

**INFLUENCE OF FOOD RESOURCES AND TEMPERATURE
ON THE DISTRIBUTION AND ENERGY BALANCE OF
BEAR LAKE SCULPIN, *COTTUS EXTENSUS***

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**PROJECT F-47-R, STUDY 5
TO THE UTAH DIVISION OF WILDLIFE RESOURCES
SALT LAKE CITY, UTAH**

June 4, 1998

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ABSTRACT--Changes in the abundance, diet, and daily ration of adult and sub-adult Bear Lake sculpin (*Cottus extensus*) were investigated seasonally along a littoral to profundal transect in Bear lake to determine if or when sculpin were food limited. During different seasons, sculpin migrated inshore or offshore. These were most pronounced for age 1+ sculpin, 35-55 mm in length. This age class was most abundant in the littoral zone, particularly in August. The migrations of age two and older sculpin were less pronounced, and most of these fish were located in the profundal zone (>30 m). The sculpin diets also changed seasonally in response to their movements and to seasonal changes in the abundance of chironomids in the littoral and metalimnetic areas, and to increases in the abundance of *Daphnia* in the profundal areas in the summer and fall. The composition of the benthic invertebrates in Bear Lake has changed considerably in recent years, primarily due to increases in *Daphnia*. An analysis of the net energetic balance of sculpin (consumption - respiratory costs) in different depth strata suggested that the migrations were food-related in June and August, but not in October and December. In all seasons, gut fullness of sculpin and daily consumption rates were less than observed in the laboratory under *ad libitum* feeding, indicating that the sculpin were strongly food limited.

INTRODUCTION

In recent years the abundance of Bear Lake sculpin *Cottus extensus* has fluctuated nearly twofold, but the reasons for these fluctuations are unknown (Wurtsbaugh and Luecke 1993). Understanding the reasons for these fluctuations of sculpin are particularly important for two reasons. First, sculpin are endemic to Bear Lake and they are listed as a Species of Special Concern. Because the lake is intensively managed for recreation and water use, we need to be certain that those activities do not harm this endemic population. Secondly, the sculpin are a major prey for the primary sport fish in the lake, cutthroat and lake trout (Nielson and Johnson 1979; Nielson and Lentsch 1988; Wurtsbaugh and Hawkins 1990), and transfer production of benthic invertebrates to these piscivores. Consequently, a healthy population of sculpin is critical for the successful management of the sport fishes in the lake.

The life history pattern of Bear Lake sculpin has been documented in earlier and ongoing studies (Loo et al. 1964; Workman and Sigler 1966; Neverman 1989; Ruzycki 1995; Ruzycki et al. In press). These studies have indicated that Bear Lake sculpin have pronounced ontogenetic and/or seasonal shifts in habitat use in the lake, but it is unknown if these migrations are related to benthic food resources and/or temperature conditions. Additionally, many of these studies have focused on the young-of-year sculpin (Wurtsbaugh and Neverman 1988; Neverman and Wurtsbaugh 1994; Ruzycki et al. In press). As such, a great deal is known about the early life history and seasonal movement patterns of young sculpin, but less information is available for sub-adult and adult sculpin.

In Bear Lake and other lacustrine systems, the abundance and distribution of benthic invertebrates vary greatly with depth (Brinkhurst 1974; Ali and Mulla 1976; Ferraris and Wilhm 1977; Merritt et al. 1984; Wurtsbaugh and Hawkins 1990). Oligotrophic lakes, such as Bear Lake, will often develop two modes in the abundance of benthic invertebrates. The first is usually located in the highly productive littoral area and another at or around

the metalimnetic interface (Brinkhurst 1974). In some seasons invertebrate abundance in Bear Lake has had this pattern (Wurtsbaugh and Hawkins 1990). Explanations of why this variance with depth occurs are weak or have been rarely attempted (Thorp and Diggins 1982).

Food resources may not be the only factor that influences the distribution of sculpin throughout the lake. Most studies on ontogenetic niche shifts have focused on how predators may differentially influence the distribution of different sized fish (Crowder and Crawford 1984; Werner and Gilliam 1984; Mittelbach and Chesson 1987; Persson and Greenberg 1990). An earlier study (Wurtsbaugh and Hawkins 1990) suggested that adult sculpin move away from littoral habitats rich in food, and migrate offshore to areas of the lake with the coldest temperatures and little food. This type of ontogenetic niche shift may reduce intraspecific competition among different life stages (Brandt 1986). Predation has also been shown to mediate habitat shifts. Another hypothesis is that this ontogenetic habitat shift in adult sculpin is to maximize growth. The shift may occur as food-limited fish try to minimize the high metabolic costs associated with life in the warm littoral waters by moving to the deep, cold, profundal. Energy-saving strategies such as this have been proposed for other species (Stockwell and Johnson 1997).

An alternative hypothesis is that by moving to the dark profundal zone adult sculpin can maximize the amount of time spent foraging. Predation can indirectly influence prey by altering prey behaviors (Stein and Magnuson 1976; Werner et al. 1983) such that if there is a foraging rate/predation risk trade off, sculpin may behave differently at different depths, and in different habitats. For example, in deep, dark areas sculpin might forage constantly (Brandt 1980) by using their lateral line to detect prey, as other sculpin do (Hoekstra and Janssen 1985). In contrast, sculpin in the littoral zone may have to reduce their foraging times during light hours to avoid predation (Greenberg and Holtzman 1987; Werner and Hall 1988).

Although the distribution and feeding ecology of sculpin is partially understood (Wurtsbaugh and Hawkins 1990), the question still remains whether or not adult and sub-adult sculpin are food limited, and why they migrate seasonally to different habitats. Several approaches can be used to determine if animals are food limited. Here we examine the distribution of food resources of the sculpin to determine if they distribute themselves along this resource. We also compare seasonal estimates of gut fullness and daily consumption in different habitats with maximum rates measured in the laboratory to address seasonal and depth-related food limitation.

METHODS

Study Area

Bear Lake is approximately 280 km² at full pool. The lake lies in the northeast corner of Utah and the southeast corner of Idaho at an elevation of 1805 m. Due to a tilt-block fault, the bottom of the lake has a gradual slope from the western shore to the deepest point of 63 m located just off the east shore. The geomorphology of the drainage system is predominantly calcareous, and calcium carbonates often precipitate in the lake. As a result, most of the lake bottom is fine marl sediment. Rock substrate is limited throughout the lake, with most being distributed within the upper 10 m of the eastern shore (personal observation). Some macrophyte growth occurs in the shallow portions of the lake, but is sparse and patchy. Bear Lake is typically dimictic, with epilimnetic temperatures reaching 19-23 °C during summer months and profundal temperatures fluctuating near 3-5 °C through the year (Wurtsbaugh and Luecke 1994). Bear Lake is intensively managed for water storage and this contributes to wide fluctuations in water levels and potentially to nutrient loading and lake productivity (Lamarra et al. 1986).

Bear Lake is oligotrophic, with limited capability to produce fish. Chlorophyll a levels are very low, with mean epilimnetic concentrations near $0.5 \mu\text{g}\cdot\text{L}^{-1}$ (Lamarra et al. 1986; Moreno 1989; Wurtsbaugh and Luecke 1994). As a result, crustacean zooplankton densities in the lake are also very low, ranging from 1-5 per liter (Wurtsbaugh and Luecke 1994). It wasn't until recently that *Daphnia* species occurred more than occasionally (Wurtsbaugh and Luecke 1993). Benthic invertebrate abundances are also very low in the lake, with typical biomasses of only $0.34 \text{ g}\cdot\text{m}^{-2}$ dry weight (Erman 1969; Erman and Helm 1971; Wurtsbaugh and Hawkins 1990). Low invertebrate abundance appears to be due to the limited primary production, and/or to the dominance of fine substrates in the lake (Wurtsbaugh and Hawkins 1990).

Bear Lake contains four endemic fish species, three of which are primarily dependent on benthic invertebrates as prey. These are the Bear Lake sculpin (*Cottus extensus*), Bonneville whitefish (*Prosopium spilonotus*), and Bear Lake whitefish (*Prosopium abyssicola*). The Bonneville cisco (*Prosopium gemmifer*) is the dominant zooplanktivore in the lake. Bear Lake cutthroat trout (*Oncorhynchus clarki utah*), the indigenous salmonid of Bear Lake, feed extensively on sculpin, as do the introduced lake trout (*Salvelinus namychush*), and larger Bonneville whitefish.

Field Studies

Seasonal Abundance

To more clearly define the seasonal migrations of sculpin during 1994 and 1995, samples were collected at eight depths along a transect bisecting the middle of the lake (Figure 1). The sampling depths were based in part on the previous study conducted by Wurtsbaugh and Hawkins (1990), and on the gradient of substrate types and temperature. The depths were chosen to reflect the changes from larger sand particles in the littoral zone (2, 3.5,

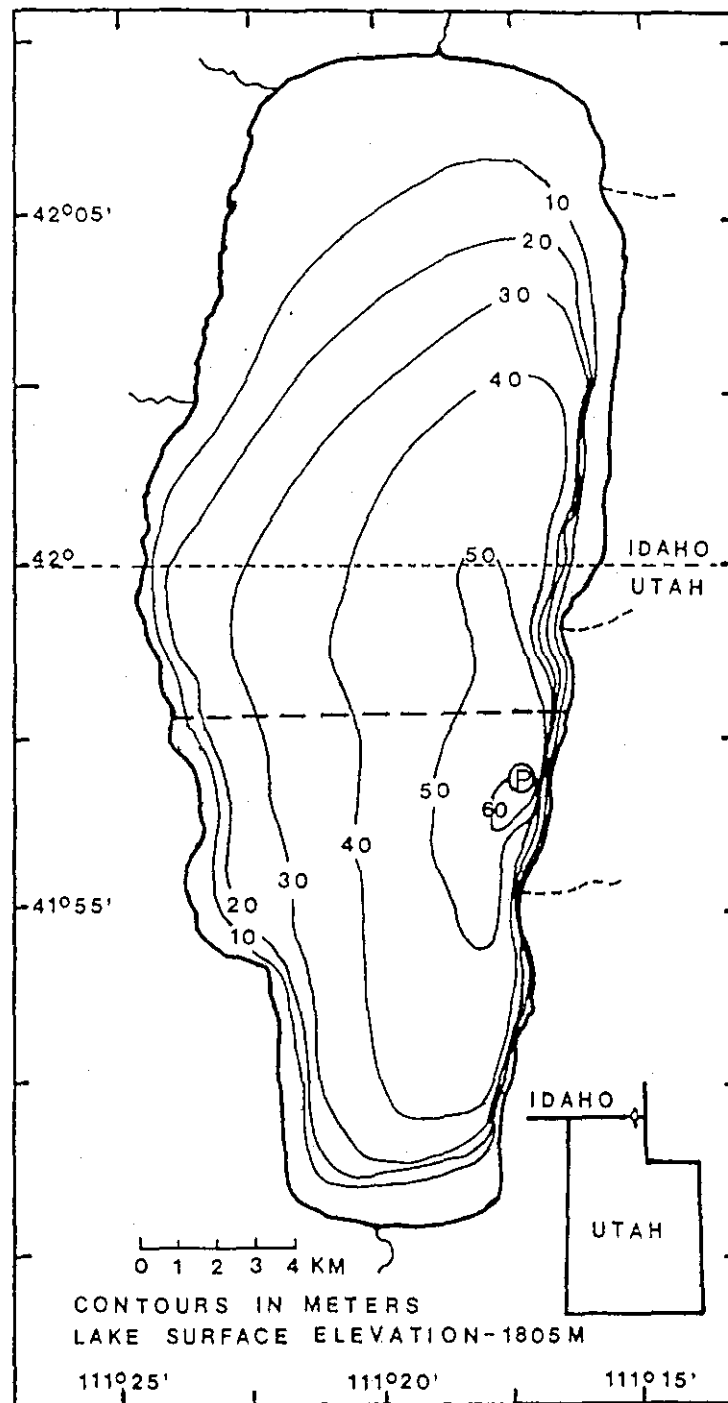


Figure 1. Morphometric map of Bear Lake showing the location of the transect (dashed line) used to sample sculpin and benthic invertebrates.

8 meters), the sand-shell-marl matrix of the metalimnetic interface (16, 25 meters), and the fine marl sediments of the profundal zone (35, 45, 55 meters). The littoral zone (2-10 m depths) was located above the thermocline. During June through September the metalimnetic interface was located between 16 and 25 meters, whereas the profundal zone (35-55 m) was well below the thermocline during the summer. In October the epilimnion eroded and the lake began to mix to a depth of 25 m. In December the lake was isothermal at 3-4°C. The photic zone of the lake extends to approximately 20-25 meters, and daytime light intensities on the bottom of the lake are sufficient for sculpin to feed visually (Neverman and Wurtsbaugh 1994). Temperature profiles were measured during each season to determine the thermal environment of sculpin captured along the transect. Representative temperature and lake elevation data are given in Wurtsbaugh and Luecke (1995) and Wurtsbaugh and Luecke (1996).

Sculpin were sampled in June, August, October and December of 1994 and 1995 using a semi-balloon otter trawl (4.9-m head-rope, 5.3-mm mesh body, and 1-mm mesh cod end), which had a 4-m wide mouth when fished. Trawls were towed at 1 m/s for 20 minutes, traversed 1.20 km, and thus fished 0.48 ha. Trawling was done at night, no earlier than 30 minutes after sunset and no later than 30 minutes before sunrise. All fish captured were enumerated and total lengths were measured.

During each of the four seasons in 1994 and 1995 depth-specific abundance estimates of three size classes of sculpin made to determine if and when adult and/or sub-adult sculpin were changing depths. Relative abundance was calculated from depth-specific trawl capture rates. Due to unknown trawl efficiency, all abundances were considered minimum estimates. Three size classes of sculpin were used to group the fish for analysis (Ruzycki 1995): 1+ year old sculpin, 30-55 mm in length; 2+ fish, 56-69 mm; 3++ and older fish, >70 mm.

The catch rates in the strata were then expanded to show the total number of sculpin between the littoral and profundal zone. Because trawls along the depth transect were closer together in the littoral zone than in the deeper waters, it was necessary to factor the catch rates to represent the different expanses between the strata. For example, density estimates in the 3.5 m strata were assumed to cover an area of 3000 m² along the transect (1200-m long x 2.5-m wide), whereas the abundances in the 45 m strata were assumed to extended over an area four times wider (12000 m²; 1200 m x 10 m). An analysis using the lake's hypsographic curve to expand to whole-lake densities yielded similar results to the calculations shown here.

Benthic Invertebrate Abundance

Benthic invertebrate abundance and biomass were measured during the day along the east-west transect line. During each season, samples were taken at 3.5, 16, and 45 m. In June and August 1994, additional samples were taken at depths of 1, 8, 25, 35, and 55 m to better define invertebrate abundances. At each depth, three samples were taken separated along the depth contour by no less than 200 m. The benthic invertebrates were collected with a 0.053 m² Ponar dredge that removed the top 15 cm of sediment. Samples were sieved through a 0.5 mm standard screen to remove the large macroinvertebrates in size classes preyed upon by sculpin.

The invertebrates were separated, identified and counted. Although detailed taxonomic classification was conducted on some groups, here we present the data in the following general taxa: cladocera, copepoda, and amphipoda, arachnoids, worms, ostracods, chironomids, and other insects. Length measurements and length-weight regressions (Wurtsbaugh and Hawkins 1990) were used to calculate the biomass of each taxa.

Diel Feeding Periodicity and Diet Analyses

The diel feeding periodicity of sculpin was determined at three depths (3.5, 16, 45 m). This was done one time in each season in 1994, and two times in each season in 1995.

Most of the same trawling procedures were used for the feeding analyses as for the abundance analyses. We sampled every 2-3 hours in 1994, and every 6 hours in 1995 using a 3.9 m head-rope trawl. This trawl was more effective in capturing sculpin during the day than the larger trawl. When densities were low, several replicate trawls were made in a depth stratum in an effort to catch adequate numbers of fish. If available, ten fish from each size class from each depth were euthanized and preserved in 10% formalin. A total of 2,618 fish were analyzed. The wet weight of each fish, without the stomach contents, was measured in the laboratory, and the contents of each stomach was dried to a constant weight.

Gut fullness was used to determine the diel feeding periodicity as well as to make consumption estimates. Gut fullness was calculated as:

$$(2) \quad F_t = G_t * 100 / W_t$$

Where F_t is gut fullness for time period t , G_t was the mean dry weight (grams) of the stomach contents for each time interval and W_t was the mean dry weight (grams) of the fish without the stomach contents. Dry fish weights were calculated from wet weights, using the following, empirically-derived equation:

$$\log (\text{dry weight, g}) = -0.6452 + 1.0526 \log (\text{wet weight}) \quad r^2 = 0.991$$

This equation accounts for a shift in percent dry weight of sculpin from 20% at 0.1 g, to 26% at 10 g.

The diet of the different size classes of Bear Lake sculpin was also determined from the ten fish from each size class of the fish captured during the diel sampling. Items found in the guts of the individual fish were identified, enumerated, and measured to provide an estimate of the taxa-specific dry biomass.

Consumption estimates

We estimated daily consumption of benthic invertebrates using the sculpin collected in the diel studies. Daily consumption (D) was calculated by the method of Bajkov (1935) because gut fullness varied relatively little over the diel cycle. With this method the mean daily gut content is multiplied by the instantaneous gut evacuation rate. The mean daily gut content was estimated from the measurements of gut weight during the 24-hr period. To convert the consumption to energy units, we assumed a caloric content of 16,700 Joules/g for the mixed food types and 20,800 Joules/g for the sculpin. Gut evacuation rates were first calculated using data from digestion experiments conducted in our laboratory (Lay (unpublished), Wurtsbaugh and Neverman 1988, and Orme and Wurtsbaugh (unpublished)). However, these rates were erroneously low, usually predicting energy intake rates below daily estimated respiration rates, and below those of other fish (He and Wurtsbaugh 1993). Consequently, we used the empirical equation of He and Wurtsbaugh (1993) to estimate gut evacuation rates as a function of temperature (T, C) and food particle size (PS, g):

$$R_g = 0.049 e^{[0.072 \cdot T - 0.060 \ln(PS)]}$$

This equation is most responsive to temperature, and relatively insensitive to estimates of prey size. Estimated instantaneous digestion rates varied from 0.10 h⁻¹ at 4.6 C, to 0.32 h⁻¹ at 20.7°C. Mean dry weights of prey were estimated to be 1700, 210 and 11 µg for littoral, metalimnetic intersect, and profundal fishes, respectively. These were based on

estimated prey sizes of 8, 4 and 1.5 mm in the respective depth strata, and on the generalized invertebrate length-weight relationship of (Wetzel and Likens 1991).

Laboratory studies

Maximum Daily consumption and Maximum Gut Fullness

Maximum daily consumption rates (C-Max) were measured in the laboratory. Groups of 30-40 sculpin from the three size classes were held in glass aquaria immersed in four temperature-controlled water baths of 5, 10, 15, and 20° C. The fish were acclimated to their experimental conditions by raising the temperatures 0.5°C per day until the desired level was reached, and then holding them at that temperature for one additional week prior to an experiment. During acclimation the fish were fed amphipods to allow them to become adjusted to this prey. Amphipods were used in the experiments, as they were readily available and because they are a common diet component of sculpin. Preliminary experiments showed that starving the sculpin 24-72, depending on temperature, would ensure that their guts would be empty prior to the experiment. In the experiments, groups of 20-30 fish in a size class were fed a measured excess of amphipods. After 72 hours the remaining amphipods were removed and weighed to determine the amount consumed. The maximum consumption rate was calculated as the mean 24-hour consumption rate (Joules fish⁻¹ day⁻¹). These rates were compared with the actual amounts consumed by sculpin from the field.

Another approach used to determine if sculpin were food limited was to determine the maximum gut fullness of sculpin. For this, groups of sculpin were acclimated to the experimental temperatures, starved, and then fed to satiation with amphipods. After feeding ceased, the fish were euthanized, and the gut fullness determined as described previously.

Calculation of the energy balance.

The energy balance (growth potential) of different-sized sculpin in the different depth strata was calculated as the difference between consumption and loss factors according to:

$$\text{Net Energy (En)} = C \cdot A - \text{SDA} - R$$

Where:

C = Daily consumption

A = Assimilation rate = 0.80

SDA = Specific Dynamic Action = $0.15 \cdot C$

R = Routine metabolic rate

Consumption rates of sculpin in the field were calculated as described above. Assimilation rates were assumed to be 80% of ingested food and specific dynamic action (SDA) was assumed to be 15% of ingested food (Wootton 1990). Respiration rates (R, joules/day) of sculpin were taken from the measurements given in Wurtsbaugh and Luecke (1993) and described by:

$$\text{Log}_{10} R = 1.055 + 1.009 \text{ Log}_{10} T + 0.0702 \text{ Log}_{10} W \quad r^2 = 0.989$$

where:

T = temperature °C

W = dry weight of the fish (g)

If net energy gain determines the sculpin movement patterns, we would expect a positive correlation between that parameter, and the distribution of the sculpin along the depth

transect. To analyze this, the net energy gain for a size class within a season was normalized by dividing the gain in each stratum by the mean for all three depth strata:

$$E_R = E_n / E_{\text{mean}}$$

where:

E_R = Relative net energy gain for a size class in a depth stratum during a season

E_n = Energy gain for a size class in a particular depth stratum during a season

E_{mean} = Mean energy gain for a size class in a stratum during a season

A value of 2, for example, would indicate that sculpin at that depth realized twice the net energy gain as they averaged for all the strata. The relative abundance of sculpin was then regressed against this parameter to determine if the fish sought out regions yielding the highest energy gain.

RESULTS

Ontogenetic changes in distribution

The seasonal distributions of sculpin of different sizes were markedly different (Table 1), as indicated by a significant age class by depth by season interaction term in an analysis of variance (ANOVA). The analysis of sculpin densities indicated, however, that there were no significant differences between years ($p > 0.05$). Figure 2 shows some of the distribution patterns of the sculpin. In June 1995 the 1+ sculpin occurred throughout the different depth strata, but the highest densities were found at the metalimnetic intersect (25-35 m) and in the shallow littoral zone. By August the distribution had shifted and most of the sculpin in this size class were in the littoral zone or upper portion of the metalimnetic

Table 1. Mean densities (#/ha) of sculpin of different age classes at different depths and in different seasons.

DEPTH (m)	JUNE			AUG			OCT			DEC		
	AGE 1	AGE 2	AGE 3++	AGE 1	AGE 2	AGE 3++	AGE 1	AGE 2	AGE 3++	AGE 1	AGE 2	AGE 3++
2	64	13	2	21	15	0	157	6	5	15	1	1
3.5	103	3	3	261	66	8	89	1	1	33	5	1
8	22	4	2	161	68	14	39	2	2	15	1	0
16	13	3	8	67	65	14	1	0	0	7	2	3
25	45	11	5	42	33	5	247	29	17	39	3	7
35	46	15	15	3	24	26	121	84	70	236	22	21
45	23	21	24	3	6	4	30	102	172	223	59	147
55	53	58	45	45	83	63	50	119	140	166	141	153

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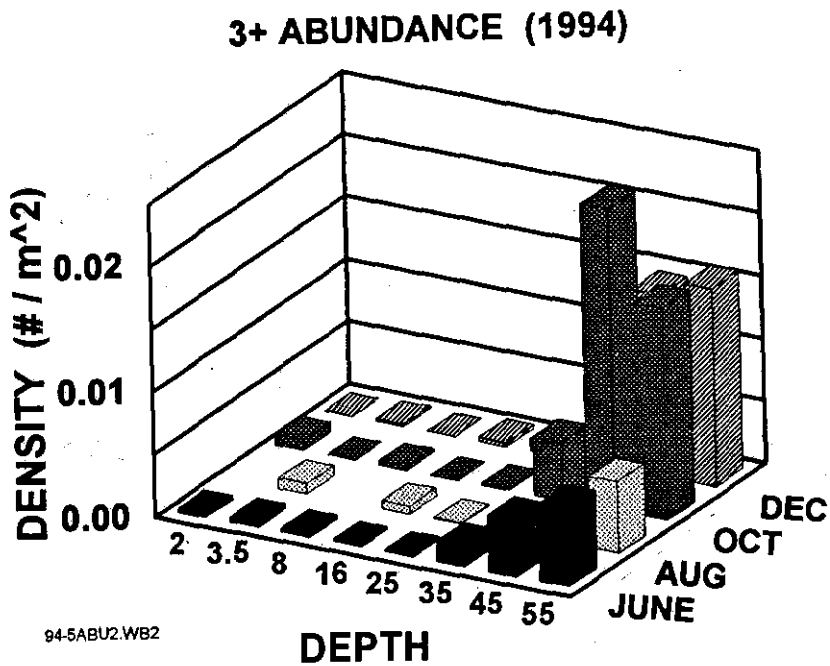
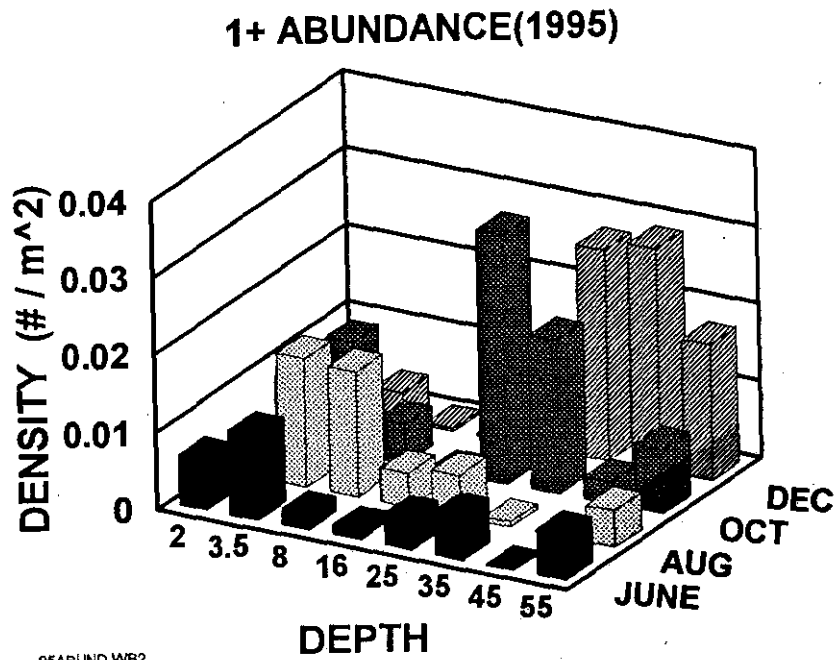


Figure 2. Examples of sculpin distribution patterns during four seasons. Above: distribution of age 1 sculpin during 1995. Below: distribution of age 3+ sculpin in 1994. Densities shown are minimums because the trawl used for sampling may be less than 100% efficient.

intersect, and very few were in the profundal region. In October a large proportion of the fish moved to the lower metalimnetic intersect, and in December they migrated even deeper and were found primarily between 35 and 45 m.

The 2+ fish were found relatively deeper than the 1+ fish throughout the year (Table 1). In June they were mostly concentrated between 25 and 55 m. In August the distribution was relatively even between the littoral and profundal zones, but with a maximum at the metalimnetic intersect (16 m). In October, and especially in December, the fish moved into the deep profundal zone.

The 3++ sculpin were located in the profundal or metalimnetic intersect throughout the year, with few using the littoral zone (Figure 2). In June the highest densities were between 35 and 55 m. In August, some of the fish shifted into the littoral zone, but most were still found in deeper waters. In October and December the 3++ fish migrated into the profundal, and were distributed much like the other size classes.

Table 1 summarizes the 1994-95 distribution data, and adjusts it to represent the different expanses between the strata. For example, densities from Figure 2 in the 3.5 m strata were assumed to cover an area of 3000 m² along the transect (1200-m long x 2.5-m wide), whereas the abundances in the 45 m strata extended over an area four times larger (12000 m²; 1200 m x 10 m). An analysis using the lake's hypsographic curve yielded similar results to the calculations shown here.

When the data were adjusted to show the abundances in different depth zones of the lake, it is apparent that the littoral zone was relatively less utilized by sculpin than were the profundal and metalimnetic interface zones (Figure 3). These data again show differential habitat use by different size classes of sculpin. Age 1+ sculpin were relatively more abundant in the littoral zone from June through October than were older age classes, but even then, less than 50% of the young fish occurred in the shallow water. Older sculpin

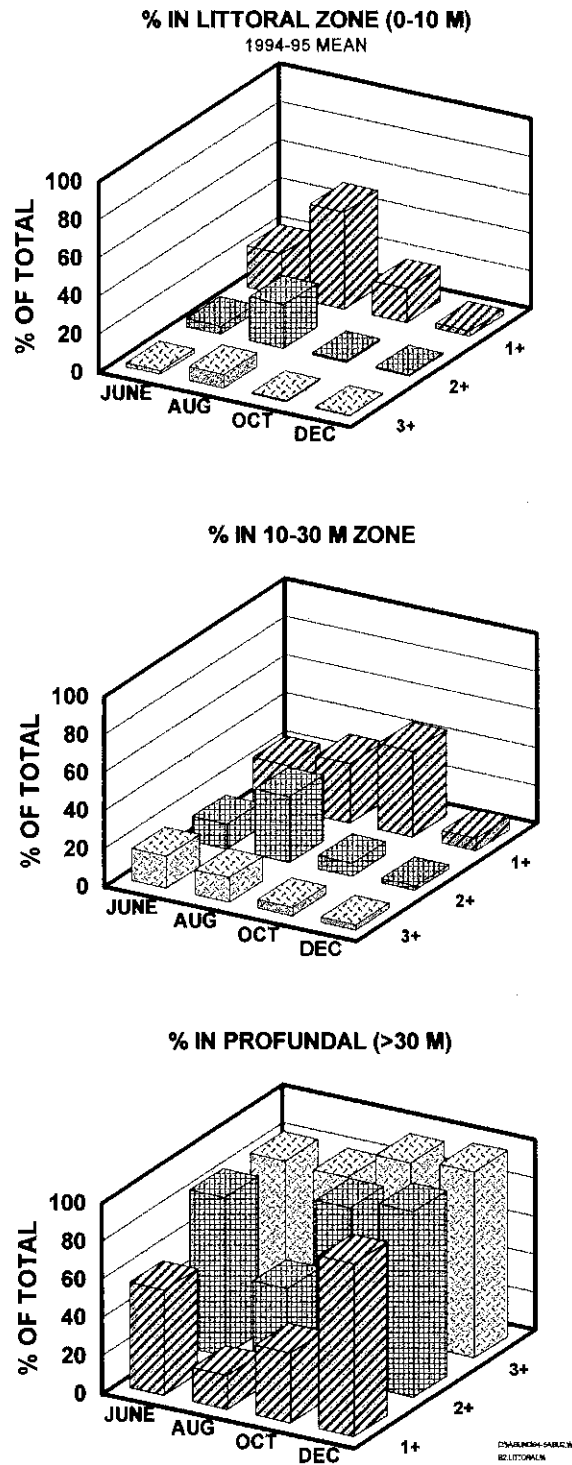


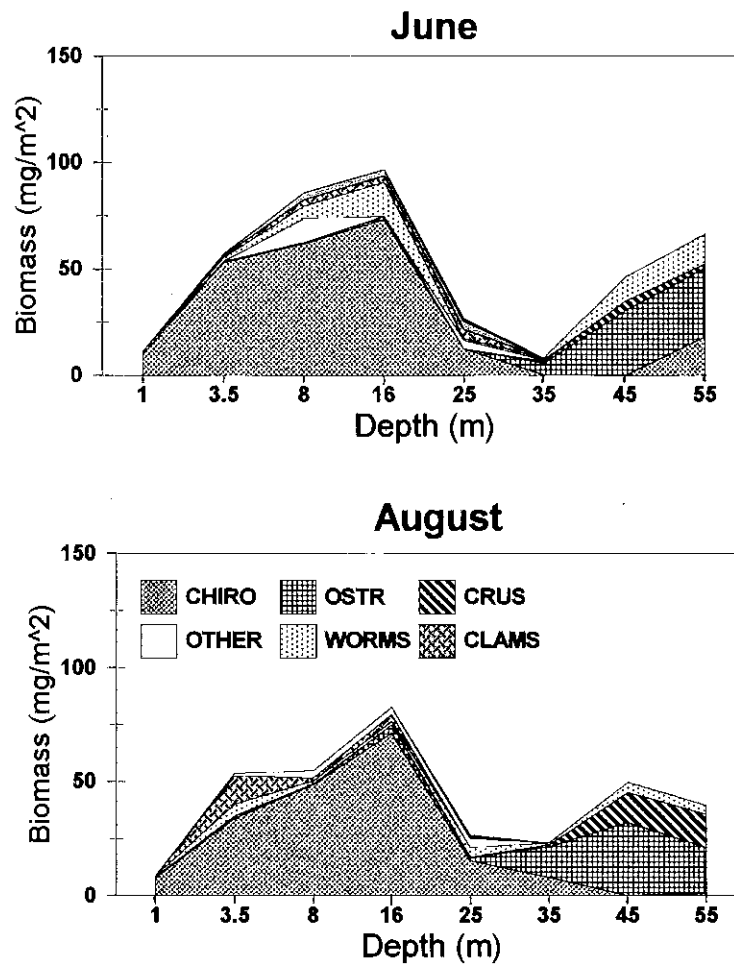
Figure 3. These data show the mean 1994 and 1995 distribution of sculpin of three size classes (+1, +2, +3) in three depth strata of Bear Lake. The distributions are corrected for the amount of area in the lake that are covered by those depth strata. Note reversal of age classes of fish in the last frame. The average between-year variance (SE) was 15% of each mean.

used the littoral zone even less, and were most abundant there in midsummer. The metalimnetic interface (10-30 m) had an intermediate abundance of sculpin, with differential temporal use by the different size classes. The profundal zone in Bear Lake harbored the largest proportion of each size class during most of the year. In June and December, more than 50% of all size classes occurred in water >30 m. In August and October the 2+ and 3++ fish were still concentrated in the deeper waters, and only 1+ sculpin were not abundant there. Because 1+ sculpin are more abundant than the other size classes, the littoral zone supports a greater total number of fish during these seasons than do the other strata.

Benthic Invertebrate Prey Abundance

Biomasses and densities of benthic invertebrates varied markedly with changes in depth. In June, chironomids and ostracods dominated the biomass of prey available (Figure 4). Prey biomass was low at 1 m but increased up to a depth of 16 m due to increasing densities of chironomids. The low biomass in the 1-m area may have been due to this area being inundated for only 1-2 months prior to sampling. Below the shallow littoral zone, invertebrate biomass declined with depth to 35 m as chironomids declined. In the deep profundal zone biomass increased again due to an abundance of ostracods, chironomids and crustaceans. The crustacean component was dominated by *Daphnia*, but also included some copepods.

In August, the biomass distribution was similar to that observed in June. Biomass was again low at 1 m and completely dominated by chironomids. Biomass increased substantially with depth up to 16 m due to chironomids, decreased between 25 and 35 m, and then increased again at the two deepest profundal stations. At 55 m approximately 40% of the biomass was due to *Daphnia*.



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Figure 4 . Biomass of benthic invertebrates in Bear Lake during June and August, 1994. Items shown in heavy shading are the primary food items of sculpin.

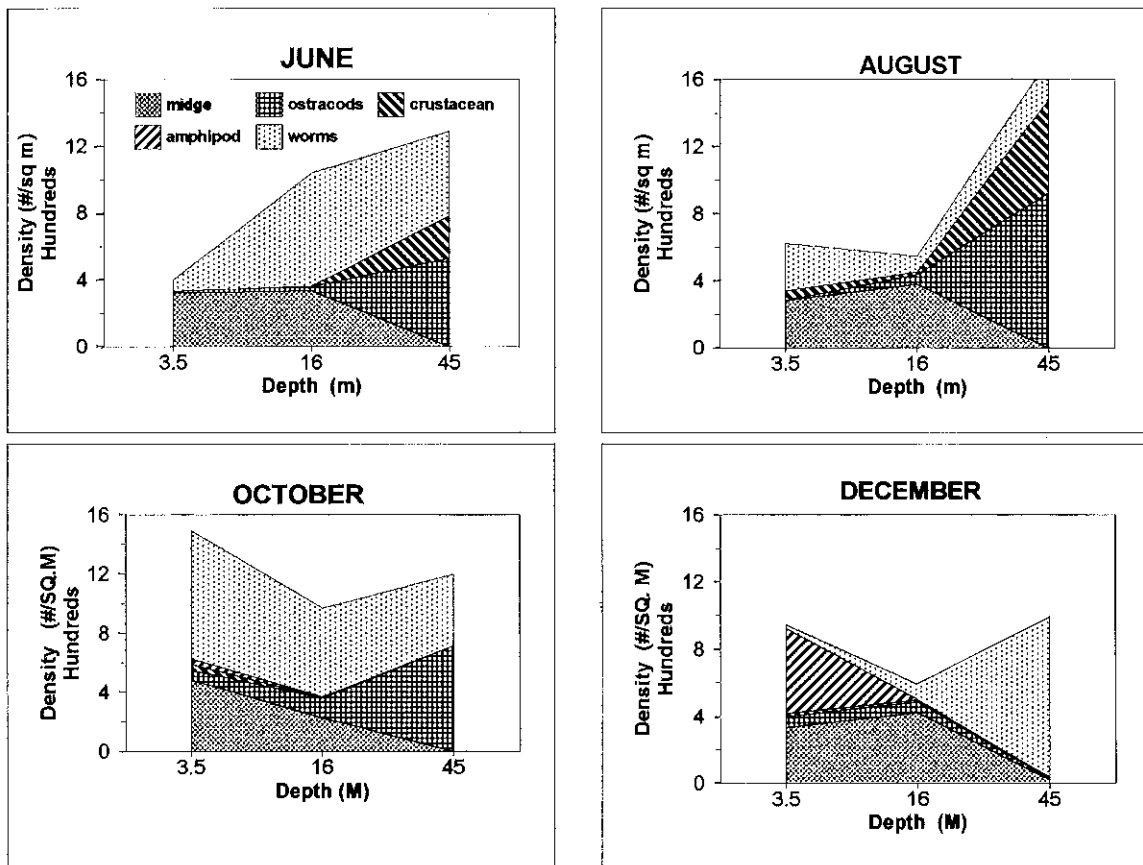
The seasonal analysis revealed substantial differences in prey abundance and distribution between the June-August period, and the October and December periods (Figure 5). Densities of organisms either varied little with depth (October and December), or increased with depth (June, August). In June the increases were due to larger numbers of worms (annelids and nematodes), ostracods, and crustaceans. The increase at 45 m was particularly apparent during August, when the combined densities of ostracods and crustaceans reached 1,500 m⁻². In October, overall densities were relatively stable between depths, but ostracods replaced chironomids in the deeper strata. In December, chironomids and amphipods were abundant at 3.5 m. At 16 m only chironomids were abundant, and at 45 m only worms were plentiful.

Invertebrate biomass, which is probably the best indication of the availability of prey for sculpin, also varied substantially between the June-August period, and the October and December periods (Figure 6). June and August had similar low prey biomass, and relatively little variability in the total biomass among the three depths. In October, prey biomass increased 2 to 5-fold in the littoral and metalimnetic interface zones, due to increases in chironomids and amphipods at 3.5 m, and ostracods at 16 m. In December, prey biomass was very high in the littoral zone due to increases in chironomids. Biomass decreased markedly with depth, however, and extremely little prey was available in the profundal zone (45 m).

Sculpin Diets

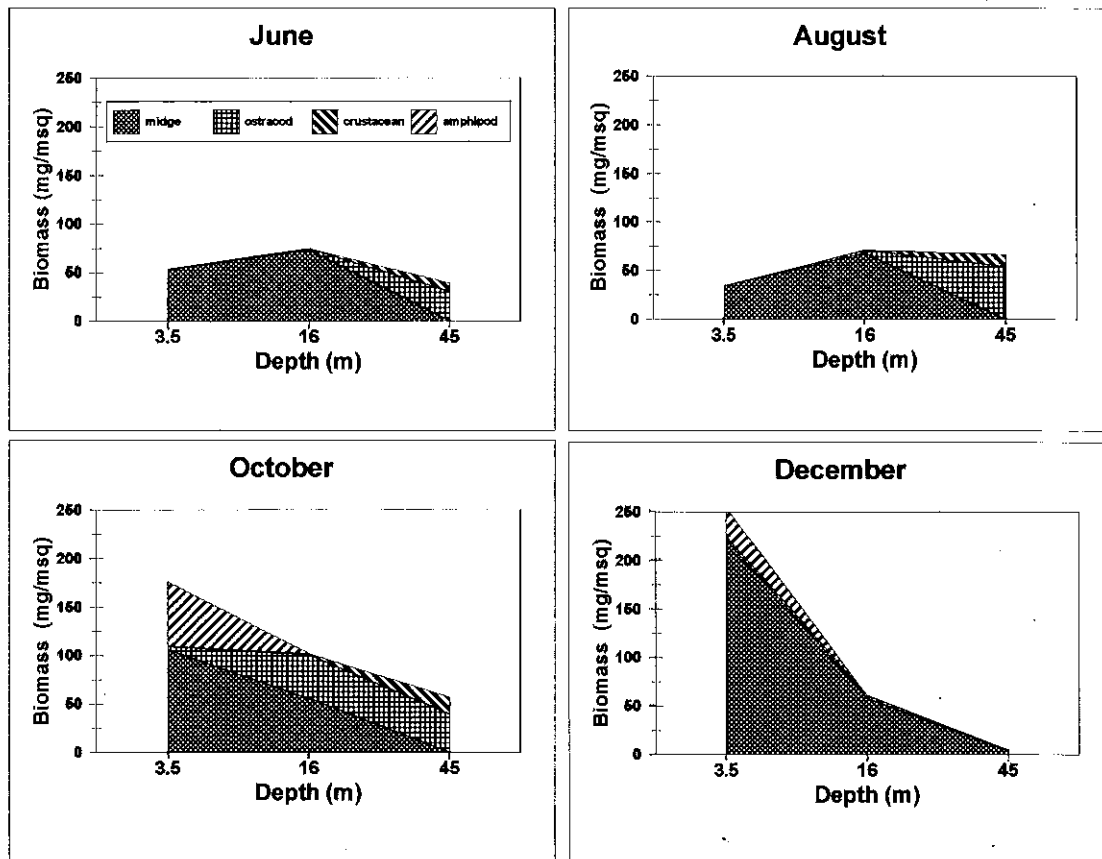
The sculpin diets reflected changes in prey availability in different seasons and different depths. A detailed analysis of the diets is shown in Appendix 1. This information is summarized in Figure 7.

Diets changed relatively little as fish size changed. Chironomids represented approximately 20-30% of the diet for all size classes. Ostracods were the most important



B_invert2.wb2

Figure 5. Densities of benthic invertebrates in Bear Lake during four seasons of 1994.



BINUMS.WB2

Figure 6. Benthic invertebrate biomass in Bear Lake during four months in 1994. Shown are the principal diet items of sculpin. Oligochaetes are not included in the graph, as they were seldom eaten by sculpin. CHIRO - chironomid larvae and pupae; OST = ostracods; CRUS = crustaceans (primarily *Daphnia*); AMPH = amphipods.

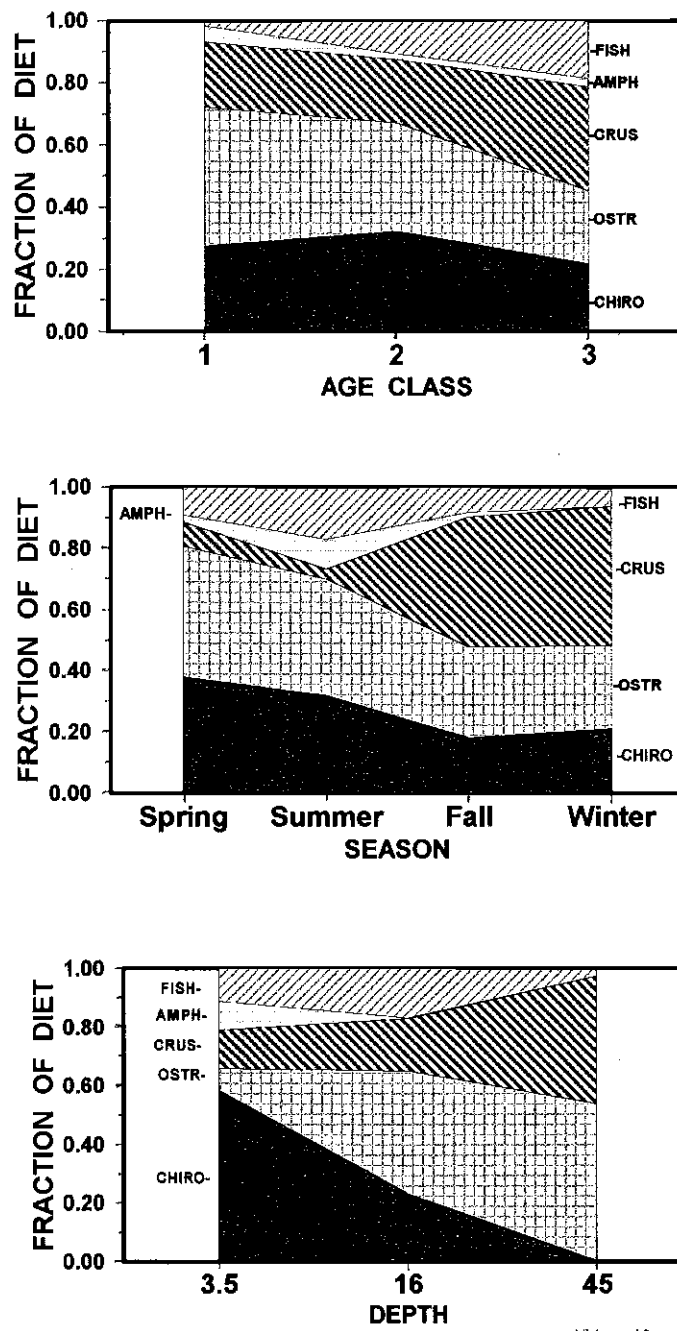


Figure 7. Summary of Bear Lake sculpin diets during 1994 and 1995. Above: Diet variation with changes in age class. Middle: Seasonal diet changes. Below: Changes in diet with depth.

prey, contributing 50% of the prey biomass for the smallest sculpin, and 25-37% for the other two size classes. Crustaceans (*Daphnia*) were also important, representing 20-38% of the diet of all size classes. Fish (primarily other sculpin) became relatively more important as the sculpin grew, but only represented about 20% of the diet in the largest size class. Amphipods contributed a small amount to the diets of all size classes.

Seasonal changes in diets were most responsive to changes in the abundances of *Daphnia* and amphipods. In the spring (June), the diets were dominated by ostracods, chironomids, and lesser amounts of other prey. In the summer the diets were similar to those in the spring, but the importance of amphipods in the diet had increased. In the fall and winter when *Daphnia* were more available, nearly 50% of the diet consisted of these crustaceans, and they were even more important in the diets of the largest sculpin which resided primarily in the profundal zone where these invertebrates were most abundant (cf. Figure 4, Appendix 1).

Diet changes were most apparent with changes in depth strata (Figure 7, bottom). At 3.5 m in the littoral zone chironomids represented 60% of the prey, and the remainder was divided among the other prey categories. Amphipods were only important as a diet item in the littoral area. At greater depths, chironomids became less important in the diets, and they were insignificant for the fish at 45 m. With increasing depth, ostracods and crustaceans (*Daphnia*) became increasingly dominant in the diet.

Food consumption of sculpin

Laboratory studies

Sculpin fed amphipods *ad libitum* in the laboratory consumed large rations. Maximum gut fullnesses were near 5% of the body weight of the sculpin. Maximum daily rations were influenced by body size and by temperature (Table 2). Daily rations ranged from 390

Table 2 . Maximum consumption rates of sculpin in laboratory experiments. The 3+ fish at higher temperatures may have been stressed, and consequently not eaten as much as possible.

AGE CLASS	TEMPERATURE (C)	Consumption	
		G/FISH/D	J/FISH/D
1+	5	0.031	522
1+	10	0.049	818
1+	15	0.157	2625
1+	20	0.169	2832
1+	5	0.023	385
1+	10	0.049	820
1+	15	0.100	1674
2+	5	0.039	648
2+	10	0.086	1434
3+	10	0.335	5602
3+	15	0.367	6151
3+	20	0.545	9122

CONSUME2.WB2.SUMMARY

joules/day for the smallest size class of sculpin kept at 5 C, to 9100 joules/day for the largest sculpin at 20 C. Maximum daily ration (R_{\max}) was defined by:

$$\text{Log } R_{\max} = 2.04 + 0.279 (\text{Age}) + 0.060 C \quad n = 12, \quad r^2 = 0.924, \quad p < 0.001$$

where:

Age = Age class (1, 2 or 3)

C = Temperature

Field studies

Field studies of gut fullness indicated that diel changes in feeding were limited. Figure 8 shows an example of gut fullnesses during one of the 12 diel studies that were conducted. For age 1+ sculpin gut fullness was generally highest at 45 m, and lowest at 16 m. The stomachs were fuller at night than during midday. Age 2+ sculpin had a similar pattern, with the exception that gut fullnesses were similar at 3.5 and 16 m. Age 3++ sculpin showed the least diel variation in stomach fullness, and nearly all the stomachs from fish collected at 3.5 m were empty. Maximum gut fullness indices were generally much lower than the maxima observed in the laboratory. Only when a sculpin had digested another fish (usually another sculpin), did gut fullness approach (or surpass) the 5% maxima observed in the laboratory.

The results of the diel studies were summarized by taking the average gut fullness for a size class of fish over the 24-h period (Figure 9; Appendix 2). A 3-way ANOVA was used to test differences in gut fullness in the different age classes, seasons, and depth strata (Table 3).

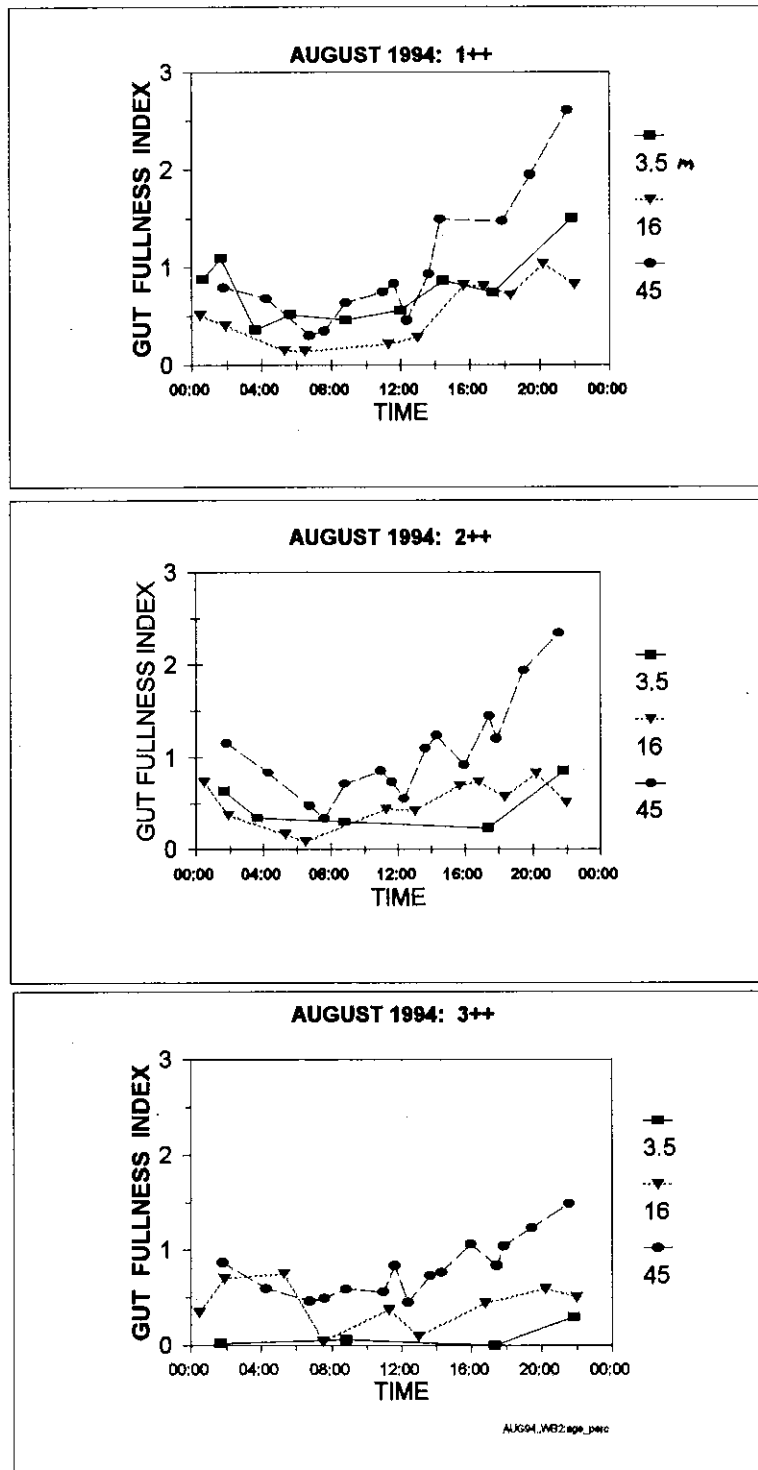
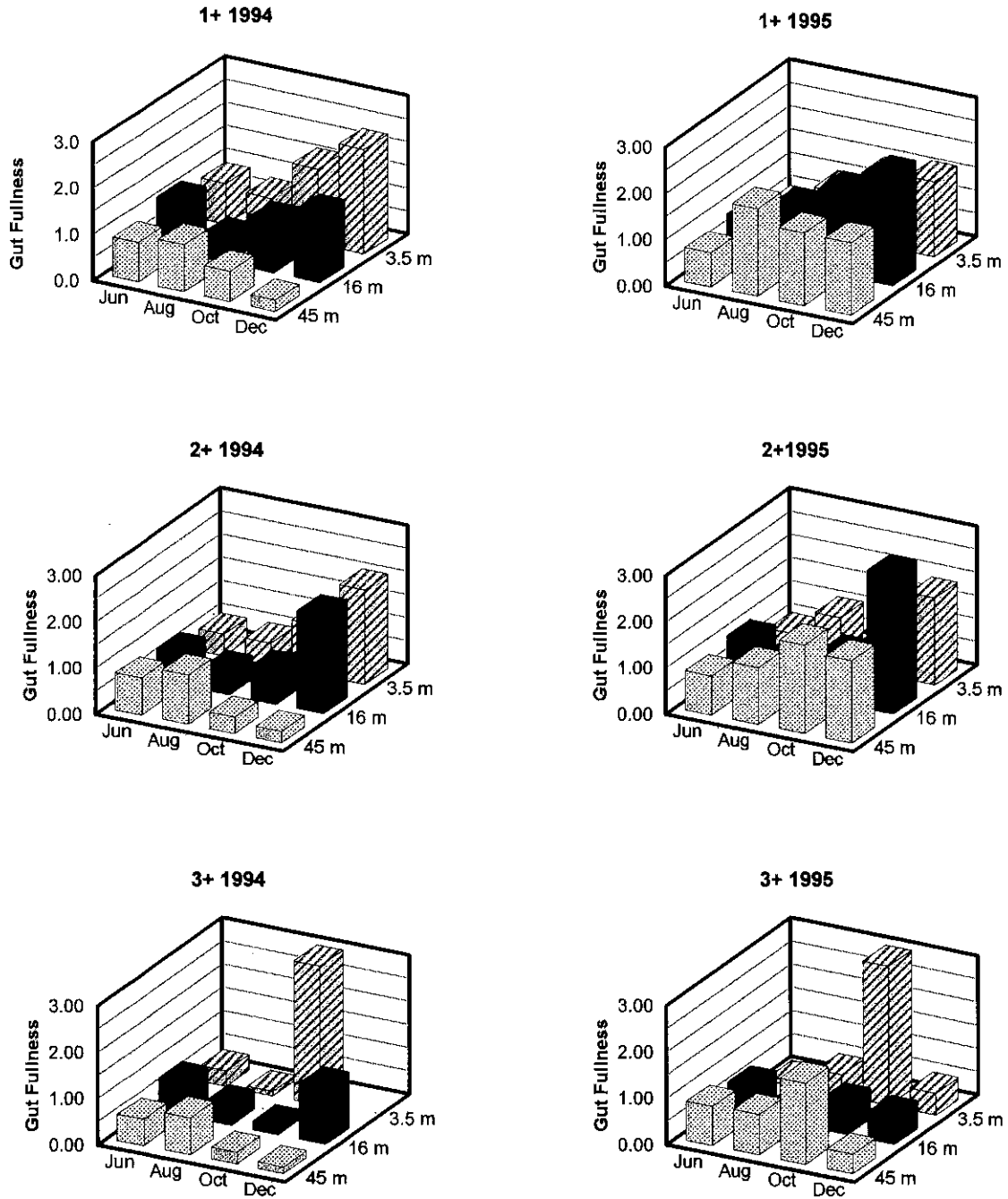


Figure 8. Diel changes in the gut fullness indices of Bear Lake sculpin of three different size classes in three different depths during the month of August, 1994. Each point shows the mean gut fullness of 4-10 sculpin.

Sculpin Gut Fullness Index (%) 1994-1995



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Figure 9. Mean gut fullness indices of Bear Lake sculpin in 1994 and 1995 at three depths and during four seasons.

Table 3. Analysis of variance of gut fullness data of Bear Lake sculpin. Samples with less than 5 fish captured over the diel period were excluded from the analysis.

Source	SS	DF	MS	F	P
Age	2.901	2	1.451	7.42	0.002
Year	1.724	1	1.724	8.82	0.005
Season	2.080	3	0.693	3.55	0.021
Depth	0.032	2	0.016	0.08	0.922
Error	9.582	50	0.196		

Gut fullnesses were highest for age 1+ and lowest for 3++ sculpin. Fullnesses were significantly higher in 1995 than in 1996, and they were significantly higher in October and December than in other months. A subsequent ANOVA indicated that there was a significant ($p < 0.001$) season x depth interaction. This was most evident in 1994 where gut fullnesses declined in deeper waters in October and December, but remained high in shallower water. Surprisingly, gut fullness did not vary significantly with depth.

Gut fullness was significantly correlated with the biomass of invertebrates available in a particular depth strata and season ($p < 0.001$; Figure 10). Gut fullnesses were particularly low in the profundal zone during December when negligible amounts of prey were available, and particularly high in the littoral zone during the same month when prey abundance was at its maxima. Despite the strong correlation, there was still considerable scatter in the data. In part, this was a consequence of relatively small numbers of sculpin available from some trawls, so that the mean daily gut fullness was frequently calculated

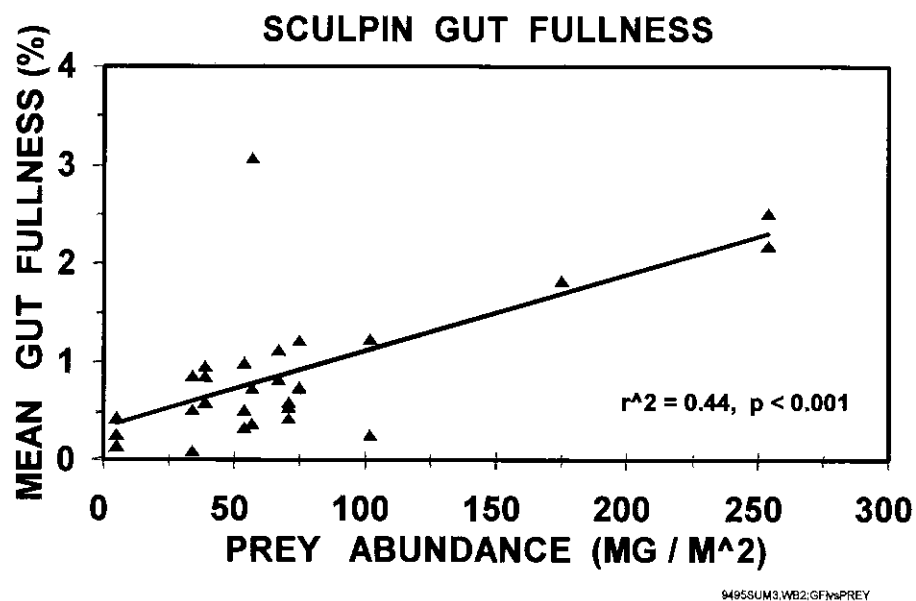


Figure 10. Relationship between the biomass of prey in different strata and seasons, and the gut fullness of sculpin during 1994. Gut fullness was calculated as the daily average gut content. The outlier with a gut fullness >3% was for a sample where only 8 fish were available to determine the daily average. Data sets where less than 5 fish were available were highly variable, and were removed from the analysis.

with less than 10 fish (Appendix 2). Net energy return was also correlated with prey abundance (Figure 11; $p < 0.002$), and was particularly high in the littoral zone in October and December, and low in the profundal zone in December.

Although gut fullness was not correlated with depth, estimated consumption rates were almost always higher in the warmer, shallower strata, than in the deeper waters (Figure 12). This is because gut evacuation rates increase exponentially with temperature, so that equal volumes of food in the gut are processed much faster in warm water than in the cold profundal waters.

Although food consumption rates were higher in shallow than in deeper waters, estimates of the net energy balance (growth potential) did not show distinct overall patterns with temperature (Figure 13). Other patterns were, however, evident. In 1994 the littoral zone (3.5 m) yielded increasingly high net energy balances for 1+ and 2+ sculpin as the seasons progressed from June through December. This increase reflects the increasing food supply in the littoral zone, combined with the low metabolic costs there in December when the littoral zone was cold. The energy balance analysis suggests that the 3++ fish maintained the highest energy balances in 1994 by remaining in deeper waters from June through October (Figure 13). In December, however, the energy balance was very low at 45 m. For 1995, the energy balance analysis suggested that the metalimnion intersect (16 m) and profundal areas (45 m) usually provided the highest growth potential for all size classes of sculpin (Figure 13).

The comparison of relative net energy gain with distribution patterns indicated that sculpin sought out areas for good growth in June and August, but not in October and December (Figure 14). A regression analysis of the June and August data indicated a significant correlation between the percentage of the fish within a strata, and the relative net energy gain in that stratum ($p < 0.03$). Analysis of Figure 14 indicates that during these months the fish tended to avoid areas of low relative energy gain, but that there was limited

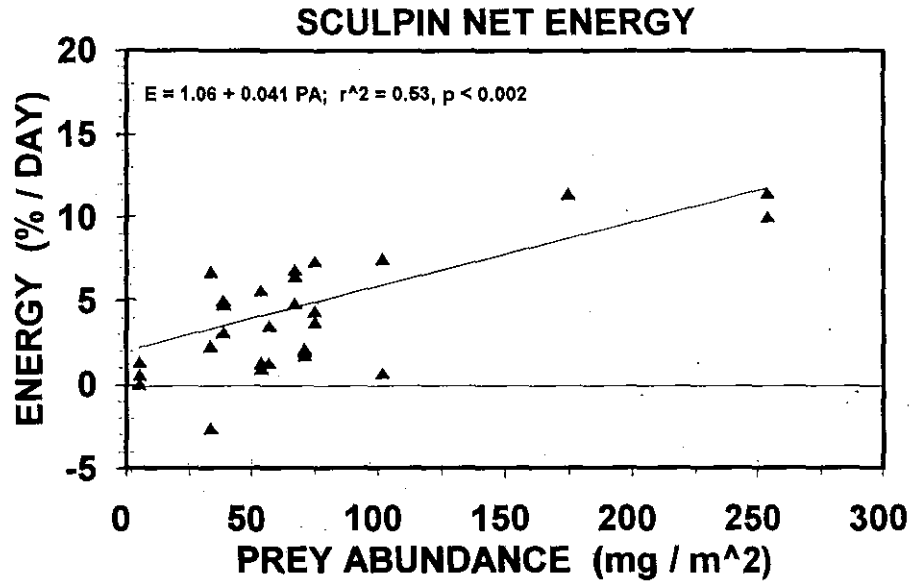
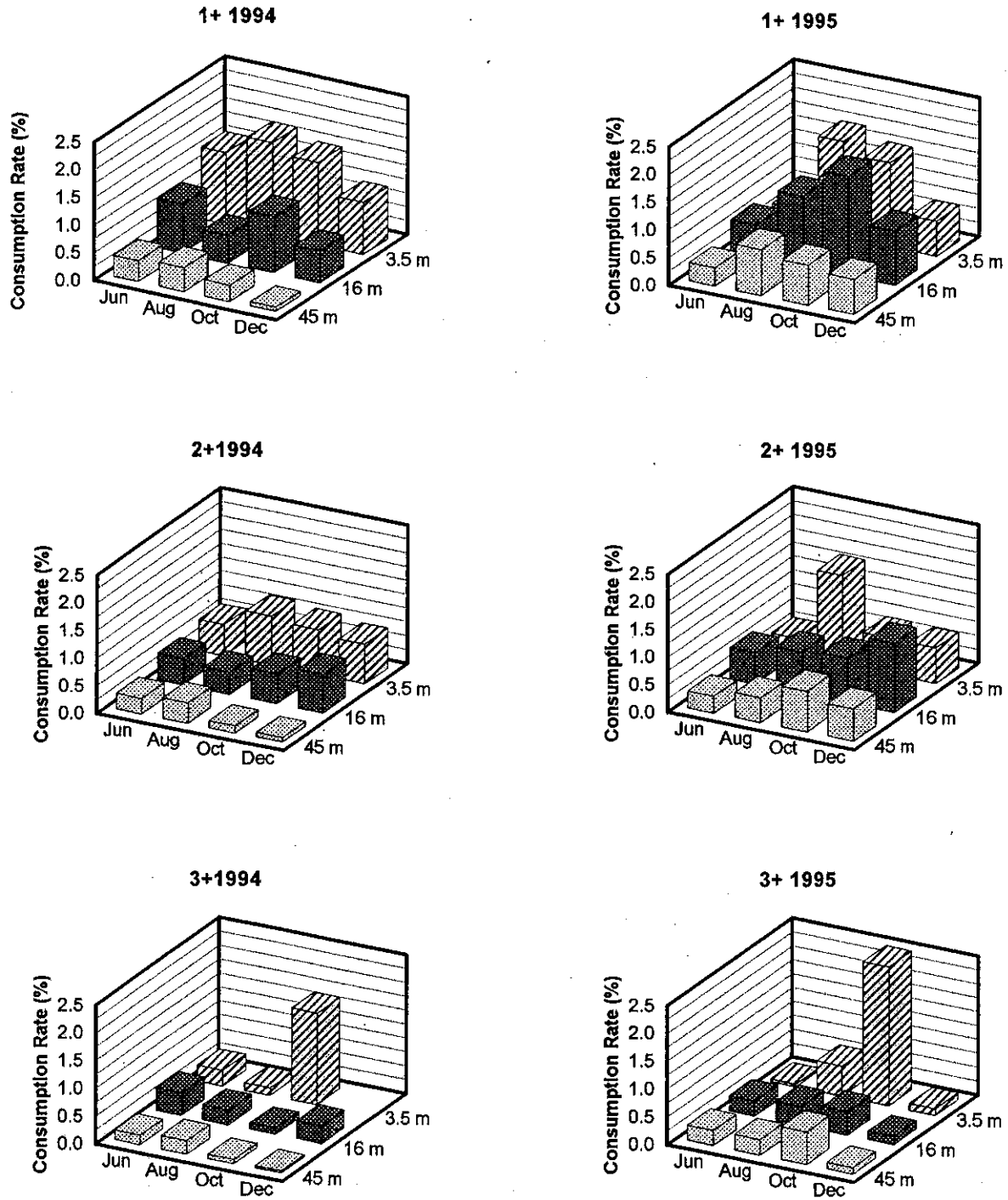


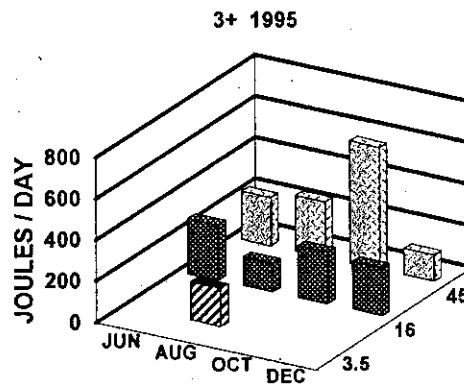
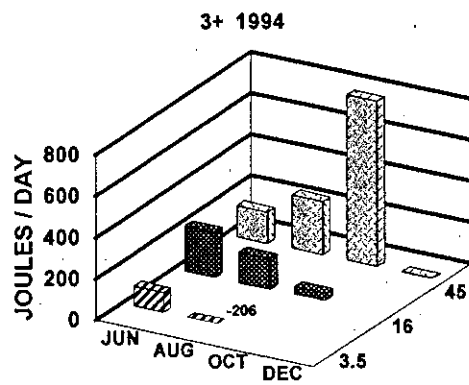
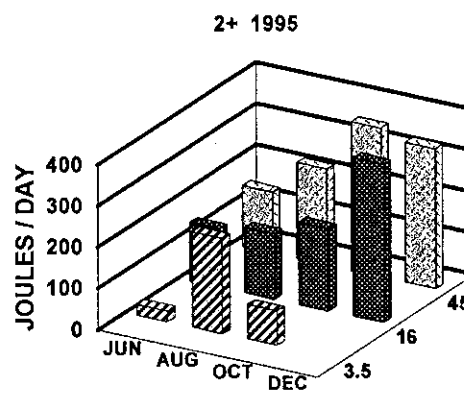
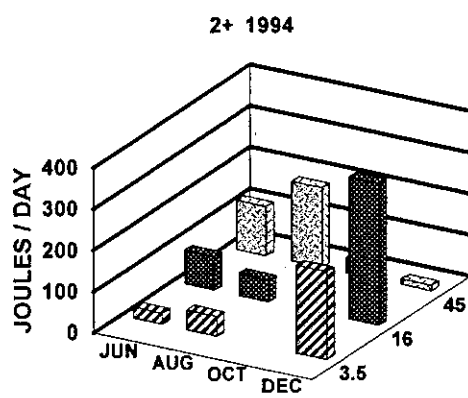
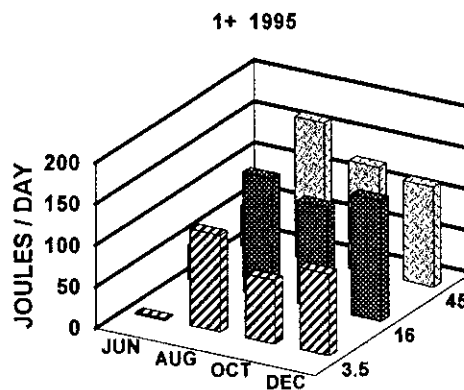
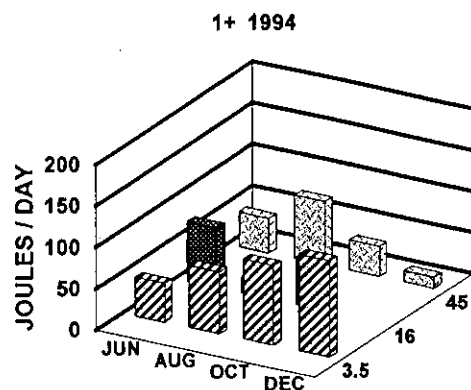
Figure 11. Estimated energy balance realized by Bear lake sculpin in different depth strata and seasons, as a function of the prey biomass available in the strata. One outlier, with an energy balance of 25% was removed from the analysis. For the outlier, there were only eight fish available to estimate the energy balance.

Sculpin Consumption Rate (% / Day)



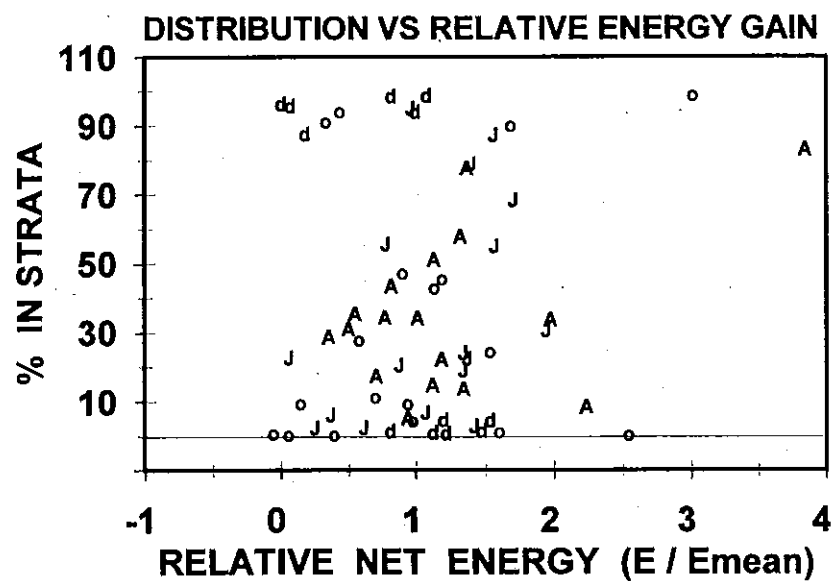
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Figure 12. Estimated consumption rates (%/day) of sculpin in four seasons and three depth strata during 1994 and 1995.



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Figure 13 . Energy balance estimates of sculpin from different depths, months, and size classes in Bear Lake during 1994 and 1995. The balance was calculated as the difference between assimilation and the sum of SDA and respiration, and is a measure of growth potential. Samples with less than 5 fish available were not graphed.



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Figure 14. Relative net energy gain of sculpin in the three different depths strata for each season, compared to the percent of sculpin of that size class found in a strata (from Fig. 3). The symbols represent the months that samples were collected during 1994 and 1995. The relationship between relative net energy and % in strata was significant for the June-August period, but not in October and December

selection for areas with high growth potential. In October there was no significant correlation between net energy gain and distribution. In December the correlation was significant but negative--i.e., the fish avoided the littoral zone with the highest net energy gain and were in the profundal where prey abundance and net energy gain was low.

DISCUSSION

The diet and food consumption analysis of the sculpin indicates that they were strongly food-limited in Bear Lake. Gut fullness indices and daily energy intake estimates seldom approached levels attained in the laboratory where the sculpin had unlimited food. Additionally, gut fullness and consumption rates in the field were positively correlated with food abundance, also suggesting food limitation. The correlation analysis suggests that prey abundances would need to increase about 2.5-fold before sculpin would become satiated in the field.

The food limitation is consistent with a limited amount of benthic invertebrate food available in Bear Lake. In August, for example, the mean amount of food available along the transect was only 40 mg dry weight m^{-2} . Even the maxima of 255 mg m^{-2} observed in the littoral zone in December ranks among the lowest biomasses reported for temperate lakes (Morgan et al. 1980). The low biomass of benthic invertebrates is consistent with the oligotrophic nature of the lake (Lamarra 1980). The large size and depth of the lake also contribute to low benthic invertebrate abundance, as large, deep lakes often have lower biomasses than do small lakes with relatively large littoral zones (Brinkhurst 1974). Additionally, the dominant marl substrate is a relatively poor habitat for many benthic invertebrates as Wurtsbaugh and Hawkins (1990) found that chironomid larvae were 180 times more abundant in rocky areas than in soft-bottomed substrates. The benthic invertebrate biomass we found in 1994 was considerably less than reported by Wurtsbaugh and Hawkins (1990). This is likely due to the larger mesh size (500 μM) used

to sieve the invertebrates in 1994 than was used in the earlier study (200 μ M). The changing lake elevation due to water withdrawals and spring filling may have also contributed to differences between years.

The composition of the benthic invertebrate prey has changed from the earlier study (Wurtsbaugh and Hawkins 1990). In the previous study, *Daphnia* and ostracods contributed relatively little to the biomass in the profundal region. In contrast, we found that these invertebrates contributed significantly to the profundal biomass in August and October. The change in *Daphnia* reflects the change found in the plankton of Bear Lake in recent years (Chapter 1). However, in the plankton the *Daphnia* increase was not noted until 1995, whereas we found large numbers in the benthos in 1994. This is consistent with the results of Bouwes and Luecke (1993) who studied *Daphnia* distribution in 1993 and found that during the day these cladocerans were 10-times denser near the sediments than in the water column. During the night these benthic *Daphnia* moved into the water column. These results suggest that the recent increase of *Daphnia* may have begun earlier in the profundal sediments, and subsequently extended into the water column. Alternatively, the present abundance of *Daphnia* may reflect a shift of *Daphnia* from the sediments to the water column, similar to the change observed in adult Bonneville cisco during the same period. It is possible that the increasing number of benthic sculpin over the past four years (Wurtsbaugh and Luecke, in preparation) has caused the *Daphnia* to move into the water column during the day.

The diets of the sculpin were consistent with the increase in *Daphnia*. In 1987 *Daphnia* were insignificant in the diets of sculpin throughout the year (Wurtsbaugh and Hawkins 1990), whereas in 1994 and 1995 this cladoceran contributed 25% of the overall diet, and 44% of the diet of sculpin inhabiting the profundal region. A recent increase of *Daphnia* in the diets of whitefish and other species has also been noted (B. Nielson and S. Tolentino, personal communication).

The benthic invertebrate prey densities and biomass may be controlled by the sculpin movement patterns. From June through August the biomass of invertebrates was relatively similar at 3.5, 16 and 45 m. During these months, sculpin densities were also relatively similar in the three strata. However, as sculpin evacuated the shallower depths in the fall and winter, invertebrate biomasses increased in the shallow water. In December, when most of the sculpin had moved to the profundal region, invertebrate biomass increased even more in the littoral zone, and decreased to very low levels in the profundal region. Thus predation pressure from sculpin could be important in controlling their invertebrate prey base. However, because whitefish and suckers also utilize these prey, an interpretation based solely on sculpin must be treated cautiously.

The sculpin distribution analysis indicated that the littoral zone may be less important for the sculpin than previously thought. When viewed along the entire transect and over all seasons, a relatively small proportion of each size class of sculpin inhabit the littoral zone. The detailed analysis indicated this was particularly evident in the 1-m deep transect where we caught very few sculpin. During our monitoring work on Bear Lake, which is conducted in midsummer, we have found high densities of sculpin in the littoral zone. However, because the profundal zone is so expansive it harbors significant numbers of sculpin even in midsummer, and in other seasons most sculpin are located in the deep waters. However, age 1+ and YOY sculpin (Ruzycki 1995) do make significant use of the littoral areas from June through October.

Wurtsbaugh and Hawkins (1990) suggested that sculpin should inhabit the littoral or metalimnetic interface zones because the previous analysis of benthic invertebrates indicated that there has more food available there than in the profundal zone (Wurtsbaugh and Hawkins 1990). The analyses reported here, however, indicate that sculpin gut fullness was not significantly related to the depth they inhabit. This is not surprising given that our benthic invertebrate data reveal moderate to high biomasses of benthic invertebrates in the profundal region. Because the profundal *Daphnia* and ostracods are

epibenthic, they may be easily preyed upon by sculpin. Consequently, in some seasons, the *availability* of prey in the profundal and metalimnetic interface zones may equal or even exceed that in the shallower areas where many of the chironomids live in the sediments.

The bioenergetic analysis of net energy gain only partially explained the distribution patterns of the sculpin. In June and particularly in August sculpin avoided areas where net energy gain was low and concentrated instead in strata providing a greater balance between food intake and respiratory costs. However, even in these months the correlations were not strong. In part, the relatively poor correlations could be related to a sampling artifact. In many seasons, we could not capture enough sculpin in some strata to provide a reliable estimate of their consumption, and consequently, the net energy gain. For example, age 3++ sculpin were seldom captured in the littoral zone after August, so we could not determine their energy balance there. If sculpin moved out of these zones because net energy gain there was low, we would not have been able to detect it. The diel gut fullness analyses suggest that the older sculpin may not feed effectively in the shallow littoral zone, as they frequently had little food in their guts throughout the day, even though other size classes were feeding. The lack of feeding in the shallow water by 3++ fish may be a predator-avoidance behavior.

The analysis of net energy gain was not useful for understanding sculpin distribution in the fall and particularly during winter. By December nearly all of the sculpin had moved out of the littoral zone and inhabited the profundal zone, even though benthic invertebrates, consumption, and energy gain there were all extremely low. The calculated energy balance of the few sculpin remaining in the littoral zone during December indicated that they should grow much faster than those that moved to deeper waters. This was because littoral zone prey abundance was high, and respiratory costs were low because temperatures had declined to 4.6 °C. Nevertheless, only a few percent of the sculpin remained in the littoral zone until December. Other factors must override the bioenergetic considerations. Possible mechanisms include avoiding predators (whitefish, trout) that can

move into the littoral zone when waters cool, and anticipation of very cold littoral zone temperatures (ca. 2 °C) that occur from January-March.

Our analyses have shown very complex movement and feeding patterns in Bear Lake sculpin. Although interesting, this complexity complicates the ecological analysis of the species. For example, a traditional bioenergetic analysis (Kitchell et al. 1977) would be extremely difficult to do for the sculpin because the growth and thermal history of the fish are convoluted. Because many other species of fish also undergo complicated ontogenetic and seasonal shifts in distribution, care must be exercised in applying these models. Our use of temperature-specific digestion rates overcame this problem, but required a large time investment to acquire diel samples of gut fullness.

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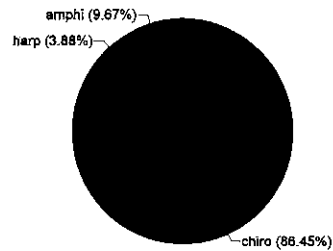
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Appendix 1 Bear Lake sculpin diet composition from June, August, October and December time periods. Samples were collected from three depth strata in Bear Lake, and analyzed for three size classes of fish.

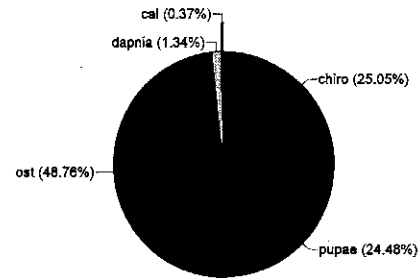
Sculpin Diet

June 3m depth, 1+ size class



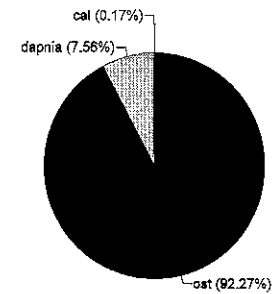
Sculpin Diet

June 16m depth, 1+ size class



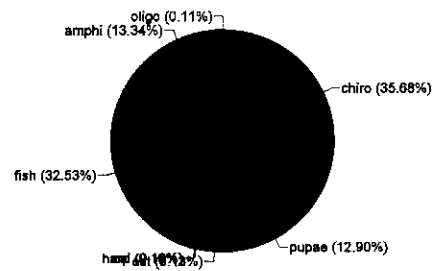
Sculpin Diet

June 45m depth, 1+ size class



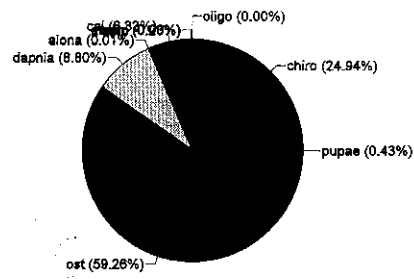
Sculpin Diet

June 3m depth, 2+ size class



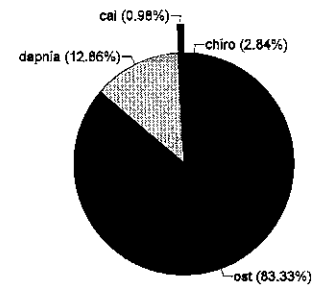
Sculpin Diet

June 16m depth, 2+ size class



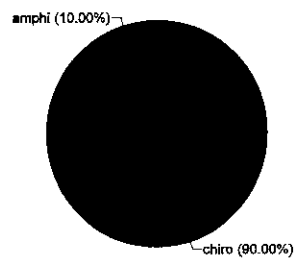
Sculpin Diet

June 45m depth, 2+ size class



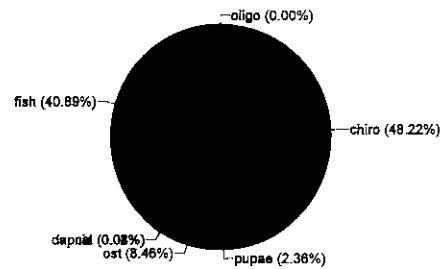
Sculpin Diet

June 3m depth, 3+ size class



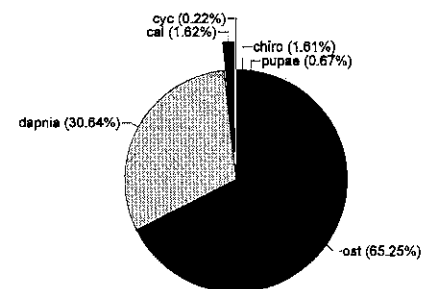
Sculpin Diet

June 16m depth, 3+ size class



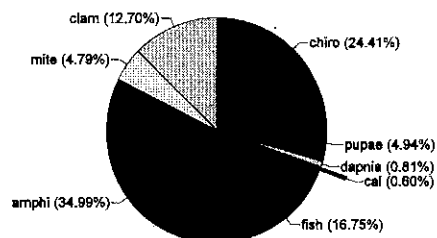
Sculpin Diet

June 45m depth, 3+ size class



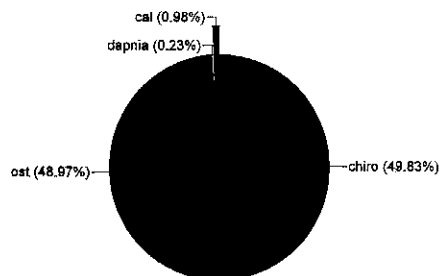
Sculpin Diet

August 3m depth, 1+ size class



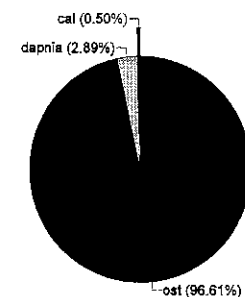
Sculpin Diet

August 16m depth, 1+ size class



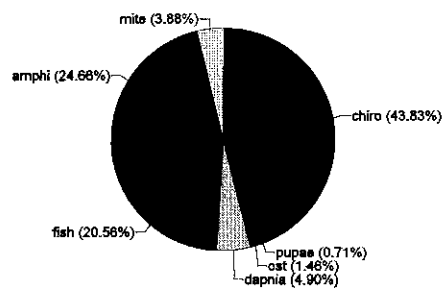
Sculpin Diet

August 45m depth, 1+ size class



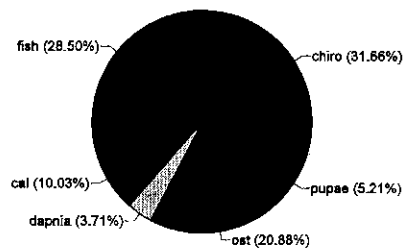
Sculpin Diet

August 3m depth, 2+ size class



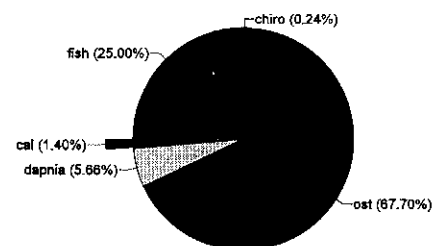
Sculpin Diet

August 16m depth, 2+ size class



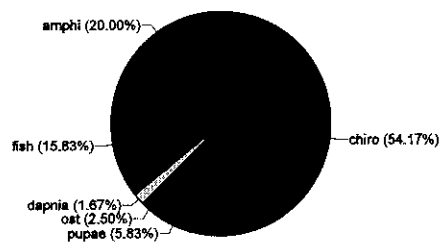
Sculpin Diet

August 45m depth, 2+ size class



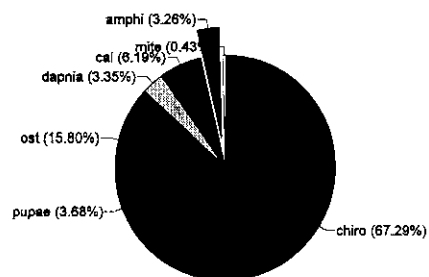
Sculpin Diet

August 3m depth, 3+ size class



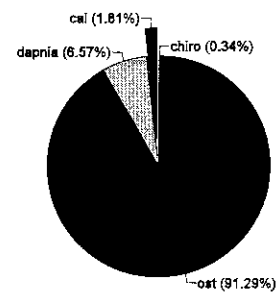
Sculpin Diet

August 16m depth, 3+ size class



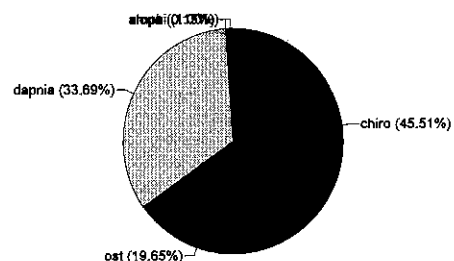
Sculpin Diet

August 45m depth, 3+ size class



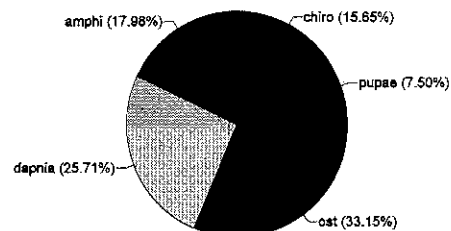
Sculpin Diet

October 3m depth, 1+ size class



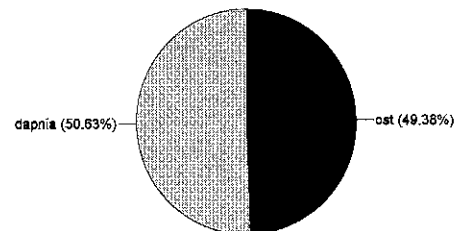
Sculpin Diet

October 16m depth, 1+ size class



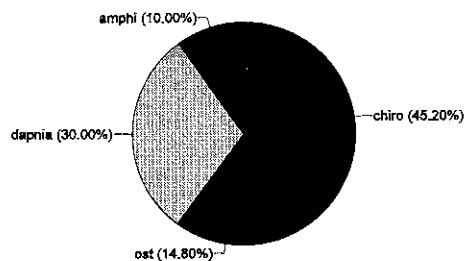
Sculpin Diet

October 45m depth, 1+ size class



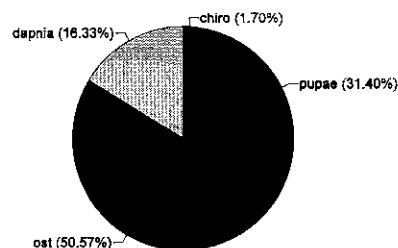
Sculpin Diet

October 3m depth, 2+ size class



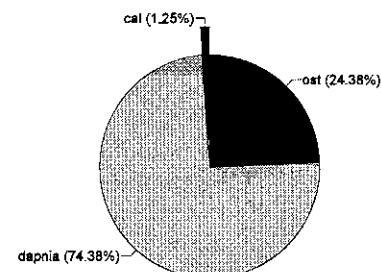
Sculpin Diet

October 16m depth, 2+ size class



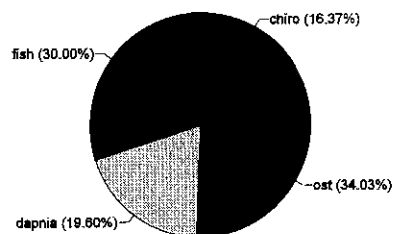
Sculpin Diet

October 45m depth, 2+ size class



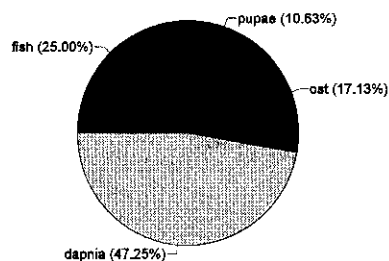
Sculpin Diet

October 3m depth, 3+ size class



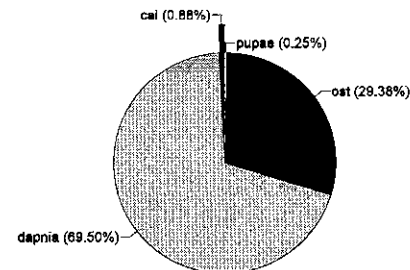
Sculpin Diet

October 16m depth, 3+ size class



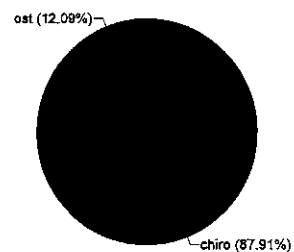
Sculpin Diet

October 45m depth, 3+ size class



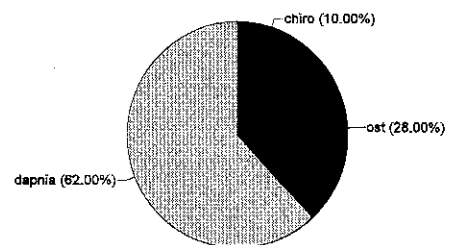
Sculpin Diet

December 3m depth, 1+ size class



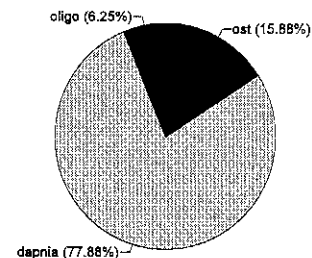
Sculpin Diet

December 16m depth, 1+ size class



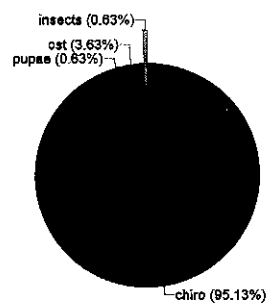
Sculpin Diet

December 45m depth, 1+ size class



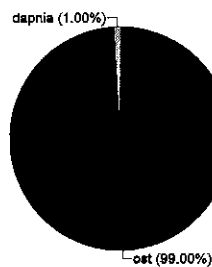
Sculpin Diet

December 3m depth, 2+ size class



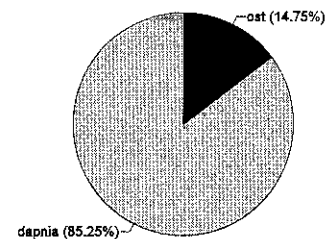
Sculpin Diet

December 16m depth, 2+ size class



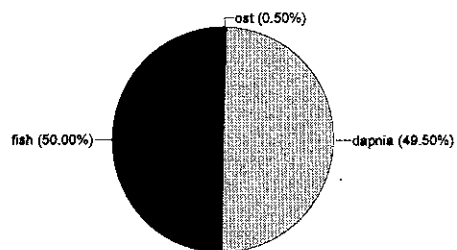
Sculpin Diet

December 45m depth, 2+ size class



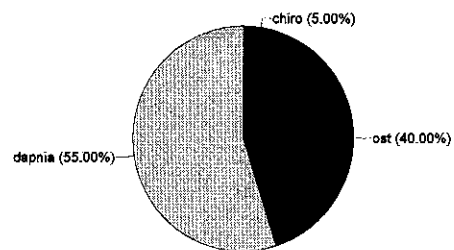
Sculpin Diet

December 3m depth, 3+ size class



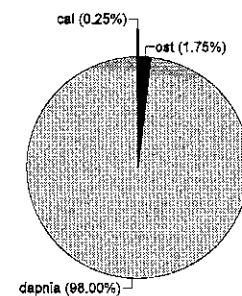
Sculpin Diet

December 16m depth, 3+ size class



Sculpin Diet

December 45m depth, 3+ size class



Appendix 2. Gut fullness, consumption, respiration, and net energy estimates for Bear Lake sculpin during 1994 and 1995. Samples with less than 10 individual fish are shown in italics.

Year	Season	Age	Depth (m)	N	Mean Wet weight (g)	Mean Gut fullness Ind.	Temp. (C)	Digestion rate (r)	Consumption J/D	Respiration J/D	Net Energy J/D
1994	june	1++	3.5	152	0.75	0.99	16.4	0.234	156	54	47
1994	june	1++	16	57	0.87	1.22	11.0	0.180	173	41	72
1994	june	1++	45	47	0.75	0.96	5.0	0.139	90	16	42
1994	june	2++	3.5	38	1.85	0.51	16.4	0.234	206	106	28
1994	june	2++	16	32	1.86	0.75	11.0	0.180	235	71	81
1994	june	2++	45	34	2.12	0.85	5.0	0.139	238	35	119
1994	june	3++	3.5	19	7.89	0.33	16.4	0.234	622	309	95
1994	june	3++	16	25	4.15	0.74	11.0	0.180	538	129	221
1994	june	3++	45	69	3.97	0.59	5.0	0.139	316	56	149
1994	Aug	1++	3.5	87	0.99	0.86	20.7	0.319	246	84	75
1994	Aug	1++	16	93	1.03	0.59	12.8	0.205	113	53	20
1994	Aug	1++	45	56	1.05	1.12	5.1	0.140	151	21	76
1994	Aug	2++	3.5	24	1.83	0.51	20.7	0.319	279	133	49
1994	Aug	2++	16	99	2.13	0.54	12.8	0.205	222	91	53
1994	Aug	2++	45	128	2.40	1.12	5.1	0.140	358	39	193
1994	Aug	3++	3.5	7	6.33	0.10	20.7	0.319	195	332	-206
1994	Aug	3++	16	16	6.19	0.43	12.8	0.205	539	201	149
1994	Aug	3++	45	140	4.37	0.82	5.1	0.140	491	61	257
1994	Oct	1++	3.5	37	0.76	1.83	11.8	0.168	210	39	97
1994	Oct	1++	16	23	0.68	1.24	11.8	0.190	144	36	57
1994	Oct	1++	45	47	0.93	0.73	5.6	0.145	89	21	36
1994	Oct	2++	3.5	2	1.75	1.16	11.8	0.168	321	73	135
1994	Oct	2++	16	2	1.74	0.77	11.8	0.190	239	73	83
1994	Oct	2++	45	47	2.41	0.37	5.6	0.145	123	44	37
1994	Oct	3++	16	3	5.07	0.19	11.8	0.190	177	160	-45
1994	Oct	3++	45	59	4.38	0.26	5.6	0.145	161	68	37
1994	Oct	3++	3.5	8	7.38	3.07	11.8	0.168	3847	211	2289
1994	Dec	1++	3.5	34	0.91	2.51	4.6	0.100	206	17	117
1994	Dec	1++	16	1	1.10	1.61	4.6	0.113	182	20	98
1994	Dec	1++	45	37	0.89	0.43	4.6	0.135	47	17	13
1994	Dec	2++	3.5	6	1.82	2.18	4.6	0.100	373	29	213
1994	Dec	2++	16	4	2.43	2.23	4.6	0.113	583	36	343
1994	Dec	2++	45	32	2.05	0.26	4.6	0.135	69	32	13
1994	Dec	3++	3.5	0							
1994	Dec	3++	16	1	6.17	1.21	4.6	0.113	847	71	479
1994	Dec	3++	45	28	4.89	0.14	4.6	0.135	93	60	0
1995	Jun	1++	3.5	66	0.87	0.51	10.1	0.149	60	37	2
1995	Jun	1++	16	46	0.89	0.91	9.7	0.164	119	36	41
1995	Jun	1++	45	30	1.00	0.82	5.4	0.143	106	22	47
1995	Jun	2++	3.5	8	1.98	0.53	10.1	0.149	146	68	27
1995	Jun	2++	16	23	2.01	1.03	9.7	0.164	321	66	142
1995	Jun	2++	45	53	2.41	0.89	5.4	0.143	293	42	149
1995	Jun	3++	3.5	1	5.44	0.10	10.1	0.149	84	144	-90
1995	Jun	3++	16	9	6.38	0.62	9.7	0.164	653	156	269
1995	Jun	3++	45	52	3.75	0.86	5.4	0.143	452	58	235
1995	Aug	1++	3.5	71	1.11	1.08	19.0	0.282	310	84	117
1995	Aug	1++	16	24	1.15	1.40	13.5	0.215	317	61	145
1995	Aug	1++	45	12	1.08	2.09	5.5	0.144	297	24	170
1995	Aug	2++	3.5	44	1.86	1.11	19.0	0.282	546	123	232
1995	Aug	2++	16	55	2.07	0.93	13.5	0.215	391	95	159
1995	Aug	2++	45	53	2.37	1.30	5.5	0.144	424	42	233
1995	Aug	3++	3.5	10	5.57	0.45	19.0	0.282	711	277	185
1995	Aug	3++	16	16	4.59	0.49	13.5	0.215	476	170	139
1995	Aug	3++	45	69	4.08	0.89	5.5	0.144	513	63	271
1995	Oct	1++	3.5	36	0.66	1.69	12.5	0.177	176	38	77
1995	Oct	1++	16	13	0.69	2.04	12.4	0.199	250	39	124
1995	Oct	1++	45	18	1.02	1.73	5.8	0.147	237	24	130
1995	Oct	2++	3.5	5	1.72	0.87	12.5	0.177	246	76	84
1995	Oct	2++	16	5	2.09	1.13	12.4	0.199	443	87	201
1995	Oct	2++	45	40	2.18	2.04	5.8	0.147	620	42	361
1995	Oct	3++	3.5	4	8.18	5.06	12.5	0.177	7426	241	4585
1995	Oct	3++	16	8	4.77	0.68	12.4	0.199	634	161	251
1995	Oct	3++	45	40	3.89	1.80	5.8	0.147	1008	64	591
1995	Dec	1++	3.5	53	1.13	1.78	4.6	0.100	184	20	99
1995	Dec	1++	16	10	0.93	2.63	4.6	0.113	252	18	146
1995	Dec	1++	45	89	1.01	1.73	4.6	0.135	215	19	121
1995	Dec	2++	3.5	24	2.10	2.00	4.6	0.100	398	32	226
1995	Dec	2++	16	1	1.62	3.70	4.6	0.113	634	27	385
1995	Dec	2++	45	44	2.39	1.88	4.6	0.135	578	35	340
1995	Dec	3++	3.5	4	6.11	0.46	4.6	0.100	281	71	112
1995	Dec	3++	16	6	7.21	0.58	4.6	0.113	479	80	231
1995	Dec	3++	45	82	5.09	0.43	4.6	0.135	282	62	128

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