in the water column at night. Open symbols are from fish captured on the bottom of the lake. Each point represents the mean for ten sculpin. The shaded area indicates the time from evening to morning civil twilight on 14 August. Triangles: 14-15 August 1985. Circles: 16-17 September 1985. Instantaneous digestion rates[10] of sculpin during the night were calculated from the exponential decline in the weight (W) of food in the guts over time (t): August, $W_{t2} = W_{t1}\ e^{-0.27(t)}$, $r^2 = 0.92$; September, $W_{t2} = W_{t1}\ e^{-0.23(t)}$, $r^2 = 0.92$.

swimming speeds of 1-2 body lengths per second decrease growth rates less than 25% in well-fed juvenile salmon[11]. Consequently, the metabolic costs of routine swimming are probably not so large as to cancel the threefold growth advantage of inhabiting the warm metalimnion at night.

Post-feeding thermotaxis may be a common phenomenon affecting not only sculpin, but a wide range of ectothermic animals. Under experimental conditions some reptiles, amphibians and other species of fish seek higher temperatures after feeding[12,13]. Also, bioenergetic studies on reptiles[14,15] and amphibians[16] have shown that post-feeding thermotaxis increases their feeding, digestion and growth. Our results indicate that daily vertical migration and behavioural thermoregulation can also be important in controlling growth processes of fish.

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