5-1995

Ontogenetic Habitat Shift of Juvenile Bear Lake Sculpin (Cottus extensus)

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ONTOGENETIC HABITAT SHIFT OF JUVENILE BEAR

LAKE SCULPIN (<u>COTTUS</u> <u>EXTENSUS</u>)

by

James R. Ruzycki

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Aquatic Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1995

ABSTRACT

Ontogenetic Habitat Shift of Juvenile Bear

Lake Sculpin (Cottus extensus)

by

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Utah State University, 1995

Major Professor: Dr. Wayne A. Wurtsbaugh
Program: Aquatic Ecology

Bear Lake sculpin (Cottus extensus) exhibited an
ontogenetic habitat shift during their first year of life.
Soon after hatching in the littoral zone, the fry swam to
the surface where they dispersed throughout the lake. Most
juveniles that initially settled in the profundal zone
returned to the littoral zone during their first summer.
Patterns in the daily growth increments of otoliths
confirmed the history of habitat residence and the
individual size at the habitat switch. We used this
habitat shift to test a μ/g model incorporating a growth
rate-mortality risk trade-off. A trade-off occurred in the
littoral zone because both growth rate and mortality risk
were greater in this habitat. Given initial profundal
residence, the directed movement of juveniles to the more
profitable littoral zone was consistent with model

predictions. Contrary to model predictions, juvenile sculpin initially occupied both habitats and switched habitats at a wide range of sizes. Lack of a discrete switch size may have resulted, in part, from the lack of a strong trade-off or from an inability of fish to respond facultatively to environmental variables at the large spatial scale of this system.

(59 pages)

ACKNOWLEDGMENTS

This work could not have been completed without the assistance of many people. I would like to thank Paul Chase, Clayton Housely, Clyde Lay, and Rick Orme for their many hours of assistance in the field and in the laboratory. My thanks to all my fellow graduate students who gave support through the whole process, especially to Nick Bouwes, who shared many hours of labor and discussion.

I extend my thanks to my committee members, Chuck Hawkins and Frank Messina, for their help with the experimental design and thesis review. I would especially like to thank my major advisor, Wayne Wurtsbaugh, who guided me through the entire process. Without his knowledge and guidance this work could not have been enjoyable or even possible.

Finally, I owe many thanks to my wife, Patti Howard, for her encouragement and for enduring so many years in Utah. Without her support this work would never have been accomplished. I hope the next three years pass more quickly.

James R. Ruzycki

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INTRODUCTION

Ontogenetic habitat shifts have been described for many aquatic species and ontogenetic shifts in resource use are nearly universal for fishes (Werner and Gilliam 1984). Body size can influence a fish's ability to use a resource that varies among habitats (Werner and Hall 1988). For several freshwater fish species, small changes in body size have been demonstrated to influence habitat use during the initial year of growth (e.g., Mittelbach 1981; Rice et al. 1987; Post and McQueen 1988; Luecke et al. 1990). Furthermore, body size often changes by orders of magnitude during the first year (Miller et al. 1988).

Ontogenetic changes in habitat use may be mediated by predation. Predators may influence their prey directly by removing individuals, or indirectly by altering prey behavior (Stein and Magnuson 1976; Mittelbach and Chesson 1987; He and Kitchell 1990). Risk of mortality has been experimentally demonstrated to alter the use of foraging habitats (e.g., Werner et al. 1983; Gilliam and Fraser 1987; Holbrook and Schmitt 1988; Abrahams and Dill 1989; Tabor and Wurtsbaugh 1991). Mortality risk due to predation is also strongly related to body size (Miller et al. 1988; Werner and Hall 1988). Predation may therefore affect habitat choice of vulnerable size classes of fish, and because this vulnerability varies with body size, habitat choice may vary ontogenetically.

Growth rate may affect how long an individual is

susceptible to a size-related predation risk (Crowder et al. 1987; Post and Prankevicius 1987). If so, growth rates and predation may influence ontogenetic niche shifts. To maximize future fitness potential, an individual would theoretically minimize present mortality risk while maximizing growth potential. In many aquatic communities a habitat that is optimal for growth may also have a higher predation risk (Werner et al. 1983). Many fish may therefore be confronted with a trade-off between a risk of mortality (μ) and growth rate (g), expressed as the ratio μ/g (Werner et al. 1983). This trade-off affects the habitat choice of vulnerable size classes of fish, and if this vulnerability varies with body size, habitat choice may vary ontogenetically.

Here, we examined the potential for an ontogenetic habitat shift by Bear Lake sculpin (<u>Cottus</u> <u>extensus</u>), a species endemic to Bear Lake Utah/Idaho, USA. The depth distribution of age-0 juveniles appeared to vary seasonally. These sculpin hatch during late spring in the littoral zone but are soon located throughout the lake, inhabiting both the cold profundal and the warm littoral zones. The juvenile sculpin located in the profundal zone undergo a diel vertical migration (DVM) into warmer metalimnetic waters that increases digestion rates and consequently growth rates (Wurtsbaugh and Neverman 1988; Neverman and Wurtsbaugh 1994). This behavior suggests

temperatures in the profundal are not optimal for growth. Bottom trawl catches during 1991 and 1992 suggested that juveniles, which initially locate in the profundal zone, recruit to the littoral zone during their first summer. The relatively warmer littoral zone temperatures should also be more favorable for growth (Neverman and Wurtsbaugh 1994), and densities of invertebrate prey are higher there than in the cold profundal zone (Wurtsbaugh and Hawkins 1990).

During the summer the littoral zone also contains a relatively large population of age-1 and older sculpin. Large Bear Lake sculpin are known to cannibalize smaller sculpin (Wurtsbaugh and Hawkins 1990). A growth rate/ predation risk trade-off may therefore exist for juvenile sculpin during their initial year. For this phenomenon to occur, fish must grow faster and be more vulnerable in the same habitat (Werner and Hall 1988). For age-0 Bear Lake sculpin, these constraints may exist in the littoral habitat.

By examining the distribution of juvenile Bear Lake sculpin during their initial year, and by evaluating their daily otolith increments, we tested the hypothesis that age-0 juveniles undergo an ontogenetic habitat switch. We also tested a model that incorporated a mortality risk/growth rate trade-off. We hypothesized that juvenile sculpin, which initially locate in the profundal zone, move to the littoral zone upon reaching a certain size. Juvenile

mortality was predicted to be mediated through predation and individual size, whereas growth rates were predicted to be primarily temperature dependent.

MATERIALS AND METHODS

Study Area

Bear Lake is located in northeast Utah and southeast Idaho (Fig. 1). It is a 282 km², tilt-block lake at an elevation of 1805 m, with a maximum depth of 63 m. Most of the bottom sediment is fine marl at depths beyond 23 m (Smart 1958). Shallower water substrate is dominated by sand on gradual slopes and gravel, cobble, and boulders on the precipitous eastern shore. Macrophytes are rare except in the far northern section of the lake. The lake is typically dimictic, with summer surface temperatures reaching 19-21°C and bottom temperatures remaining year-round at 3-5°C (Lamarra et al. 1986). The lake is oligotrophic, with mean summer epilimnetic chlorophyll concentrations near 0.5 mg·m⁻³ (Lamarra et al. 1986; Moreno 1989).

Bear Lake sculpin consume primarily benthic invertebrates (Wurtsbaugh and Hawkins 1990). Mean annual benthic invertebrate biomass is very low (0.34 g·m⁻² dry weight) compared to other temperate systems. The benthic invertebrate biomass also declines rapidly between the depths of 15 and 35 m with the taxa consumed by sculpin being 10-12 times greater in biomass in shallow water than in the profundal (Smart 1958; Wurtsbaugh and Hawkins 1990).

The Bear Lake sculpin is one of four endemic fishes in Bear Lake. The other three endemic species include
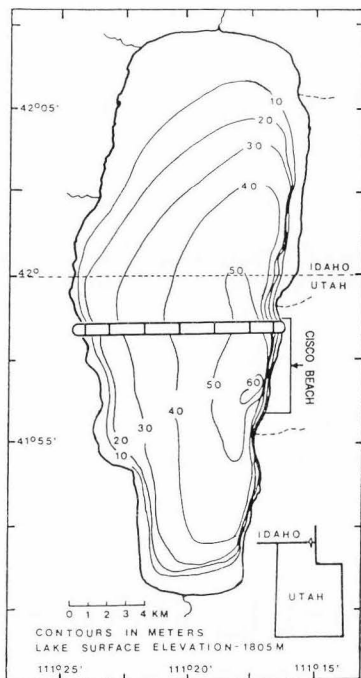
Fig. 1.   A bathymetric map of Bear Lake. The two nominal
habitats studied, profundal and littoral zone, are at
depths of 30-50 m and 2-8 m, respectively. The bracket on
the eastern shore delineates a major spawning area for
sculpin (Cisco Beach). The neuston net transects are shown
as vertical lines extending from Cisco Beach to the
opposite shore.

Bonneville cisco (<u>Prosopium</u> <u>gemmifer</u>), Bonneville whitefish
(<u>Prosopium</u> <u>spilonotus</u>), and Bear Lake whitefish (<u>Prosopium</u>
<u>abyssicola</u>). Other dominant fish species include cutthroat
trout (<u>Oncorhychus</u> <u>clarki</u>), Utah sucker (<u>Catostromus</u>
<u>ardens</u>), and the introduced lake trout (<u>Salvelinus</u>
<u>namaycush</u>). Bear Lake sculpin are an important forage fish
that, along with cisco, sustain the salmonid sport fishery
(Nielson 1981). Adult Bear Lake sculpin are commonly preyed
upon by cutthroat trout and lake trout (Nielson 1981), and
small juveniles are preyed upon by whitefish and larger
sculpin (Wurtsbaugh and Hawkins 1990).

Field Studies

<u>Habitat Demarcation</u>

For the purposes of this investigation, the lake was
divided into two habitat types based on environmental
variables expected to influence the mortality risk and
growth rate of juvenile sculpin. The two habitats were
nominally classified as the littoral zone (2-8 m depth) and
the profundal zone (30-50 m depth). The littoral zone is
located above the thermocline from June through August,
whereas the profundal zone is located well below the
thermocline during this period (Fig. 2). Because of the
possibility of horizontal diel sculpin movement, the 9-29 m
intermediate depths were not sampled to allow for sample
independence by spatially segregating the habitats.
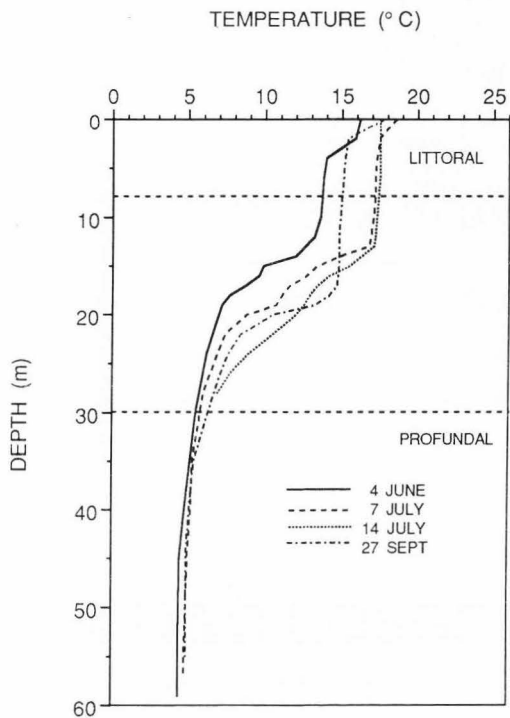
Fig. 2.   Temperature profiles on four dates during 1992
illustrating the temperature differential between the
profundal and littoral habitats.

Hatching and Dispersal

Before sampling juvenile sculpin in the profundal and littoral habitats, the timing of sculpin hatching was verified. This information allowed us to predict when the 1992 sculpin cohort would become vulnerable to the bottom trawl gear used to sample benthic sculpin. Hatching dates were also important for verifying daily increments of growth in otoliths.

The onset of sculpin hatching was determined by viewing the development of sculpin egg masses over known sculpin spawning habitat. By snorkeling, egg masses were monitored weekly beginning 9 May 1992 and monitoring continued until hatched egg cases were observed (23 May 1992). The onset of free-swimming behavior of the larvae was monitored with neuston nets (35 by 100-cm mouth opening, 500-μm mesh body and buckets). Beginning 23 May 1992, surface waters were sampled at weekly intervals until we captured no sculpin larvae for 2 consecutive weeks. Beginning 0.5 h after sunset, the nets were pulled for 15 min along seven north-south transects located 0.1, 1, 3, 5, 7, 9, and 10 km west of a major spawning location on the east shore. The western-most transect was approximately 0.1 km from the west shore (Fig. 1). The transects were sampled sequentially in an east to west direction. Two nets (port and starboard) were pulled simultaneously at approximately 1 m·s^{-1} and were adjusted to sample immediately below the

water surface. An absence of larval sculpin in neuston nets was subsequently used as an indication of the onset of the benthic residence of juveniles.

Juvenile and Adult Distribution

To determine the spatio-temporal distribution of age-0 and older sculpin in their benthic habitat, we trawled biweekly from 18 June to 23 September and again on 11 November 1992 with a semi-balloon otter trawl (2.9-m head rope, 5.3-mm mesh body, and 1-mm mesh net liner in the cod end). The trawl was pulled at 1 m·s⁻¹ for 20 min. Every 2 wk, we selected eight profundal and twelve littoral sites to trawl. Profundal sites were trawled during the day, because juvenile sculpin vacate the bottom at night (Wurtsbaugh and Neverman 1988). Littoral sites were trawled at night. Juvenile sculpin were measured to the nearest 0.5 mm and subsamples were retained for diet and otolith analysis. Age-1 and older sculpin were measured to the nearest 1.0 mm. A subsample of juveniles and age-1 and older fish were blotted dry and weighed to the nearest 0.1 mg to develop length-wet weight relationships.

A habitat-specific index of juvenile abundance (A) was determined from trawl capture rates by assuming the trawl captured all sculpin in its path (i.e., 100% efficiency):

(1) $A = (TC) HA \cdot TA^{-1}$

where TC is the mean number of fish captured in a trawl, HA is the benthic habitat surface area, and TA is the area sampled in our standardized trawl (0.0024 km²). The surface areas of the profundal zone (100 km²) and the littoral zone (40 km²) were calculated from a hypsographic curve.

Otolith Observations and Analyses

Habitat-specific growth rates, evidence for a habitat shift, and fish length at this habitat shift were determined from daily growth rings of otoliths from juvenile sculpin collected with the bottom trawls. Because of their larger size, sagittal otoliths were used exclusively. By using a dissecting microscope, both sagittal otoliths were removed from fish. Dissected otoliths were immediately cleansed in bleach (sodium hypochlorite) to remove adhering tissue, rinsed in deionized water, and stored in 95% ethanol (Secor et al. 1991). Otoliths were then dried and each pair was mounted on a glass microscope slide using a thermoplastic polymer (Crystal Bond 509, Aremco Products Inc.). Complete daily increment counts were possible on 80% (n = 157) of the whole otoliths from fish collected through 26 August 1992 without grinding or polishing. Using a compound light microscope, increments were counted twice from the primordium to the edge along a transect free of any secondary primordia (Szedlmayer and Able 1992). The mean increment count was used for all analyses. All otolith radius measurements were made on the anterior segment along

the anterior (rostrum) to posterior (postrostrum) axis with a calibrated ocular micrometer at 400 or 1000 magnification. The anterior radius was preferred over the posterior because of a high incidence of secondary primordia on the posterior portion of the otoliths.

To validate aging of fish from counts of daily increments, we analyzed 9-12 otoliths from fish collected every 2 wk from July through August 1992. Increment counts were then compared to the interval between the hatching date estimate in the lake and sample date. Three independent counts of increments were also made on a subset of otoliths by separate observers to verify the counts of the primary observer. To validate otolith size as a predictor of fish size, 121 otoliths from fish 9.5-32 mm standard length (SL) were linearly measured from the primordium to the anterior rostral projection (Secor et al. 1991) and compared to fish SL.

Juvenile sculpin were also reared in the laboratory to verify otolith age measurements. Eggs were collected from the lake on 22 May 1992 and hatched the same day in transport to the laboratory. The fry were placed in a 250-L aquarium and fed an ad libitum diet of live invertebrates. After 21 d, 10 fish were sacrificed and their otoliths were removed and mounted as described previously. Increment counts were made for each fish and otoliths were compared to otoliths dissected from day-of-hatch specimens.

Substantial supportive evidence of a habitat shift of juvenile sculpin was also evident in the contrast of the daily increments of the otoliths. This contrast was compared from fish collected in both littoral and profundal habitats. An abrupt change from high contrast to low contrast was used as a mark to identify a switch from the profundal to the littoral habitat. Juveniles that inhabit the relatively cold profundal zone undergo a daily vertical migration into the warmer metalimnion at night, which probably induces daily increments of high contrast. Sub-daily temperature fluctuations have been demonstrated to increase the contrast between the microzones of the daily growth increments of juveniles of other species (Campana and Neilson 1985; Neilson and Geen 1985). Fish SL at the time of the habitat switch was determined by measuring the radius of the otolith at the outermost increment of high contrast.

To verify the difference in contrast of daily increments deposited under the different temperature regimes, 10 sculpin were held for 7 d in 250-L laboratory aquaria under a 24-h, 10°C temperature cycle (15°C at night and 5°C during the day) to mimic the temperature regime of the juveniles undergoing a DVM in the profundal zone. For the duration of the experiment (3-25 November 1993), fish were exposed to a natural photoperiod of ambient light entering through laboratory windows. After 7 d, the temperature

regime was returned to a constant 18°C to simulate temperatures of a habitat switch from the profundal zone to the littoral zone. An additional control group of 10 fish were reared at a constant temperature of 18°C throughout the experiment. All fish were fed excess rations of invertebrate prey each day at 09:00. During the period of temperature fluctuation, feeding was approximately 1 h after temperatures were reduced to the 5°C daytime temperature. Prey items were then removed from the test chambers prior to the switch to the 15°C nighttime temperature. This feeding cycle mimicked that of juveniles in the offshore region of Bear Lake (Neverman and Wurtsbaugh 1994). At the end of 14 d, fish were sacrificed and their otoliths removed. The contrast of the individual daily increments in the two temperature treatments and in wild fish was then compared.

The change in contrast of the otolith increments of wild fish made it easy to distinguish between fish inhabiting the different habitats. This method, however, is partly subjective and an alternative method of distin-guishing habitat choice and size at habitat switching was desirable.

Because of the correlation between otolith radius and fish body length, increments produced in the warm littoral zone were hypothesized to be greater in width than the increments produced by fish inhabiting the cold profundal

zone. Twenty-seven fish were selected from the biweekly
bottom trawl collections (1 July-26 August 1992; size
range, 12-24.5 mm SL). The width of the initial 10
increments on either side of the habitat switch mark was
measured and compared (Neilson and Geen 1985).

Habitat-specific daily growth rates were determined
from measurements of the daily increment width of otoliths.
The contrast of the increments was used to assign the
habitat in which the increments were deposited. An easily
observed section of the otolith was located and the radius
at this position was measured. The width of the 10 incre-
ments on either side of this radius measurement was deter-
mined, and the mean daily width of these 10 increments was
calculated. Daily increment width was then converted to
daily growth rate ($mm \cdot d^{-1}$) based on a regression of fish SL
on otolith radius (R). Growth in length was then converted
to growth in mass based on a regression of wet mass on SL.

Calculation of Mortality Risk

The habitat-specific risk of mortality (μ) was
estimated using the following parameters: (1) consumption
rates of juveniles by older sculpin determined from diet
analyses; (2) a size-dependent function of the consumption
of juvenile sculpin by older sculpin determined in the lab-
oratory; and (3) the estimated biomass of age-1 and older
sculpin in each habitat. Consumption (C) was estimated
using a simple equation based on the frequency of occur-

rence of juveniles in age-1 and older sculpin stomachs
(Bajkov 1935):

(2) $C = N(B) \cdot V^{-1}$

where N = number of ingested juveniles for each kg of age-1
and older sculpin, B = biomass ($kg \cdot ha^{-1}$) of age-1 and older
sculpin in each habitat, and V = gut evacuation time in
days. For the diet analysis, age-1 and older sculpin were
randomly selected from every sample date (total $\underline{n}$ = 269).
Gut evacuation times were set at 16 h for the warm littoral
zone and 32 h for the colder profundal zone (He and
Wurtsbaugh 1993). Total length (TL in mm) of age-1 and
older sculpin was converted to wet mass (m in g) based on a
regression of mass on length. Density ($number \cdot ha^{-1}$) of age-
1 and older sculpin was estimated from trawl catches in the
same manner as for juveniles. The biomass of older sculpin
(B, $kg \cdot ha^{-1}$) in each habitat was then computed for each
month (June-August). Because only 5% of the examined adult
stomachs contained juvenile sculpin, a size-specific
consumption rate could not be calculated from the field
data. Consumption values were therefore based on the mean
size of the juveniles found in the diets of age-1 and older
sculpin. To determine individual juvenile mortality risk,
however, the size-dependent vulnerability to cannibalism
had to be estimated.

     To do this we measured size-dependent cannibalism in

the laboratory using laboratory-reared juveniles. All experiments were conducted at 15°C, and all fish were temperature acclimated for at least 14 d prior to experimentation. Experimental light levels were approximately 1.5 $\mu E \cdot m^{-2} \cdot s^{-1}$, an intensity that can support near-maximal levels of visual predation by sculpin (Neverman and Wurtsbaugh 1992). On five dates during the spring and summer of 1992, 10 juveniles from one of four nominal size classes (8, 12, 16, 20, and 24 mm SL) were placed in 40-L aquaria partitioned with a 1-mm mesh screen. This partition allowed the prey to acclimate without threat from the predator located on the opposite side of the aquaria. After 5 min the partition was removed. Each aquarium contained one adult sculpin predator (mean size = 60 mm, range = 58-63 mm) acclimated without food for 1 d prior to the experiment. We ran five replicates for each prey size class and recorded the number of juveniles consumed and the percent capture success of adults during the initial hour. An adult would often make a series of strikes and pursue the juvenile fish before it was finally captured and consumed. Each single strike by an adult sculpin was evaluated separately and only scored as a success if it resulted in the juvenile being eaten. A regression of the number of prey consumed during the initial hour as a function of juvenile length was then used to scale consumption from the mean size of juveniles in wild age-1

and older sculpin diets to individual juvenile size.

Calculation of μ/g

Because of the transient nature of age-1 and older sculpin densities in each habitat, the μ/g ratio was calculated for each of the 3 mo (July-September 1992) for which there were juvenile abundance and growth data. Although sculpin hatched during late May and early June, juvenile abundance for June was not possible because juveniles were not captured in our bottom trawls until 1 July 92. Furthermore, due to the opaqueness of their otoliths, juvenile growth rates were not calculated beyond September 1992.

RESULTS

Field Studies

Hatching was initially observed on 23 May 1992. No
further monitoring of spawning substrate and hatching
activity was conducted after this date. We captured 1,197
yolk-sac larvae in 22 neuston net trawls from 23 May
through 6 June 1992. Highest catch rates occurred on 29
May. No larval sculpin were captured at the surface in 14
neuston trawls on 13 and 19 June. We captured 97% of the
larvae within 1 km of the eastern shore, although only 32%
of the trawling effort was conducted in this area. Capture
rates were consistently low at mid-lake and west-shore
transects, indicating that the rocky eastern shore is a
primary spawning site for sculpin.

During most of the summer, the abundances of juvenile
sculpin were higher in the littoral zone than in the
profundal zone. Abundance estimates for juvenile sculpin
from bottom trawls were, however, unexpectedly low in both
the littoral and profundal zones during June and July (Fig.
3). The low catch rates may have been a function of poor
trawl efficiency because the fish were small (< 15 mm SL)
during this period. Low catch rates in the profundal zone
may have persisted for a longer period than in the littoral
zone because of the slower growth rate in the deeper,
colder water (see below). During August and September,
abundance appeared to increase in both zones with littoral

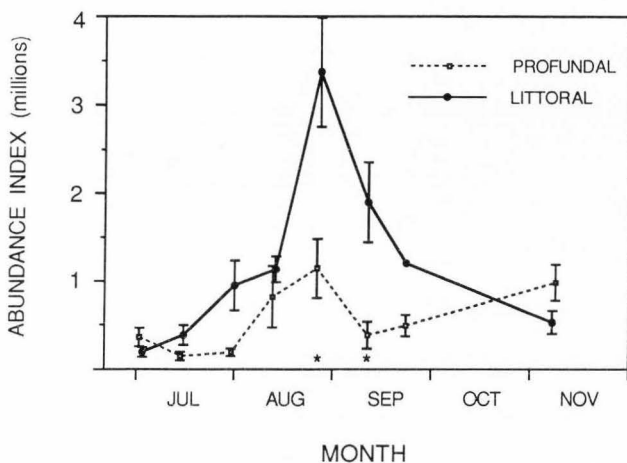Fig. 3. Profundal (30-50 m) and littoral (2-8 m) zone juvenile abundance indices as determined from bottom trawl catches. For each profundal sample date, n = 8 except Nov. where n = 6. For each littoral sample date, n = 12 except Nov. where n = 8. Error bars indicate ± 1 SE. Asterisks on the x-axis denote dates when abundance estimates were significantly different between habitats (t-tests; $p < 0.0063$).

abundance continuing to exceed that in the profundal. By 11 November, however, juvenile abundances in the littoral zone had decreased markedly.

Juvenile sculpin captured in the littoral zone were consistently larger than fish in the profundal zone (Fig. 4). Note, however, that when the June size estimate is excluded, the slopes of the lines for the littoral and profundal zones are approximately parallel, suggesting similar growth in the two zones. This is likely an artifact of the relatively small profundal juveniles recruiting to the littoral zone during the course of the summer, reducing the mean size there (see below). Size-frequency distributions of juveniles captured in the two zones also demonstrate that the littoral zone had some fish similar in size to the smaller offshore sculpin, but that many more large juveniles were present in the shallow water (Fig. 5).

From late June to September, density estimates of sculpin age-1 and older were 2-5 times greater in the littoral zone than in the profundal region (Fig. 6). In late-September and mid-November, however, profundal zone estimates exceeded littoral zone estimates. The large variance on any sample date in both juvenile abundance estimates and age-1 and older sculpin density estimates is likely a function of the habitat heterogeneity encountered by including the entire lake area in the sampling regime.
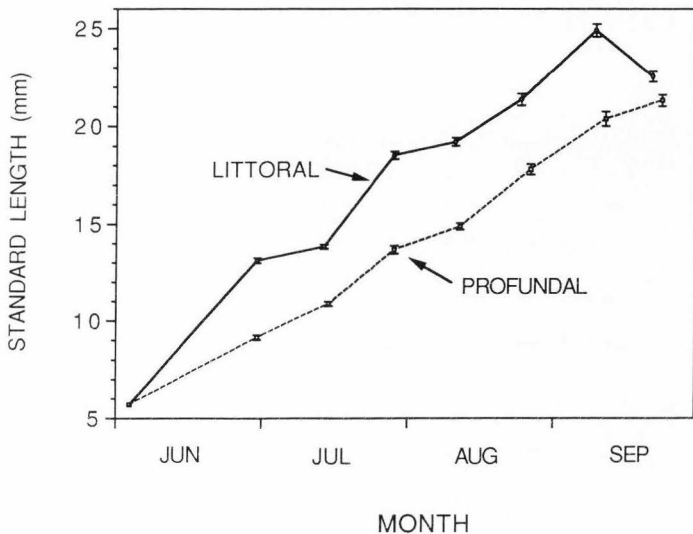
Fig. 4. Changes in the standard lengths of juvenile
sculpin captured in the littoral and profundal zones of
Bear Lake with a bottom trawl (1 July - 23 Sept. 1992). The
June size estimate is from the 6 June neuston net samples.
Error bars indicate ± 1 SE.
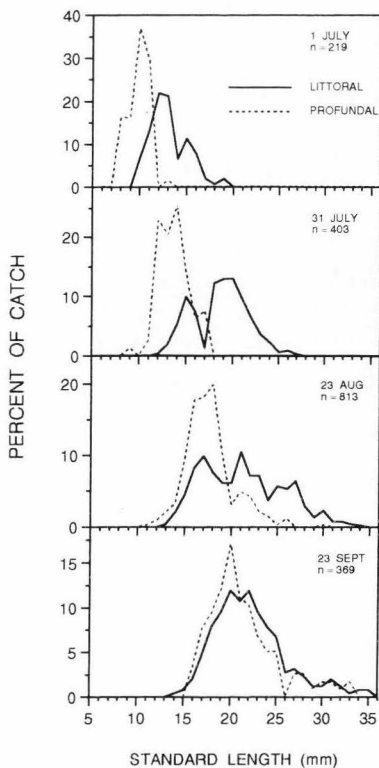
Fig. 5. Size-frequency distributions of juvenile sculpin captured with the bottom trawls in the littoral and profundal zones during 1992. The abundances used to estimate the frequency polygons were tabulated at 1-mm intervals. Sample sizes and dates are indicated.
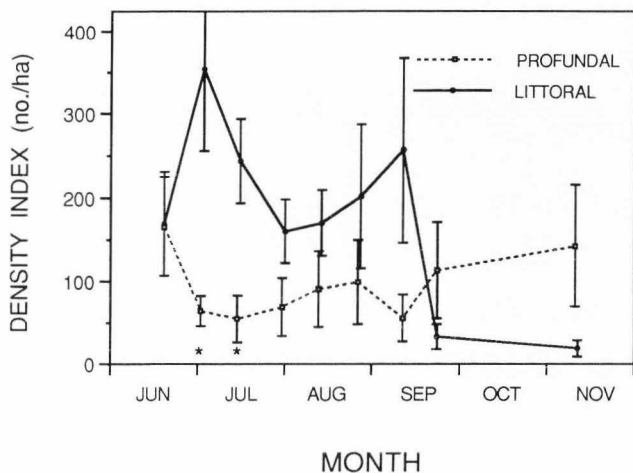
Fig. 6. Profundal and littoral zone density indices of age-1 and older sculpin as determined from the same bottom trawl catches used to determine juvenile abundance. For each profundal sample date, n = 8 except Nov. where n = 6. For each littoral sample date, n = 12 except Nov. where n = 8 Error bars indicate ± 1 SE. Asterisks on x-axis denote dates when density estimates were significantly different between habitats (t-tests; p < 0.0056).

Otolith Observations and Analyses

Major evidence for the occurrence of a habitat switch was recorded in an individual fish's pattern of daily otolith growth. Juvenile sculpin captured in the profundal zone had greater contrast between daily increments than did the outer increments of fish captured in the littoral zone (cf. Fig. 7 a,b). All of the examined otoliths of juveniles captured in the profundal zone had daily increments that were easily observed and high in contrast (e.g., Fig. 7a). Complete increment counts were possible on 88% ($\underline{n}$ = 50) of the otolith pairs of fish captured in the profundal habitat. Moreover, none of the otoliths of profundal fish showed a change in contrast of the increments until September when littoral zone fish began to migrate offshore. In comparison, complete increment counts were possible on 77% ($\underline{n}$ = 107) of the otolith pairs of fish captured in the littoral habitat. Of these, 93% showed a change in the contrast of the increments. Furthermore, all otoliths with a contrast change had high contrast increments beginning near the primordium and lower contrast increments near the outer edge. This evidence also suggests that the high contrast increments were formed in the pro-fundal zone, and the switch to the littoral zone resulted in increments of lower contrast. Additionally, the mean daily increment widths of the increments on either side of the habitat switch mark (profundal = 3.1 μm, littoral = 5.4
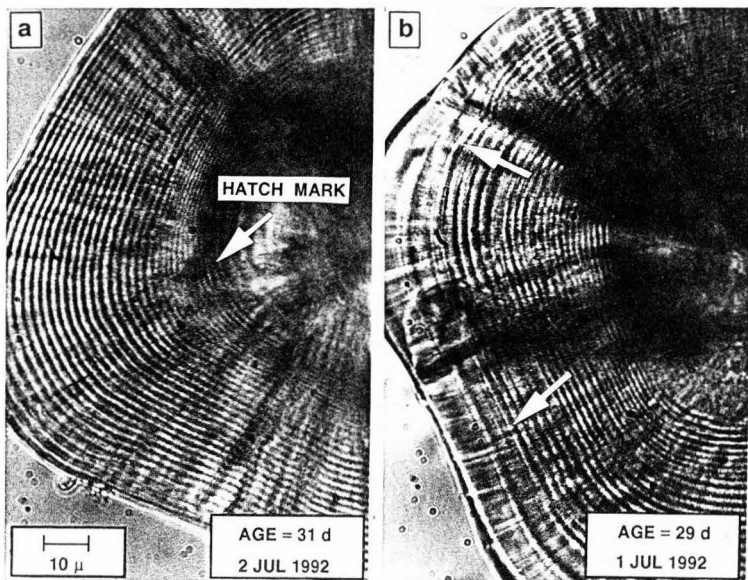
Fig. 7.   Photomicrograph of sagittal otoliths of sculpin
captured in the profundal zone (a) and the littoral zone
(b). Note the high contrast increments of the profundal
inhabitant beginning at the arrow and extending to the
outer edge. Also note the abrupt change in contrast of the
increments of the littoral inhabitant as indicated by the
arrows. Age and date of capture of each individual are
indicated. Although of lower contrast, daily increments of
littoral inhabitants are discernable.

μm) were significantly different ($\underline{n}$ = 37; paired $\underline{t}$-test, $\underline{p}$ < .001).

Validation analyses of otoliths indicated that increments were formed daily. A linear regression between day of the year and increment count was significant ($\underline{r}^2$ = 0.99, $\underline{p}$ < 0.001) and had a slope of 1.006 (Fig. 8). This slope was not significantly different from 1.00 (ANCOVA, $\underline{p}$ = 0.260; Appendix A.3), suggesting that increment formation was daily. The x-intercept of this line was the 148th day of the year ($\underline{SE}$ = 7.4), which corresponds to 28 May 1992. This date is not significantly different from our observation of initial sculpin hatching on 23 May 1992 ($\underline{t}$-test, df = 1, $\underline{p}$ > 0.05), nor from peak catch rates of yolk-sac larvae in the neuston nets on 29 May 1992 ($\underline{t}$-test, df = 1, $\underline{p}$ > 0.05), also suggesting that increment formation was daily. The three independent counts of increments on a sub-set of otoliths indicated no significant difference among reader counts (ANOVA, $\underline{p}$ > 0.99; Appendix A.4).

Increment counts of fish raised in the laboratory were also used to validate daily increment formation. Fish sacrificed 21 d after hatching had a mean increment count of 20.5 ($\underline{SD}$ = 1.05, $\underline{n}$ = 10). Although the counts were in close agreement with age, the increments formed by the laboratory fish were not as distinct as those of wild individuals captured in the profundal zone. This non-distinct increment formation inhibited laboratory
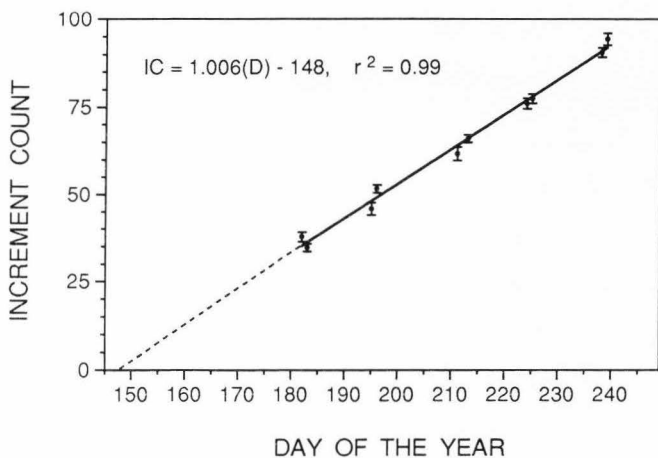
Fig. 8. Mean number of daily otolith increments (IC) from juvenile sculpin collected on different days of the year (D). Sculpin hatching was initially observed on the 143rd day of the year. Error bars indicate ± 1 SE, n = 111.

validation of the change in the increment contrast of fish exposed to the 24-h, 10°C temperature cycle. Although daily increments were observable, there was no apparent change in the contrast of the increments of fish that were initially exposed to the 24-h temperature cycle and subsequently switched to the constant temperature regime.

Juvenile Growth Rate

Habitat-specific growth rates, as measured from otolith increments, indicated faster growth in the littoral habitat than in the profundal habitat. To validate otolith radius (R) as a predictor of fish size (SL), juvenile SL was regressed against otolith radius and was well described by the linear relationship (Fig. 9):

(3) $SL = 4.45 + 42.01R$, $\underline{n} = 184$, $\underline{r}^2 = 0.96$

Conversion of SL to wet mass for juveniles was described by the equation:

(4) $m = (1.18 \cdot 10^{-5}) SL^{3.11}$, $\underline{n} = 189$, $\underline{r}^2 = 0.97$

where m = wet mass (g), and SL = standard length (mm). By using equations 3 and 4, and measurements of otolith radii and daily increment widths, absolute growth (G) in wet mass ($g \cdot d^{-1}$) in the littoral zone and profundal zone was regressed against individual length and was best described by the following equations:
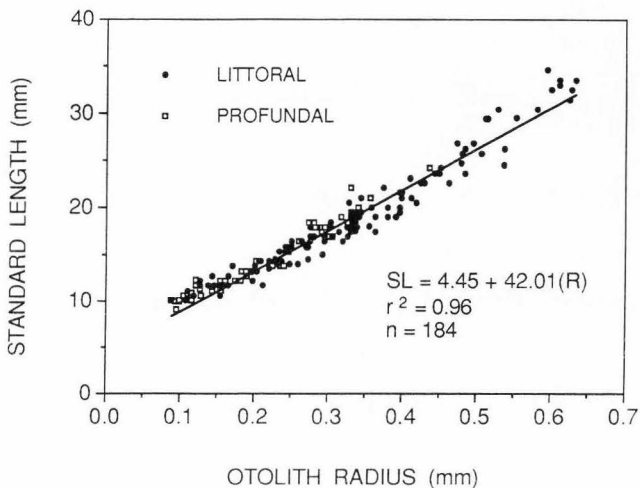
Fig. 9. Otolith radius (R) versus standard length (SL) relationship for juvenile sculpin.

(5) $G = (1.16 \cdot 10^{-6}) SL^{2.88}$, $\underline{n} = 55$, $\underline{r}^2 = 0.93$

(6) $G = (1.64 \cdot 10^{-6}) SL^{2.51}$, $\underline{n} = 64$, $\underline{r}^2 = 0.97$

The slopes of these regressions were significantly different (ANCOVA, $\underline{F} = 10.0$, $\underline{p} < 0.01$; Table A.3).

Juvenile Mortality Risk

From July through mid-September, the biomass of predatory sculpin in the littoral zone was 1.5 to 3.0 times higher than in the profundal zone. Based on these numbers, and temperature-dependent digestion rates, the consumption of age-0 juveniles by age-1 and older sculpin was estimated to be 1.5 to 12.8 times higher in the littoral zone than in the profundal during this same period. Similarly, mortality risk (μ) for age-0 juveniles was always higher in the littoral zone until late-September. Field estimates of the biomass of and consumption by age-1 and older sculpin, and the mortality risk of age-0 juvenile sculpin are shown in Table A.1. The conversion of age-1 and older sculpin total length (TL) in mm to wet mass (m) in g was best described by the function:

(7) $m = (1.82 \cdot 10^{-5}) TL^{2.84}$, $\underline{n} = 361$, $\underline{r}^2 = 0.97$

In the laboratory tests, small juveniles were very susceptible to predation by adult sculpin, but this vulnerability decreased as the juveniles grew (Fig. 10). When adult sculpin preyed on the 8-mm SL juveniles, over
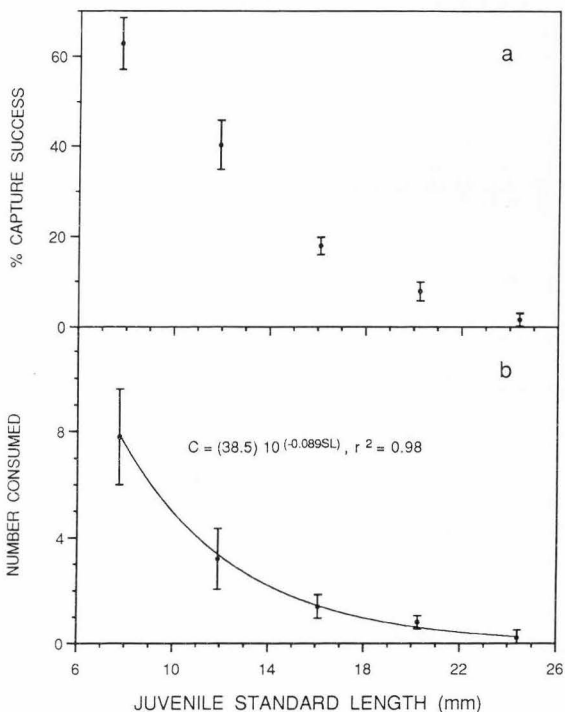
Fig. 10. Mean capture success per strike, and consumption (C) estimates of 60-mm sculpin preying on juveniles in laboratory experiments. Percent capture success and consumption were measured over the initial hour of each trial. Error bars indicate ± 1 SE.

60% of their strikes were successful, but only 1% of the
attacks on 24-mm juveniles were successful. Similarly,
approximately 80% of the 8-mm juveniles were consumed by
adults during the first hour, whereas only 2% of the 24-mm
juveniles were eaten (Fig. 10). The change in consumption
rate of juveniles by age-1 and older sculpin (C) as a
function of juvenile size (SL) was best described by the
power function:

(8) $C = 38.52(10^{-0.089SL})$, $\underline{n} = 25$, $\underline{r}^2 = 0.98$, $\underline{p} < 0.01$

Only eight juvenile sculpin were observed in the
stomachs of the 167 age-1 and older sculpin examined.
Sample sizes were therefore too small to calculate a size-
dependent function of the rate of cannibalism from field
sampling alone. The mean size of all juveniles found in
age-1 and older sculpin diets (18.8 mm, range = 7.6-27.4
mm) and the mean frequency (4.9%) were used as starting
points to model size-specific consumption. Consumption was
then scaled for individual juvenile size using equation 8
to determine the mortality risk for each 1-mm size class.

Mortality Risk-Growth
Rate Trade-Off

From July through September, a mortality risk-growth
rate trade-off existed in the littoral habitat as both a
higher mortality risk and growth rate occurred there. The
relative importance of growth was greater, however, as the

μ/g ratios for all sizes of juvenile sculpin were always lower in the littoral habitat compared to the profundal (Fig. 11). That is, the optimal ratio (minimal μ/g) consistently occurred in the littoral habitat regardless of juvenile size. The model, therefore, predicts that juveniles should initially inhabit the littoral area and remain there for their first summer. Observations of the otoliths of juveniles captured in the littoral zone, however, indicated that most of the fish initially located in the profundal zone.

Measurements of the otolith radius at the habitat switch mark, furthermore, indicated that the juvenile sculpin migrated from the profundal to the littoral zone at a wide range of sizes (range = 8-24 mm SL, mean = 16.2 mm, $\underline{SD}$ = 4.2, $\underline{n}$ = 169; Fig. 12). Early in the summer, juveniles switched habitats at smaller sizes than they did during August and September. From June through July, most juveniles switching from the profundal to the littoral zone were larger than the average-sized juvenile in the profundal zone.
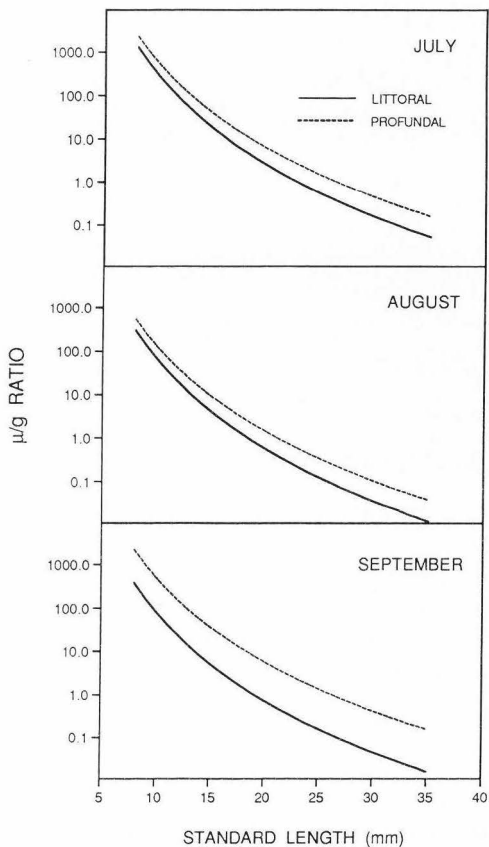
Fig. 11. The habitat-specific mortality risk-growth rate
(μ/g) ratios for juvenile sculpin during July, August, and
September 1992.
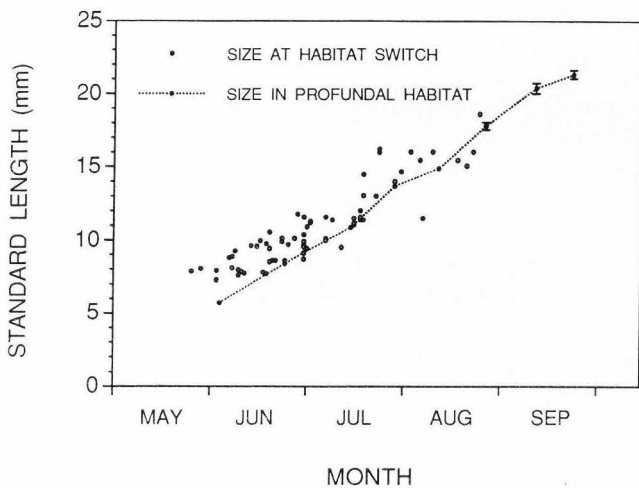
Fig. 12. The standard length of juvenile sculpin at the time of the habitat switch as determined from otoliths. The line depicts the mean size of juveniles in the profundal habitat as determined from bottom trawl catches. Error bars indicate ± 1 SE.

DISCUSSION

During the summer of 1992, age-0 juvenile sculpin that initially located in the profundal zone switched habitats by migrating to the littoral zone. Three lines of evidence indicated that juvenile Bear Lake Sculpin shifted habitats through ontogeny: habitat-specific abundances, size-frequency distributions, and changes in the pattern of daily otolith increments. In the littoral zone, juvenile sculpin experienced a trade-off between growth rate and mortality risk as both growth rate and mortality risk were greater in this habitat. The optimal μ/g ratio also occurred in the littoral zone during this summer period, indicating that the growth rate difference was more important than the increase in mortality risk.

Ninety-three percent of all the age-0 fish captured in the littoral zone showed a change in the contrast of their daily increment patterns. Furthermore, few age-0 juveniles returned to the profundal zone before September as evidenced by the consistent contrast of the daily increments of fish captured there. This nonrandom, primarily uni-directional movement of age-0 sculpin from the profundal to the littoral zone during July and August is consistent with the model. This pattern of movement also suggests that once juvenile sculpin encountered the littoral habitat, they did not return to the less profitable profundal habitat before September. It is not clear why larger juveniles began to

move offshore during September contrary to model predictions. This annual offshore migration of adults and larger juveniles is currently being investigated.

The change in contrast of otolith increments with movement to the littoral zone was also accompanied by a significant increase in the width of the daily increments and a concomitant increase in summer growth rate. Although the laboratory-reared fish exposed to a temperature cycle did not develop increments higher in contrast than those exposed to constant temperatures, poor contrast may be an artifact of laboratory conditions. Others have reported nondistinct increment formation in laboratory-reared fishes (see Campana and Neilson 1985).

Our μ/g model predicted that profundal inhabitants should recruit to the littoral zone regardless of their body size (Fig. 11), but the profundal residents switched to the littoral habitat at a wide range of sizes. Given initial profundal residence, this habitat shift is consistent with the model. Results of the examination of the otoliths of sculpin captured in the littoral zone also suggested that more large profundal residents are migrating than small individuals (Fig. 12). Although the model predicted that all fish should migrate, these larger fish would incur a relatively lower probability of mortality in the littoral habitat than smaller migrants. We cannot be sure, however, that larger fish emigrated from the

profundal region at a faster rate than did smaller fish. Smaller fish may have emigrated at the same rate but may have been cannibalized in the littoral habitat before they were captured in our trawls.

The primary benefit of switching habitats appears to be an increase in growth rate. By moving to the littoral zone, juveniles increased the temperature of their environment (and the prey density; Wurtsbaugh and Hawkins 1990) and, according to otolith measurements, significantly increased their absolute growth rate. Observed movements into the littoral zone to increase growth rate are consistent with other behavior of the age-0 juveniles. Neverman and Wurtsbaugh (1994) suggested that age-0 Bear Lake sculpin located in the cold profundal migrate into the water column at night to the relatively warmer metalimnion to increase digestion rates and consequent growth rates. This diel, migratory behavior also suggests that temperature, not food, is limiting growth in the profundal zone. Furthermore, by increasing their growth rates, age-0 juveniles may be increasing their probability of survival by decreasing the time they are vulnerable to predation (Houde 1987; Rice et al. 1987; Miller et al. 1988; Luecke et al. 1990).

Initial habitat residence was not well predicted by the model because contrary to model predictions many juveniles initially resided in the profundal habitat. Given

the apparent benefit of the littoral zone, it is not clear why the fish initially dispersed from a warm, food-rich spawning habitat to the profundal zone. This contradictory behavior may develop for a variety of reasons and two hypotheses appear plausible. First, larval sculpin may be attempting to disperse from a densely-populated spawning area. Second, larval sculpin may not be able to select a specific habitat because of their poor swimming ability.

The initial dispersal away from the spawning habitat by juveniles would also be consistent with an avoidance mechanism of the adult spawning population. Because we could not trawl over rocky substrate, we were unable to estimate the density of the adult spawners. It is likely, however, that adult densities were very high, because nest-site densities exceeding $3 \cdot m^{-2}$ have been measured (J. Ruzycki, unpubl. data). The swim-up behavior that likely induces initial dispersal away from the shallow water spawning habitat may be a mechanism to avoid cannibalism.

Once larval sculpin hatch, habitat selection early in life may be a function of surface water currents. There is some evidence that suggests storm events may trigger sculpin hatching. During 1991, high neuston net catches of larval sculpin occurred at the eastern shore 2 d after a storm event that produced large waves (J. Ruzycki, pers. obs.). Large storms may potentially produce sufficient surface water and alongshore currents (Dillon and Powell

1976; Strub and Powell 1987) to disperse larvae. Currents also are known to be important for the dispersal and survival of ichthyoplankton in marine and estuarine environments (e.g., Simpson 1987; Weinstein 1988) as well as fresh-water systems (Houde and Forney 1970). Larvae are also captured near the surface in neuston nets. Planktonic behavior may increase dispersal via surface water currents. Given the potential for currents, and the weak swimming ability of larval fish, early habitat selection may not be possible for larval sculpin.

Although habitat switching behavior was indicated empirically, and predicted by the model, there was no size threshold at which juvenile sculpin switched habitats as has been reported for other species (Post and McQueen 1988; Werner and Hall 1988). Lack of a discrete size threshold at the habitat shift may be indicative of how juvenile sculpin switch to or select habitats.

It is not likely that juvenile sculpin respond facultatively through an assessment of predation pressure. Bear Lake is probably too large for an inefficient swimmer, such as a sculpin, to avoid predation by retreating to a refuge habitat. Relatively small, structurally complex systems such as those inhabited by bluegill (Lepomis macrochirus) may enable these juveniles to respond facultatively to an environmental variable (Mittelbach 1986). This idea is supported by Post and McQueen's (1988)

observation that horizontal, diel migrations by juvenile yellow perch (Perca flavescens) did not occur in larger systems where the distances traveled were > 200 m. In Bear Lake, a juvenile sculpin that moved from the profundal to the littoral zone would also have to make > 200 m migrations.

If sculpin are not responding facultatively to prey or predator abundance, then another mechanism of dispersal away from the profundal zone must be responsible for movement to the littoral zone. The diel vertical migration to the metalimnion may displace profundal inhabitants. Although not measured, currents within the metalimnion or along the bottom of the epilimnion (Dillon and Powell 1979; Wetzel 1983) may contribute to sculpin dispersal. If these currents are primarily unidirectional, they could incrementally displace fish residing each night near the metalimnion. Diel vertical migrations by juvenile fish in estuaries have been shown to transport these species to favorable habitats (Fortier and Leggett 1983; Boehlert and Mundy 1988). This incremental displacement may also contribute to the higher frequency of larger fish switching habitats (Fig. 12) because the larger, presumably older, fish would have spent more nights in this metalimnetic water mass.

The difference between the mortality factors of each habitat may be too small to operate as a strong selective

factor. According to our estimates of age-1 and older sculpin consumption, there were 11 juvenile sculpin$\cdot$ha$^{-1}\cdot$d^{-1} consumed in the littoral zone during July. This is equivalent to a 0.017 probability of mortality$\cdot$d^{-1} (μ), and is approximately one order of magnitude lower than that reported by Werner and Hall (1988) for juvenile bluegill < 60 mm SL in the open water of their experimental ponds. Perhaps this relatively lower probability of mortality is not a strong enough selective factor to induce discrete habitat selection.

This study revealed that the distribution, behavior, and ontogenetic habitat selection of a juvenile fish during the initial 4 mo of life may be controlled by a complex set of factors not well described by a simple μ/g trade-off model. We believe the observed inconsistencies between age-0 juvenile sculpin behavior and model predictions are a function of the spatial scale of this system, the swimming ability of juveniles, and a lack of facultative responses. The evidence from this study suggests that applications of the μ/g model to this type of system may be limited. Further understanding of sculpin habitat selection through ontogeny will require a more thorough investigation of the manner in which individual fish migrate between habitats and the flexibility of habitat choice.

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APPENDIX

Table A.1. The mean biomass (B) in kg·ha⁻¹ of, and consumption (C) in number·ha⁻¹·d⁻¹ of age-0 juveniles by, age-1 and older sculpin, and the mortality risk (μ) as the probability of mortality per day for age-0 juveniles. All the results for each modeled date and habitat are shown. The estimated biomass is based on 100% trawl efficiency. Lower, actual trawl efficiency would raise these estimates.

Date	Littoral Zone			Profundal Zone		
	(B)	(C)	(μ)	(B)	(C)	(μ)
7/1/92	0.320	11.24	0.0118	0.100	0.88	0.0012
7/15/92	0.224	9.86	0.0364	0.089	0.78	0.0027
7/31/92	0.215	11.58	0.0024	0.131	1.15	0.0023
8/12/92	0.394	13.86	0.0024	0.194	1.71	0.0001
8/26/92	0.354	12.48	0.0007	0.238	2.09	0.0001
9/11/92	0.383	13.74	0.0014	0.133	1.17	0.0013
9/26/92	0.057	3.58	0.0006	0.271	2.38	0.0024

Table A.2. The mean neuston net catches ($\underline{n}$ = number of tows) of larval sculpin ($\pm$ 1 $\underline{SE}$) during 1992.

Distance from	Mean catch $\pm$ 1 SE.			
east shore				
(km)	23 May	29 May	6 June	13 June
	($\underline{n}$ = 7)	($\underline{n}$ = 7)	($\underline{n}$ = 8)	($\underline{n}$ = 7)
0.1	8.5 $\pm$ 3.9	221 $\pm$ 20.2	113 $\pm$ 24.5	0
1	5.5 $\pm$ 0.35	58 $\pm$ 4.6	65 $\pm$ 27.2	0
3	1 $\pm$ 0.71	0	4 $\pm$ 0.71	0
5	0	6 $\pm$ 4.2	1 $\pm$ 0.35	0
7	0	1 $\pm$ 0.71	1 $\pm$ 0.35	0
9	0	2 $\pm$ 0.71	0	0
10	0	0	0	0

Table A.3. Analysis of covariance results from the comparison of the slopes of age-0 sculpin growth rates $(g \cdot d^{-1})$ as a function of fish standard length (SL). The growth rates were compared among the littoral and profundal habitats.

Source	SS	df	MSE	F	p
SL·HABITAT	0.082	1	0.082	10.00	0.002
HABITAT	0.010	1	0.010	1.28	0.260
SL	17.01	1	17.04	2090	0.000
ERROR	0.937	115	0.01		

Table A.4. Analysis of variance results from the comparison of the daily increment counts of 96 otolith pairs by three independent readers.

Source	SS	df	MSE	F	p
READER	0.083	2	0.042	0.00	0.99
ERROR	6020.0	93	64.70		