THE UNIVERSITY OF CALGARY

Direct and Indirect Effects of Interference Competition in Size-Structured Rainbow Trout (*Oncorhynchus mykiss*) Populations

by

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ABSTRACT

Dominance hierarchies formed by size-dependent interactions occur in salmonids living in lotic systems. I investigated whether older and larger rainbow trout (*Oncorhynchus mykiss*) influenced the spatial distribution, growth, and mortality of age-0 rainbow trout living in lentic systems. I manipulated populations in three lakes by varying the intensity of interactions towards age-0 trout to investigate size-dependent processes within size-structured populations. Age-0 rainbow trout are spatially restricted by the presence of older conspecifics, using shallower, more complex and less profitable habitats, therefore avoiding open water habitats. The intensity of spatial restriction depended on body size. Growth rates of age-0 trout varied inversely with the intensity of interactions with older conspecifics, whereas their mortality rates varied directly. In the presence of older trout, mortality rates were strongly size-dependent. These results demonstrate that size-dependent processes such as interference competition and predation may affect population dynamics of age-0 rainbow trout in lentic systems.

ACKNOWLEDGEMENTS

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INTRODUCTION

Many animals species have size-structured populations (Ebenman and Persson 1988) with complex interactions among individuals. The type and intensity of interactions that an individual encounters during its life history depends partly on body size (Peters 1983). Among fishes, competition and predation vary in intensity with body size. Fishes are a useful taxon to examine size-dependent interactions because they often grow through 4-5 orders of magnitude of body mass (Peters 1983). They express strong size-dependent competitive and predator/prey interactions which have received considerable empirical and theoretical attention (Werner and Gilliam 1984; Walters and Juanes 1993; Werner and Anholt 1993; Persson et al. 1996).

Resource use by fish tends to change with age (size) and habitat segregation within species often reflects competition among individuals of different age and size classes (Werner et al. 1983b; Tonn et al. 1992). Many fish species are opportunistic feeders and ontogenetic changes allow them to be facultatively piscivorous (Amundsen 1994; Lynott et al. 1995). In fact, intraspecific predation (cannibalism) is common in fishes (Smith and Reay 1991). In streams, interference competition is the overriding process that controls the use of space and food resources (Grant 1990; Gregory and Griffith 1996), growth, mortality (Marschall et al. 1995), and population dynamics of fishes (Elliot 1990).

Most empirical work on size-dependent interactions within lake fishes has been studied at a small scale such as in enclosures, ponds, and laboratory tanks (Werner et al. 1983b; Tabor and Wurtsbaugh 1991; Johnsson 1993; Eklöv and Diehl 1994). These experiments at small scales do not allow sufficient behavioural plasticity typical of fishes due to the limited availability of natural habitats that fish experience in the wild. These experiments can not realistically assess population-level phenomenon such as mortality. Therefore, it is necessary to experiment at the population level to understand the consequences from the interactions (Tonn et al. 1994; Persson et al. 1996).

In this study, I assess the effects and consequences of size-dependent interactions among size-structured rainbow trout (*Oncorhynchus mykiss*) populations in lentic systems. I "created" populations that differed in size-structure and experimented at the whole-lake scale. Therefore, I could examine the implications of the interactions at the population level. I manipulated three lake systems by varying the intensity of interactions between two age classes. I measured short-term behaviours of the youngest age class of rainbow trout (age-0) such as use of resources like space and food through ontogeny at a fine spatial scale. I also measured the population level responses such as growth and mortality resulting from the short term behaviours.

Gilliam and Fraser (1987) demonstrated that fish that minimize their mortality rate (μ) relative to gross foraging rate (f) (minimize μ/f), maximize their growth and survival. The experimental design allowed me to draw inferences about the proximate mechanisms involved in size class interactions and to test empirically at the population level Gilliam and Fraser's (1987) theoretical predictions that small-bodied fish select habitats that minimize the ratio of mortality rate to gross foraging rate.

I present the thesis as two independent research chapters. The first chapter tests the hypothesis that lentic populations of rainbow trout are spatially structured based on interference competition driven by size-dependent aggressive abilities of the rainbow trout. The second chapter tests the hypotheses that growth of age-0 rainbow trout populations is indirectly controlled by the presence of older conspecifics through direct effects on resource use and that mortality of age-0 rainbow trout populations is size-dependent and directly controlled by the presence of older conspecifics.

CHAPTER 1

Is spatial distribution of age-0 rainbow trout influenced by the presence of larger conspecifics in lentic systems?

1.1 Introduction

Spatial segregation of species in freshwater fish assemblages is relatively common (Werner et al. 1977; Brandt et al. 1980; Laughlin and Werner 1980; Olson et al. 1988; Rossier 1995) and is also observed between age and size classes within species (Werner et al. 1983b; Magnan and FitzGerald 1984; Kneib 1987; Tonn et al. 1992; O'Connell and Dempson 1996). This habitat partitioning within species is usually a consequence of competition due to partial overlap in resource use among individuals of different size or age classes (Keast 1977; Polis 1984; Werner and Gilliam 1984; Venne and Magnan 1995). Competition occurs whenever individuals jointly use a limiting resource (exploitative competition) or individuals directly interfere with one another (interference competition), yielding reduced fitness by decreasing efficiency in food acquisition or increasing metabolic costs. Empirical research on fishes has demonstrated that size-dependent interactions within size- and age-structured populations determine recruitment and population dynamics (Persson 1987; Tonn et al. 1992; Post et al. in press). Exploitative competition within a species affects population cycling (Hamrin and Persson 1986) and growth patterns (Persson 1987). Interference competition can govern population dynamics in fish species (Borgstrøm et al. 1993; Post et al. in press).

Interference competition determines temporal and spatial patterns of habitat use

(Gregory and Griffith 1996). Interference competition within size-structured populations usually favours larger individuals, forcing smaller ones into less profitable habitats (Fausch 1984; Metcalfe 1986; Grant 1990). The extreme form of interference behaviour is predation. Many studies have demonstrated that young fish modify their habitat use to reduce risk to interference or predation such as avoiding open water and selecting shallow, vegetated inshore areas (Werner et al. 1983b; Holopainen et al. 1991; Tabor and Wurtsbaugh 1991; Tonn et al. 1992). The use of habitats that provide refuge, or at least partial refuge is common in freshwater fishes (Savino and Stein 1982; Mittelbach 1986; Gotceitas and Colgan 1989; Persson and Eklöv 1995; Eklöv and Persson 1996). Refuge can be broadly defined to include any strategy that decreases predation risks and examples of refuges encompass spatial, temporal, group living, and movement reduction (Sih 1987; Walters and Juanes 1993).

Most of the work on size-dependent interactions has focused on interspecific predation and its direct effects on prey species (Werner et al. 1983a; Tonn et al. 1992; L'Abée-Lund et al. 1993). However, intraspecific predation (cannibalism) may be equally important (Polis 1981; Dominey and Blumer 1984; Foster et al. 1988) especially when life-history stages differ considerably in size. Therefore, inter- or intra-specific aggression, whether it results in cannibalism or predation or not, typically results in interference competition and differential habitat selection by smaller and younger individuals.

The spatial and temporal distribution of small or young fish is often also associated with seasonal changes in resource levels leading to changes in habitat profitability (Werner and Hall 1976; Hall and Werner 1977; Werner et al. 1983b; Hamrin and Persson 1986).

Therefore, individuals can benefit from changing their distributional behaviour through time. By choosing habitats with high prey abundance, small or young individuals may face a tradeoff between foraging in profitable habitats or remaining in less profitable habitats near cover with lower risks of predation or agonistic encounters (Walters and Juanes 1993). This tradeoff is most important for small fish because they are particularly vulnerable to size-selective predators and larger aggressive competitors. One strategy utilized by juvenile fish then, is a diurnal migration where they move to risky and profitable habitats at dusk to feed when risks are lower (Clark and Levy 1988).

Dominance hierarchies formed by size-dependent interactions occur in salmonid populations living in lotic systems (Li and Brocksen 1977; Fausch 1984; Abbott et al. 1985; Grant 1990; Huntingford 1993). The interactions are a result of competition between individuals through aggressive behaviour to obtain stream positions which provide the greatest net energy gain (Fausch 1984; Grant and Noakes 1988). Stream salmonids have to compromise between limiting energy expenditure while swimming against a current and increasing exposure to drifting invertebrates. There is also the presence of potential predation risk (Huntingford et al. 1988). Therefore, because lotic systems are structured physically and biologically in features such as current velocity, prey availability, and predation risk, dominance hierarchy develops to defend territory or optimal stream position (Fausch 1984; Metcalfe 1986; see review Huntingford 1993).

These same salmonid species also live in lentic systems, where they do not experience the same physical and biological gradients as in lotic systems. It is not presently known whether salmonids living in lentic systems show the same biological (size) structure. The goal of this study is to determine whether lentic populations are spatially structured based on interference competition driven by size-dependent aggressive abilities as are lotic populations, despite the obvious differences in spatial structure between lentic and lotic systems.

Most experiments dealing with size-dependent interactions among fish have been conducted in small systems, such as aquaria, laboratory streams, enclosures, ponds, or sections of ponds as the experimental units. These conditions restrict a fish's behaviour due to the limited availability of alternate habitats. It is therefore critical to use whole-system experiments to study size-dependent interactions to incorporate both spatial and temporal natural variability in these interactions (Tonn et al. 1994; Persson et al. 1996). Conversely, most surveys of the spatial distribution of fish at a larger scale (whole lake) do not allow detailed analysis at the smaller scale over which fish make behavioural decisions and at a scale that covers the early ontogeny.

Experiments should be replicated, but the replicated randomized experiment is rarely used at the whole system level (Hurlbert 1984). Due to practical problems and the costs involved, replication in whole lake experiments is unrealistic in most situations. Carpenter (1989) demonstrated that the number of replicates necessary to obtain significant treatment effects, when the effects are present, is so high that under most conditions it is not feasible to carry out replicated whole lake experiments using traditional statistical technique due to high interannual variation and interecosystem variability. In this study, I present a multi-lake experiment which encompasses finer scale temporal and spatial distribution and examine interactions at the population level. I manipulated three lake systems with partial replication. Therefore, the resources were invested in developing a more detailed mechanistic analyses on three lakes rather than less intense sampling on more lakes as would be required in a fully replicated design. This design is less powerful than a fully replicated design due to the inter-lake variability, but it is more powerful than a survey type of experiment, because I allocated randomly the treatments and I created fish populations from the same genetic origin. I can not reject *a priori* that the observed effects are due to the lakes themselves, but because I allocated my treatments randomly and the populations had the same origin, I interpret the effects as treatment effects and consider the possibility of lake effects.

I studied the size-dependent interactions among age-classes of rainbow trout (*Oncorhynchus mykiss*). They experience size-dependent predation (cannibalism) (Tabor and Wurtsbaugh 1991; Post et al. unpublished manuscript), competitive interference (Li and Brocksen 1977; McCarthy et al. 1992), and exploitative competition (Post et al. in press). Adult rainbow trout spawn in streams and juveniles migrate from streams into lakes at ages ranging from shortly after hatch to age-3 (Northcote 1969; Scott and Crossman 1973; Hayes 1987, 1988; Rosenau 1991). Therefore, several age- and size-classes co-occur in lakes. Previous studies have shown that adult rainbow trout use the epilimnion in lakes (Wurtsbaugh et al. 1975; Warner and Quinn 1995) and typically prefer temperatures in the range of 18 °C (M^cCauley and Pond 1971; Cherry et al. 1975), and other work suggests that age-0 rainbow trout tend to occupy the shallow littoral zone (Johannes and Larkin 1961; Tabor and Wurtsbaugh 1991; Post et al. in press). Post et al. (in press) demonstrated that age-0 and older rainbow trout overlap in use of space and food resources.

The goal of my research is to understand the processes by which rainbow trout of different ages and sizes interact and how that is expressed in their use of space in lakes. My approach involves varying the size-structure in experimental rainbow trout populations and contrasting the use of spatial and food resources in the populations. Specifically, I will test whether: (1) habitat selection in age-0 rainbow trout is related to differential food concentrations among habitats; (2) habitat selection in age-0 rainbow trout is in response to temperature variation among habitats; (3) habitat selection in age-0 rainbow trout and diurnal variation in habitat use is in response to an avoidance of interference or cannibalistic interactions with older conspecifics.

1.2 Methods

1.2.1 Study area

The study was carried out in three lakes located on the southern interior plateau of British Columbia (Figure 1.1), 40 km southeast of Merritt (50° 07' N, 120° 47' W). The lakes are situated within a 0.56 km^2 area and consequently experience similar climatic and geological conditions. Their morphometries are similar (Table 1.1 and Figure 1.2, 1.3, 1.4). These mesotrophic lakes range from 15 to 30 $mg \cdot L^{-1}$ in total phosphorus and 300 to 500 $mg \cdot L^{-1}$ in total dissolved solids. Two of the lakes were fishless (due to winterkill) at the time of stocking and the third had a very low density of age-1 rainbow trout with a known size structure and abundance. All lakes had been stocked with rainbow trout in previous years.

All three lakes were stocked with rainbow trout reared from gametes collected from adults of a native population in Tunkwa Lake, British Columbia. I used fish with a wild ancestry as opposed to a hatchery ancestry because innate predator avoidance has been reduced through domestication in steelhead fry (Berejikian 1995). The fish were reared at the Fraser Valley Trout Hatchery in Abbotsford, B.C.. Two age classes were used for the experiment: age-0 trout which had hatched about one month prior to the experiment and age-1 trout which were 1 year-old fish. The fish were stocked in early July 1994, which corresponded to the timing of recruitment from streams into lakes for a proportion of the age-0 rainbow trout population in that region.

Figure 1.1 Location of the study site in south-central British Columbia, Canada.

Table 1.1 Morphometry and location of the experimental lakes in south-central British Columbia.

Lake	**Bluey 1**	**Bluey 2**	**Kentucky Pothole**
Treatment	Age-0 / Age-1	Age-0 + Age-1	Age-0
Surface area (ha)	2.0	1.4	2.1
Perimeter (m)	710	508	601
Mean depth (m)	3.0	3.5	5.4
Maximum depth (m)	6.5	7.2	11.2
Mean secchi disk depth (m)	4.4	4.1	4.1
Latitude	49° 52' 40" N	49° 52' 50" N	49° 53' 30" N
Longitude	120° 33' 35" W	120° 33' 35" W	120° 33' 30" W

Figure 1.2 Bathymetric map of Bluey 1 Lake, the Age-0 / Age-1 treatment. Depth contours in m.

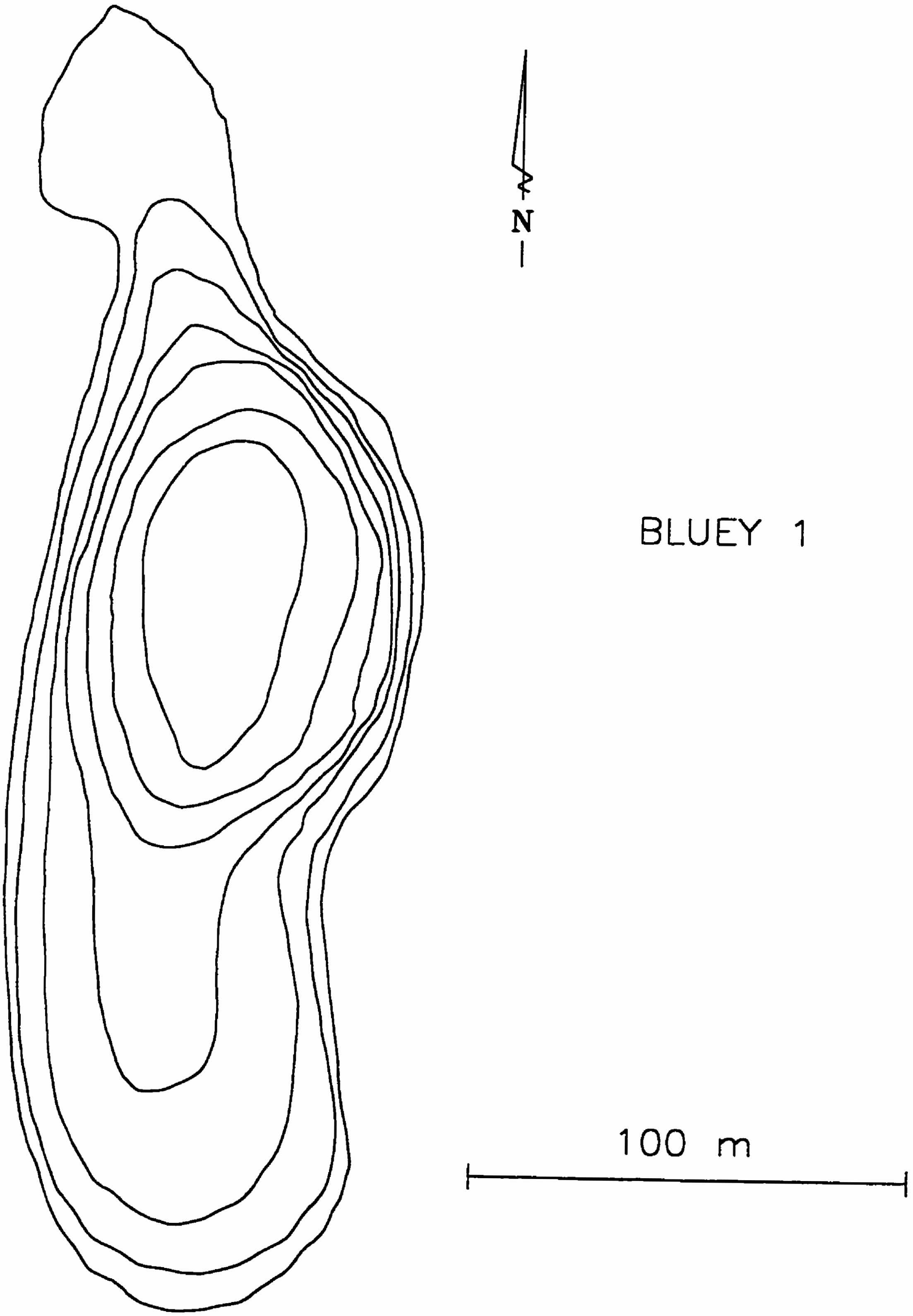

N
BLUEY 1
100 m

Figure 1.3 Bathymetric map of Bluey 2 Lake, the Age-0 + Age-1 treatment. Depth contours in m.

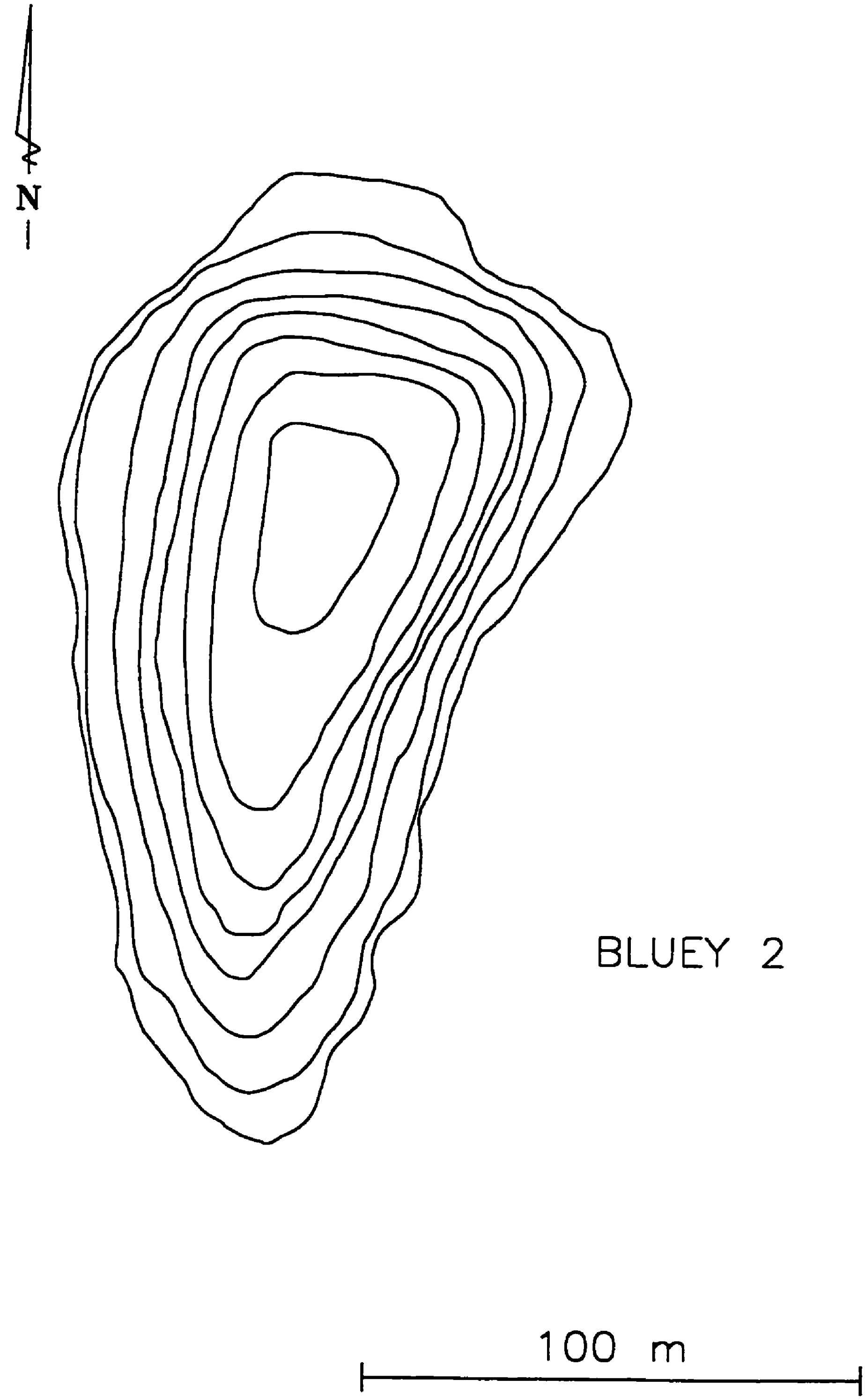
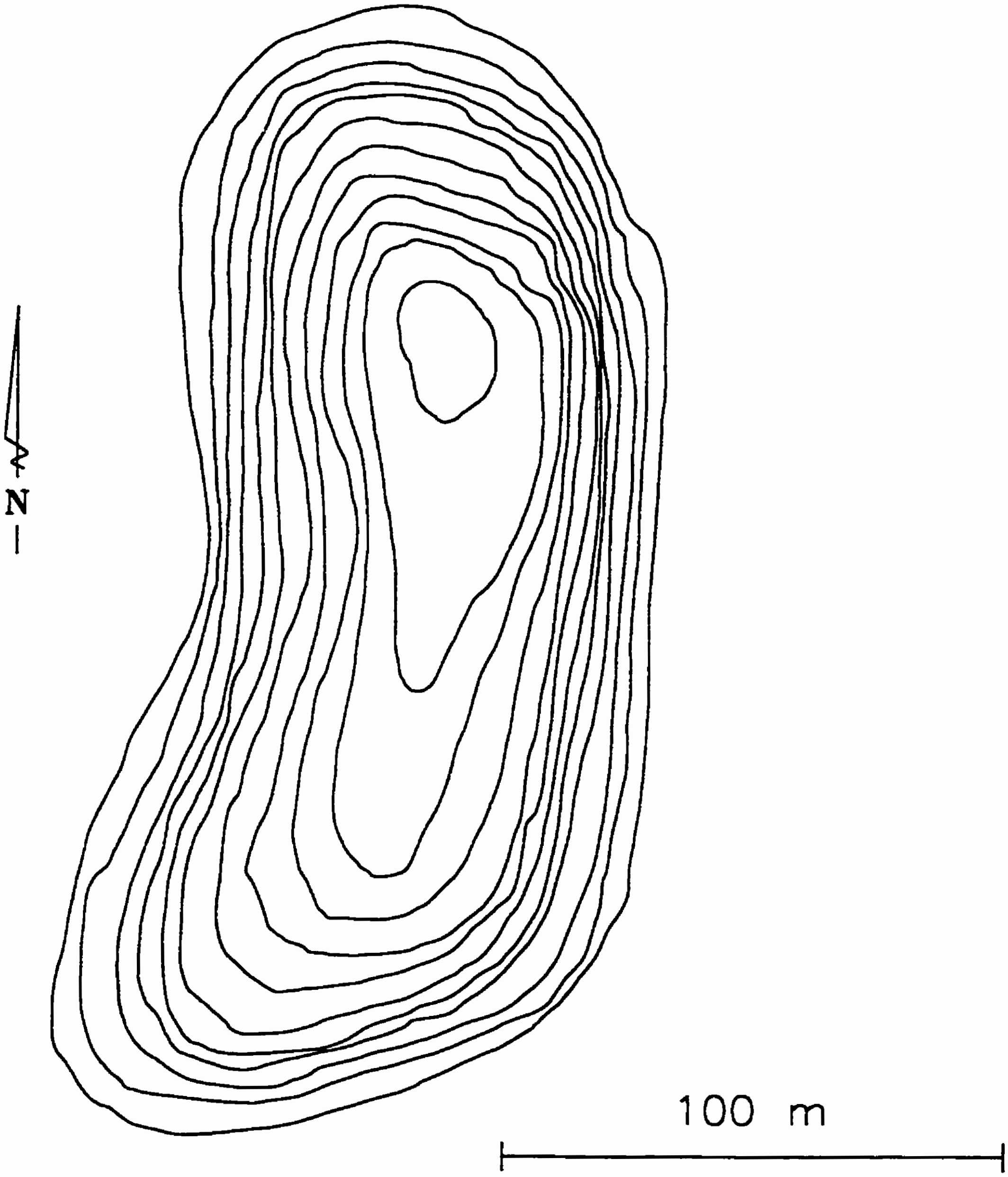

N
BLUEY 2
100 m

Figure 1.4 Bathymetric map of Kentucky Pothole Lake, the Age-0 treatment. Depth contours in m.

KENTUCKY POTHOLE



1.2.2 Experimental design

The main objective of this project was to examine the spatial distribution of age-0 rainbow trout among lakes with different size-structured populations. The experiment involved three stocked trout populations with different size-structures. Bluey 1 was stocked with both age-0 and age-1 rainbow trout (referred as the Age-0 / Age-1 treatment) where both age classes were present throughout the entire experiment. Kentucky Pothole (referred as Age-0 treatment), received only age-0 rainbow trout, so that inter-age-class interactions could not occur. These two lakes acted as references for comparison to an experimentally perturbed system, Bluey 2. This treatment involved adding age-1 rainbow trout to the lake on August 19 which had previously contained only age-0 rainbow (referred to the Age-0 + Age-1 treatment).

All three lakes were stocked with age-0 fish at a target density of 10 800 · ha^{-1}. Two size groups of age-0 trout were stocked simultaneously in all three lakes: 70% averaged 27 mm ± 1.15 (SD) long and a mass of 0.17 ● 0.03 (SD) g, whereas the other 30% averaged 37 mm ± 2.35 (SD) long and a mass of 0.50 ± 0.11 (SD) g. Bluey 1 lake was also stocked with age-1 rainbow trout measuring 157.9 ± 25.4 (SD) mm and weighing 44.8 ± 20.7 (SD) g at a target density of 750 · ha^{-1}. Bluey 2 received age-1 trout that measured 209.4 ± 14.9 (SD) mm and weighed 101.2 ± 24.6 (SD) g and the target density was 750 · ha^{-1}. Rainbow trout longer than 150 mm are facultative piscivores (Beauchamp 1987, 1990; Post et al. unpublished manuscript).

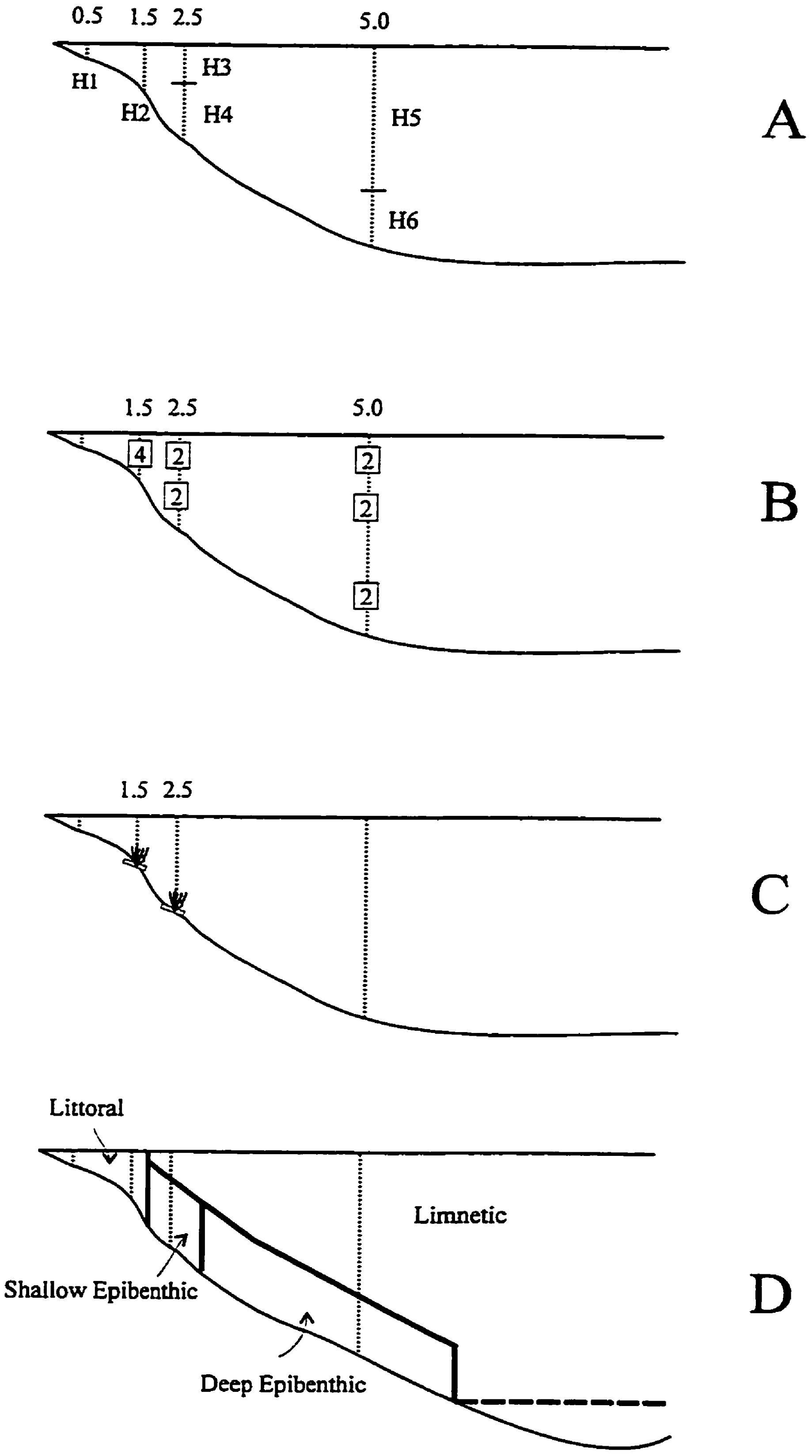
The study lasted 60 days and involved an intensive sampling of the spatial distribution of both age classes of trout and their primary prey organisms, the zooplankton and benthos communities. The period allowed ontogenetic changes to occur and extended from the end of July 1994 to the end of September 1994. Each lake was sampled eight times during that period. The first sampling day was dropped from all analyses, because age-0 trout had not yet grown to a size sufficiently large to be captured with gillnets in all lakes. So for all analyses, I refer to sampling days 1 through 7. The period between sampling days varied between 5 and 10 days. The addition of yearlings in Bluey 2 (Age-0 + Age-1 treatment) occurred between sampling days 3 and 4.

I sampled six habitats (Upper Littoral, Lower Littoral, Shallow Epibenthic, Deep Epibenthic, Midshore Limnetic, and Limnetic) to cover all possible habitats used by the trout. However, for the analyses I grouped both Littoral and both Limnetic habitats together and used four main habitats (Littoral, Shallow Epibenthic, Deep Epibenthic, and Limnetic) because the Upper Littoral represented a low percentage of the total lake volume (Table 1.2) and the Midshore Limnetic had a low proportion (mean = 0.01) of the total catches. The two Littoral habitats were referred to as Upper (H1) and Lower (H2) Littoral (Figure 1.5A), and were located at the 0.5 m and 1.5 m depth contours respectively. The Midshore Limnetic (H3) and the Shallow Epibenthic (H4) habitats were situated at the 2.5 m contour, with the Midshore Limnetic representing the top 1 m and the Shallow Epibenthic the bottom 1.5 m (Figure 1.5A). At the 5 m contour I sampled two habitats. The lower 1.5 m represented the Deep Epibenthic habitat (H6), and the Limnetic (H5) was the upper 3.5 m. The Upper and Lower Littoral, Shallow Epibenthic, and Deep Epibenthic were all situated within 1.5 m strata from the bottom of the lakes. Fish were sampled in all six habitats, whereas the zooplankton community was sampled in

Table 1.2 Total lake volumes (m^3) and volumes of the habitats sampled in the lakes.

	Age-0 / Age-1		**Age-0 + Age-1**		**Age-0**	
Habitats	volume	% total	volume	% total	volume	% total
H1	1832	3.1	1173	2.5	1363	1.6
H2	4947	8.4	3839	8.1	3102	3.5
H3	4109	7.0	2087	4.4	1918	2.2
H4	6164	10.5	3131	6.6	2877	3.3
H5	32077	54.6	30773	64.8	70747	81.4
H6	9619	16.4	6454	13.6	6900	7.9
Littoral	6779	11.5	5012	10.6	4465	5.1
Shallow Epibenthic	6164	10.5	3131	6.6	2877	3.3
Deep Epibenthic	9619	16.4	6454	13.6	6900	7.9
Limnetic	36186	61.6	32860	69.2	72665	83.6
Total volume	**58748**		**47457**		**86907**	

Figure 1.5 A. Location of the six sampling habitats and the four gillnet sampling depths in dotted line. B. Location of the zooplankton samples and number of samples per habitat. The first depth from the surface is at 1 m, the next at 2 m, and the deepest at 4 m. C. Depth of the macroinvertebrate samples. D. Division of the lake for volume calculations of each habitat. The thick dashed line represents the 6 m depth.


0.5
1.5
2.5
5.0
H1
H2
H3
H4
H5
H6
A
1.5
2.5
5.0
4
2
2
2
2
2
B
1.5
2.5
C
Littoral
Limnetic
Shallow Epibenthic
Deep Epibenthic
D

five habitats (Figure 1.5B). The macroinvertebrate community was sampled in two habitats (Lower Littoral and Shallow Epibenthic) (Figure 1.5C) and temperature and oxygen concentration were collected in all habitats.

1.2.3 Sampling procedures

Fish

I used Lundgren multiple-mesh experimental gillnets to sample age-0 fish which are slow sinking nets made with monofilament nylon. They are 11.4 m long and are divided into four panels of different mesh sizes (13 mm, 16 mm, 20 mm, and 25 mm stretched mesh). I used gillnets of four different heights (0.5, 1.5, 2.5, and 5.0 m) to sample all the habitats of the lake. I delineated the 2.5 m and the 5.0 m nets with a thin string through the entire length of the net at 1.5 m from the bottom which separated both epibenthic habitats from the limnetic habitats (Figure 1.5A). Fish caught above the string in both nets belonged to the limnetic habitats (H3 and H5). I established 10 fixed sites uniformly along each of the 0.5 m and 1.5 m depth contours for the two littoral habitats and six sites for each 2.5 m and 5.0 m depths. On each sampling day, between one and five sites were selected randomly from the ten sites for each of the littoral habitats (H1 and H2), and between one and three sites were selected from the six sites for each of the other two depths. Nets were set at those sites and I attempted to obtain a sample of approximately 200 fish on each set to have a good estimate of the spatial distribution. Consequently, the lakes were sampled with different efforts due to differences in growth rates, mortality rates, and activity levels which all influence gillnet catchability. All nets were set in the water for 1 h, and the fish were collected twice, once in the afternoon (between 12:30 and 14:30) and once at dusk. Nets set at dusk were set 0.5 h before sunset and were retrieved 0.5 h after sunset. I sampled both time periods because rainbow trout forage more intensively at dusk (Angradi and Griffith 1990; Beauchamp 1990; Tabor and Wurtsbaugh 1991), which may affect their spatial patterns in presence of older conspecifics.

A different set of gillnets was used to sample the age-1 fish during the day. They were sampled on every second sampling day in the Age-0 / Age-1 treatment and all four days following the addition of age-1 fish in the experimental treatment lake (Age-0 + Age-1). Yearlings were sampled in three habitats; the 1.5 m (Littoral), the 2.5 m (Shallow Epibenthic), and the 5.0 m (Limnetic and Deep Epibenthic). Nets of two different heights were used to sample these habitats (2.3 m and 4.9 m). These nets were gangs of seven panels, each with a different mesh size (ranging from 25 to 89 mm stretched mesh) and measuring 14.6 m in length for a total length of 102.2 m.

The fish caught in all habitats were measured (fork length, to the nearest mm), weighed (to the nearest 0.01 g), counted, and age-class was recorded. A random sub-sample of 3-10 fish per habitat were kept and stored in 4% formaldehyde for diet samples. Only the stomach contents of the age-0 rainbow trout caught at dusk were analyzed because this was the most intensive foraging period. The stomach contents of the fish kept per habitat were combined and a description of the diet was specific to each habitat on each sampling day. The fish collected on each sampling day were combined per habitat and dissected. A total of 1532 fish were dissected for diet analysis. All non-zooplankton (later referred as macroinvertebrates) prey in the sample were removed, counted, and identified to order or to family using a dissecting microscope (25 x). Only identifiable parts were counted such as head, thorax, or abdomen. The remaining sample containing the zooplankton was diluted and a sub-sample was taken to obtain an approximately 300 individuals and total density was then calculated. The zooplankton were identified to genus and counted using a dissecting microscope (25 x). The number of prey were then calculated per individual fish. The percentage that each prey category contributed to the total number of prey in all stomachs (percentage of total number) was used for analysis. A lake-wide diet for each sampling day was calculated for each treatment lake by weighting each diet observation obtained per habitat by the catch data of that habitat.

Zooplankton

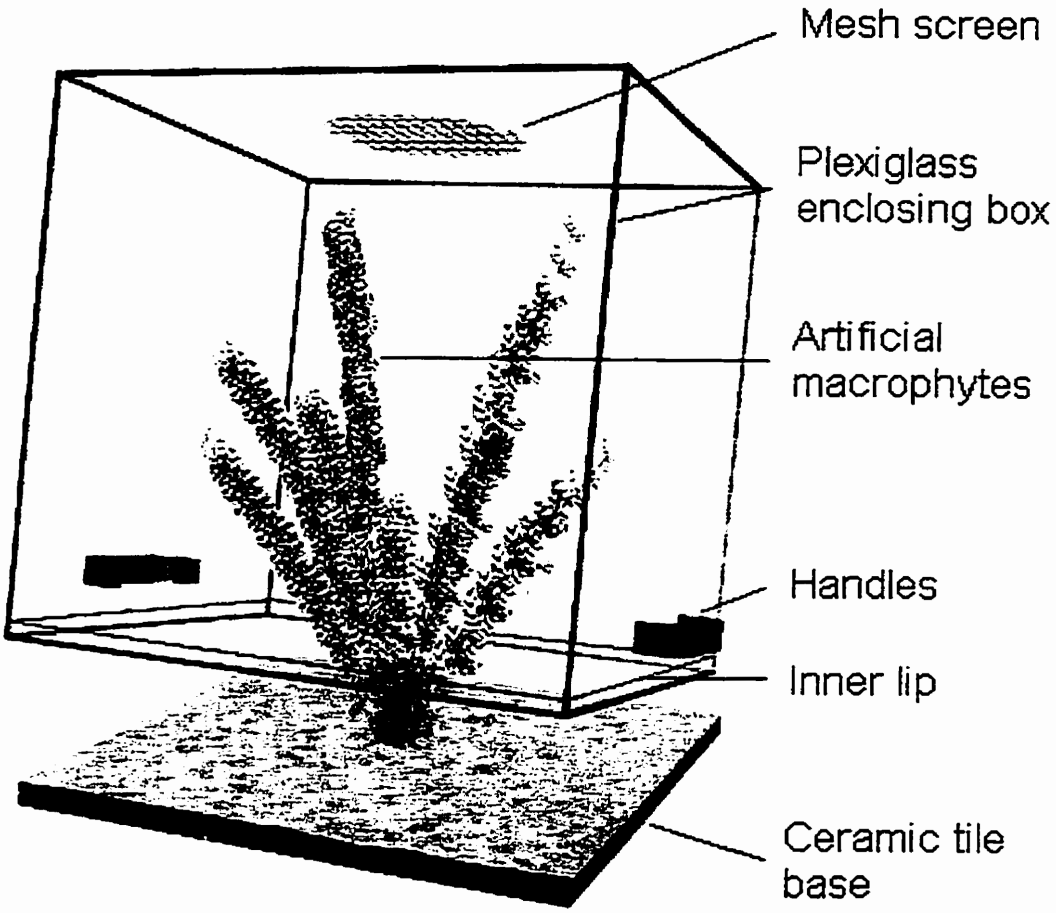
I used the relative abundance and biomass of zooplankton in each habitat to test the alternate hypothesis that fish select habitats in response to prey abundance. The zooplankton community was sampled each sampling day between the Day and Dusk gillnetting periods. The zooplankton samples were collected in five of the six habitats (Figure 1.5B) and the Upper Littoral habitat (H1) was not sampled because it was too shallow. I collected samples with a Schindler trap which collects a volume of 31.25 l of water. A sieve with an 84-µm mesh was connected to the bottom of the trap where the plankton was collected. The samples were collected where nets were set to collect fish. On each sampling day, four Lower Littoral habitat (H2) sites were sampled at 1-m depth and these samples were combined. Two samples were collected at 2-m depth for the

Shallow Epibenthic habitat (H4) and two at 4-m for the Deep Epibenthic habitat (H6) (Figure 1.5B). Six samples were collected and combined for the Limnetic habitat, including two samples from 1-m depth in the Midshore Limnetic (H3) sites and four samples in H5 (2 at 1 m and 2 at 2 m). The zooplankton samples were then preserved in 70 % ethanol, and all the zooplankton were identified in the laboratory to genus and measured to the nearest mm using a dissecting microscope (25 x). Length measurements represent the total length of the organism excluding antennae, terminal setae, appendages, and cerci. Biomass of individuals was obtained from length-weight regressions (Post 1984) for each taxon. A total biomass of zooplankton was then calculated for each habitat, on each sampling day.

Macroinvertebrates

Macroinvertebrates were sampled four times during the study period with a passive apparatus (Figure 1.6). The macroinvertebrates sampled included both benthic organisms and pelagic organisms such as Amphipods, Diptera pupae, Mites, and Hemipterans. All the lakes were sampled on sampling days 1, 3, 5 and 7. The equipment used is a ceramic tile (20 cm x 20 cm) placed with its rough surface facing up, with 12 fronds of plastic "macrophytes" (measuring 9 and 18 cm in height) glued in the middle. These macrophytes simulated the lake bottom flora and were similar to one species present in the lakes (*Myriophyllum* sp.). The tiles were then deposited by a snorkelling diver at two depths (Figure 1.5C) which corresponded to the bottom of the Lower Littoral (H2) habitat at 1.5 m, and the Shallow Epibenthic (H4) at 2.5 m. Five replicates were

Figure 1.6 Sampling device for macroinvertebrates (from Benoît et al. unpublished manuscript).


Mesh screen
Plexiglass enclosing box
Artificial macrophytes
Handles
Inner lip
Ceramic tile base

placed at each depth and the locations were chosen by randomly selecting sites from 20 fixed sites at each depth. It was previously determined that after four days, the colonized invertebrate taxa on the sampler were strongly concordant with prey items found in the stomachs of rainbow trout (Benoît et al. unpublished manuscript). The tiles were covered and retrieved after four days with an open Plexiglass box (Figure 1.6) by a snorkelling diver. Once out of the water, the water in the box flowed out the bottom through a 500-μm mesh and the invertebrates were retained on the mesh in the box. The fronds and the surface of the tile were washed with a high pressure water jet. Then all the invertebrates were collected and stored in 70% ethanol. In the laboratory the invertebrates were sorted, identified to order or family, and counted with the use of a dissecting microscope. The invertebrates were blotted to remove superficial water and each taxon was weighed as a group to the nearest 0.1 mg with an analytical balance.

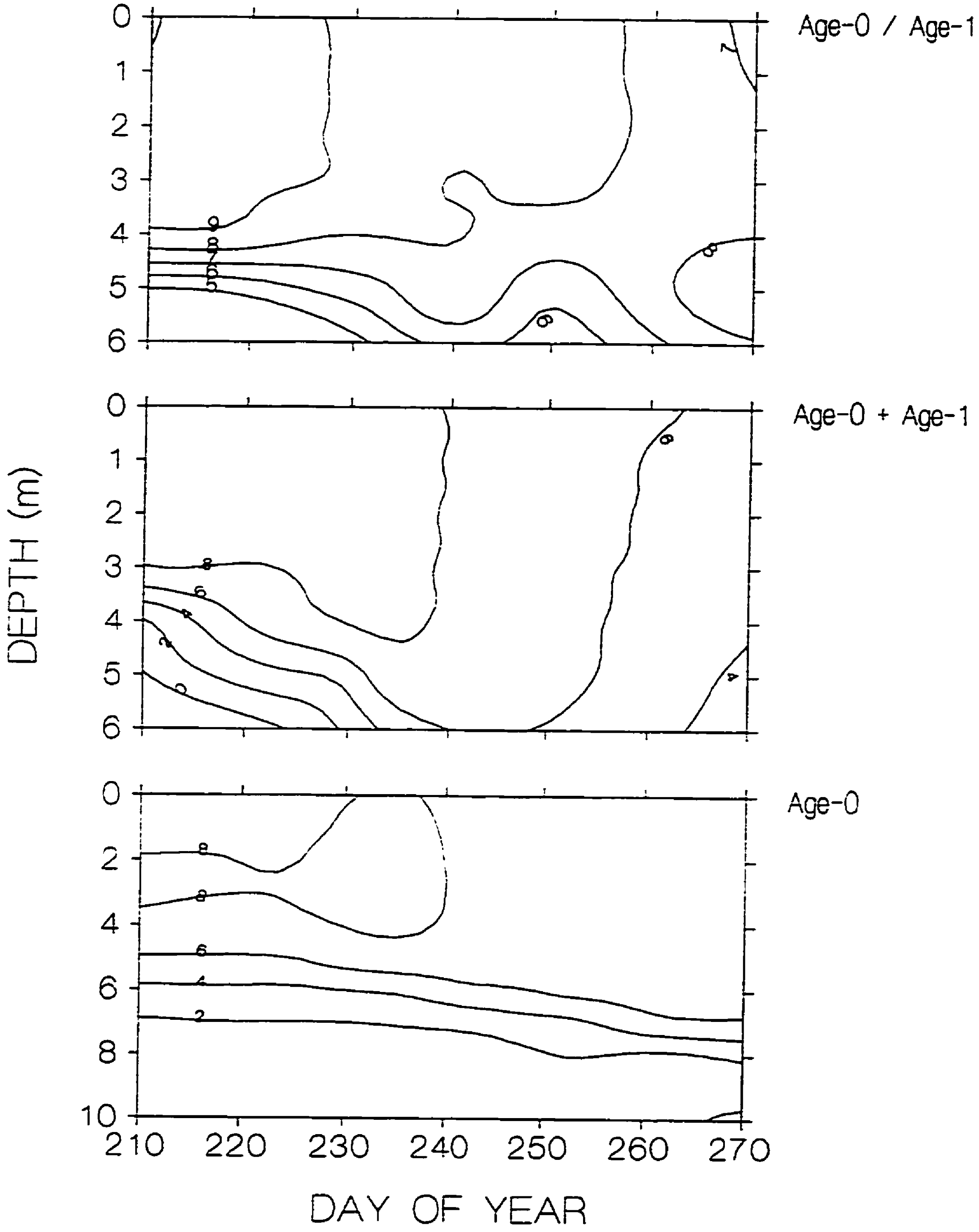
1.2.4 Data analysis

I present the density of the age-0 fish as catch per unit effort (CPUE), which represents the number of fish caught in a vertical standing gillnet in one hour expressed as the # fish $\cdot$ $(m^2)^{-1} \cdot h^{-1}$. CPUE can not be used for interpreting the spatial patterns of fish populations across predetermined habitats among lakes with varying morphometry. The morphological differences among lakes affect the size of specific habitats relative to others. If one tries to describe the spatial distribution of a population across habitats varying in volume, the CPUE will not be comparable across lakes and will not reflect the proportions of the total fish population in each habitat. Therefore, I standardized CPUE by multiplying it by the water volume of the particular habitat and used this value as a "Population Index". To calculate the volumes in each habitat, I divided the lake profile into the 4 habitats (Figure 1.5D). The Littoral habitat was the volume which included everything shallower than 2 m. The Shallow Epibenthic covered everything within 1.5 m off the bottom and between 2 and 3 m depths. The same 1.5 m strata along the bottom comprised the Deep Epibenthic, but between 3 and 6 m depth. The Limnetic strata encompassed all the rest of the lake above the 6 m depth contour which delineated the upper boundary of the anoxic hypolimnion. All spatial distribution analyses were based on the Population Indices.

The lakes were all similar in area, but differed in volume and shape (Table 1.1, 1.2). I calculated habitat volumes for all lakes based on a maximum depth of 6 m. I assumed that the number of fish below 6 m was negligible in all lakes for the following reasons. The percentage of the total volume of water below six meters was negligible in the two shallower lakes (1 and 4 %) and according to the oxygen profiles throughout the experiment for the deepest lake (Age-0 treatment) (Figure 1.7), it was reasonable to assume that there were few fish below 6 meters due to low oxygen concentrations (less than 4 ppm). Rainbow trout are rarely found where oxygen levels are below 3 $mg \cdot L^{-1}$ (Jones 1982; Ayles et al. 1976; Rowe and Chisnall 1995).

The spatial distribution dataset comprised Population Indices for each habitat over seven sampling days. In many gillnets, I caught no fish, so the data were not normally distributed and the variances were not homogeneous. I consequently used a two-step process to analyze these data. First, I assessed the spatial distribution of age-0 rainbow

Figure 1.7 Oxygen concentration (mg · L^{-1}) isopleths for each lake from end of July until end of September. Data were collected in all habitats at 1 m intervals.


Age-0 / Age-1
Age-0 + Age-1
Age-0
DEPTH (m)
DAY OF YEAR
0
1
2
3
4
5
6
8
10
210
220
230
240
250
260
270

trout among different treatment lakes and over time with a 3-factor ANOVA (Wilkinson 1992) by using only the non-zero values of the Population Indices in an unbalanced design with replicates varying from one to ten for each habitat. After a log transformation of the non-zero values, the data were normalized and variances were homogeneous. I conducted the ANOVA for only the Dusk data because from 388 nets set during the day for the whole study, 167 had no fish, hence many cells had no observations. Only 48 out of 346 nets set at Dusk had no fish, and I had to delete sampling day 1 from the 7 sampling days in the analysis because on one occasion there was a cell with no observations.

The second part of this two-step process involved analyzing all net catches including the zero values by examining the presence or absence of fish in nets across sites and treatments. These analyses helped determining the use of habitats by the age-0 fish. The capture success of the nets was modeled using a logit model (Hosmer and Lemeshow 1989; Collett 1991). I analyzed capture success using a logistic regression on the success of a net (caught fish or did not catch fish) with the LOGIT function from a supplementary module for SYSTAT (Steinberg and Colla 1991). I performed this regression to determine how factors including Treatment, Habitat, Sampling Day, and Pre/Post Addition influenced the capture success of a gillnet. I first contrasted the capture success among the three lake treatments and then I ran a separate model for each treatment for the 3 independent variables. Sampling Day was the only continuous variable. To maintain consistency with the 3-factor ANOVA, I omitted Sampling Day 1 from the analysis. There was a total of 150 nets for the Age-0 / Age-1 treatment, 148 for the Age-0 + Age-1, and 48 for the Age-0 lake. The low number of nets in the Age-0 lake was due to its high catch rates.

The basic form of the model in this study to obtain the predicted probability of catching a fish in a net P(x) was represented as:

$$P(x) = \frac{\exp\,(\beta_0 + \beta_1 x_1 + \dots \beta_p x_n)}{1 + \exp\,(\beta_0 + \beta_1 x_1 + \dots \beta_p x_n)} \tag{1}$$

where x_i (i = 1, 2, ..., n) denotes a predictor variable and β_i (i = 1, 2, ..., n) is the associated regression parameter. The logistic transform of this probability (the log of the odds) leads to the logistic model where:

$$\ln\left(\frac{P(x)}{1-P(x)}\right) = \beta_0 + \beta_1 x_1 + \dots \beta_p x_n \tag{2}$$

The regression coefficients were obtained through maximum-likelihood estimates.

I analyzed the spatial distribution of zooplankton using a single-factor ANOVA on the total zooplankton biomass per litre for each lake separately with Habitat as the main effect using sampling days as replicates. Mean densities per habitat for all lakes are plotted with the spatial distribution of the age-0 fish. To test the alternate hypothesis that the fish distribution correlates with zooplankton density, I calculated Spearman's coefficient of rank correlation (Sokal and Rohlf 1995) between the fish distribution at dusk and the zooplankton density in the four habitats. I calculated this coefficient for each sampling day in each treatment. To reject the null hypothesis that there is no correlation between the two sets of rankings with a sample size of 4, I required a perfect correlation

($r_s = 1$). Therefore, I used this analysis only to qualitatively describe patterns since the small sample size made it impossible to test the hypothesis with power.

The spatial pattern of macroinvertebrates was analyzed similarly but with only two habitats. I performed a single-factor ANOVA on the total biomass per tile with Habitat as the main effect for each lake and tested it over all sampling days pooled. Data for both zooplankton and macroinvertebrates analyses were log transformed to stabilize variances. To facilitate presentation, descriptive statistics were back-transformed, resulting in asymmetric 95 % confidence limits.

1.3 Results

1.3.1 Spatial distribution of age-0 and age-1 rainbow trout

The spatial distribution of age-0 rainbow trout varied day to dusk, over time and among treatments (Figure 1.8, 1.9). The catch rates during the day (Figure 1.8) were extremely low in the Age-0 / Age-1 treatment for the three last sampling days. There was a considerable percentage of fish during the day in the Littoral habitat in all 3 sampling days before the addition in the Age-0 + Age-1 treatment but it dropped on the last 2 sampling days and not many fish were present in the Limnetic habitat after the addition (Figure 1.8) as opposed to sampling day 1. In the Age-0 treatment, the age-0 fish tended to use the Limnetic habitat more than the other habitats during most of the sampling days. There was an increase in the use of the Limnetic habitat through time in the Age-0 / Age-1 treatment at dusk (Figure 1.9). This pattern was also observed in the experimental lake (Age-0 + Age-1) after the addition of age-1 (Figure 1.9). The Limnetic habitat had also fish before the addition.

The 3-factor ANOVA showed significant Treatment * Habitat, Treatment, and Habitat effects (Table 1.3). The Population Indices differed among treatments and the significant interaction demonstrated a difference in the spatial distribution of age-0 rainbow trout among the three treatments (Figure 1.10). In the continuous presence of older conspecifics (Age-0 / Age-1), the fish distributed themselves more uniformly across the four habitats (Figure 1.10) whereas in the Age-0 + Age-1 treatment fish used the Deep Epibenthic habitat significantly more than the Littoral and Limnetic habitats. In the

Figure 1.8 Daytime distribution of age-0 rainbow trout for each treatment for the seven sampling days from end of July to end of September. Data are means of replicate nets from each habitat presented as percentage of Total Population Index. The arrows indicate the time of addition of age-1 to the experimental lake (Age-0 + Age-1). LIT = Littoral, SE = Shallow Epibenthic, DE = Deep Epibenthic, and LIM = Limnetic. The number of fish sampled on each day is displayed.

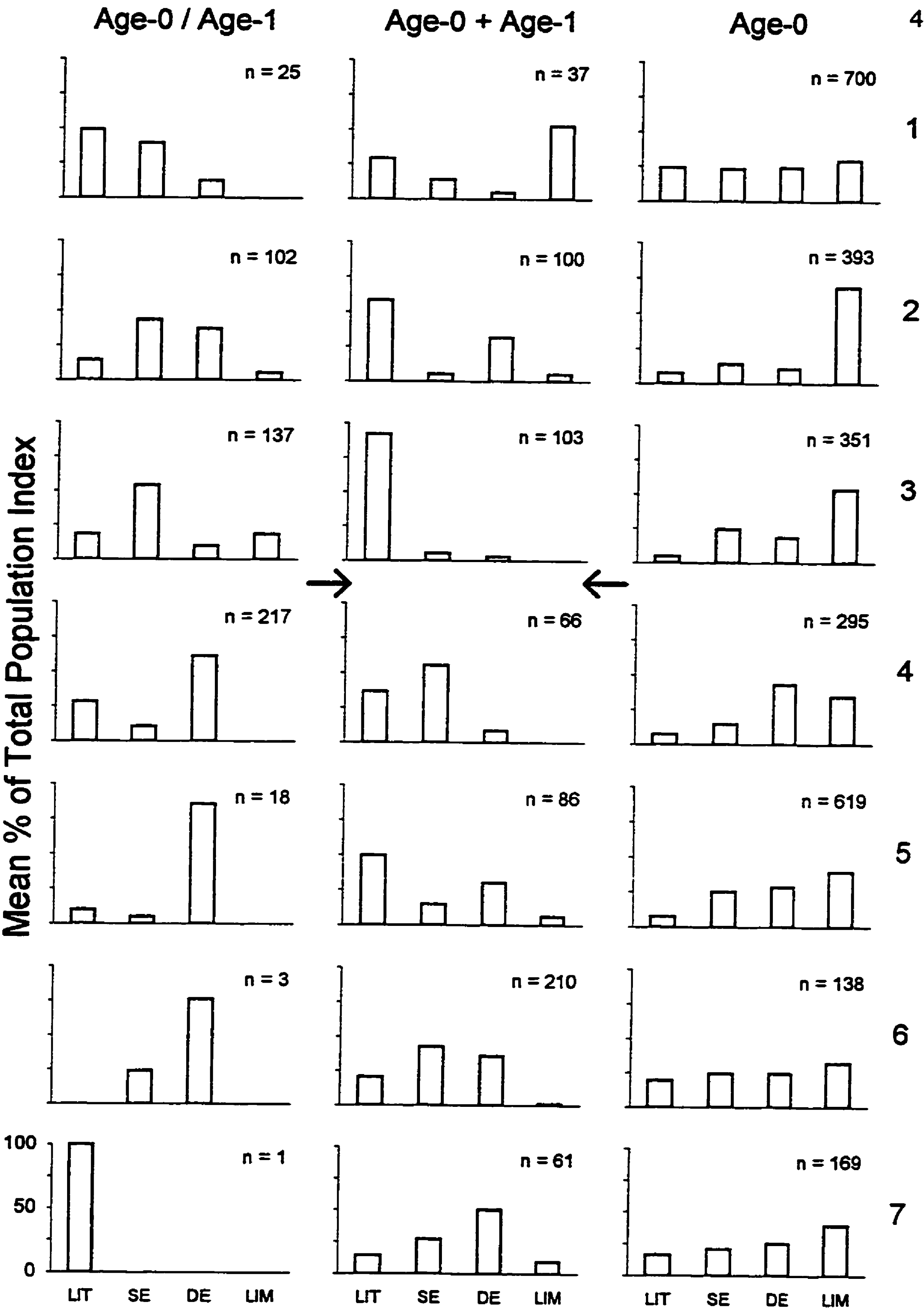

Age-0 / Age-1
Age-0 + Age-1
Age-0
Mean % of Total Population Index
n = 25
n = 37
n = 700
1
n = 102
n = 100
n = 393
2
n = 137
n = 103
n = 351
3
n = 217
n = 66
n = 295
4
n = 18
n = 86
n = 619
5
n = 3
n = 210
n = 138
6
100
50
0
n = 1
n = 61
n = 169
7
LIT
SE
DE
LIM
LIT
SE
DE
LIM
LIT
SE
DE
LIM

Figure 1.9 Dusk distribution of age-0 rainbow trout for each treatment for the seven sampling days from end of July to end of September. Data are means of replicate nets in each habitat presented as percentage of Total Population Index. The arrows indicate the time of addition of the age-1 fish to the experimental lake (Age-0 + Age-1). LIT = Littoral, SE = Shallow Epibenthic, DE = Deep Epibenthic, and LIM = Limnetic. The number of fish sampled on each day is displayed.

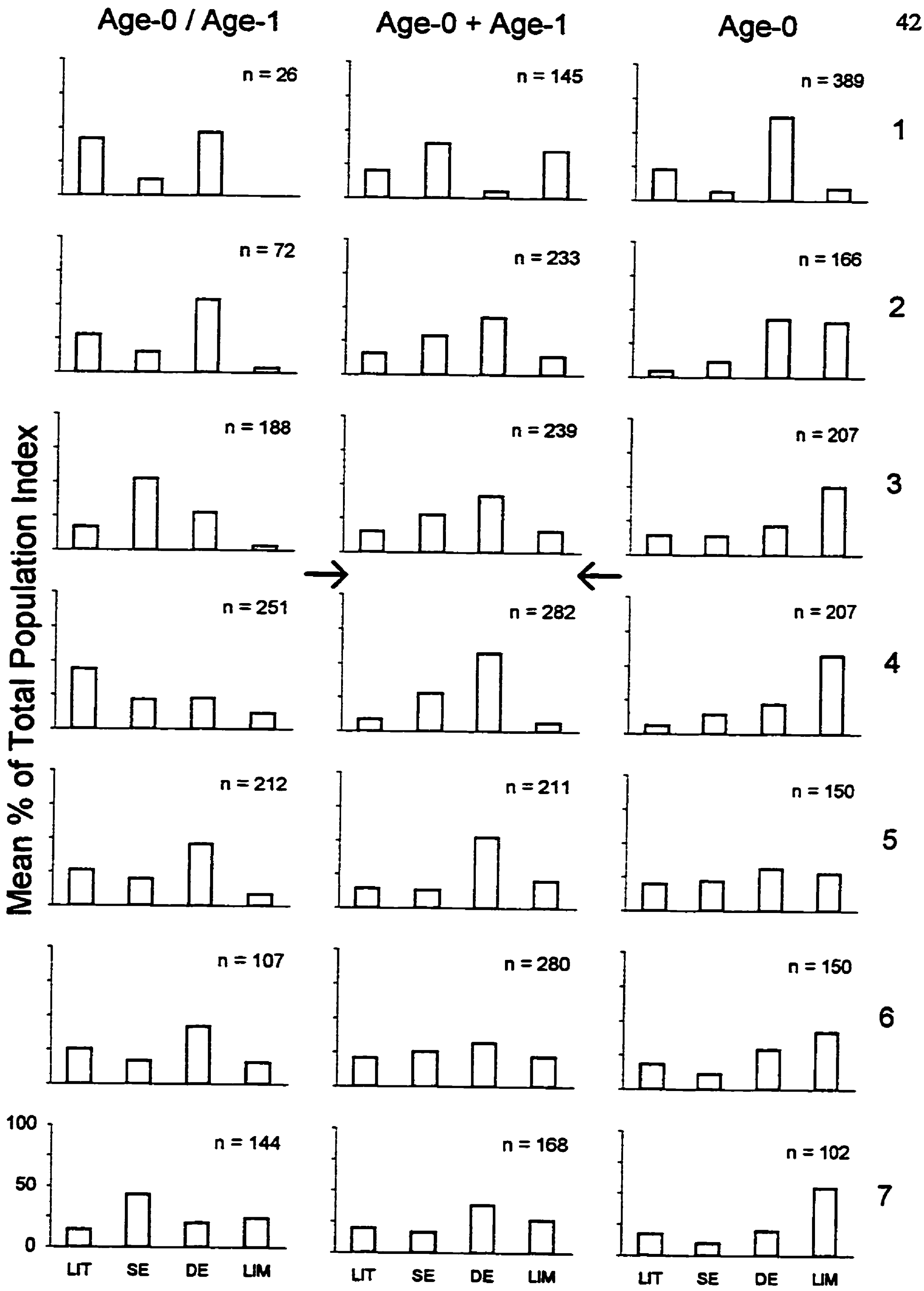
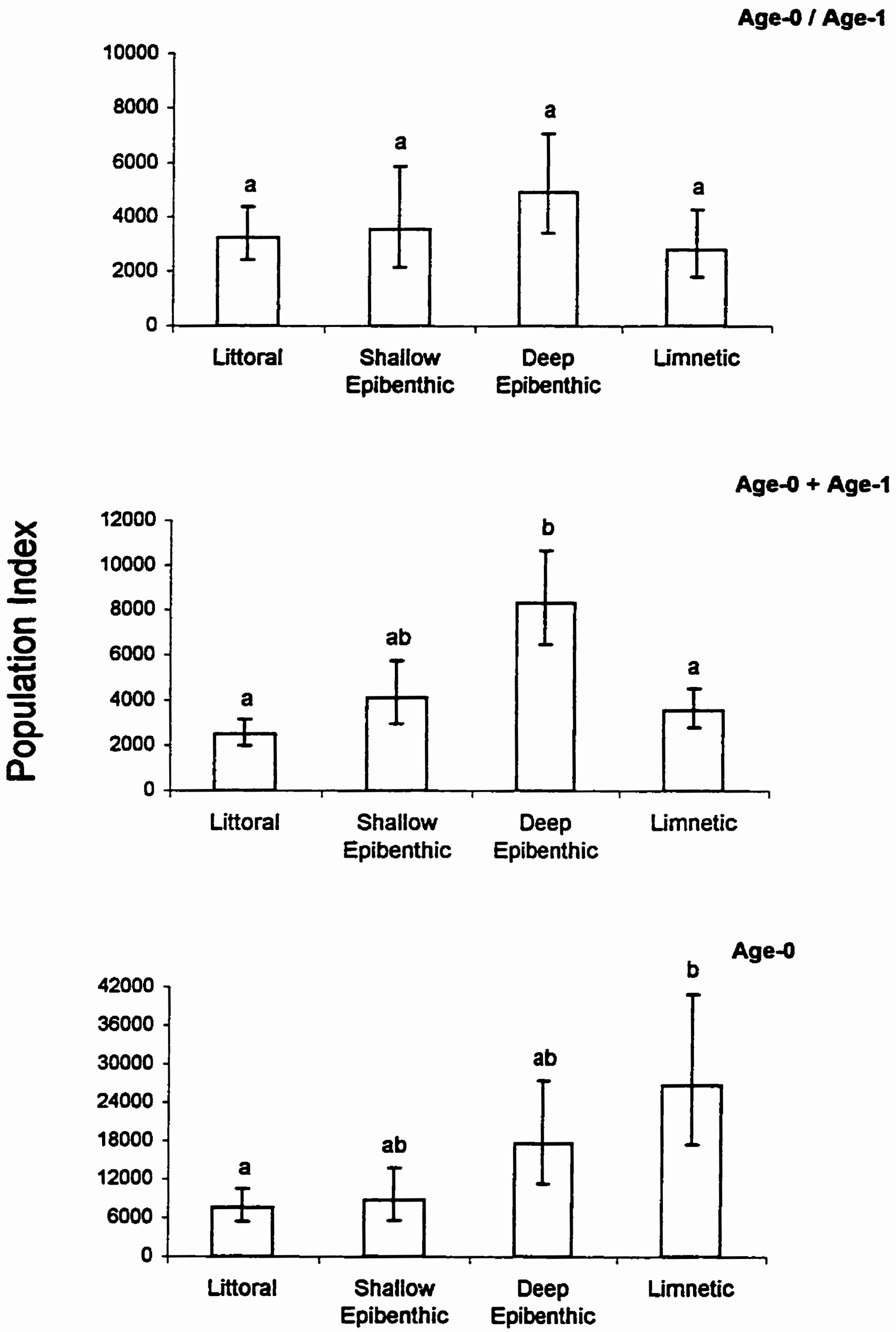

Age-0 / Age-1
Age-0 + Age-1
Age-0
Mean % of Total Population Index
n = 26
n = 145
n = 389
1
n = 72
n = 233
n = 166
2
n = 188
n = 239
n = 207
3
n = 251
n = 282
n = 207
4
n = 212
n = 211
n = 150
5
n = 107
n = 280
n = 150
6
100
50
0
n = 144
n = 168
n = 102
7
LIT
SE
DE
LIM
LIT
SE
DE
LIM
LIT
SE
DE
LIM

Table 1.3 Three-factor analysis of variance on density estimates (Population Indices) from dusk samples of the age-0 rainbow trout with respect to Treatment, Sampling Day, and Habitat over six sampling days for four habitats. All Population Indices of zero were omitted from the analysis.

Source	**SS**	**DF**	**MS**	**F-ratio**
Treatment	8.19	2	4.09	32.52***
Sampling Day	0.73	5	0.15	1.17
Habitat	3.33	3	1.11	8.80***
Treatment * Sampling Day	1.37	10	0.14	1.09
Treatment * Habitat	2.55	6	0.43	3.37**
Sampling Day * Habitat	0.70	15	0.05	0.37
Treatment * Sampling Day * Habitat	3.67	30	0.12	0.97
Error	24.05	191	0.13	

**$p < 0.01$, ***$p < 0.001$

Figure 1.10 Back-transformed means of Population Indices of age-0 fish from replicate nets containing fish for each habitat. Means are from Dusk catches over 6 sampling days for all three treatments. Error bars represent upper and lower 95 % confidence intervals. Different letters indicate a significant ($p < 0.05$) difference for a pairwise comparison on Log Population Indices using Tukey's test. Data are based on sample sizes of 1000 fish for Age-0 / Age-1 treatment, 1558 for Age-0 + Age-1, and 1371 for Age-0. The Y axes have different scales.


Age-0 / Age-1
10000
8000
6000
4000
2000
0
a
a
a
a
Littoral
Shallow Epibenthic
Deep Epibenthic
Limnetic
Age-0 + Age-1
Population Index
12000
10000
8000
6000
4000
2000
0
a
ab
b
a
Littoral
Shallow Epibenthic
Deep Epibenthic
Limnetic
Age-0
42000
36000
30000
24000
18000
12000
6000
0
a
ab
ab
b
Littoral
Shallow Epibenthic
Deep Epibenthic
Limnetic

absence of older conspecifics, the age-0 fish were significantly more abundant in the Limnetic than in the Littoral habitat. The results clearly demonstrate that fish are distributed differently among habitats across the three treatments. Approximately 80 % of the age-1 fish inhabited the Deep Epibenthic and the Limnetic habitats in both lakes containing age-1 trout (Figure 1.11).

A representation of the mean percentages of the Total Population Indices for each habitat in each lake enabled me to observe differences among treatments. The mean percentages within a habitat clearly differed among the treatments for the Dusk data (Figure 1.12). In the habitat with complex structure (Littoral), the treatment with older conspecifics (Age-0 / Age-1) had the highest percentage of age-0 fish and the treatment without older conspecifics (Age-0) had the lowest percentage. This habitat may be considered as the least risky habitat. This pattern switches for the Limnetic habitat which may be the riskiest habitat. There is approximately a 4-fold difference in the percentage of age-0 trout found in the Limnetic habitat between the Age-0 / Age-1 and Age-0 treatment at dusk (Figure 1.12). In the experimental lake, where age-1 trout were not present for half of the study period, the percentage was intermediate to the other two lakes in the Littoral and Limnetic habitats. When age-0 trout are continuously present with older conspecifics, they avoid the habitat with no physical structure (Limnetic) at dusk and utilize the habitats with structure more than age-0 fish in the absence of age-1 trout (Age-0 treatment) (Figure 1.12).

I was not able to test statistically the distributional patterns of age-0 fish during the day due to the low catches, but similar patterns to the Dusk data were observed (Figure

Figure 1.11 Mean percent of Total Population Index of the spatial distribution of age-1 rainbow trout. White bars represent the Age-0 / Age-1 treatment and dark bars the Age-0 + Age-1 treatment. Data are means of replicate nets over 4 sampling days. The 1.5 m net represents the Littoral habitat, the 2.5 m net represents the Shallow Epibenthic and the Midshore Limnetic, and the 5.0 m represents the Limnetic and the Deep Epibenthic. Error bars are one standard deviation.

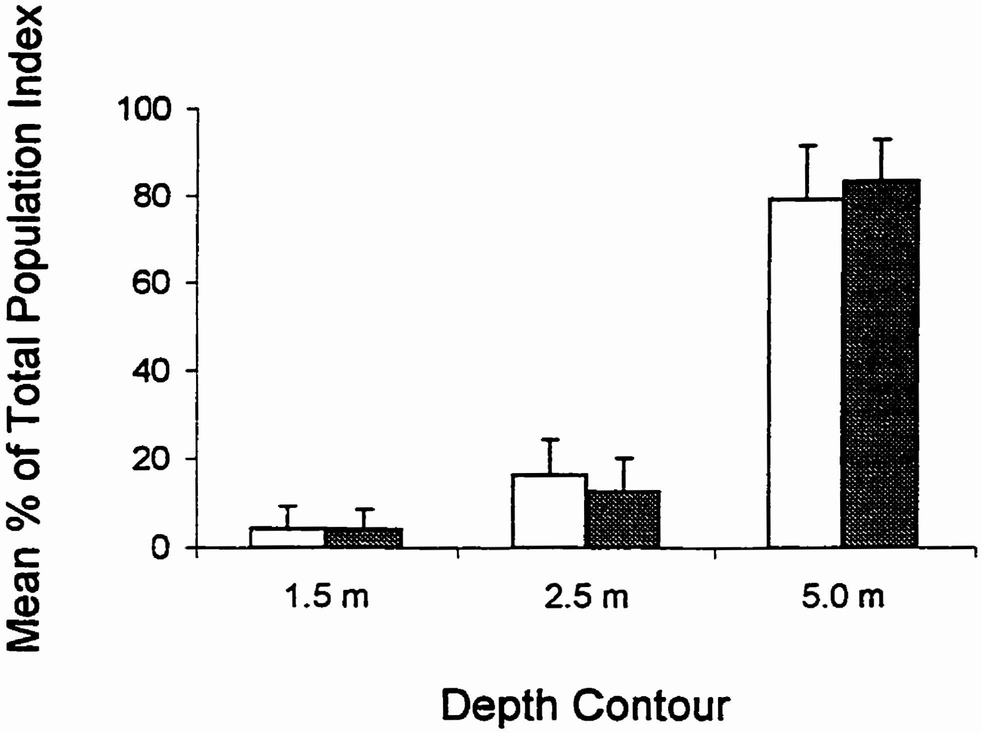
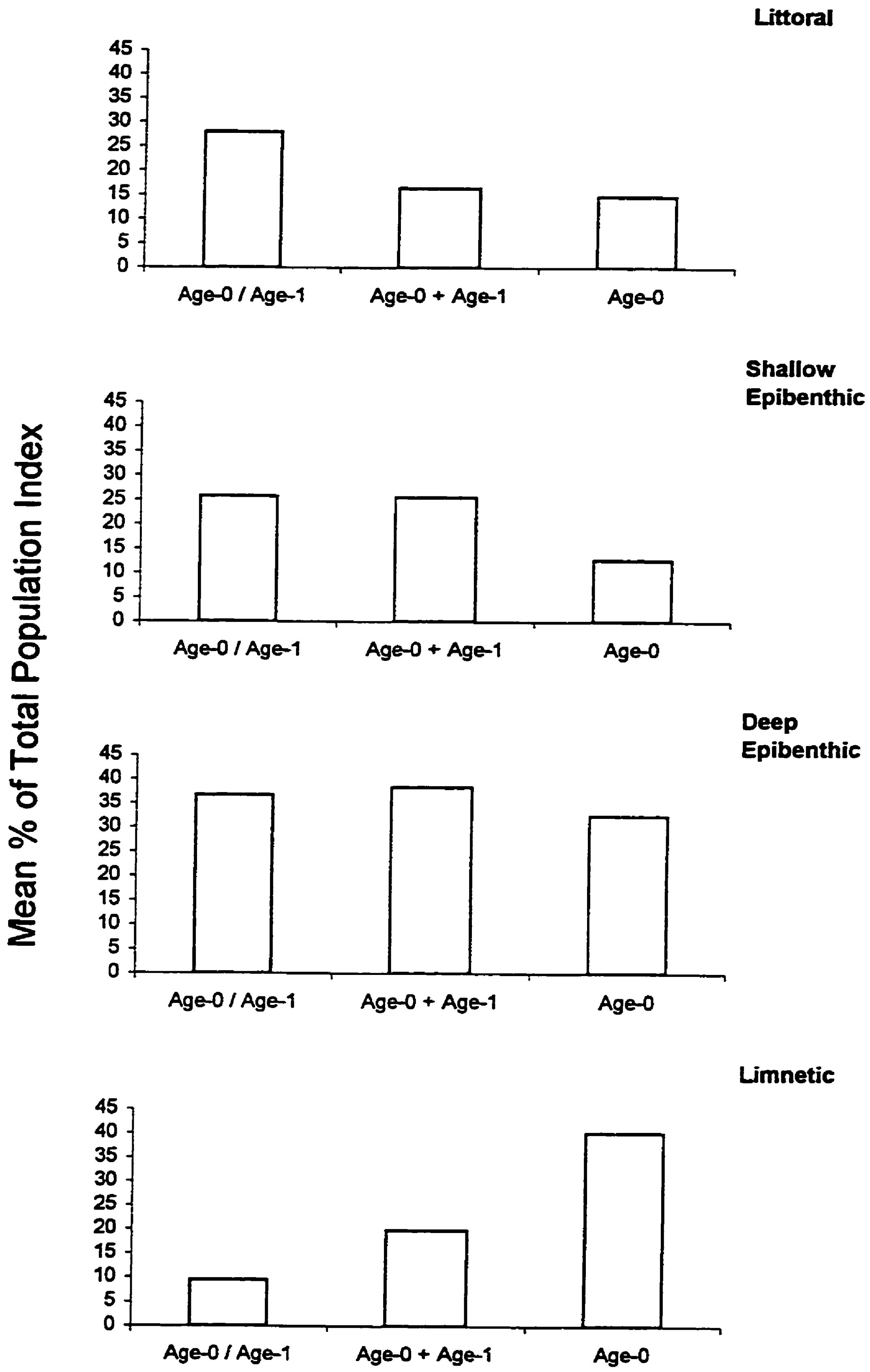

Mean % of Total Population Index
100
80
60
40
20
0
1.5 m
2.5 m
5.0 m
Depth Contour

Figure 1.12 Mean % of Total Population Index of age-0 rainbow trout for Dusk catches over 7 sampling days for all four habitats. Data represent a mean of replicate nets in each habitat for seven sampling days. Data include all catches of zero fish. Data are based on sample sizes of 1000 fish for Age-0 / Age-1 treatment, 1558 for Age-0 + Age-1, and 1371 for Age-0. Scales on Y axis differ between habitats.


Littoral
Shallow Epibenthic
Deep Epibenthic
Limnetic
Mean % of Total Population Index
45
40
35
30
25
20
15
10
5
0
Age-0 / Age-1
Age-0 + Age-1
Age-0

1.13). There was a greater difference in percentage of age-0 fish found in the Limnetic habitat between the extreme treatments (Age-0 / Age-1 and Age-0) compared to Dusk data. There was approximately a 9-fold difference (Figure 1.13). The large increase in use of the Littoral habitat in the experimental lake (Age-0 + Age-1) is partly due to sampling day 3 where 90 % of the Total Population Index was obtained from one net in the Littoral habitat for unknown reasons.

Complementary to the ANOVA of treatment effects, I performed four logistic regressions on the success rate of the nets for the Dusk catches using Treatment, Habitat, Sampling Day, and Pre/Post Addition as independent variables. Gillnet success rate varied across lakes, and among habitats within treatments. With Treatment as a categorical variable, the Age-0 / Age-1 lake was used as the reference group for the other two lakes (Table 1.4). The parameter estimates were calculated with Equation 2, and in a univariate case, the estimates of the standard errors are identical to the estimates obtained using the cell frequencies from the contingency table (Hosmer and Lemeshow 1989). Therefore no standard errors are reported for the Age-0 lake, because all nets caught fish, and the standard error calculation includes a division by the number of empty nets. The probabilities of success were calculated with Equation 1 and the Age-0 treatment yielded a probability of 1 since all nets caught fish. The lake with the continuous presence of age-1 trout had the lowest predicted probability of success, suggesting that not all nets caught fish which implies that fish are not using all habitats.

Because each lake differed in the probability of success overall, I examined differences across habitats within each lake and observed significant differences which

Figure 1.13 Mean % of Total Population Index of age-0 trout for Day catches over 7 sampling days for all four habitats. Data represent a mean of replicate nets in each habitat for seven sampling days. Sampling days six and seven were omitted in the Age-0 / Age-1 treatment. Data include all catches of zero fish. Data are based on sample sizes of 499 fish for Age-0 / Age-1 treatment, 663 for Age-0 + Age-1, and 2665 for Age-0. Scales on Y axis differ between habitats.

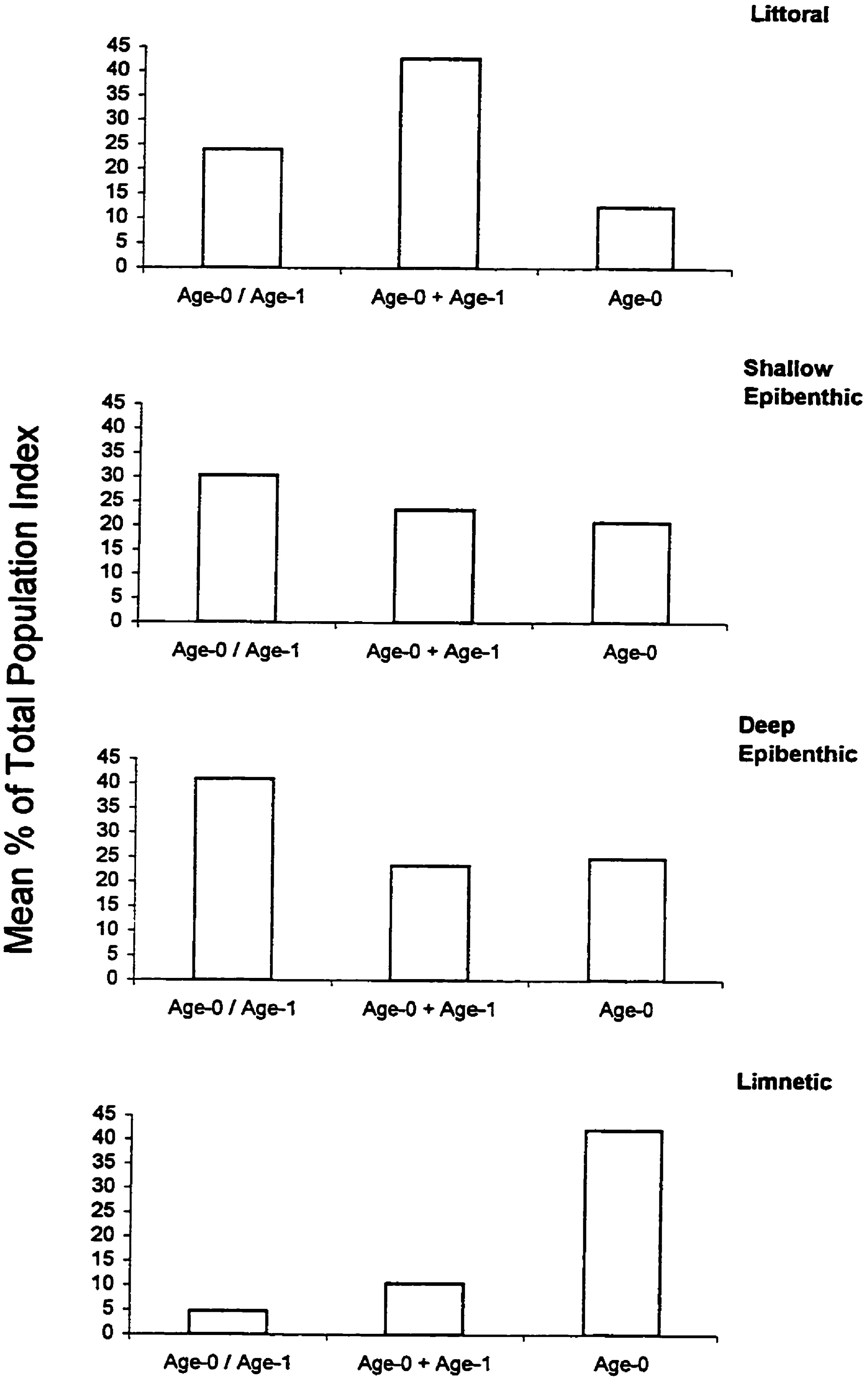

Littoral
Shallow Epibenthic
Deep Epibenthic
Limnetic
Mean % of Total Population Index
0
5
10
15
20
25
30
35
40
45
Age-0 / Age-1
Age-0 + Age-1
Age-0

Table 1.4 Logistic regression of treatment effects on dusk gillnet catch success. Treatment is used as the independent categorical variable. The model uses treatment Age-0 / Age-1 as the reference group (α). Two dummy variables were created, one for each of the other two treatments. The Age-0 + Age-1 treatment is represented with the β_1 parameter and the Age-0 with β_2. The predicted probability of success is calculated for each treatment manipulation. Sampling day 1 was omitted from the analysis.

Parameter	**Estimate**	**SE**	**t-ratio**
α	1.686	0.243	6.928***
β_1	1.147	0.459	2.499**
β_2	14.516	na	na

Treatment	**P(success)**
Age-0 / Age-1	0.84
Age-0 + Age-1	0.94
Age-0	1.00

Note: The SE and the t-ratio can not be calculated when the success rate is always 1.
na = not applicable
**p < 0.01, ***p < 0.001

were similar to the spatial distribution results (Table 1.5). No regression was performed for the Age-0 treatment due to catches in all nets. In the regressions for the other two treatments, I used the Littoral habitat as the reference group. The low predicted probability of success in the Limnetic habitat for the Age-0 / Age-1 treatment infers a low use of that habitat which may due to its greater risk. There is also a significantly lower success rate in the Limnetic habitat for the experimental lake compared to its Littoral habitat.

Sampling Day and Pre/Post Addition were both analyzed separately. Sampling Day was treated as a continuous variable and significantly affected the success rate of the nets in the lake with the continuous presence of older conspecifics (Age-0 / Age-1), but did not affect the other two lakes (Table 1.6). This supports an increase use of all habitats as observed in the spatial distribution data of the Age-0 / Age-1 treatment (Figure 1.9). This effect is observed in the predicted probability values.

In the models with the Pre/Post Addition variable, I used the Pre-Addition as the reference group (Table 1.7). There were no significant differences between the two periods in both lakes with yearlings. In the Age-0 / Age-1 treatment, there was a non-significant increase in capture success from the Pre- to the Post-period as observed in the Sampling Day model. But in the experimental lake I observed a non-significant decrease in the Post-period as would be expected if the age-1 trout affected the age-0 fish. Both analyses demonstrated an overall increased use of habitats through time in the Age-0 / Age-1 treatment and no significant increase in capture success rate through time in the Age-0 + Age-1 treatment but the Pre/Post Addition model detected a non-significant

Table 1.5 Logistic regression of habitat effects on dusk gillnet catch success. Habitat is used as the independent categorical variable. A regression model is presented for each treatment. Each model uses the Littoral habitat as the reference group (α). Three dummy variables were created to represent the other three habitats. The Shallow Epibenthic habitat parameter is represented by β_1, the Deep Epibenthic by β_2, and the Limnetic by β_3. The predicted probability of success for each habitat in each lake is calculated in the analysis. Sampling day 1 was omitted from the analysis.

Treatment	**Parameter**	**Estimate**	**SE**	**t-ratio**
Age-0 / Age-1	α	2.872	0.593	4.839***
	β_1	13.331	na	na
	β_2	13.331	na	na
	β_3	-2.760	0.681	-4.054***
Age-0 + Age-1	α	3.970	1.009	3.933***
	β_1	12.233	na	na
	β_2	12.233	na	na
	β_3	-2.361	1.104	-2.138**
Age-0	α	na	na	na
	β_1	na	na	na
	β_2	na	na	na
	β_3	na	na	na

	P(success)		
	Age-0 / Age-1	**Age-0 + Age-1**	**Age-0**
Littoral	0.95	0.98	1.00
Shallow Epibenthic	1.00	1.00	1.00
Deep Epibenthic	1.00	1.00	1.00
Limnetic	0.53	0.83	1.00

Note: The SE and the t-ratio can not be calculated when the success rate is always 1.

na = not applicable

**$p < 0.01$, ***$p < 0.001$

Table 1.6 Logistic regression of sampling day effects on dusk gillnet catch success. Sampling Day is used as the independent continuous variable. A regression model is presented for each treatment. The predicted probability of success is calculated for each sampling day in each treatment. Sampling day 1 was omitted from the analysis.

Treatment	Parameter	Estimate	SE	t-ratio
Age-0 / Age-1	α	0.292	0.655	0.4
	β_1	0.329	0.154	2.134*
Age-0 + Age-1	α	1.604	1.030	1.6
	β_1	0.289	0.244	1.2
Age-0	α	na	na	na
	β_1	na	na	na

		P(success)	
Sampling day	**Age-0 / Age-1**	**Age-0 + Age-1**	**Age-0**
2	0.72	0.90	1.00
3	0.78	0.92	1.00
4	0.83	0.94	1.00
5	0.87	0.95	1.00
6	0.91	0.97	1.00
7	0.93	0.97	1.00

Note: The SE and the t-ratio can not be calculated when the success rate is always 1.

na = not applicable

*$p < 0.05$

Table 1.7 Logistic regression of effects of pre/post addition on dusk gillnet catch success. Pre/Post Addition is used as the independent categorical variable. A regression model is presented for each treatment. The model uses the Pre-Addition category as the reference group (α). One dummy variable is created to represent the category Post-Addition. The parameter for that dummy variable is β_1. The predicted probability of success is calculated for each treatment manipulation. Sampling day 1 was omitted from the analysis.

Treatment	Parameter	Estimate	SE	t-ratio
Age-0 / Age-1	α	0.969	0.354	2.738**
	β_1	1.203	0.499	2.410
Age-0 + Age-1	α	2.890	0.726	3.979***
	β_1	-0.081	0.860	-0.094
Age-0	α	na	na	na
	β_1	na	na	na

P(success)

	Age-0 / Age-1	Age-0 + Age-1	Age-0
Pre	0.72	0.95	1.00
Post	0.90	0.94	1.00

Note: The SE and the t-ratio can not be calculated when the success rate is always 1.

na = not applicable

**p < 0.01, ***p < 0.001

lower rate after the addition as expected from interference by the age-1 trout.

1.3.2 Diet of age-0 rainbow trout

Age-0 rainbow trout in the three experimental lakes ate both macroinvertebrates and zooplankton (Table 1.8). Zooplankton dominated the diet as a percentage of number (84-93 %) but macroinvertebrates were always present in the diet and were also important diet items because they are larger-bodied than zooplankton. More specifically, in two of the lakes (Age-0 / Age-1 and Age-0 + Age-1) age-0 fish primarily ate *Daphnia* spp. (Table 1.9), whereas in the Age-0 treatment fish fed on three zooplankton taxa. These trends are present throughout the study. In the Age-0 treatment, fish switched from eating two taxa to eating primarily *Cyclops* spp. on the 6 and 7 sampling days because the populations from the other taxa had collapsed. In all lakes, the macroinvertebrate diet was diverse, dominated by Chironomidae spp. larvae, Diptera pupae, *Chaoborus* spp. larvae, and Amphipoda spp. (Table 1.10). In the continuous presence of age-1 (Age-0 / Age-1 treatment), the age-0 trout mainly fed on Diptera pupae and Chironomidae spp. larvae whereas in the other two lakes a major part of their diet consisted of taxa found in open water such as *Chaoborus* larvae, amphipods, and also terrestrial insects.

1.3.3 Spatial distribution of zooplankton and macroinvertebrates

Data on the spatial and temporal distribution of zooplankton and macroinvertebrate taxa were collected to test the alternate hypothesis that age-0 rainbow trout distributed themselves in response to spatial variation in their prey community rather

Table 1.8 Percentage of total number of macroinvertebrates (Macro) and zooplankton (Zoo) eaten by age-0 fish, weighted per Population Index. The percentages are indicated for all sampling days and a mean over all days is calculated for each treatment.

	Sampling Day							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**Mean**
				Age-0 / Age-1				
Macro	7.2	10.9	12.4	11.2	7.2	8.2	1.5	**8.4**
Zoo	92.8	89.1	87.6	88.8	92.8	91.8	98.5	**91.6**
# fish	15	38	55	77	79	32	69	
Total # fish				**365**				
				Age-0 + Age-1				
Macro	25.2	0.9	2.0	0.6	0.5	9.9	9.3	**6.9**
Zoo	74.8	99.1	98.0	99.4	99.5	90.1	90.7	**93.1**
# fish	61	80	90	79	93	99	96	
Total # fish				**598**				
				Age-0				
Macro	1.3	2.0	0.8	0.6	1.0	47.3	61.9	**16.4**
Zoo	98.7	98.0	99.2	99.4	99.0	52.7	38.1	**83.6**
# fish	75	71	89	93	69	85	87	
Total # fish				**569**				

Table 1.9 Percentage of zooplankton taxa eaten by age-0 fish, weighted per Population Index. Taxa that made up less than 0.1 % of the diet are indicated by an asterisk and if not present in the diet sample they are indicated by a dash. The diets are indicated for all sampling days and a mean over all days is calculated for each treatment.

	Sampling Day							
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**Mean**
				Age-0 / Age-1				
Ceriodaphnia	-	-	-	0.3	0.7	1.7	0.1	**0.4**
Daphnia	99.1	100	100	99.7	99.3	98.3	99.5	**99.4**
Cyclops	-	-	-	-	-	-	-	-
Diaptomus	0.9	-	-	-	-	*	0.4	**0.2**
				Age-0 + Age-1				
Ceriodaphnia	-	-	-	-	-	-	-	-
Daphnia	99.8	96.2	99.2	100.	100.	13.1	3.6	**73.1**
Cyclops	-	-	-	*	*	0.1	*	*
Diaptomus	0.2	3.8	0.8	*	*	86.8	96.4	**26.8**
				Age-0				
Ceriodaphnia	-	-	-	-	-	-	-	-
Daphnia	23.7	80.6	71.4	29.1	0.4	-	1.1	**29.5**
Cyclops	-	-	-	-	-	99.1	98.9	**28.3**
Diaptomus	76.3	19.4	28.6	70.9	99.6	0.9	-	**42.2**

Table 1.10 Percentage of total number of macroinvertebrate and terrestrial insect taxa eaten by age-0 fish, weighted per Population Index calculated for each habitat. Taxa that made up less than 0.1 % are indicated by an asterisk and those not present in the diet are indicated by a dash. The diets are indicated for all sampling days and a mean over all days is calculated for each treatment. Miscellaneous category includes taxa which occur in 0.1 % or less of the mean diet for all treatments. It is composed of the following taxa (Coleoptera, Ostracoda, Turbellaria, Ceratopogonidae, Araneae, Anisoptera, Hirudinea, and Trichoptera).

				Sampling Day				
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**Mean**
				Age-0 / Age-1				
Ephemeroptera	*	0.4	0.1	0.1	0.1	0.5	0.4	**0.2**
Trichoptera larvae	-	-	-	-	-	0.1	0.1	*
Chironomidae larvae	0.5	70.8	27.0	47.4	30.5	31.2	15.9	**31.9**
Diptera pupae	0.4	17.9	59.8	42.7	54.8	40.0	19.6	**33.6**
Chaoborus larvae	*	2.9	0.3	0.4	8.7	4.3	10.7	**3.9**
Corixidae (Hemiptera)	-	-	-	-	-	-	-	-
Zygoptera	*	0.2	0.1	0.1	1.2	12.9	38.7	**7.6**
Amphipoda	0.1	3.2	0.5	0.5	0.9	7.5	4.7	**2.5**
Gastropoda	-	-	-	-	*	0.3	1.2	**0.2**
Pelecypoda	-	-	-	-	-	-	-	-
Mites (Acari)	*	2.1	12.1	8.0	2.1	1.7	0.5	**3.8**
Nematoda	-	-	-	-	-	-	0.2	*
Miscellaneous	-	-	*	*	0.1	1.6	0.4	**0.3**
Trichoptera adult	-	-	-	-	-	-	-	-
Diptera adult	-	2.4	*	0.6	1.4	*	7.7	**1.7**
Hymenoptera	-	-	-	-	0.1	-	-	*
Aphidae (Homoptera)	-	-	-	-	-	-	-	-

Table 1.10 Continued.

	Sampling Day							
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**Mean**
				Age-0 + Age-1				
Ephemeroptera	-	0.2	12.7	6.8	17.0	1.6	0.1	**5.5**
Trichoptera larvae	-	-	-	-	-	1.6	2.2	**0.5**
Chironomidae larvae	0.4	6.6	3.1	7.6	4.1	41.1	37.2	**14.3**
Diptera pupae	1.4	13.0	6.2	20.0	6.7	8.1	15.8	**10.2**
Chaoborus larvae	96.3	29.0	46.9	25.4	22.7	9.2	8.4	**34.0**
Corixidae (Hemiptera)	0.1	-	-	-	0.2	0.4	1.0	**0.2**
Zygoptera	-	0.9	0.5	4.0	2.7	4.6	0.2	**1.8**
Amphipoda	1.7	47.5	28.1	34.7	18.8	19.2	10.4	**22.9**
Gastropoda	-	-	1.5	-	-	8.3	1.1	**1.6**
Pelecypoda	-	0.3	0.1	0.1	0.1	2.7	0.9	**0.6**
Mites (Acari)	-	-	-	-	-	0.5	0.1	**0.1**
Nematoda	-	-	0.2	-	-	-	-	*****
Miscellaneous	0.1	-	*	0.6	-	0.6	*	**0.2**
Trichoptera adult	-	-	-	0.1	0.6	0.1	0.1	**0.1**
Diptera adult	*	2.3	0.4	0.5	7.2	1.7	16.9	**4.2**
Hymenoptera	-	0.1	-	0.1	20.1	*	2.2	**3.2**
Aphidae (Homoptera)	-	-	0.2	0.1	-	0.1	3.5	**0.6**
				Age-0				
Ephemeroptera	-	-	45.0	3.1	0.2	0.3	0.3	**7.0**
Trichoptera larvae	-	-	-	-	*	1.1	-	**0.2**
Chironomidae larvae	25.6	37.2	4.7	13.2	5.2	26.5	14.8	**18.2**
Diptera pupae	1.3	0.2	0.9	2.0	0.1	1.6	0.6	**1.0**
Chaoborus larvae	57.0	14.1	5.9	2.4	2.3	14.7	8.4	**15.0**
Corixidae (Hemiptera)	-	-	-	2.5	1.2	-	0.8	**0.6**
Zygoptera	*	-	0.3	6.7	2.4	2.7	0.9	**1.9**
Amphipoda	15.4	44.5	35.2	53.7	37.5	25.0	10.8	**31.7**
Gastropoda	-	-	-	-	-	0.1	0.3	**0.1**
Pelecypoda	-	-	-	1.2	0.1	1.7	1.7	**0.7**
Mites (Acari)	-	-	-	-	-	-	1.1	**0.2**
Nematoda	-	-	1.8	5.9	4.0	2.5	2.0	**2.3**
Miscellaneous	-	-	0.2	0.2	0.2	-	0.2	**0.1**
Trichoptera adult	-	-	-	1.3	*	-	0.5	**0.3**
Diptera adult	0.6	3.9	5.8	7.0	4.9	23.7	34.7	**11.5**
Hymenoptera	-	0.1	0.4	0.6	41.3	*	18.3	**8.7**
Aphidae (Homoptera)	-	-	-	-	0.4	-	4.7	**0.7**

than in response to presence of larger conspecifics. Zooplankton biomass varied among habitats and through time in each treatment lake (Figure 1.14). The Littoral habitat had the lowest density for most of the sampling days in all three lakes which implies that it was not a profitable habitat for foraging on zooplankton. The mean biomass differed by approximately an order of magnitude among lakes with a mean of 3261 $mg \cdot L^{-1}$ for the Age-0 / Age-1 treatment, 2135 $mg \cdot L^{-1}$ for the Age-0 + Age-1, and 376 $mg \cdot L^{-1}$ for Age-0. A one-factor ANOVA for each treatment identified significant differences in prey densities across habitats (Age-0 / Age-1: $F_{3,24} = 4.303$, $p < 0.05$; Age-0 + Age-1: $F_{3,24} = 5.762$, $p < 0.01$; Age-0: $F_{3,24} = 7.893$, $p < 0.01$). In all 3 lakes the Littoral habitat had the lowest zooplankton biomass and in all instances it was significantly lower than in Limnetic habitat (Figure 1.15). In the continuous presence of older conspecifics (Age-0 / Age-1), the Limnetic habitat had a low percentage of fish and a high density of zooplankton.

With a small sample size of 4, the correlation patterns (mean = 0.57) between zooplankton biomass and age-0 rainbow trout distribution in the Age-0 lake (Figure 1.16) suggest that the fish choose habitats based on zooplankton prey availability at dusk. For the Age-0 / Age-1 treatment, the correlations were mostly negative (mean = -0.21). The experimental addition lake (Age-0 + Age-1) was intermediate with a mean of 0.37, but the three last sampling days had high correlations.

Macroinvertebrates biomass varied between habitats and across sampling days (Figure 1.17). A one-factor ANOVA was conducted on the biomass between habitats for each lake, and there was a significant difference between the two habitats sampled in only the experimental lake (Age-0 / Age-1: $F_{1,38} = 1.158$, $p > 0.05$; Age-0 + Age-1: $F_{1,38} =$

Figure 1.14 Zooplankton density per sampling day per habitat for all three treatments. Littoral data are presented by the thick dashed line, Shallow Epibenthic by the thick solid line, Deep Epibenthic by the thin solid line, and Limnetic by the thin dashed line. The ordinates have different scales.

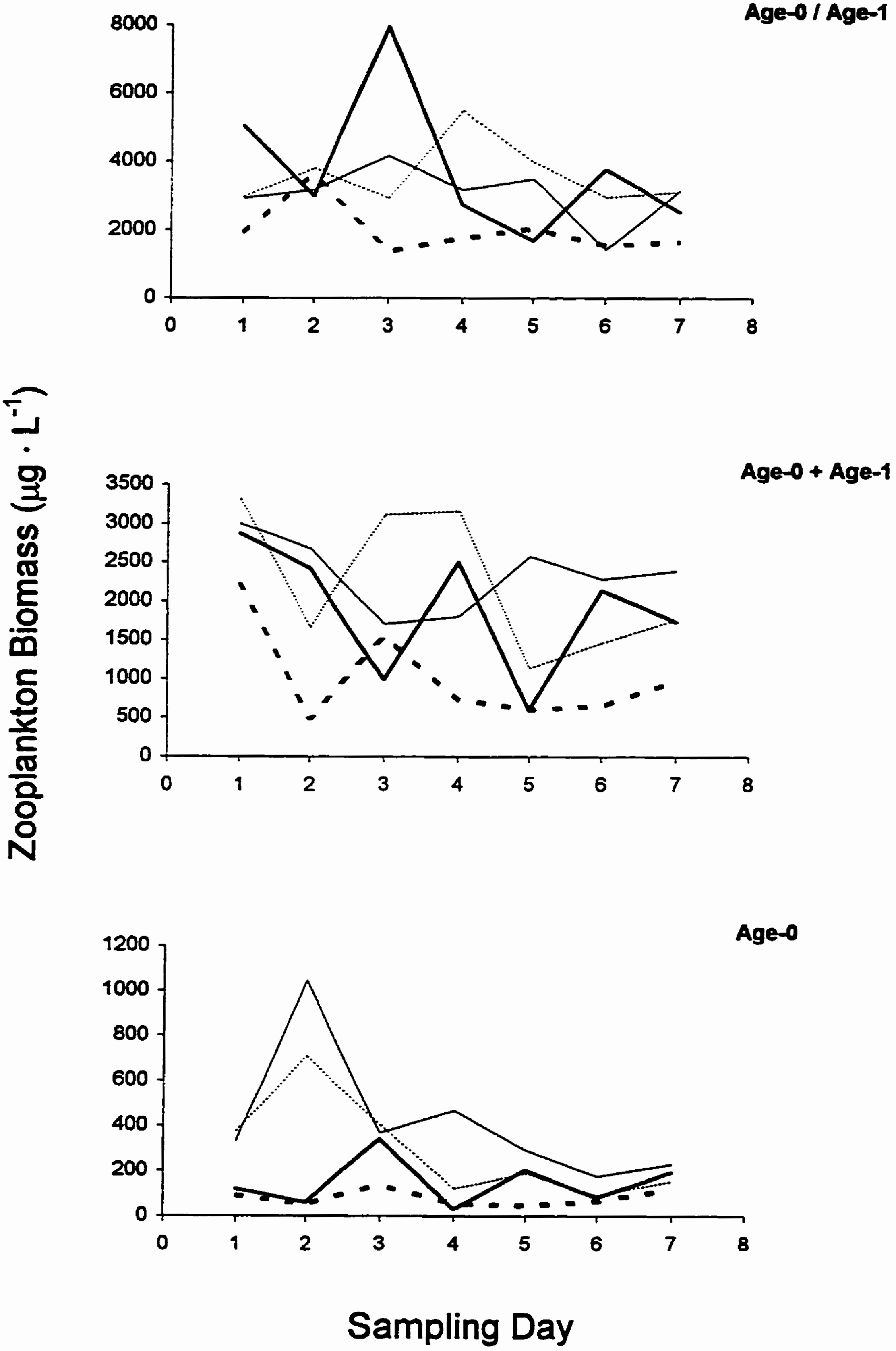

Age-0 / Age-1
8000
6000
4000
2000
0
0
1
2
3
4
5
6
7
8
Age-0 + Age-1
3500
3000
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
Zooplankton Biomass ($\mu g \cdot L^{-1}$)
Age-0
1200
1000
800
600
400
200
0
0
1
2
3
4
5
6
7
8
Sampling Day

Figure 1.15 Back-transformed means of total zooplankton biomass ($\mu g \cdot L^{-1}$) from 7 sampling days with 95 % confidence intervals for each habitat per lake. Different letters indicate a significant ($p < 0.05$) difference for a pairwise comparison on Log biomass using Tukey's test. Dark bars are plotted against the right axis and represent the mean % of the Total Population Index of age-0 trout at dusk.

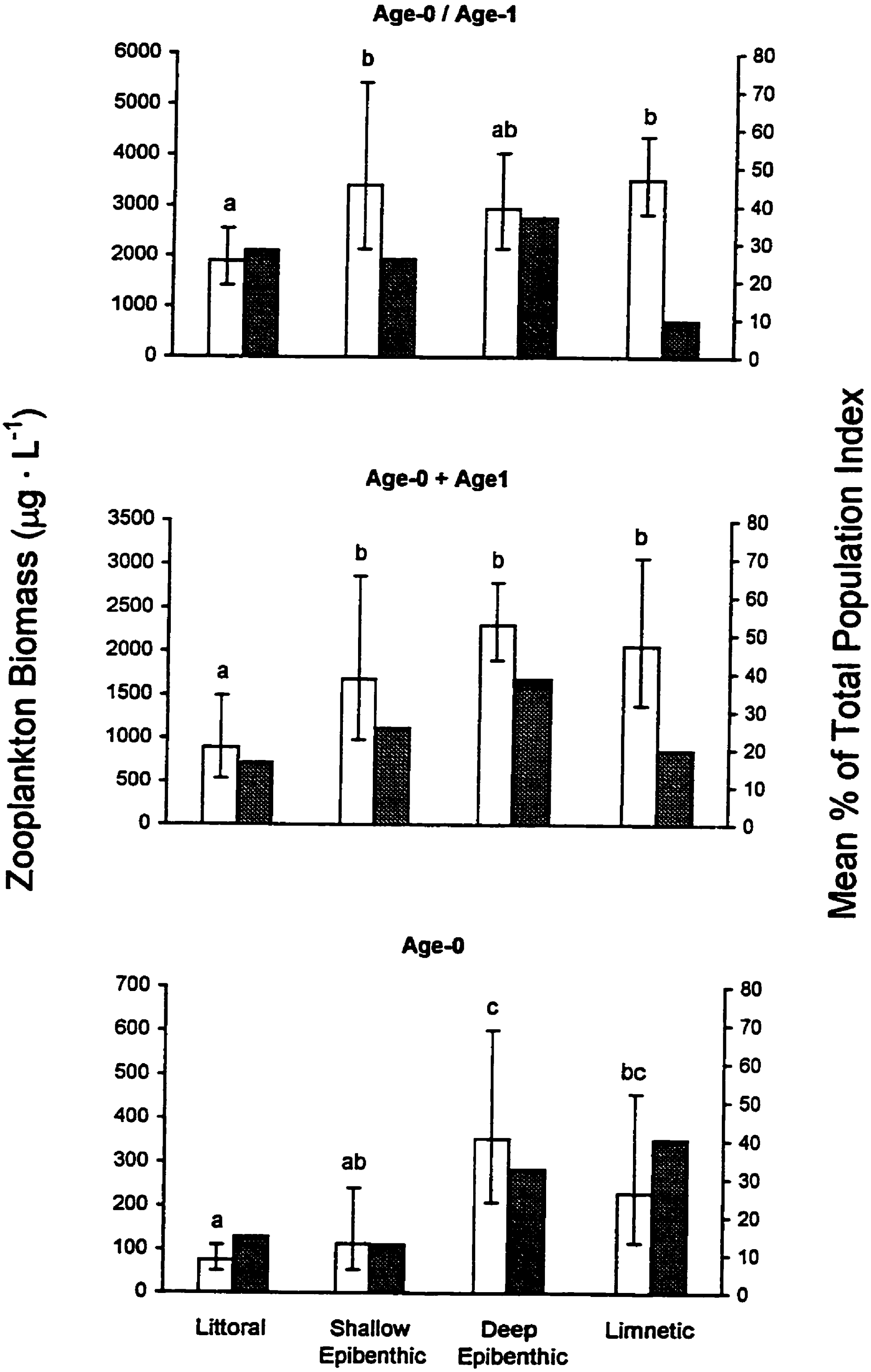

Age-0 / Age-1
Age-0 + Age1
Age-0
Zooplankton Biomass (µg · L-1)
Mean % of Total Population Index
6000
5000
4000
3000
2000
1000
0
3500
3000
2500
2000
1500
1000
500
700
600
500
400
300
200
100
80
70
60
50
40
30
20
10
a
b
ab
b
a
b
b
b
a
ab
c
bc
Littoral
Shallow Epibenthic
Deep Epibenthic
Limnetic

Figure 1.16 Spearman's rank correlation for dusk fish distribution at and zooplankton density ($\mu g \cdot L^{-1}$) during the study. All correlations are based on the ranks of the four habitats.

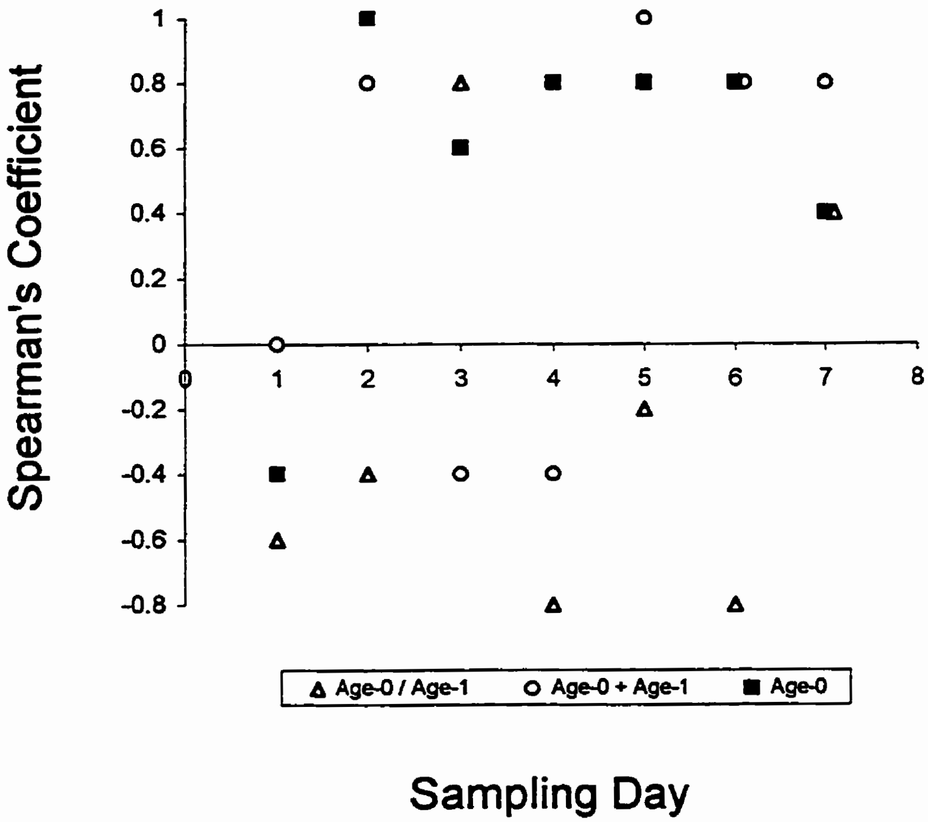
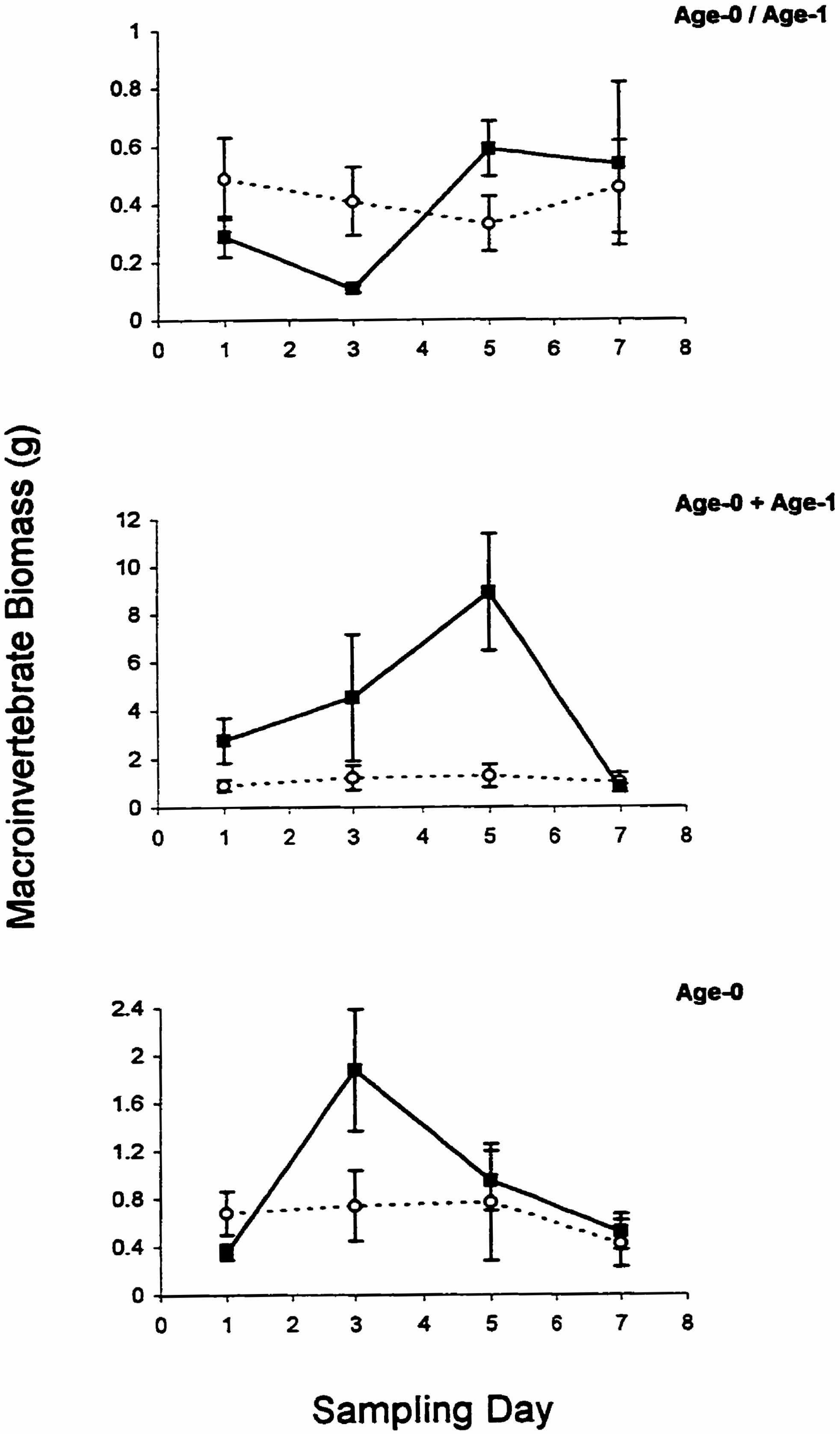

Spearman's Coefficient
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
0
1
2
3
4
5
6
7
8
△ Age-0 / Age-1
○ Age-0 + Age-1
■ Age-0
Sampling Day

Figure 1.17 Total macroinvertebrate biomass (mean ± SE) per tile for 4 sampling days. Means are calculated from five replicates. The Littoral data is presented by a dashed line, and Shallow Epibenthic by a solid line.


Age-0 / Age-1
1
0.8
0.6
0.4
0.2
0
0
1
2
3
4
5
6
7
8
Age-0 + Age-1
12
10
8
6
4
2
0
0
1
2
3
4
5
6
7
8
Age-0
2.4
2
1.6
1.2
0.8
0.4
0
0
1
2
3
4
5
6
7
8
Macroinvertebrate Biomass (g)
Sampling Day

9.765, $p < 0.01$; Age-0: $F_{1,38} = 2.035$, $p > 0.05$) (Figure 1.18). There is no evidence in two of the lakes (Age-0 / Age-1; Age-0) that age-0 rainbow trout choose habitats based on macroinvertebrate abundance since there were not significant differences in macroinvertebrate abundance between the two habitats. The trend in the experimental addition treatment (Age-0 + Age-1) shows more age-0 trout in the Shallow Epibenthic habitat than the Littoral habitat which is positively correlated to a significant difference in macroinvertebrate abundance between habitats (Figure 1.18).

1.3.4 Water temperature and oxygen concentrations

Water temperatures in all habitats and in all lakes decreased from the beginning of the experiment at the end of July to the end of September (Figure 1.19). The differences between lakes in temperature within a habitat were never greater than 2 °C (Figure 1.19). The pattern across habitats within a lake was consistent among the three treatments with the Deep Epibenthic habitat being the coldest early in the experiment and the Littoral the warmest throughout most of the period (Figure 1.20). During the first three sampling days in all three lakes, the temperature in the Deep Epibenthic habitat was much lower than in the other three habitats and close to 18 °C (Figure 1.20). The possibility of the distribution being driven by oxygen concentrations was rejected since all habitats were well oxygenated throughout the experiment (Figure 1.7).

Figure 1.18 Back-transformed means and 95 % confidence intervals of total macroinvertebrate biomass (g) per tile from 4 sampling days for two habitats and for each lake. Significant differences ($p < 0.05$) between habitats are indicated by an asterisk. Dark bars are plotted against the right axis and represent the mean % of the Total Population Index of age-0 trout at dusk.

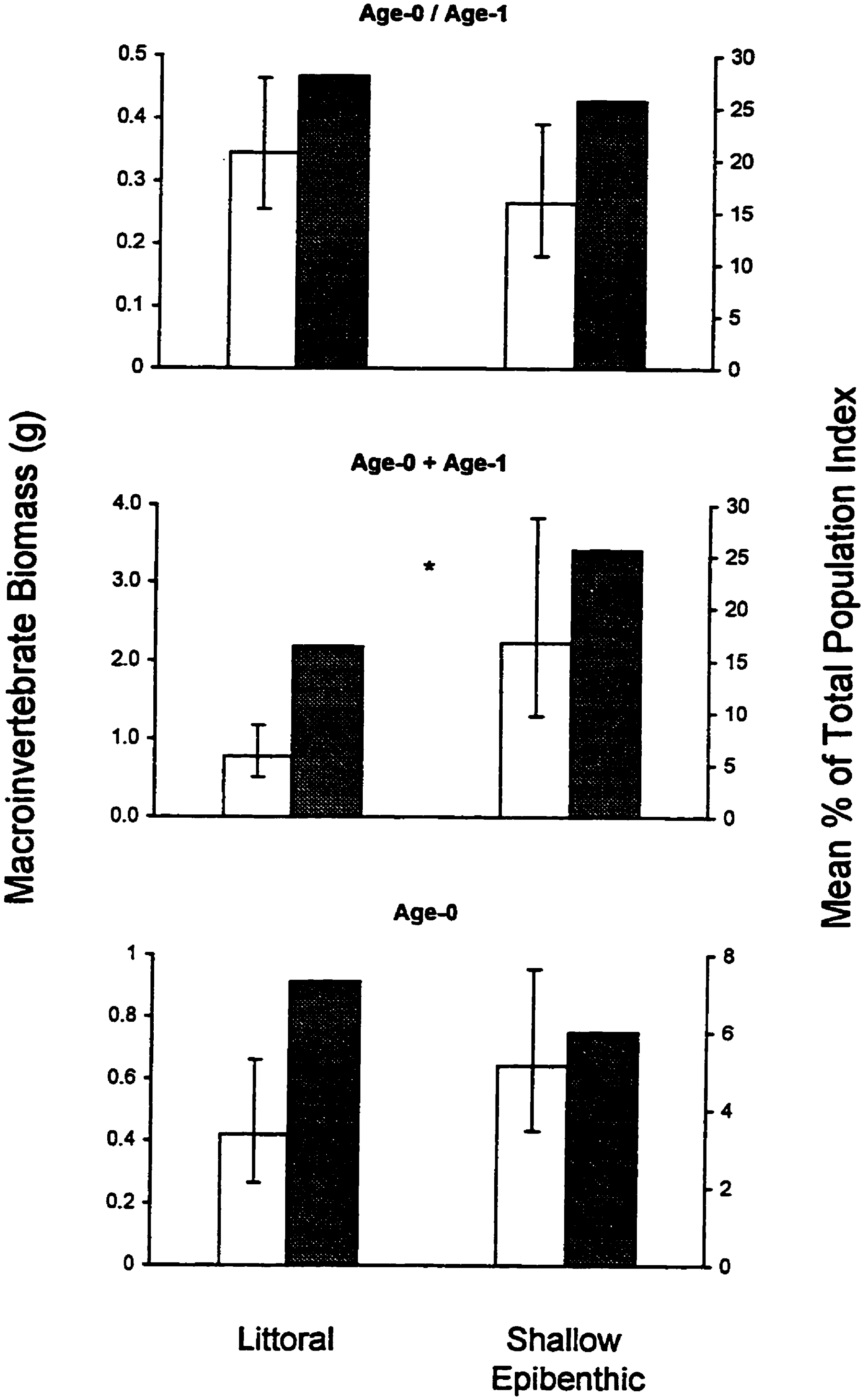

Age-0 / Age-1
0.5
0.4
0.3
0.2
0.1
0
30
25
20
15
10
5
0
Age-0 + Age-1
4.0
3.0
2.0
1.0
0.0
*
30
25
20
15
10
5
0
Age-0
1
0.8
0.6
0.4
0.2
0
8
6
4
2
0
Macroinvertebrate Biomass (g)
Mean % of Total Population Index
Littoral
Shallow Epibenthic

Figure 1.19 Habitat-specific mean temperatures (°C) of each sampling day for each treatment. The Age-0 / Age-1 treatment is represented by the thin solid line, the Age-0 + Age-1 treatment by the dashed line, and the Age-0 treatment by the thick solid line.

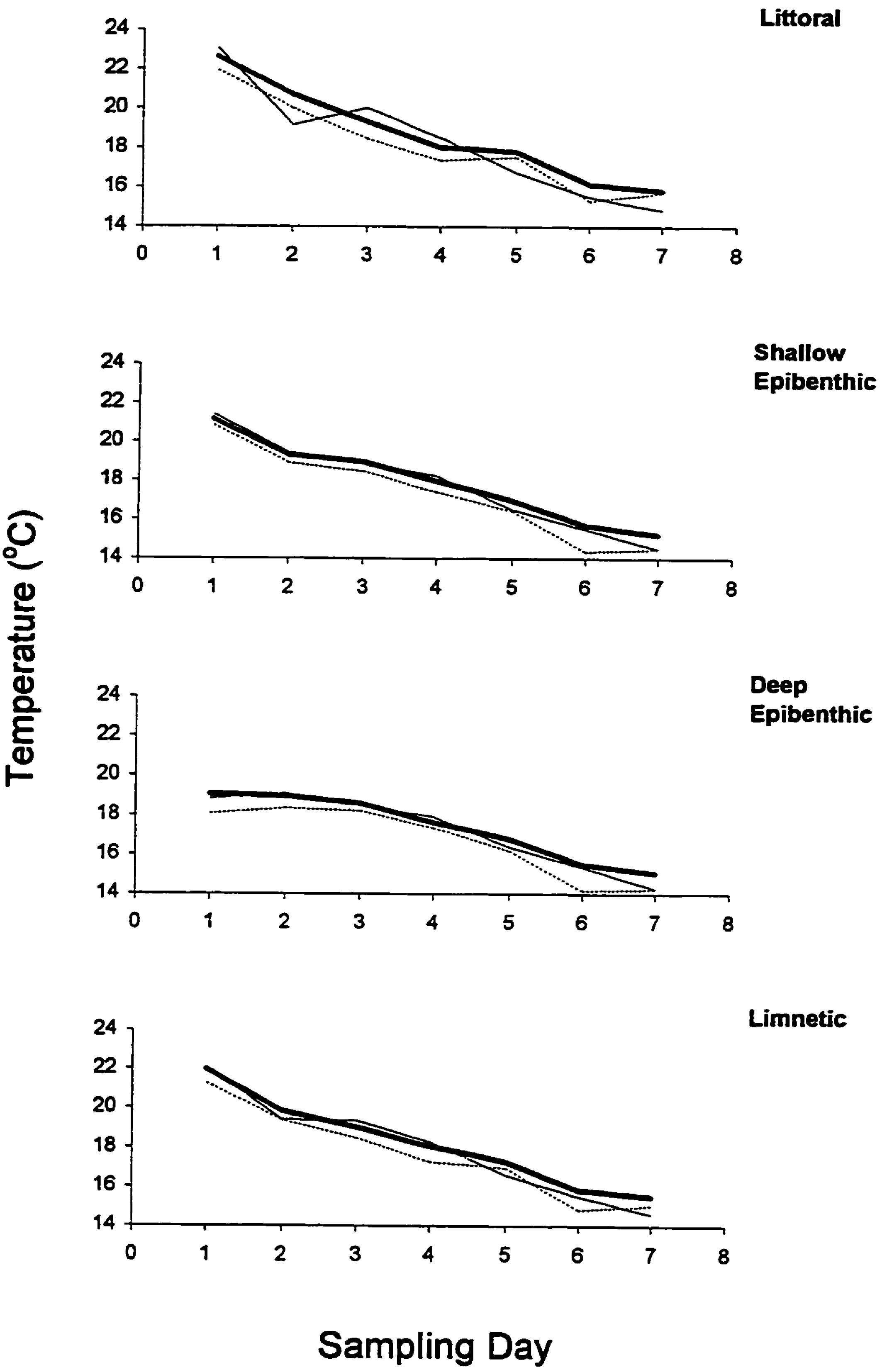
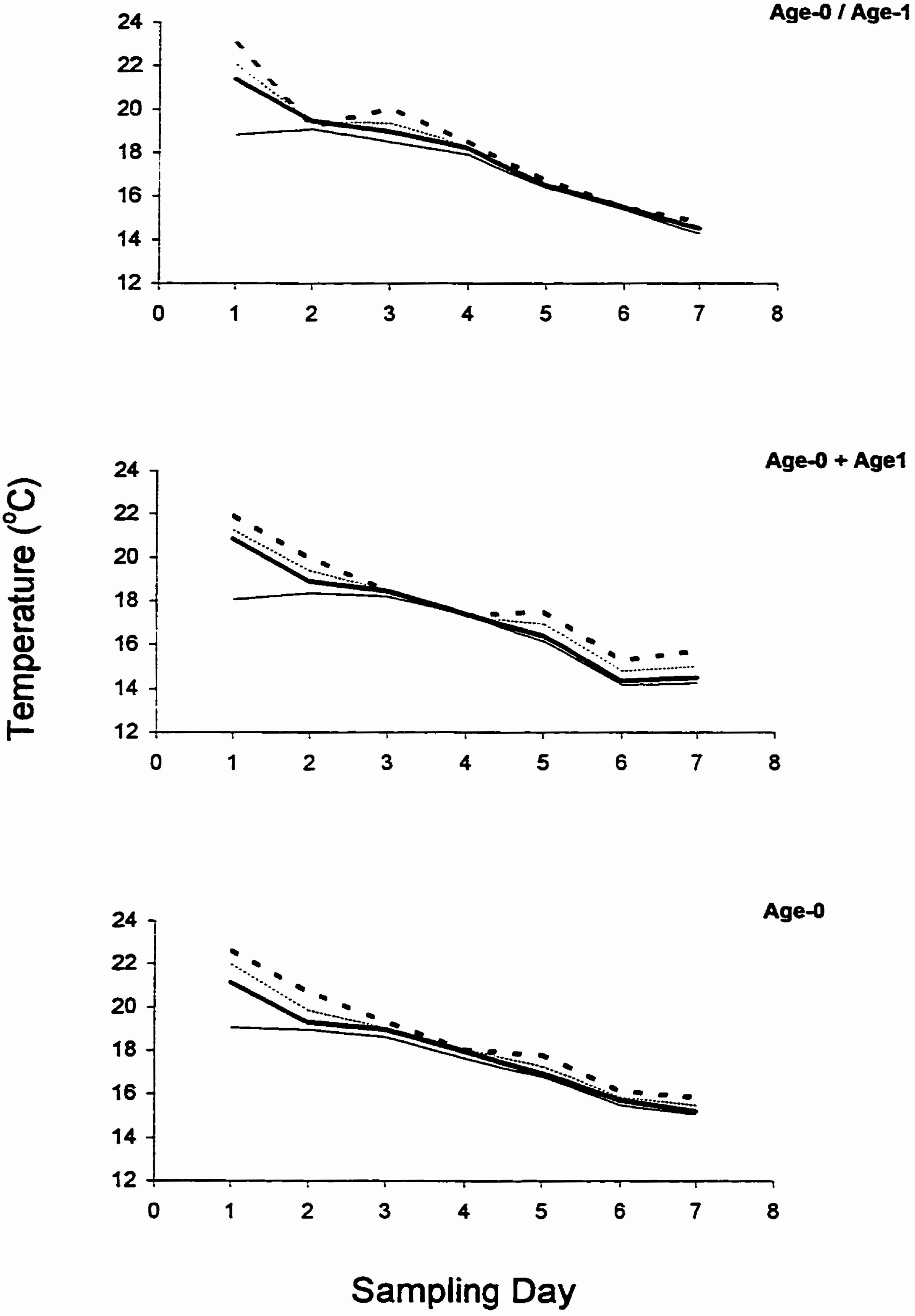

Littoral
24
22
20
18
16
14
0
1
2
3
4
5
6
7
8
Shallow Epibenthic
24
22
20
18
16
14
0
1
2
3
4
5
6
7
8
Deep Epibenthic
24
22
20
18
16
14
0
1
2
3
4
5
6
7
8
Limnetic
24
22
20
18
16
14
0
1
2
3
4
5
6
7
8
Temperature (°C)
Sampling Day

Figure 1.20 Treatment-specific mean temperatures (°C) of each sampling day for each habitat. Littoral data is presented by the thick dashed line, Shallow Epibenthic by the thick solid line, Deep Epibenthic by the thin solid line, and Limnetic by the thin dashed line.


Age-0 / Age-1
Age-0 + Age1
Age-0
24
22
20
18
16
14
12
0
1
2
3
4
5
6
7
8
Temperature (°C)
Sampling Day

1.4 Discussion

The spatial distribution of age-0 rainbow trout differed among the three lakes. The experimental treatments themselves and observations of the spatial distribution of older conspecifics, planktonic and benthic prey and of temperature and oxygen concentrations allowed assessment of several alternate hypotheses for the spatial distribution of the age-0 trout. The selection of experimental treatments was intended to test the primary hypothesis that the spatial distribution of age-0 rainbow trout resulted from inter-cohort interactions, as commonly observed in fluvial salmonids (Fausch 1984; Grant 1990; Huntingford 1993).

The results observed which are consistent with an "inter-cohort effect" could possibly be a lake effect. I do not disregard this posibility, but because the treatments were allocated at random, the fish populations were created from the same genetic origin, and the results are consistent with the hypotheses, I interpret the effects as treatment effects. I understand that this experimental design was not as powerful as a fully replicated design, but I was faced with a tradeoff between obtaining biological details and statistical power. Due to the problems with the logistics in obtaining statistical power, I opted for the biological details to support the "inter-cohort" effect and present several alternate hypotheses.

The spatial distribution of juvenile fishes is usually controlled by two factors: the presence of predators or aggressors and food availability. Because these factors are linked spatially, younger fish often face a tradeoff between risk of predation or interference and food profitability (Werner et al. 1983a; Gilliam and Fraser 1988). In this study, I observed the direct effect of this tradeoff by comparing the spatial distribution of age-0 trout across treatments that potentially differed in intensity of size-dependent interactions. The effect of this tradeoff can be detected in spatial distribution of age-0 fish in relation to prey availability and risk of interference. Gilliam and Fraser (1987) demonstrated that fish that minimize their mortality rate (μ) relative to gross foraging rate (f) (minimize μ/f), maximize their growth and survival. In the Age-0 lake, fish appeared to be distributed according to prey abundance as would be predicted by Gilliam and Fraser (1987), because there was no risk of predation or interaction by older conspecifics. But in the continuous presence of age-1 fish, age-0 trout apparently avoided the habitats with high zooplankton biomass at dusk. These observations imply that the age-1 trout probably inhibited the younger fish from occupying the most productive habitats. The results do not support the alternate hypothesis that the age-0 would choose habitats based on zooplankton prey availability when older conspecifics are present, but they do choose habitats with more zooplankton when alone. This apparent dominance of productive habitats by older and larger individuals is also observed in salmonids living in lotic systems (Fausch 1984; Grant 1990) and in other species such as scorpions (Polis 1988). The avoidance of habitats with high prey density was observed in the greater use of the Littoral habitat in the continuous presence of older conspecifics which had a significant lower prey abundance than the Limnetic habitat. The low use of the Limnetic habitat appeared to be a facultative behaviour since in the absence of older conspecifics, a high percentage of age-0 trout inhabited the Limnetic where prey density was significantly higher than in the Littoral habitat. An alternate hypothesis could be that the Limnetic habitat in the Age-0 / Age-1 treatment had much less volume than in the Age-0 treatment, but this hypothesis can be rejected because the difference in volume was approximately 35 % whereas the difference in % of Total Population Index was approximately 900 % during the day and 400 % at dusk.

Because older fish were most abundant in the Deep Epibenthic and Limnetic habitats, the avoidance of the Limnetic habitat and greater use of the Littoral and Shallow Epibenthic habitats by age-0 fish in the continuous presence of older conspecifics may have been a response to reduce encounters with age-1 rainbow trout. In that lake, the capture success had the lowest predicted probability, suggesting that not all nets caught fish which implies that fish were not using all habitats. Hence, the yearlings may have inhibited access to certain habitats such as the Limnetic habitat. The avoidance of the Limnetic habitat by age-0 trout was also demonstrated in the low probability of net success from the Habitat logistic regression model. Often, the safer habitats such as the littoral zone have reduced feeding opportunities (Mittelbach 1981; Cerri and Fraser 1983; Werner et al. 1983a; Milinski 1985; Naud and Magnan 1988; Tabor and Wurtsbaugh 1991) as observed in this study. This observed behaviour may be the result of a tradeoff between foraging in habitats with abundant prey and those with a lower risk of interference or predation which may then lead to lower growth rates (see Chapter 2).

Use of structurally complex habitats such as the littoral zone is typical of juvenile rainbow trout (Johannes and Larkin 1961; Wurtsbaugh et al. 1975; Tabor and Wurtsbaugh 1991; Post et al. in press) and has been shown to reduce predation rate (Tabor and Wurtsbaugh 1991). Likewise, juveniles of other lentic salmonid species are more abundant in the littoral zone (O'Connell and Dempson 1996). As in this study, age-0 Atlantic cod (*Gadus morhua*) in the presence of age-1, use more complex habitat than when alone and avoid substrates occupied by the older year class (Fraser et al. 1996). The observations from Fraser et al. (1996) and from this study suggest that certain age classes may restrict habitat use of other age classes. Spatial segregation among age classes has been observed in many fish species (Werner et al. 1983b; Sandheinrich and Hubert 1984; Kneib 1987; Tonn et al. 1992; O'Connell and Dempson 1996). Besides fish, segregation of a size-structured population with respect to habitat use by different year-classes occurs in other animals (Polis 1988; Sweitzer and Berger 1992; Wissinger 1992).

Habitat selection by young fish does not always favour the more structurally complex littoral zone. A population of Arctic charr in Norway (Klemetsen et al. 1989) displays a segregation pattern opposite to what I observed. The adults (age mode 7) occupied the littoral zone, which was the most attractive habitat for feeding, and they were supposedly the strongest competitors. In contrast, the weakest and youngest intraspecific competitors, the parr stage (age mode 2-3), occupied the profundal zone where only one benthic prey species was common. Smolt (age mode 5) occupied the pelagic habitat. This intraspecific habitat segregation also resulted from competition for space and food and possibly also predation risk. Most spatial patterns of intraspecific competition display the opposite distribution, with younger classes occupying the littoral zone and older in the profundal and pelagic zone. Klemetsen et al. (1989) proposed that a relict anadromous life cycle can be recognized in that population of Arctic charr.

The experimental addition lake yielded very different results between day and dusk. There was no evident explanation for the high percentage of fish found in the Littoral habitat during the day before the addition of age-1 trout. The lower use of the Deep Epibenthic habitat on day 1 during day and dusk compared to the Age-0 lake was likely due to the low oxygen concentration at that depth (see Figure 1.7). After the addition of age-1 trout, there was a slight decrease in the use of the Limnetic habitat at dusk which may have been a response to the presence of age-1 trout. The absence of a greater effect of the addition may be due to the smaller difference in size between age-0 and age-1 at the time of stocking than in the Age-0 / Age-1 treatment. The difference may not have been large enough to affect the age-0 trout behaviour significantly. The Spearman coefficients in the Age-0 + Age-1 treatment were high for the last three sampling days suggesting that fish were selecting habitats with high zooplankton biomass and the age-1 trout had no effect. An experimental addition such as I performed in the Age-0 + Age-1 treatment could be conducted at several times throughout ontogeny if several experimental lakes were available. I would predict stronger effects if the addition was done early in the ontogeny when the age-0 trout were small with the effect weakening the later the addition was conducted as observed in this experiment.

A reduction in activity was observed during the day in the Age-0 / Age-1 treatment during the last 3 sampling days, because catchability of fish by gillnet is related to their activity (Rudstam et al. 1984). The reduction of activity of age-0 fish during the day may be a refuge response to the presence of older conspecifics. The use of a temporal refuge was observed in the lakes that contained age-1 rainbow trout. The increase in use of the Limnetic habitat from Day to Dusk in the Age-0 / Age-1 and the Age-0 + Age-1 treatment suggests a diel onshore-offshore migration which may be a result of diel changes in foraging benefits, agonistic encounters, and predation risk. A slight decrease in the use of the Limnetic habitat was observed in the Age-0 lake suggesting that offshore migrations at dusk were only present when age-0 cohabited with older conspecifics. These diel migrations are common in freshwater fishes (Bohl 1980; Helfman 1981; Hanych et al. 1983; Naud and Magnan 1988; Gauthier et al. 1997). It may be advantageous for age-0 to occupy riskier habitats at dusk, since encounter rates with age-1 have decreased and in lower light conditions, the number of agonistic behaviours decreases among age-0 rainbow trout (Stringer and Hoar 1955). Diel onshore-offshore movements have also been previously observed in juvenile rainbow trout in both lentic (Tabor and Wurtsbaugh 1991) and lotic systems (Riehle and Griffith 1993). In the lotic system, juvenile trout moved out of the substrate at night to feed when they were less vulnerable to day-active predators, resulting in increased feeding efficiency by avoiding predation and interference (Riehle and Griffith 1993).

The gradual increase in the use of the Limnetic habitat at dusk by the age-0 fish during the study period in the Age-0 / Age-1 treatment suggests that the age-0 fish may choose less profitable habitats to avoid costly interactions when the size difference with the older conspecifics is greatest. As they grow, age-0 fish become less vulnerable and increase their use of formerly more risky habitats. The existence of an ontogenetic shift from Littoral and Shallow Epibenthic habitats to Deep Epibenthic and Limnetic habitats observed in the spatial distribution and in the Sampling Day logistic regression implies that the relative benefits and costs associated with the available habitats, changes with the size of the age-0 fish or the difference in size of the age-0 and older trout. There was no complete shift from one habitat to another at any specific size as observed in other studies. Instead, the shift appeared more gradual suggesting constant interference or predation pressure. Tabor and Wurtsbaugh (1991) indicated that a more distinct shift occurred in age-0 rainbow trout once they reached 100-120 mm, when they move from the littoral zone to the limnetic zone. A similar shift was observed in Arctic charr, which moved between epibenthic and pelagic feeding habitats at sizes of 130-180 mm (L'Abée-Lund et al. 1993). Age-0 brook charr behaved similarly to the age-0 trout in this study; living nearshore in July and August (0-2 m depth) and moving into deeper water in September (1-3 m)(Venne and Magnan 1995). Many of the important changes that occur during the ontogenetic development of fish are essentially a result from changes in size (Miller et al. 1988). In general, as the size ratio (age-1/age-0) decreases, resource overlap increases, whereas the intensity of interference should decrease due to the smaller size difference between individuals. Such size-dependent shifts in habitat use in fish populations are often attributed to interference or cannibalism (Schlosser 1987; Foster et al. 1988).

In this study, I had no evidence of cannibalism because no age-0 fish were found in stomachs of age-1 fish. The sizes of age-0 and age-1 trout were such that cannibalism could have occurred (Beauchamp 1987, 1990; Post et al. unpublished manuscript) and with the density ratio of age-0/age-1 fish, not many successful cannibalistic encounters would be necessary to increase mortality of the age-0 class. Cannibalism is common in teleost fishes (Smith and Reay 1991) and may regulate fish populations (Ricker 1954), both directly via mortality, and indirectly by causing small individuals to modify habitat selection and behaviour. Therefore, the absence age-0 fish in stomachs of older fish does not mean that predation had no effects on age-0. Furthermore, the non-lethal effects (interference) of cannibalism may be as important as actual predation (Mittelbach 1986). Therefore, interference may have influenced the spatial patterns of age-0 rainbow trout. A similar mechanism was observed in populations of Arctic charr in Norwegian lakes (L'Abée-Lund et al. 1993). The spatial distribution of juveniles was recognized to be governed by interference because predation rate was low in all their lakes.

Interference and aggression are behaviours used to monopolize food (Johnsson and Björnsson 1994), therefore we can interpret that if age-1 rainbow trout interfered with age-0 trout, the behaviour may have been a result of controlling the rich habitats. Agonistic behaviours have been observed as early as emergence in age-0 rainbow trout (Dill 1977; Cole and Noakes 1980) and it has been suggested in previous studies that threats are relatively more frequent in older and larger fish (Stringer and Hoar 1955; Cole and Noakes 1980). Therefore, aggression seems to be an influential behaviour of age-0 rainbow trout. I suggest that this behaviour occurs in lake environments and that interference and possibly predation (cannibalistic) pressure may be controlling the use of spatial resources by age-0 rainbow trout.

In this experiment, I used the youngest two age classes of rainbow trout, recognizing that natural populations contain multiple age classes. These classes differed more than 100-fold in mass at stocking which is substantially greater than variation in mass between any other adjacent age classes. Therefore, I expected *a priori*, that size-dependent interactions would be strongest among these two size classes in this experiment. If I had used an older year-class instead of 1-year old fish, the predation interactions may have been more important. In natural populations with more size classes, the intensity of interactions between the two youngest age classes may be stronger if older conspecifics restrict age-1 trout to habitats chosen by age-0 trout in the presence of larger bodied cannibals or antagonistic conspecifics. Material presented in Chapter 2 and potential future experiments could sort out the importance of the size-dependent interactions through the first year of life where the age-0 trout grow through approximately 2 orders of magnitude in mass.

The effects of size-dependent interactions (predation, interference and exploitative competition) on size-structured fish populations can have important consequences at the population level (Ebenman and Persson 1988). To understand the mechanisms that govern the structure of a population, one needs to examine processes at the appropriate spatial and temporal scale to incorporate natural variability. By analyzing spatial patterns at the population scale I developed a better understanding of the size-dependent mechanisms that modify fish behaviour in rainbow trout populations. I demonstrated with a multiple-lake experiment that older conspecifics have a direct effect on the spatial distribution of younger ones through interference. The spatial restriction of age-0 trout observed in this study may reduce their growth and survival if the preferred or profitable habitats are limited and if their energetic costs are increased and hence affect survival (see Chapter 2). These results may suggest that lentic salmonid populations are spatially-structured based on interference competition as they are in lotic populations (Chapman 1962; Hartman 1965; Li and Brocksen 1977; Fausch 1984; Huntingford 1993; Gregory and Griffith 1996).

An understanding of the ecology and dynamics of the juvenile stage should be an essential part in assessing and managing fish populations (Houde 1987; de Lafontaine et al. 1992) because that stage is relatively important in controlling/regulating recruitment levels of freshwater fishes (Houde 1994). Walters and Juanes (1993) stressed that fish recruitment studies should give more attention to spatial habitat use by juveniles and to the behavioural mechanisms involved. This study provides indirect empirical evidence of intraspecific interactions among age-classes within lake populations of rainbow trout and the observations of age-classes segregation may be explained by interference competition.

CHAPTER 2

Size-dependent growth and mortality in age-0 rainbow trout among lakes differing in intensity of size-dependent interactions

2.1 Introduction

Animals typically exhibit one of two types of growth pattern (Lincoln et al. 1982; Sebens 1987). Determinate growth, in which adult size has a genetic component and is fixed with little variation once full body size has been achieved, is typical of birds, mammals (Sebens 1987), and insects. Indeterminate growth, in which adults continue growing throughout their life, is typical of soft-bodied marine, freshwater, and some terrestrial invertebrates, and also fish. Indeterminate growers commonly exhibit growth plasticity resulting from continuous size change as environmental conditions change either physically and/or biologically. Such environmental changes lead to size-structured populations for indeterminate growers.

Variation in size structure has important implications for the strengths of competitive and predator-prey interactions, which often depend on the size of interactants (Van Valen 1973; Peters 1983; Calder 1984). The size of an individual is often a key variable in determining vital rates such as fertility, survival, and growth rates, as well as susceptibility to predation. Roff (1992) demonstrated that in animals, a large size at birth or hatching would increase the fitness of offspring through increased resistance to starvation, improved survival, and faster growth.

Many species of fish grow through 4-5 orders of magnitude of body mass during their lives (Peters 1983) and often 2-3 orders of magnitude of this growth occurs during the first several months of life. Growth rate variation is often greatest during the first year and it can influence cohort survival and size-structure. Therefore, strong size-dependent competitive (interference and exploitation) and predator-prey interactions can occur between individuals.

For most fish species, risk of predation declines greatly as body size increases (Parker 1971; Werner et al. 1983b; Mittelbach 1984; Werner and Gilliam 1984; Miller et al. 1988; Werner and Hall 1988; Ward et al. 1989). Fish that grow fast can escape gape-limited predators (Hambright et al. 1991; Persson et al. 1996), and larger-bodied, faster growing individuals commonly have a higher probability of survival (Tonn et al. 1994; Post et al. 1997). Conversely, smaller fish suffer higher starvation mortality during their first winter due to lower energy storage (Shuter and Post 1990; Smith and Griffith 1994; Cargnelli and Gross 1996). Therefore, survivorship during the first year of life is often strongly size-dependent.

Growth of juvenile fishes depends on many factors such as prey abundance (Welker et al. 1994; Post et al. in press), quantity of food consumed (Boisclair and Leggett 1989a; Mittelbach 1981), and prey type consumed (Mills and Forney 1981; Mittelbach 1981; Boisclair and Leggett 1989b). The composition of fish communities may also affect growth rates of juveniles fishes through exploitative and interference competition and predation (Boisclair and Leggett 1989c; Persson 1986; Persson et al. 1996).

The outcome of exploitative competitive interactions within size-structured fish populations can differ depending on the relative sizes of competitors and their prey. Larger individuals often have an advantage due to their greater searching capacity and capture efficiency (Hamrin and Persson 1986; Persson et al. 1996). They are also capable of eating a wider range of prey, providing them an advantage when the size distribution of the prey community is skewed towards larger individuals (Hamrin and Persson 1986; Persson et al. 1996). Smaller individuals may be advantaged if the prey community is small-bodied because their net profitability is higher than that of large individuals (Hamrin and Persson 1986; Persson et al. 1996). Therefore, in exploitative competitive interactions, the outcome of interactions depends on the size-structure of competitors and their prey community.

Interference competition may increase use of cover and refuge habitats, decreasing foraging opportunities and growth rates (Werner et al. 1983b; Walters and Juanes 1993) because the composition and abundance of suitable prey can differ from more risky habitats. The outcome of interference competition within size-structured populations usually favours large individuals, forcing small ones into less profitable habitats (Fausch 1984; Metcalfe 1986; Grant 1990). The ultimate form of interference behaviour is predation. Juvenile fish change their diet, habitat use, and activity in response to predators (Werner et al. 1983a,b; Lima and Dill 1990; Turner and Mittelbach 1990; Persson 1993; Werner and Anholt 1993). The influences of predation risk on foraging behaviour and growth have been reviewed extensively (Sih 1987; Gilliam and Fraser 1988; Lima and Dill 1990; Werner 1992; Milinski 1993). A tradeoff exists between growth and predation risk in small fish and it is complicated because small fish can reduce their vulnerability to predation by maximizing growth rates.

In salmonid fishes, fitness later in life appears to be related to first year growth. In lotic systems, trout that are large-bodied during their first year, remain large relative to other individuals of that cohort (Chapman 1962; Abbott et al. 1985; Elliot 1985) and size is correlated positively with survival (Dill et al. 1981; Bachman 1982; Ward et al. 1989). Therefore, the size of an individual in lotic systems affects its recruitment probability. Differences in growth rate among individuals may be associated with the differences in net energy gained by foraging either in a better location or at a better time, or by the increased stress of subordinate individuals associated with interactions (Symons 1971).

Growth and survival of salmonids have been studied in nature more intensively in lotic habitats than in lakes for practical reasons. Most experimental studies on size-dependent interactions among fish have examined the behaviours at small scale in the laboratory or in field enclosures. These conditions restrict the suite of "normal" behaviours due to the limited availability of habitats that fish would experience in the wild. It is therefore necessary to use whole-system experiments to incorporate both spatial and temporal natural variability and to gain an understanding of the population and community level implications of behavioural plasticity (Tonn et al. 1994; Persson et al. 1996; Post et al. in press). Often longer-term population level implications such as mortality remain unknown.

In this study, I examine the direct and indirect effects of size-dependent interactions within lentic rainbow trout (*Oncorhynchus mykiss*) populations and draw conclusions at the population level. I tested two specific hypotheses: (1) growth of age-0 rainbow trout is indirectly controlled by the presence of older conspecifics; and (2) mortality of age-0 rainbow trout is size-dependent and directly controlled by the presence of older conspecifics. My approach included three components. First, I used whole systems (lakes) to allow a normal suite of behaviours. Secondly, I created populations of rainbow trout that varied in size-structure to examine the size-dependence of the observed processes. Thirdly, I measured both short-term behaviours (i.e. use of resources like space and food) as well as long-term effects such as growth and mortality.

2.2 Methods

2.2.1 Study system

This study involved three small lakes in south-central British Columbia (for a complete description and location of the lakes, refer to Chapter 1, Table 1.1). All three lakes were stocked with native rainbow trout which had been reared at the Fraser Valley Trout Hatchery in Abbotsford, B.C.. The lakes were all stocked with two size classes (small and large) of age-0 trout in early July 1994. Each population comprised 70 % small individuals (7 700 fish · ha^{-1}) and 30 % large individuals (3 200 fish · ha^{-1}) (Table 2.1). Both size classes were the same age at stocking, and the small class had been reared at a lower temperature to obtain the size differences. The small class weighed 0.17 ± 0.03 (SD) g and measured 27 ± 1.15 (SD) mm, whereas the large class weighed 0.50 ± 0.11 (SD) g and measured 37 ± 2.35 (SD) mm.

The large class was marked with fluorescent granular pigments to identify individuals from that class in the field. This technique entails forcing fluorescent polystyrene pigments into the dermal tissue with compressed air from a small sandblasting gun (Jackson 1959). This material is not readily detected under normal light, but it fluoresces when activated by ultraviolet light. Pigment retention seemed to be very high for the short term, as 100 % of age-0 rainbow trout (25-35 mm) retained their pigments after 130 days and mortality (4%) was equivalent to unmarked (control) fish (Phinney et al. 1967). No significant difference was observed between unmarked and fluorescent-pigment-marked age-0 coho salmon (*Oncorhynchus kitsutch*) in growth and survival after

Table 2.1 Population abundance at beginning of study and population estimates at end of study.

Treatment	Size and Age	Population Abundance			% Survival
		Start		End	
		Numbers	Density (fish·ha^{-1})	Numbers	
Age-0 / Age-1	small age-0	14685	7492	2263	15.4
	large age-0	6138	3132	1742	28.4
	age-1	1540	786	910	59.1
Age-0 + Age-1	small age-0	11420	7986	3763	32.9
	large age-0	4774	3338	1777	37.2
	age-1	1050*	750	415	39.5
Age-0	small age-0	15420	7413	5965	38.7
	large age-0	6446	3099	2550	39.6
	age-1	0	0	0	-

* Fish stocked halfway through the experiment on August 19, 1994.

one year (Phinney 1974). In conjunction with this field experiment, I conducted a laboratory experiment to identify the mark retention of the large class at the hatchery. A sample of fish from those marked for the field experiments were kept at the hatchery to observe mark retention. After 85 days, only 2 (0.4 %) out of 490 trout had no observable marks.

2.2.2 Experimental design

The experiment involved stocking three lakes with the same abundances and size classes of age-0 rainbow trout, but varying the density and duration of the presence of older conspecifics. I used age-1 rainbow trout (as older conspecifics) which are known to interact either by interference or predation on age-0 trout (see Chapter 1; Post et al. in press, unpublished manuscript). One lake was stocked with only age-0 and was therefore free of inter-age class interactions throughout the whole experiment referred to hereafter as the Age-0 treatment. The Age-0 / Age-1 lake was stocked with a high density of older trout (786 age-1 $\cdot$ ha^{-1}) in addition to the age-0 fish. A third lake contained no age-1 fish for the first half of the experiment and was stocked with age-1 at 750 $\cdot$ ha^{-1} on August 19, 1994 which was halfway through the experiment, referred to hereafter as Age-0 + Age-1 treatment. The age-1 trout in the Age-0 / Age-1 treatment measured 157.9 ± 25.4 (SD) mm and weighed 44.8 ± 20.7 (SD) g at stocking. Using Miller's et al. (1988) equation which predicts capture success of a predator as a function of the predator-prey size ratio, age-1 fish would be 62.3 % successful at catching small class and 42.3 % successful for the large class. Hence, the two size-classes of age-0 fish should have experienced a 47 %

difference in mortality rate. The age-1 trout stocked in the Age-0 + Age-1 lake measured 209.4 ± 14.9 (SD) mm and weighed 101.2 ± 24.6 (SD) g at stocking.

The study was conducted during 80 days from July 11, 1994, and ended on September 29, 1994. This period covered the natural growing season, from hatching to when feeding activity and growth drop due to reduced temperatures (Keast and Eadie 1984; Cargnelli and Gross 1996).

2.2.3 Sampling procedures

Fish

Fish were sampled on 8 occasions during the study period with respect to size, diet, and spatial distribution and they were also sampled intensively at the end of the experiment to estimate overall mortality and growth rates. The first two sampling days were dropped from all analyses because the small class of age-0 trout were not yet large enough to be netted in all lakes. Therefore, the spatial distribution and diet description of both size classes of age-0 trout was obtained from 6 sampling days. Fish were collected twice on each sampling day with Lundgren multiple-mesh experimental gillnets. The nets were set for 1 h, once in the afternoon (between 12:30 and 14:30) and once at dusk. The nets were 11.4 m long and were divided into four panels of different mesh sizes (13 mm, 16 mm, 20 mm, and 25 mm stretched mesh). I used gillnets of four different heights (0.5, 1.5, 2.5, and 5.0 m) to be able to sample all the habitats of the lake. A minimum of four nets (one of each height) and a maximum of 16 were set randomly at predetermined sites on each sampling day. I attempted to obtain a sample of approximately 200 fish on each set. Diurnal activity was calculated from the number of fish caught during the day divided by the number of fish caught at dusk.

The fish caught on each sampling day in all habitats were measured (fork length, to the nearest millimetre), weighed (to the nearest 0.01 gram), counted, and the size-class was determined by examining the fish under an ultraviolet light. A random sub-sample of 3-10 fish per habitat from each size class were kept and stored in 4% formaldehyde for diet samples. Only the stomach contents from dusk captured fish were analyzed. A total of 1532 fish were dissected for diet analysis. All the non-zooplankton ("macroinvertebrates") and zooplankton in the stomach sample were sorted, and counted using a dissecting microscope (25 x). The mean number of prey per fish was then calculated. Length measurements were obtained for zooplankton to calculate biomass using taxon-specific length-to-weight regressions (Post 1984). The weights of macroinvertebrates taxa ingested were obtained from mean weights of the same taxa found in age-0 rainbow trout diet (J.R. Post, unpublished data). A lake-wide description of diet for each size cohort was created by calculating a mean diet across all habitats and weighting it by the Population Index for each habitat (see Chapter 1). This lake-wide diet description was partitioned into zooplanktonic and macroinvertebrate prey categories.

The population size of each size class of age-0 rainbow trout was estimated at the end of the experiment based on five days of intensive gillnetting (Post et al. in press). The estimates were made using the sum of the catches over the 5-day period corrected for size-dependent vulnerability to the gillnet sampling. This transformation is necessary since larger fish are depleted faster than small fish because they are more vulnerable to gillnetting. This transformation was determined using mark and recapture experiments on age-0 rainbow trout that varied substantially in size (Post et al. in press). The experiments were conducted within these lakes and other similar small lakes.

Zooplankton

The zooplankton community was sampled on the eight sampling days at each lake between the Day and the Dusk gillnetting period. Zooplankton were sampled with a Schindler trap, which collects 31.25 l of water which is then sieved through an 84-µm mesh. The samples were collected at the same net locations where fish were sampled. The zooplankton samples were then preserved in 70 % ethanol, and once in the laboratory all the zooplankton were identified to genus and measured to the nearest mm using a dissecting microscope (25 x). Length measurements were obtained with an eyepiece micrometer and biomass of individuals was calculated from length-weight regressions (Post 1984) for each taxa. The samples from each habitat were combined and weighted per habitat volume to a single sample for each sampling day. Zooplankton availability ($\mu g \cdot L^{-1}$) was then calculated for the whole lake as the arithmetic mean of the eight sampling days.

Macroinvertebrates

Macroinvertebrate abundance was measured four times during the study period with an artificial substrate sampler (see Chapter 1). Artificial substrates were deposited by a diver at 1.5 m and 2.5 m. Five replicates were placed at each depth and the locations were chosen by randomly selecting sites from 20 fixed sites. It was previously determined that a four-day period was sufficient for invertebrate colonization (Benoît et al. unpublished manuscript). The artificial substrates were retrieved after four days by a diver with an open Plexiglass box (Figure 1.6). Once out of the water, the water in the box flowed out the bottom through a 500-µm, circular (11 cm in diameter) mesh and all the invertebrates were retained on the mesh. The fronds and the surface of the tile were washed with a high-pressure water jet into the box. Then all the invertebrates were collected and stored in 70% ethanol. In the laboratory the invertebrates were sorted by order or family and counted with the use of a dissecting microscope. The invertebrates were blotted to remove superficial water and weighed to the nearest 0.1 mg with an analytical balance. Macroinvertebrates availability ($mg \cdot tile^{-1}$) is estimated by the arithmetic mean biomass of all samples per lake at 1.5 m and 2.5 m.

2.2.4 Data analysis

Daily instantaneous mortality rates were estimated from initial population size (N_0) and vulnerability-adjusted, catch-per-unit-effort population estimates obtained at the end of the experiment (N_t) (Ricker 1975):

$$\textit{Instantaneous Mortality Rate} = \frac{-\log_e\left(\frac{N_t}{N_0}\right)}{t} \qquad (1)$$

Daily instantaneous growth rates (Ricker 1975) were calculated from mean mass at stocking (W_0) and the vulnerability-adjusted, mean mass of trout caught at the end of the experiment (W_t):

$$Instantaneous \quad Growth \quad Rate \;=\; \frac{\log_e\left(\frac{W_t}{W_0}\right)}{t} \qquad (2)$$

Von Bertalanffy growth curves were fitted to the fork lengths of all measured fish for both size classes in each treatment using the Quasi-Newton algorithm within the NONLIN function in SYSTAT (Wilkinson 1992).

A multiple regression model ($R^2 = 0.65$) of the growth rate of age-0 rainbow trout based on food availability developed from a larger set of lakes (Post et al. in press) was used to test the hypothesis that the presence of older trout reduces growth rates below that expected based simply on invertebrate prey availability where :

$$\begin{gathered} Growth \quad Rate \;=\; 3.488 \;+\; 0.034 * Ephemeroptera \;+\; \\ 0.058 * Chironomidae \;+\; 0.001 * Amphipoda \;-\; 0.004 * Ceriodaphnia \end{gathered} \qquad (3)$$

This model was used only for the small class of age-0 rainbow trout in this experiment because size at stocking was equivalent to the fish used by Post et al. (in press). The units of the macroinvertebrate taxa are mg per artificial sampler and the zooplankton taxa are µg per L.

2.3 Results

Instantaneous mortality rates varied from 1.3 % to 2.3 % across treatments and the rates tended to be higher for the small class within treatments (Figure 2.1). The rates were directly related to the presumed intensity of interactions for both small and large classes of age-0 rainbow trout. The differences observed between the size classes within a treatment were also directly related to the presumed intensity of interactions. In the absence of older conspecifics, mortality of both size classes was low and the rate of the small class was only 2 % greater than the rate of the large class. In the continuous presence of older conspecifics the mortality rate of the small class was 49 % greater than the rate of the large class and 80 % greater than the rate observed in the absence of age-1 trout. In the experimental addition treatment, there was a 13 % difference between the two size classes. These results suggest that the presence of age-1 rainbow trout increases mortality of age-0 trout and that the effect is size-dependent.

A von Bertalanffy growth curve (Ricker 1975) was fitted to each size class for the three treatments (Figure 2.2). In all treatments, the asymptotic length of the small class was shorter than that of the large class (Table 2.2) and the rate of decrease in length increments (K) was always greater for the small class. The K value for the small class in the Age-0 / Age-1 treatment was 79 % greater than the rate of the large class within that treatment. This suggests that the small class attained the asymptotic length much faster. The differences between the K values were less in the other two treatments, 30 % for the Age-0 + Age-1 treatment and 28 % for the Age-0 treatment. Growth rates across treatments were inversely related to the presumed intensity of interactions and to mortality

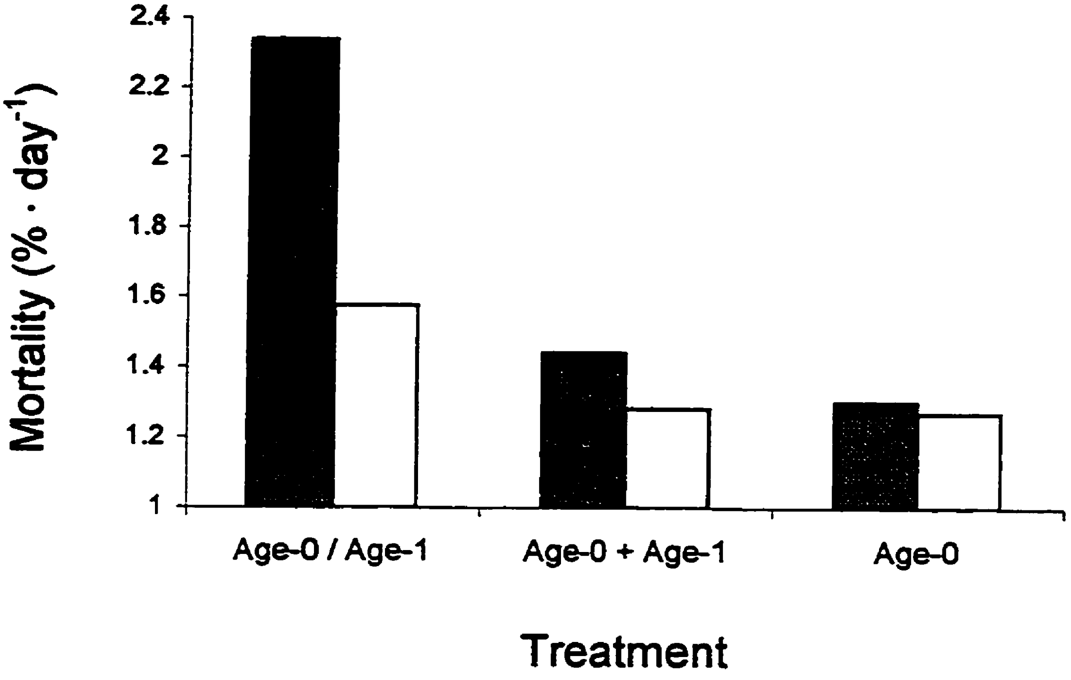
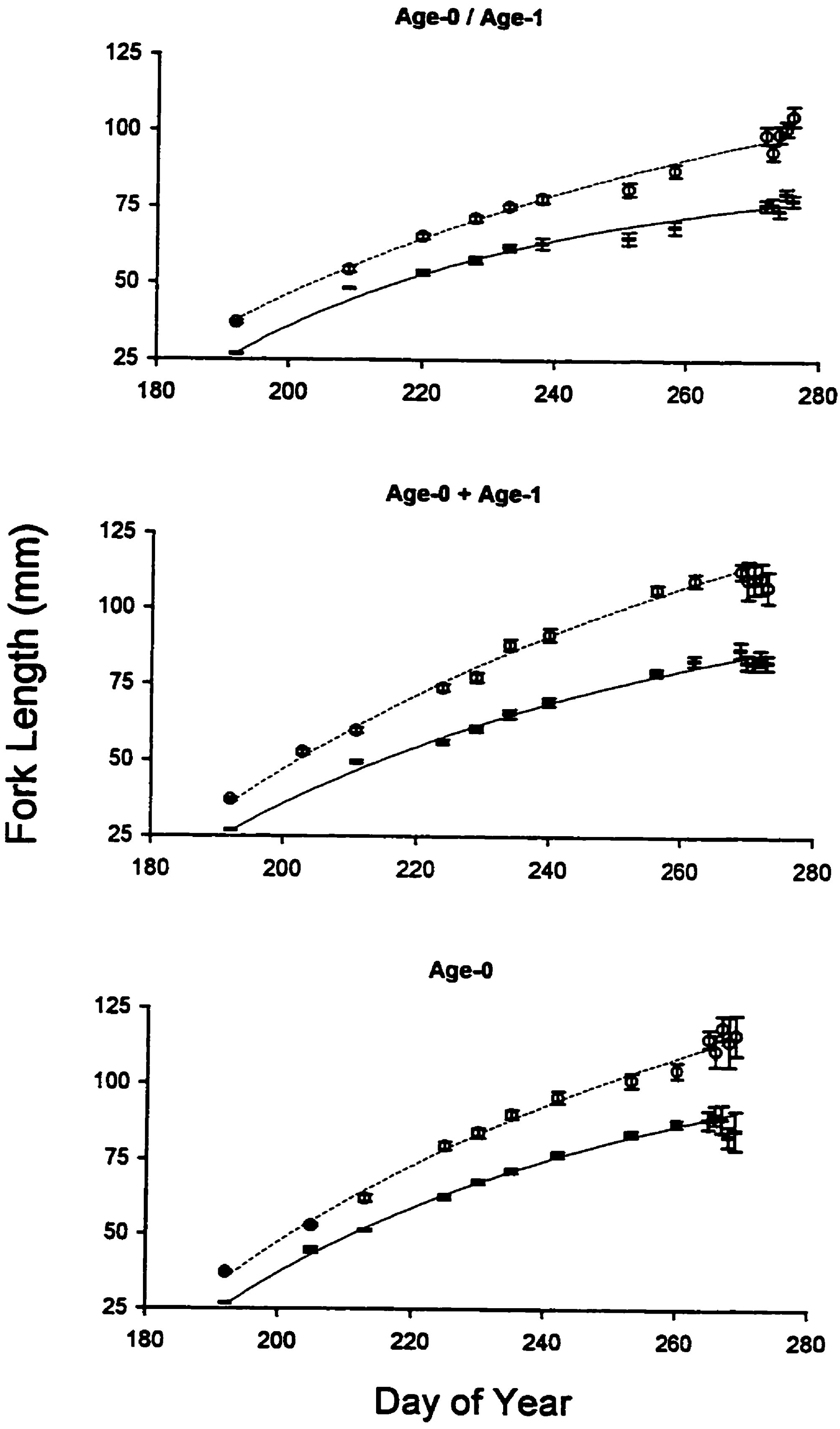

Mortality (% · day^{-1})
2.4
2.2
2
1.8
1.6
1.4
1.2
1
Age-0 / Age-1
Age-0 + Age-1
Age-0
Treatment

Figure 2.2 Fitted von Bertalanffy growth curves of fork length (FL) for each treatment. Dashed lines represent the large class and solid lines the small class. Error bars are 95 % confidence intervals on individual estimates of fork length.


Age-0 / Age-1

Age-0 + Age-1

Age-0

Table 2.2 Parameter estimates for von Bertalanffy growth curves based on Day and Dusk catches for the two size classes of age-0 rainbow trout are shown with standard errors in parentheses for all fitted coefficients. Equation used is as follows, $L_t = L_\infty * (1- \exp(-K * (t - t_0)))$ where L_∞ is the asymptotic size, K is the rate at which the curve approaches the asymptote, and t_0 is the hypothetical time at which the size of the fish is zero.

Treatment	Size Class	Sample size	L_∞ (mm)	K	t_0 (days)	R^2
Age-0 / Age-1	small	822	88.1 (1.5)	0.0195 (0.0010)	173 (1)	0.81
	large	1186	139.4 (2.3)	0.0109 (0.0004)	163 (1)	0.78
Age-0 + Age-1	small	1465	114.6 (1.9)	0.0136 (0.0005)	173 (1)	0.77
	large	1277	175.7 (3.2)	0.0105 (0.0003)	170 (1)	0.82
Age-0	small	1633	119.0 (1.7)	0.0154 (0.0005)	176 (1)	0.83
	large	1243	167.4 (3.1)	0.0120 (0.0004)	172 (1)	0.85

(Figure 2.3). The small class had faster mass-specific growth in all treatments which is probably a result of a higher scope for growth.

The diets of age-0 rainbow trout in the three study lakes included both zooplankton and macroinvertebrates (see Chapter 1, Table 1.8, 1.9, and 1.10). One potential explanation for the differences in growth rates among treatments would be related to the prey availability in each lake. The growth rates were inversely related to the lake-wide mean abundance of zooplankton (Figure 2.4) suggesting that growth differences among treatments can not be explained by the abundance of zooplankton prey. Differences in macroinvertebrate abundance across lakes also can not explain observed growth differences. The experimental addition treatment had the highest mean biomass of macroinvertebrates (Figure 2.4) and the others had similar and low biomasses.

Aggregate measures of the availability of zooplanktonic and macroinvertebrate prey in the 3 experimental lakes do not explain observed growth differences. Because fish tend to feed selectively on some invertebrate taxa, such aggregate measures need not to provide good predictions of growth. Post et al. (in press) provide an empirical model from 19 lake-years of data that predicts growth of age-0 rainbow trout based on the abundance of the specific invertebrate taxa that explain a significant proportion of growth variance. This model provides a useful tool to examine deviations from the null hypothesis that growth is strictly a function of the availability of key invertebrate taxa. In the Age-0 treatment, observed growth of age-0 rainbow trout was 12 % greater than predicted by the model based on specific prey abundance (Table 2.3). Observed growth of age-0 trout in the Age-0 / Age-1 treatment was 0.4 % less than predicted by the model. And

Figure 2.3 Instantaneous growth rates for age-0 rainbow trout from each treatment. Dark bars represent the small class and white bars the large class. Rates are calculated from known weights at stocking and vulnerability-adjusted weights from gillnet catches at end of experiment.

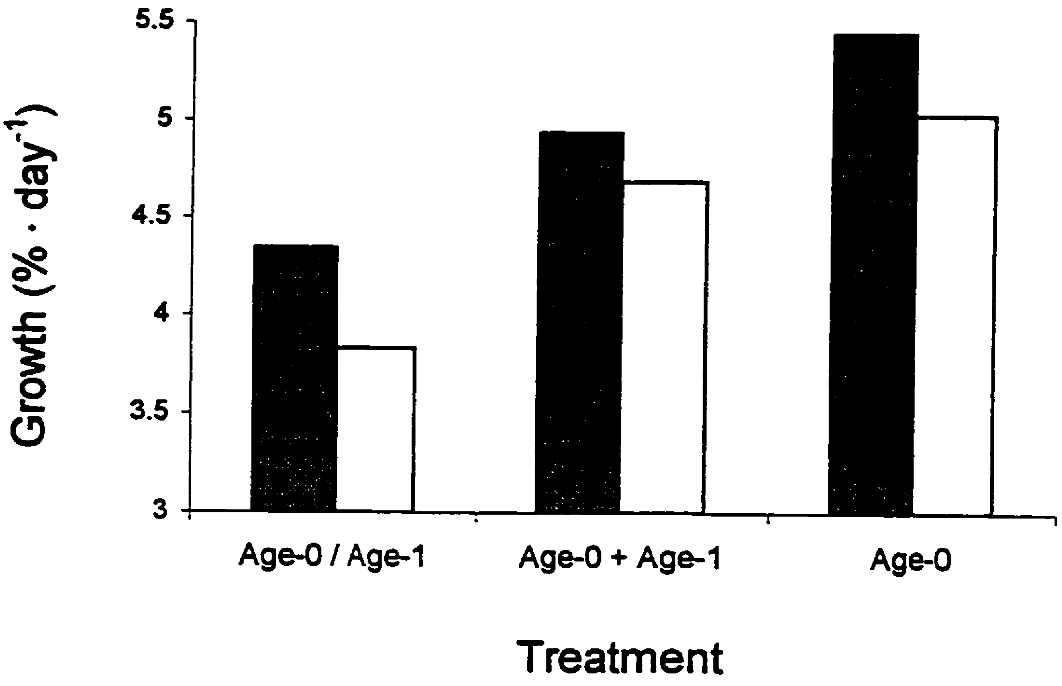
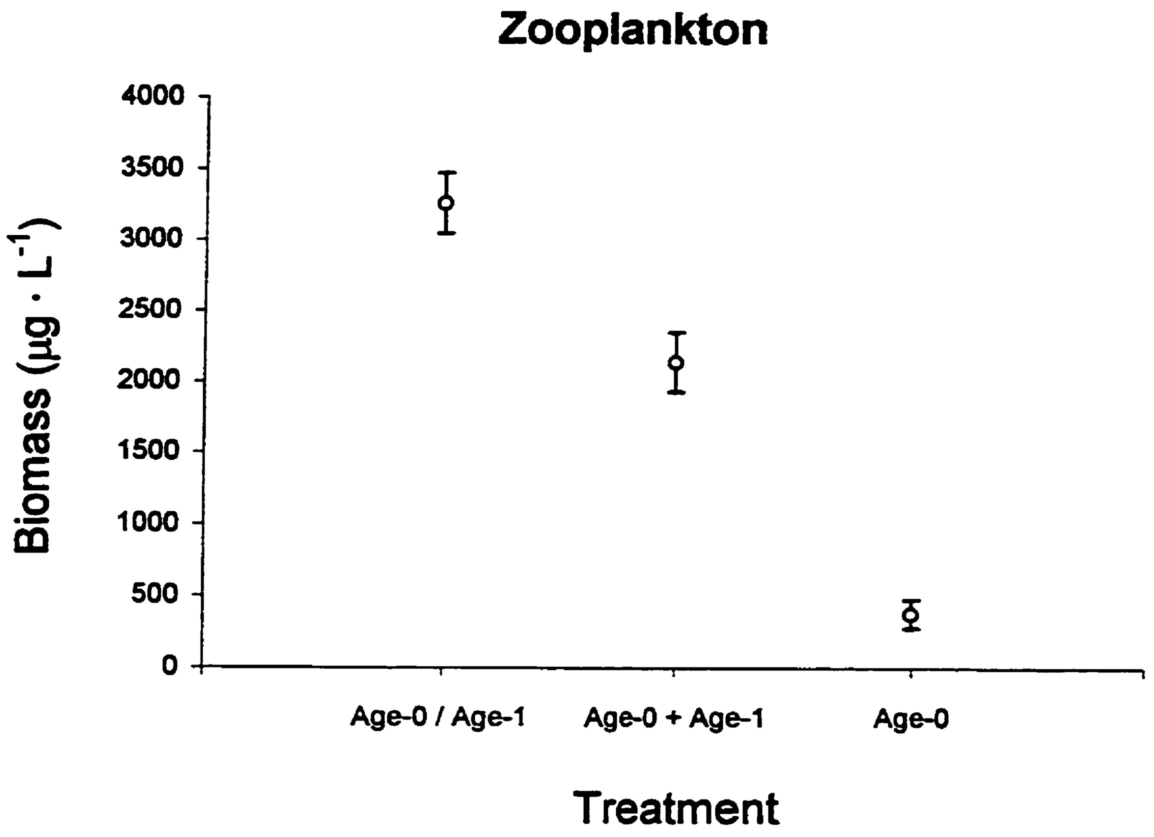

Growth (% · day⁻¹)
5.5
5
4.5
4
3.5
3
Age-0 / Age-1
Age-0 + Age-1
Age-0
Treatment

Figure 2.4 Prey availability in each treatment. Zooplankton data are means of samples from 8 sampling days which represent samples from each habitat all weighted per habitat volume and combined. Macroinvertebrate data are mean biomass per tile of 40 replicates collected over 4 sampling days where 5 samples were set at two different depths (1.5 and 2.5 m) on each sampling day. Error bars represent 1 standard error.


Zooplankton

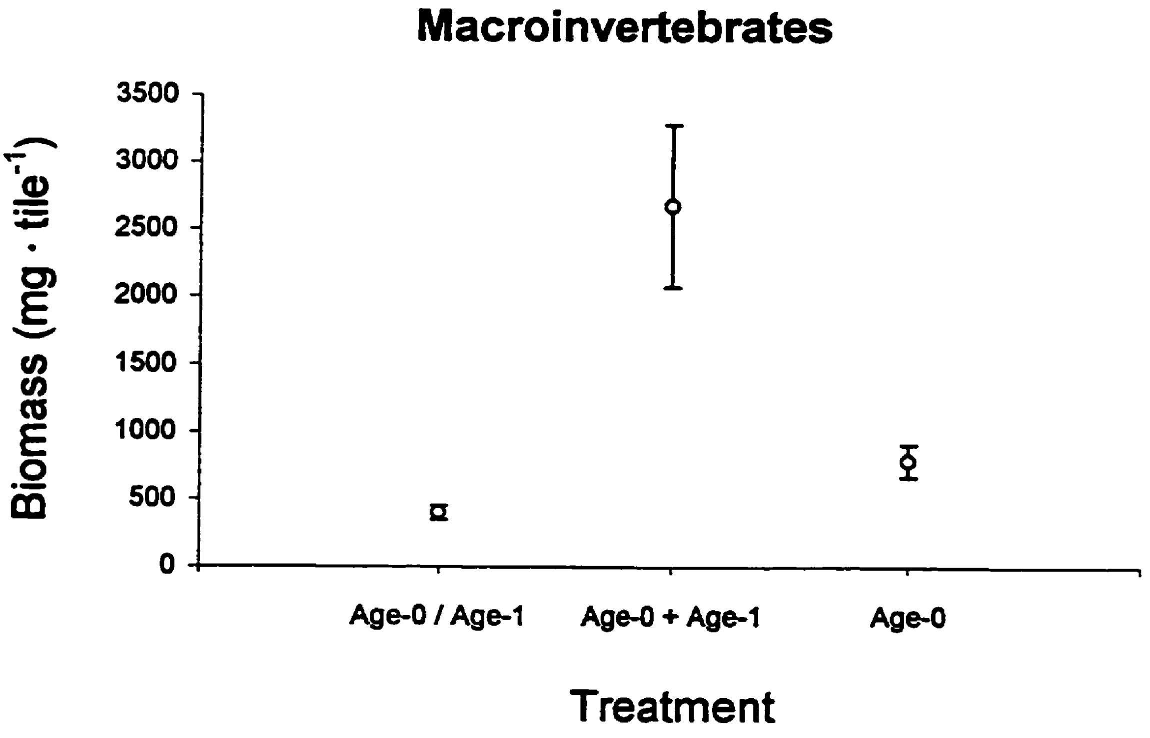

Macroinvertebrates

Table 2.3 Deviations (%) from expected growth predictions obtained from a multiple regression on age-0 growth based on prey availability (from Post et al. in press) for the small class of age-0 rainbow trout.

Treatment	**Deviation (%)**
Age-0 / Age-1	-0.4
Age-0 + Age-1	0.1
Age-0	12

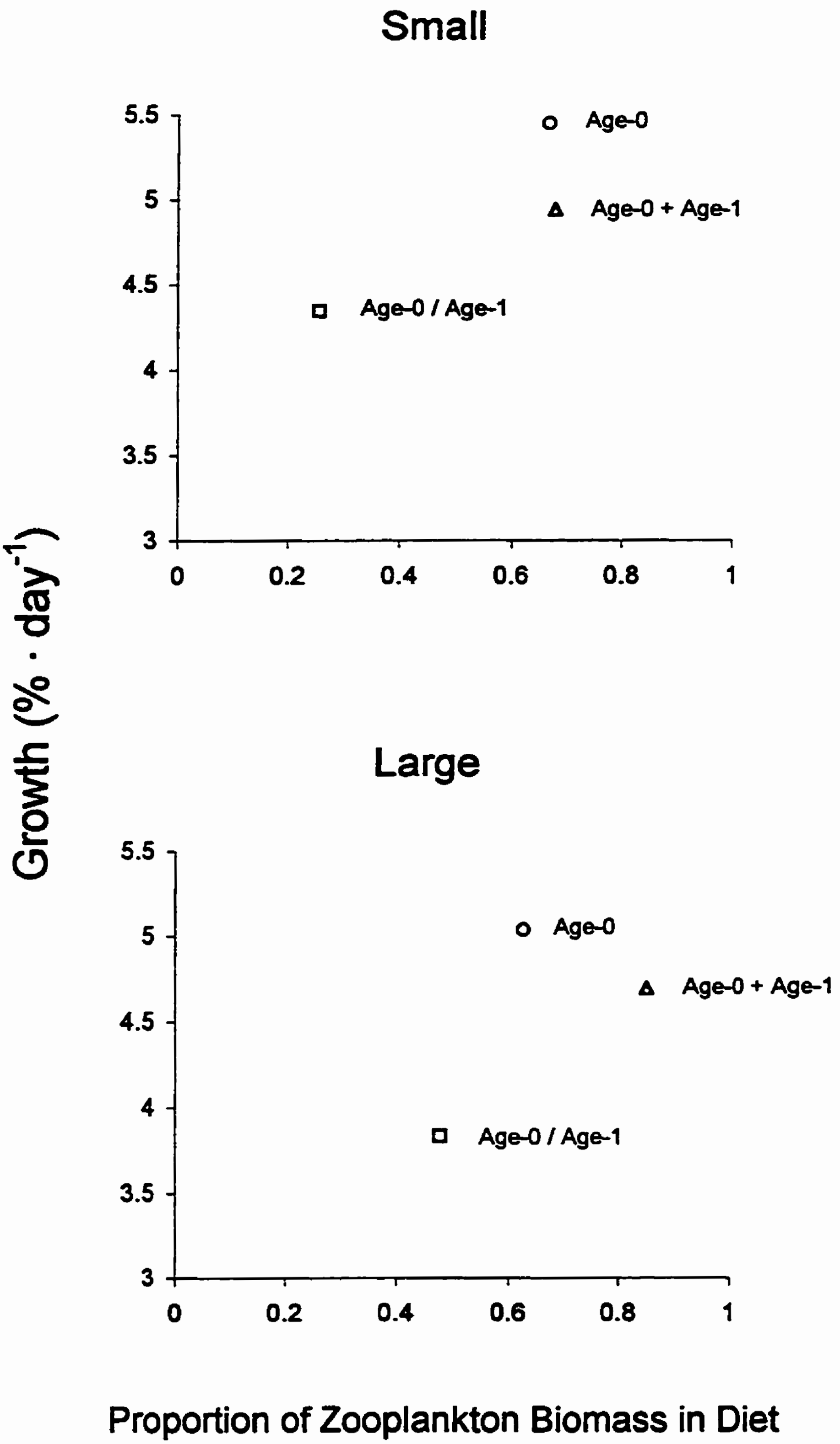
observed growth in the intermediate treatment (Age-0 + Age-1) was 0.1 % more than predicted.

It is possible that diet differences across treatments may explain the observed differences in growth rates observed. The proportion of zooplankton biomass of the age-0 fish diet differed across treatments (Figure 2.5). The mean diets from both size classes in the Age-0 + Age-1 and the Age-0 treatments comprised mainly zooplankton, whereas it was less than 50 % of the diet of both size classes in the Age-0 / Age-1 treatment (Figure 2.5). The mean diet of the large class in the continuous presence of age-1 trout included more zooplankton than in the diet of the small class.

Stomach contents of fish collected at dusk were used to test the hypothesis that differences in growth rates among the treatments may have been related to the amount of food the fish ingested. The mean stomach contents over the entire experiment differed between treatments and between size classes (Figure 2.6). In the Age-0 treatment, the age-0 fish had a lower percent of stomach contents than in the other two lakes, but growth rates were higher. In the Age-0 / Age-1 treatment, the age-0 trout had higher stomach contents than those from the Age-0 lake but had lower growth rates. In the Age-0 + Age-1 treatment, age-0 trout had higher stomach contents than in the other two lakes and had intermediate growth rates. In all three treatments, the small class had more food when caught than the large class, and had higher growth rates. These results can not explain the differences in growth rates among the treatments and suggest that the presence of age-1 rainbow trout may affect the feeding behaviour of age-0 trout.

The gillnet catch data collected during daytime and dusk in the experimental lakes

Figure 2.5 Relationship between growth and proportion of zooplankton biomass in stomach contents. Data are means of the six sampling days where the data is weighted per habitat-specific Population Index on each day.

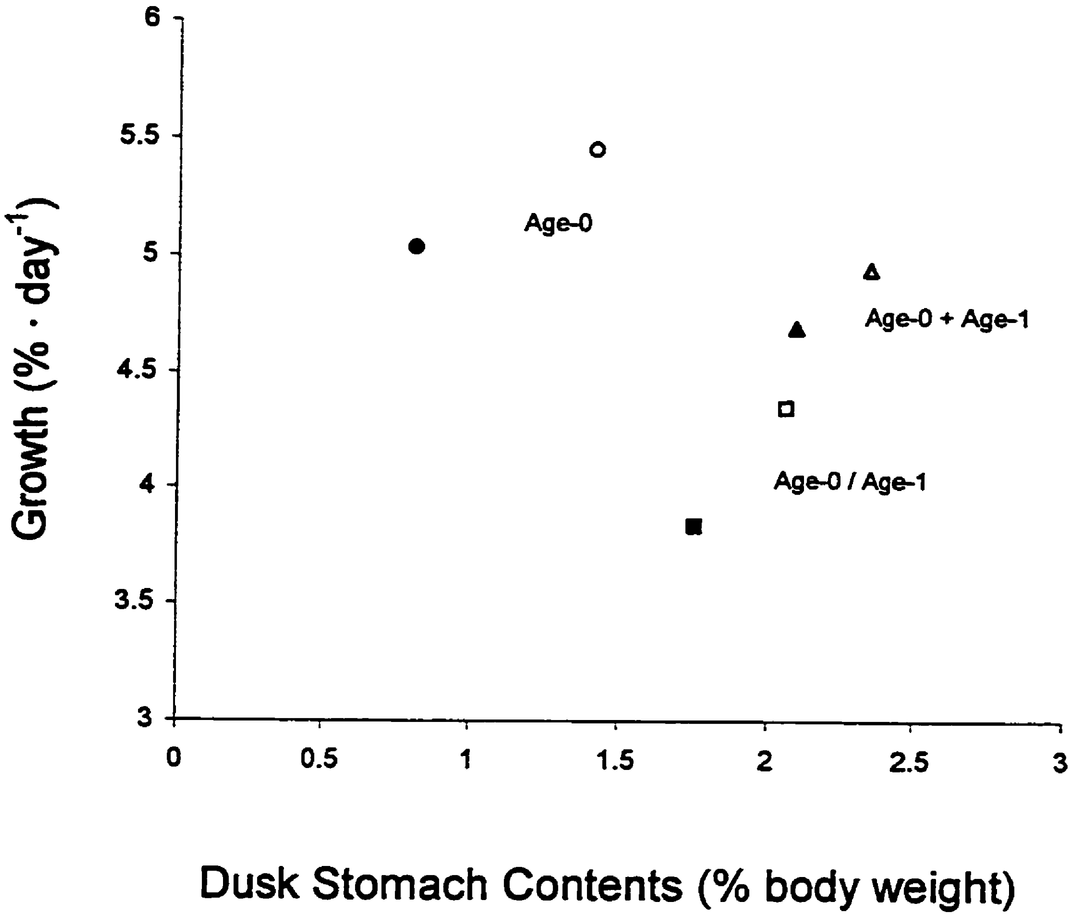


Small

Large

Growth (% · day^{-1})
Proportion of Zooplankton Biomass in Diet
5.5
5
4.5
4
3.5
3
0
0.2
0.4
0.6
0.8
1
Age-0
Age-0 + Age-1
Age-0 / Age-1

Figure 2.6 Growth in relation to mean stomach contents (% body weight). Data are means of the six sampling days where the data is weighted per habitat-specific Population Index on each day. Open symbols represent the small class and closed symbols represent the large class.


Growth (% · day^{-1})
6
5.5
5
4.5
4
3.5
3
0
0.5
1
1.5
2
2.5
3
Dusk Stomach Contents (% body weight)
Age-0
Age-0 + Age-1
Age-0 / Age-1

allowed examination of the temporal patterns of activity by the two size classes of age-0 trout as a function of the presence, absence or experimental introduction of older conspecifics. In the absence of age-1 trout, gillnet catches of age-0 trout during the day were approximately equal to catches at dusk for both size classes (Figure 2.7) suggesting no temporal restriction of activity. In contrast, in the two lakes containing older conspecifics, daytime catches ranged from 34 - 53 % of dusk catches. Interestingly, the restriction appeared to be more severe for the larger than the smaller class.

Habitat use by age-0 rainbow trout varied among treatments (see Chapter 1, Table 1.3 and Figure 1.10) and between size classes within treatments (Age-0 / Age-1: $G = 114.54$, $df = 3$, $p < 0.001$; Age-0 + Age-1: $G = 27.21$, $df = 3$, $p < 0.001$; Age-0: $G = 21.26$, $df = 3$, $p < 0.001$). In the absence of age-1 trout, close to half of the Total Population Index of both size classes of age-0 trout occupied the Limnetic habitat (Figure 2.8). In the continuous presence of age-1 trout, the majority of the small class occupied the Littoral habitat and most of the large class occupied both Epibenthic habitats. There was no large difference between the spatial distribution of the two size classes of age-0 trout in the experimental addition lake.

Figure 2.7 Diurnal activity of the age-0 rainbow trout across the three treatments. Data are total gillnet catches during the day over total catches at dusk for the six sampling days. Sampling effort was the same for both day and dusk. Open symbols represent the small class and closed symbols the large class.

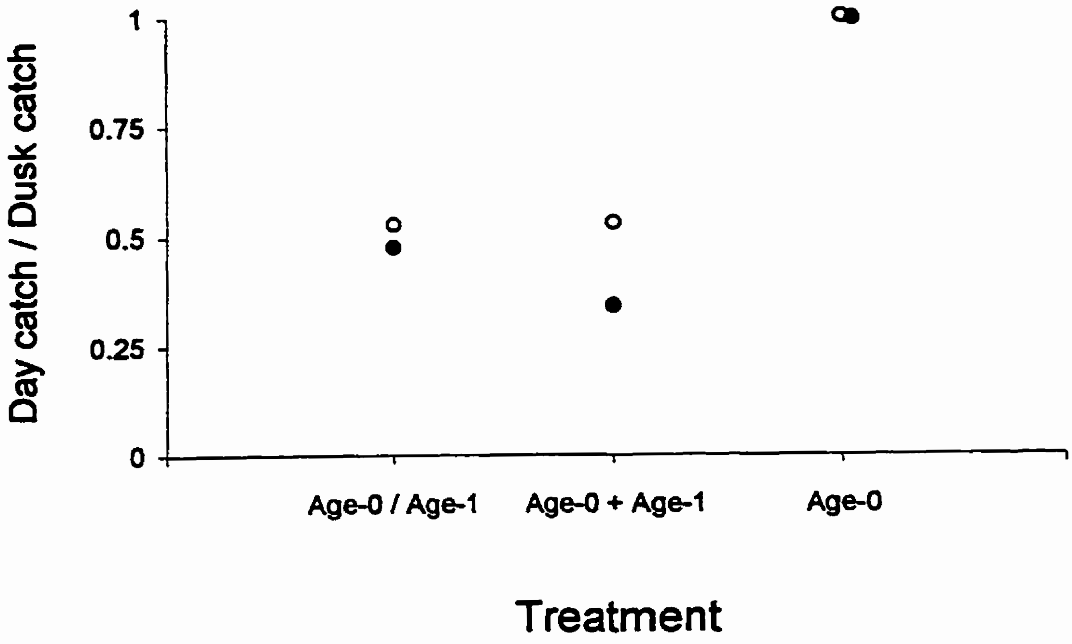
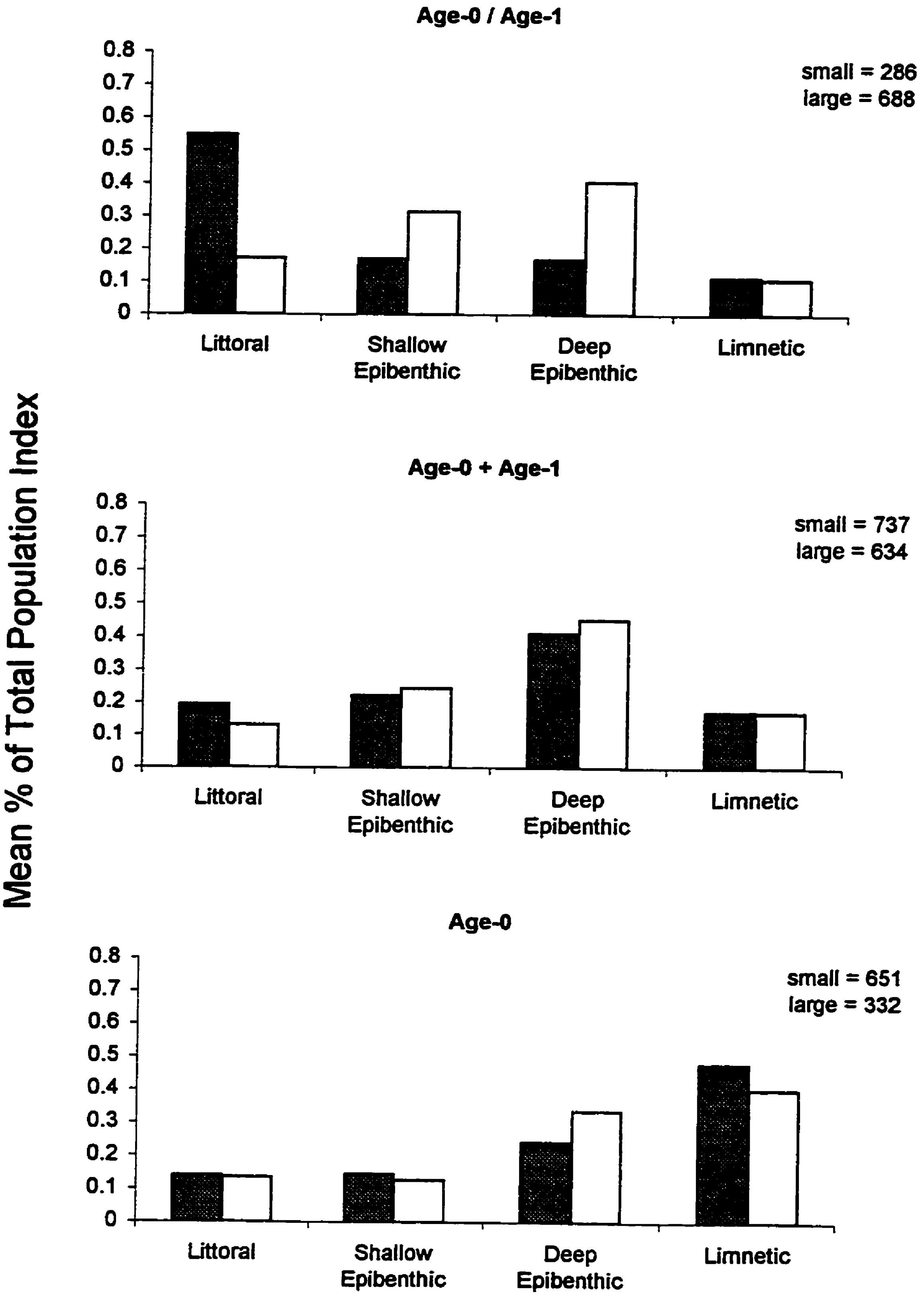

Day catch / Dusk catch
1
0.75
0.5
0.25
0
Age-0 / Age-1
Age-0 + Age-1
Age-0
Treatment

Figure 2.8 Mean percent of Total Population Index for Dusk catches over 6 sampling days for all four habitats. Data represent a mean of replicate sampling days in each habitat. Dark bars indicate small class and white bars large class.


Mean % of Total Population Index
Age-0 / Age-1
small = 286
large = 688
Age-0 + Age-1
small = 737
large = 634
Age-0
small = 651
large = 332
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Littoral
Shallow Epibenthic
Deep Epibenthic
Limnetic

2.4 Discussion

I examined whether the presence of older conspecifics affected growth and mortality of age-0 rainbow trout by creating populations that varied in size structure. I present empirical evidence that age-0 rainbow trout mortality is size-specific and varies in strength with the presumed intensity of interactions with older conspecifics and that growth is inversely related to the presumed intensity of interactions probably due to some combination of interference competition and predation. There are a number of potential explanations for the differences in growth across the three treatments and I present here the results from this study and other work which help identify the possible factors responsible for the differences.

Prey availability often governs of growth of fishes (Welker et al. 1994; Post et al. in press). In this experiment, density of zooplankton did not explain the differences in growth rates among the treatments and in fact zooplankton density was inversely related to observed age-0 trout growth rates. Because aggregate measures of prey availability such as total biomass could not explain the differences in growth rates among lakes, I used a regression model derived by Post et al. (in press) which was based on specific prey taxa and assessed whether the observed growth rates could be explained by the availability of the particular taxa. The results suggested that the presence or absence of age-1 rainbow trout may have had an impact on age-0 growth independent of prey availability. In the absence of older conspecifics the deviation was positive whereas in the continuous presence of age-1 trout the deviation was negative. Therefore, at the whole lake scale, prey availability could not explain all the growth variation among populations, but information on the intensity of interactions with older conspecifics did add to the understanding of growth variance.

Differences in growth rates among the treatments could not be explained by the amount of food the fish ingested. The data suggested that the presence of age-1 rainbow trout may have affected the behaviour of age-0 trout and yielded a greater amount of food ingested at dusk. Contrary to these results, other studies have reported a reduction in food intake due to interference by predators (Power et al. 1985; Schmitt and Holbrook 1985). An explanation for the differences observed between the extreme treatments could be that in the continuous presence of large conspecifics (Age-0 / Age-1 treatment), the age-0 would forage intensively at dusk when they are less vulnerable to predation and would be less active during the day as a result of a tradeoff between feeding and mortality risk. This would explain their greater stomach contents than the trout in the Age-0 lake, which could feed during both day and dusk and therefore have lower stomach content at any particular time. The amount of food found in the stomachs of age-0 fish in the Age-0 + Age-1 lake is harder to interpret because age-1 trout were not continuously present. Intense foraging at dusk in age-0 rainbow trout has been observed in other studies (Angradi and Griffith 1990; Tabor and Wurtsbaugh 1991). This tradeoff behaviour is supported in an indirect measure of diurnal activity levels of the fish among the extreme treatments. Because gillnet catchability is a function of activity level, it seems that activity did not change between day and dusk in the Age-0 treatment, whereas in the Age-0 / Age-1 treatment fish were apparently twice as active at dusk as during the day. This suggests that the presence of age-1 trout restricts the daytime activity of age-0 trout. This reduction in activity in the presence of predators is common in many species (see review by Lima and Dill 1990). The restriction in temporal activity appeared more severe for the larger class, because they occupy similar habitats to age-1 fish and may experience more competition during the day. This lower activity level during the day was also observed in small-scale pond experiments with age-0 rainbow trout (Tabor and Wurtsbaugh 1991). During the day, in the presence of predators, age-0 rainbow trout fed little, whereas in the absence of a predator, age-0 rainbow trout were observed feeding. More active individuals encounter food at a faster rate than less active individuals (Grant and Noakes 1987b; Werner and Anholt 1993) so that temporal restriction in activity would explain the differences in growth between the extreme treatments. Similar behaviour has been observed in juvenile sockeye salmon (*Oncorhynchus nerka*) which feed during short periods at dawn and dusk (Clark and Levy 1988) as a result of diel changes in the relationship between potential feeding rates and predation risks.

In addition to being temporally restricted in activity, age-0 rainbow trout restricted their activity spatially in the presence of older conspecifics, by using shallower and more complex habitats. Habitats that serve as refuges, such as the littoral zone, allow reduced encounter rates between predators and prey and lower predator efficiency (see Chapter 1). This increased use of refuges in the presence of predators is observed in other studies (Power et al. 1985; Schlosser 1987; Tabor and Wurtsbaugh 1991; Eklöv and Diehl 1994; Persson et al. 1996). The spatial distribution of both size classes differed in the Age-0 / Age-1 treatment and most of the smaller class inhabited the Littoral habitat, which is a low-risk habitat in lakes with rainbow trout (Post et al. unpublished manuscript). This difference in distribution between the two size classes suggests size-dependent tradeoffs between predation risk and foraging profitability among individuals that differ in size within a cohort. The fitness outcomes of these tradeoffs are critical for smaller fish because by selecting low risk habitats which may have lower prey abundance, growth rates will be low, resulting in an increase time spent at sizes vulnerable to predation. The majority of large age-0 fish in the Age-0 / Age-1 treatment inhabited the deeper water habitats where a large proportion of the older conspecifics were present (see Chapter 1). This behaviour was observed by Johnsson (1993) who found larger rainbow trout significantly more willing to risk exposure to a conspecific predator to get access to food than were small trout. I suggest that this habitat segregation between the two size classes is mediated by the age-1 through interference and predation pressure. This segregation is also observed in other species (Werner et al. 1983b; Sandheinrich and Hubert 1984; Gilliam and Fraser 1988; Tonn et al. 1992; O'Connell and Dempson 1996) where the small size class is more vulnerable. The difference in habitat use between the two size classes was indicated in the difference of their diet. The small class, which mainly inhabited the Littoral habitat, ingested a higher proportion of macroinvertebrates than did the large class. This suggests that the small class may have been forced to eat more macroinvertebrates due to the lower availability of zooplankton in that habitat (see Chapter 1, Figure 1.15) as opposed to the large class which inhabited the Epibenthic habitats. Differences in habitat use has also been reflected in the diets of perch between lakes with and without predators (Persson et al. 1996). Due to the greater use of the Littoral habitat by the small size class, where resources may be less available (see Chapter

1), intraspecific competition among smaller size classes may be intensified (Mittelbach 1986; Foster et al. 1988) and could lead to density-dependent growth. Mittelbach (1986) provided empirical evidence that resources are often limiting in the spatial refuges such as the littoral zone.

In the continuous presence of older conspecifics (Age-0 / Age-1 treatment) where zooplankton abundance was the highest of all three lakes and macroinvertebrates abundance the lowest, the age-0 trout mainly fed on macroinvertebrates. However, in the other two lakes with lower abundance of zooplankton and higher abundance of macroinvertebrates than in the Age-0 / Age-1 treatment, the fish fed primarily on zooplankton and growth rates were relatively higher. This may be a result of the low or nonexistence spatial and temporal restriction in those two treatments. Mills and Forney (1981) showed that the net energy return of yellow perch (*Perca flavescens*) feeding on benthic invertebrates was lower than for those feeding on zooplankton. They demonstrated that first-year growth of yellow perch from Lake Oneida, New York was substantially lower in years when their diet shifted from *Daphnia pulex* to benthic invertebrates. This shift occurred when *D. pulex* populations collapsed. A similar phenomenon may have occurred in this experiment. The higher proportion of macroinvertebrates in the diet of trout from the Age-0 / Age-1 treatment may be one of the reasons for the lower growth rates observed. Optimal foraging theory predicts a lower net energy gain for juvenile fish feeding on prey found in vegetation and sediments than on zooplankton prey because of the suboptimal prey size and the high minimal handling time in sediments (Mittelbach 1981). The differences in diet of age-0 fish between the Age-0 /

Age-1 treatment and the other two treatments is indicated by their observed spatial distribution (Figure 2.8) which suggest that they were not able to exploit sufficiently their preferred prey (zooplankton). This spatial limitation has led to the use of habitats poor in zooplankton prey abundance (see Figure 1.15 and 1.16 in Chapter 1).

The spatial restriction of age-0 rainbow trout induced by older conspecifics indirectly affects age-0 trout by limiting them to forage in habitats with lower prey profitability, therefore yielding lower growth rates. I suggest that the possible causes of differences in growth were interference competition and predation which led to differences in energetic costs, habitat use, and diet of age-0 rainbow trout among the three treatments. Differences in growth result from the presence of predators in experiments at smaller scales. In an enclosure experiment, age-0 chum salmon (*Oncorhynchus keta*) had consistently lower growth rates in the presence of age-1 coho predators than in their absence (Hargreaves and LeBrasseur 1986), apparently due to behavioural interactions with age-1 coho such as direct attacks and "harassment". In a pond experiment, large piscivorous perch (*Perca fluviatilis*) restricted the habitat use of age-0 perch, which then led to reduced growth (Eklöv and Diehl 1994). In sections of ponds, the smaller size class of bluegills were forced to feed in less profitable habitats due to the high risk of predation in profitable habitats and significantly depressed growth (Werner et al. 1983a). Therefore, my interpretations of spatial restriction and growth reduction in age-0 trout in the presence of older and large conspecifics appear to be general across the spatial scales of experiment.

Growth reduction prolongs the time spent at vulnerable sizes to predators, therefore increasing the predation risk. I demonstrated that mortality may vary with the intensity of interactions with older conspecifics. This can be related to the intensity of attack rates of age-1 trout on age-0 conspecifics, which increases a population's mortality rate (Post et al. unpublished manuscript). The results obtained from the Age-0 / Age-1 treatment may indicate that there were strong size-selective mortality rates in the continuous presence of older conspecifics. Such size-selective mortality rates have been shown in numerous studies (Parker 1971; Werner et al. 1983b; Hargreaves and LeBrasseur 1986; Gunn et al. 1987; Post and Prankevicius 1987; West and Larkin 1987).

The presence of age-1 rainbow trout may have increased mortality of age-0 trout in a size-dependent manner. Using Miller et al.'s (1988) equation predicted that the small class was 47 % more vulnerable to predation than the large class. The mortality rate of the small class estimated at the end of the experiment in the Age-0 / Age-1 treatment was actually 49 % greater than the large class. Therefore, Miller et al.'s (1988) equation of capture success seems to explain the difference in mortality rates for that treatment. The difference in mortality between the small classes in the Age-0 + Age-1 and the Age-0 treatment indicates that the small class in the experimental addition treatment was vulnerable to age-1 predation. The mortality rates of the large class from the Age-0 + Age-1 and the Age-0 treatments had similar values which suggest that the causes of mortality for the large class in the experimental addition treatment may not have been due to age-1 predation, but to other factors. In fact, according to the lengths of the age-1 at stocking and the lengths of age-0 in the Age-0 + Age-1 treatment, the predator-prey ratio for the large class was equal to 2.5 which yields a capture success of zero using the equation. Therefore, the larger class had reached a size at which it was no longer susceptible to predation by conspecifics since predation is highly dependent on the relative size of predators and their prey.

Mortality rates of age-0 rainbow trout observed in the Age-0 treatment and for the large class in the Age-0 + Age-1 treatment are probably due to piscivorous birds which were seen in all three lakes (belted kingfishers, *Megaceryle alcyon*; common loons, *Gavia immer*; great blue heron, *Ardea herodias*), or wandering garter snakes (*Thamnophis elegans vagrans*) and large Hemiptera and Coleoptera which were also observed in shallow water nearshore. Piscivorous birds are known to prey on age-0 rainbow trout (Tabor and Wurtsbaugh 1991; Post et al. in press). The results imply that mortality rates in age-0 rainbow trout are strongly size-dependent in the presence of older conspecifics and that mortality due to external factors is not size-selective. Although external sources of mortality do not appear to be size-selective between the 2 size classes of age-0, there is evidence that it is size-selective between age classes (Table 2.1 and see Post et al. in press).

In natural systems adult rainbow trout spawn in streams and juveniles live for some variable period in streams before migrating into lakes (Northcote 1969; Scott and Crossman 1973; Hayes 1987, 1988; Rosenau 1991). The timing of migration may have important implications for future survival and growth. Therefore, an understanding of the early life history requirements of rainbow trout in lake systems has important implications for recruitment. Hayes (1988) proposed that age-0 rainbow trout migrating early in the lake would have a competitive advantage over later migrating age-0 fish as a consequence of greater size attained in the lake due to warmer temperature and greater food abundance (Hayes 1995). This greater size would lead to greater survival, but the fish would be vulnerable to predators for a longer period. The age-0 fish would then be faced with a tradeoff between mortality and growth before entering a lake and they would encounter the same tradeoff once in the lake. Hayes (1995) pointed out that the timing of migration to lakes by age-0 rainbow trout may depend on the amount of cover in the nearshore habitat. In a lake with abundant nearshore refuge, fish would migrate early, whereas in a lake with little nearshore refuge, fish would migrate late.

Overall, the results from this experiment suggest that interference competition among age- and size-classes of rainbow trout has indirect and direct costs that translated into poorer growth and lower survival of the smallest class. This lower growth in the age-0 rainbow trout is due probably to a combination of the direct energetic costs spent by avoiding the older conspecifics and to indirect costs due to a change in foraging behaviour such as prey selection, feeding period, and habitat use. These nonlethal effects by the predators through interference competition can be as important as the actual killing of the prey (Mittelbach 1986). Adaptive behavioural responses such as choice of activity level and of habitat are mediated by tradeoffs between resource acquisition and mortality risk (Werner 1992; Walters and Juanes 1993) and these tradeoffs change with size as observed in this study. These size-specific behaviours are similar to those present in lotic salmonids, where dominance status correlates positively with size (Grant and Noakes 1987a, 1988; Gotceitas and Godin 1991), and dominant individuals tend to occupy the most rewarding locations (Fausch 1984; Metcalfe 1986; Grant 1990; Huntingford 1993).

Decreased growth rates of age-0 trout in the presence of predators has been demonstrated in other fish species at small scales (Werner et al. 1983a; Hargreaves and LeBrasseur 1986; Tabor and Wurtsbaugh 1991; Eklöv and Diehl 1994), but at these small scales it is unrealistic to assess the size-survival linkage which is crucial to understand at the population level. By using whole-lake experiments, I was able to draw conclusions at the population level and I investigated some factors which could have explained the differences in growth rates and I concluded that the effects of interference and predation may have been important factors in controlling growth of age-0 rainbow trout.

An understanding of the ecology and dynamics of the early life history governed by size-dependent interactions should be an integral part in assessing and managing fish populations. The performance of an individual represents a balance between maximizing foraging and growth rates and minimizing mortality rates due to predation. This study on size-dependent interactions provides information for understanding mechanisms governing survival and recruitment in fishes in lentic systems, and may be applied to other size-structured organisms. Although I can not directly reject the hypothesis that the results reported here are simply due to a "lake effect", the coincidence between the results and ecological theory suggests that the observed patterns in spatial and temporal distribution, growth, and survival are due to interactions between age- and size-classes of rainbow trout. It can also be supported by the fact that the treatments were allocated randomly and created fish populations from the same genetic origin.

CONCLUSIONS

1- Age-0 rainbow trout avoided the open water habitat and occupied shallower and more structurally complex habitats in two lakes that also contained older conspecifics compared to one lake without older conspecifics.

2- Smaller individuals occupied shallower habitats than large individuals in the presence of older conspecifics.

3- The spatial and temporal distribution of age-0 rainbow trout could have resulted from size-dependent tradeoffs between interference avoidance and habitat profitability.

4- Growth rates of age-0 rainbow trout populations in the experimental lakes could not be explained simply by prey availability.

5- The intensity of interactions with older and larger conspecifics may have indirectly affected growth of age-0 rainbow trout by altering the spatial and temporal use of resources and/or directly by imposing an energetic cost.

6- Water temperature and oxygen concentration could not completely explain differences in growth or spatial distribution of age-0 rainbow trout among lakes.

7- Mortality rates of age-0 rainbow trout varied directly with the presumed intensity of interactions with older conspecifics. In lakes with older conspecifics, larger individuals survived better than did small fish.

8- External sources of predation for age-0 rainbow trout, such as piscivorous birds, may have been an important mortality source. They do not appear to be size-selective within age-classes whereas they may be selective between age-classes, favouring higher survival of older and larger size classes.

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IMAGE EVALUATION
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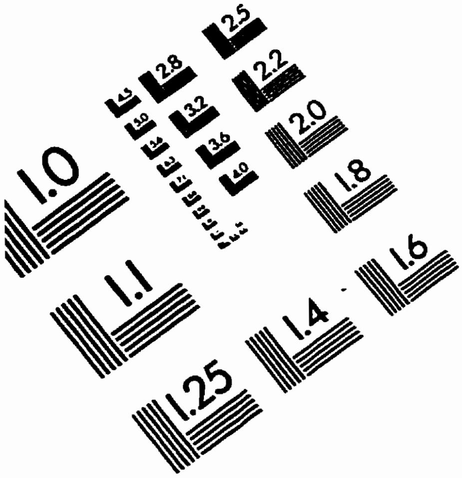

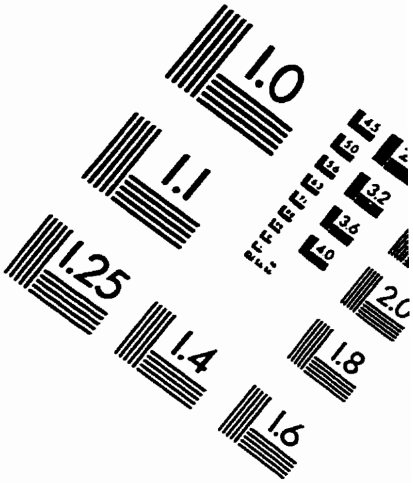

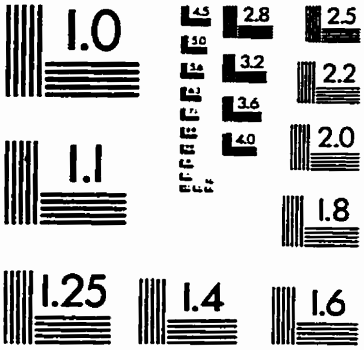

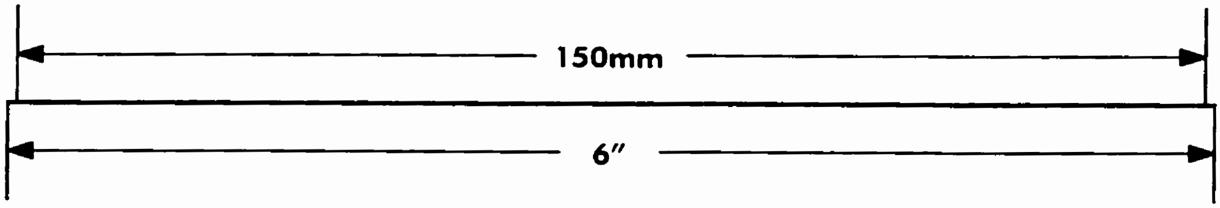

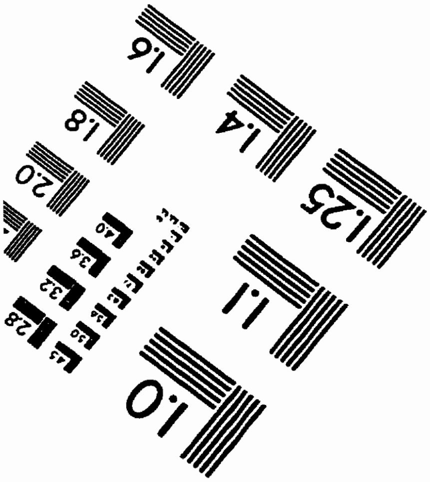

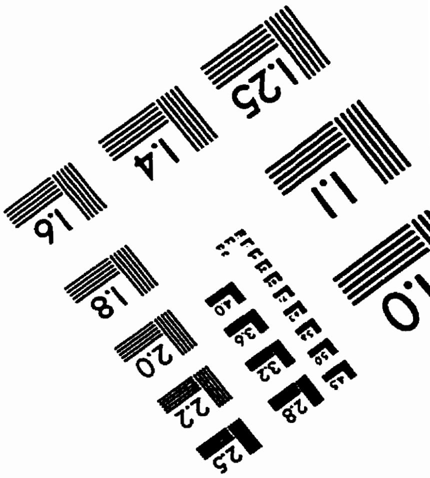

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