The Fish Community in the Pend Oreille River, Idaho:

Response to Higher Winter Water Levels

By

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December 2001

Abstract

We conducted a 2 year assessment in the Pend Oreille River, Idaho during 1999 and 2000 to identify changes in fish community and population structure associated with 3 years of higher winter lake levels. We stratified the 44.25 km section of the river from Albeni Falls Dam upstream to the U.S. 95 Highway Bridge, near Sandpoint, Idaho into similar strata that were sampled during 1991 and 1992, when the winter lake levels were reduced by 3.5 m from November through March. Nighttime electrofishing was the sampling method used in this survey, similar to that in 1991 and 1992. We collected over 13,000 fishes representing 19 species in the Pend Oreille River during 1999 and 2000. Community structure was significantly different in the Pend Oreille River although catch per effort of warmwater fishes varied among years and species. Population structure of largemouth bass *Micropterus salmoides* and black crappie *Pomoxis nigromaculatus* differed from 1991 and 1992 when water levels were drawdown to 3.5 m with incrreased abundance of larger and older fish. We used a competing models approach and found that a number of environmental factors contribute to year-class strength in largemouth bass, black crappie, and pumpkinseed. Spring water temperatures prior to and during the bass spawning season were significant along with winter water temperatures in February. Spring refill timing and quality of the growing season were also significant. Although the sign of the coefficient for drawdown elevation was negative, the relationship was not significantfor largemouth bass although it was significant for pumpkinseed and black crappie. Although individual species analyses provided conflicting information on the effects of higher lake levels in the Pend Oreille River we believe that drawdown interacts with spring and winter conditions that ultimately determine the strength of the year-class

for warmwater fishes in the Pend Oreille River. Our analysis demonstrates that multiple environmental factors contribute to year-class strength although the years of higher winter levels coincided with years of larger and older fish, independent of the influence of water temperatures on timing and quality of spawning conditions and the quality of the growing season.

Introduction

The kokanee <u>Oncorhynchus</u> <u>nerka</u> population in Lake Pend Oreille, Idaho has been declining for more than 3 decades. A number of hypotheses have been offered to explain the kokanee decline including reduced winter lake levels resulting in loss of suitable shoreline spawning habitat (Maiolie and Elam 1993). To test whether lake levels are related to kokanee survival, researchers from the Idaho Department of Fish and Game and the University of Idaho developed a proposal in 1994 (LPO Technical Committee 1994) requesting the U.S. Army Corp of Engineers to provide 3-years of higher winter lake levels. Beginning in 1996 through 1999, under the authority of the Northwest Power Planning Council, the maximum winter drawdown of Lake Pend Oreille was reduced from 3.5 m (lake elevation 625.1 m) to 2.1 m (lake elevation 626.5 m).

One possible incidental benefit of higher winter water levels in Lake Pend Oreille is increasing over-wintering habitat for warmwater game fishes in the Pend Oreille River, upstream from Albeni Falls Dam. DuPont (1994) reported a disproportionately low number of larger game fishes in the Pend Oreille River that he attributed to high winter mortality caused by the lack of suitable winter habitat. Typically, warmwater fishes prefer winter habitats with dissolved oxygen > 3mg/L, water velocities < 1 cm/s and temperatures > 1° C, characteristics generally found in areas adjacent to a main river (Knight et al. 1995; Carlson 1992; Pitlo 1992; Sheehan et al. 1990). DuPont (1994) found that under the normal 3.5 m winter drawdown in Lake Pend Oreille, habitat suitable for over-wintering warmwater fishes was approximately 4% of the summer level. Furthermore, he suggested that if drawdown were limited to 2 m, a 7.5 fold increase in

suitable winter habitat would result, and presumably translate into improved survival of warmwater game fishes.

Higher winter lake levels provided an opportunity to test the hypothesis that low abundance of warmwater fishes was associated with the paucity of suitable over-winter habitat in the Pend Oreille River. To test this hypothesis, we sampled the Pend Oreille River following 3-years of higher winter water levels in 1999 and 2000, and compared these data with data collected prior to the lake level experiment (DuPont 1994). The objectives of this study were to:

1. Assess differences in fish community structure following 3-years of higher winter water levels in the Pend Oreille River, Idaho;

2. Determine and compare population dynamics of size and age structure of selected warmwater fishes among sampling years; and

3. Determine the influence of winter water elevation and other environmental factors on year-class strength of selected warmwater fishes in the Pend Oreille River, Idaho.

Study Area

The Pend Oreille River begins at the outlet of Lake Pend Oreille located in northern Idaho at an elevation of 628.5 m (2061 ft) above mean sea level (msl; Figure 1). Our study area was the upper portion of the river, extending from Albeni Falls Dam upstream 44.25 km to the U.S. Highway 95 bridge near the City of Sandpoint, Idaho. This section of river is operated as a run-of-the-river reservoir, with flows ranging seasonally from 617 to 2,044 m^3 (11,200-73,000 cfs). At full pool, the surface area of the river is approximately 3,887 ha, the maximum depth is 48.5 m, and the average depth is 7.1 m (Dupont 1994). About 161 km of the shoreline, including sloughs and islands, have a gentle to moderate slope consisting mostly of fine sediments (< 4 mm), while about 16 km of shoreline is rocky, consisting of rip-rap (DuPont 1994).

Waters upstream of Albeni Falls Dam are typically drawndown annually from late fall to early spring for flood control and winter electrical power generation (Dice 1983). Water levels are drawndown in mid-September, reach low pool by early-November, and remain low until spring. In mid-April, water levels are raised and generally reach full pool by early June. Under normal reservoir operations, maximum winter drawdown is 3.5 m (target lake elevation of 625.1 m above msl), but from 1996 through 1999, maximum winter drawdown was reduced to 2.1 m (target lake elevation of 626.5 m above msl). This reduction in drawdown increased the winter surface area of the Pend Oreille River by approximately 7 % (Karchesky, unpublished data), which consisted mostly of shallow backwaters and sloughs. In 2000, winter drawdown was increased to 2.9 m, resulting in an intermediate drawdown elevation of 625.7 m above msl.

To insure all shoreline habitats were adequately sampled, the study area was divided into three strata similar to those delineated by DuPont (1994; Table 1). Littoral strata were divided according to substrate size and orientation to the main river channel. Each stratum was divided in 1.0-km sites, and a minimum of three sites within each stratum were randomly selected for sampling based on a stratified random sampling design (Schaffer et al. 1996).

Methods

Fish Collection

Fishes were sampled from the Pend Oreille River during full pool conditions (July

- August) in 1999 and 2000 at randomly selected sites within each of the three strata

using an electrofishing boat. We used a constant electrical output of 400 volts at 3 to 5

amps operated parallel to shore in waters generally < 1.3 m deep. One sampling unit

consisted of 10-minutes of electrofishing effort (the amount of time the electrodes are

activated), and as many fish as possible were collected without regards to species or size.

Captured fish were returned to the water after being identified, and measured for total

length (mm). Scales were collected from largemouth bass, black crappie and

pumpkinseed (See Appendix 1 for scientific names). Approximately six scales were

removed from the area near the extension of the left pectoral fin, below the lateral line

(DeVries and Frie 1996). Electrofishing was repeated at each selected site for three

consecutive nights during a sampling period to minimize nightly variation.

Data Analysis

Electrofishing data collected in 1991 and 1992 were used to provide information

concerning the characteristics of the Pend Oreille River fish community under 3.5 m

winter drawdown conditions (DuPont 1994). This earlier study used similar sampling

techniques, sampled the same three littoral strata and was conducted during the same time

periods as this study. For comparative analysis, data were separated into four sampling

periods: 1991 and 1992 (i.e. normal 3.5 m winter drawdown), and 1999 and 2000 (i.e.

following the 2.1 m experimental drawdown). All statistical analyses were conducted with SYSTAT (Wilkinson 1998) and JMP (SAS Institute 2000) software.

Fish community structure — Differences in fish community structure were assessed among sampling periods on the basis of species abundance. Mean catch-per-unit-effort (CPUE) was used as an index of abundance for each species in each habitat stratum, by sampling period. CPUE was calculated as the number of fish caught per 10 minutes of electrofishing effort. Catch data for largemouth bass, black crappie, pumpkinseed, yellow perch, northern pikeminnow, mountain whitefish, redside shiner, peamouth, tench, bullheads (pooled from brown and yellow), suckers (pooled from bridgelip, longnose, and largescale), and trout (pooled from rainbow trout, cutthroat trout, brown trout) were used to test for differences in species composition (see Appendix I for list of scientific names). Multivariate analysis of variance (MANOVA) was used to determine spatial and temporal effects in CPUE data. If significance were determined, individual species analysis of variance (ANOVA) tests were conducted and if significance were found, a least significant difference test (Fisher's LSD, $P < 0.05$) was used to determine pairwise differences among strata and years. To meet the assumption of homogenity of variance, data were log transformed prior to analysis (Kleinbaum et al. 1998).

Changes in fish community structure were further evaluated using a feeding guild approach on the premise that changes in habitat conditions can often lead to changes in food resources, resulting in changes in the trophic structure of the fish community (Karr et al. 1986). We used published accounts of diets and feeding habits (Scott and Crossman 1990) to assign fishes to feeding guilds following a trophic classification

scheme similar to Karr et al. (1986) and Bramblett and Fausch (1991; Table 2). We computed mean catch-per-unit-effort (number of fish by feeding guild/10-min electrofishing effort) for each habitat stratum by sampling period. Differences in feeding guild abundance were tested using the same multivariate approach described above. For analyses of fish community structure, we omitted age-0 fish since large annual fluctuations in their relative abundance may lead to misinterpretation of results (Angermeir 1987).

Size and Age Structure — We evaluated differences in population structure of largemouth bass, black crappie, and pumpkinseed among years by comparing size and age distributions. Length frequency graphs of selected warmwater fishes were constructed from electrofishing data for each year, and compared using Kolmogorov-Smirnov test for k-samples (Kiefer 1958). If significant differences were detected, a 2-sample Kolmogorov-Smirnov test (Conover 1999) was used to determine where differences occurred ($\alpha = 0.05$).

We assessed differences in age structure of selected warmwater species based on the proportion of fish in each age-class collected during each sampling year. Age determinations of selected warmwater species were made using scales collected during electrofishing on a minimum of 10-fish/10-mm length class. Scales were dried, cleaned and pressed into acetate slides. Impressions were magnified (46x) on an Anacomp microfiche projector and age determinations made by counting the number of annuli on each scale (Ambrose 1983). The number of fish in each age-class was estimated by extrapolation of aged subsamples in proportion to the overall length distribution.

Differences in age structure were tested among years using a chi-square contingency table ($\alpha = 0.05$; Conover 1999).

Factors Influencing Year-Class Strength — In effort to assess factors influencing year-class strength of largemouth bass, black crappie and pumpkinseed in the Pend Oreille River, electrofishing data collected from Dupont (1994) and our 2-year study were compared with reservoir environmental factors that might be related to recruitment. We used CPUE of age-1 fish as an index of year-class strength for each sampling year. This was based on results previous studies that found in Northwestern waters year-class strength of warmwater species is generally determined by first winter survival (Liter 1991; Bowles 1985), and therefore age-1 fish abundance is considered a better indicator of year-class strength. CPUE was expressed as the number of age-1 fish (as determined from our age structure analysis) collected per 10 minutes of electrofishing effort. We used catch data collected from only stratum 3 (backwaters), as abundance of these species were higher in these areas (Dupont 1994), and we felt it to be more representative of yearly variation in year-class strength.

The relationship between year-class strength and various environmental variables were evaluated using a two- stage completing model approach (Kirk Steinhorst, University of Idaho, personal communication). Analysis of variance (ANOVA) was used for initial examination of yearly differences in CPUE of age-1 fish. If significant differences by year were detected, year was removed from the model and replaced using an environmental covariant to predict yearling abundance above that explained by the overall year effect. This procedure provided a means of evaluating the influence of various environmental factors on age-1 fish abundance. We explored a number of

reservoir environmental variables that we speculated were related to strong and weak year-class formation. Winter water elevation, timing of spring refill, length of growing season and various seasonal averages of water temperature were computed for years when fish were age-0.

Mean daily river temperatures for all years were obtained from the U.S. Army Corps of Engineers through readings at Albeni Falls Dam. From these data, mean monthly temperatures were computed for months associated with spawning and early juvenile development (May - July) and first winter (December-February). Water temperatures were also used to evaluated the quality of growing season for each year-class by calculating the number of degree-days $> 10\,^{o}$ C. This was preformed using the formula (Bowles 1985):

$$D_{10} = \sum_{i=1}^{j} \frac{(C_i - 10) + (C_{i=1} - 10)}{2} d_{i,i+1}$$

where: D_{10} = degree days $> 10\,^{o}$ C,

C_i = mean temperature (C) on recording date i,

i = sampling dates i=1 to j, and

$D_{i,\,i+1}$ = number of days between consecutive temperature sampling (i to i+1).

Mean daily water elevations (meters above mean sea level) were obtained for each year from the U.S. Army Corps of Engineers through readings at the Hope recording station on Lake Pend Oreille. Water elevations were used to characterize two environmental factors. The first, timing of spring refill, calculated as the number of days

from January first to reach full pool. The second, was winter drawdown elevation associated with the first winter of a cohort.

Results

Fish Community Structure

Species composition— A total of 13,049 fish representing 19 species and 6 families was used to compare littoral fish assemblages in the Pend Oreille River, Idaho (Table 2). The largest number of fish sampled was in 2000 (n = 4,537), and the fewest in 1991 (n = 2,318; Table 2). Results of the MANOVA using species CPUE as the response variable revealed significant differences ($\alpha = 0.05$) in community structure occurred among years (Wilkes Criterion = 0.087, P < 0.001). However, results from the individual species ANOVA revealed that only catch rates of black crappie significantly (P<0.001) increased following higher winter water levels (1999 and 2000), and only mountain whitefish (P<0.001) and suckers (P<0.001) significantly decreased (Figures 2 and 3). We found no other evidence that species abundance differed between pre- and post-high winter water years.

Also, results from the MANOVA revealed significant fish community differences among littoral strata (Wilkes Criterion = 0.035, P < 0.001). In general, catch rates of cyprinids, salmonids, and catostomids were highest in littoral habitats along the main river channel (strata 1 and 2), whereas catch rates of centratchids, percids and ictalurids were highest in backwater habitat (stratum 3). Two-way interaction between year and strata was not detected (Wilks Criterion = 0.1637, P = 0.067).

Species differences in abundance among years were variable and largely related to the warmwater and coldwater fishes. Results from individual species ANOVA revealed that catch rates of largemouth bass and pumpkinseed were significant among years. Fisher's LSD determined that largemouth bass CPUE was significantly (P=0.001) lower in 1991 than in all other years, and significantly higher in 1999 than in 2000. Catches of pumpkinseed also were significantly (P<0.001) lower in 1991 than in other years. No other yearly differences in pumpkinseed CPUE were found. CPUE of the following species did not differ significantly by year: yellow perch (P=0.074), northern pikeminnow (P=0.263), tench (P=0.312), redside shiner (P=0.077), and bullheads (brown and yellow; P=0.234). Catch rates of trout species were significantly higher in 1991 than in all other years. Overall, trout species accounted for < 5 % of the species composition in 1991.

Trophic structure — Of the 19 species collected in the Pend Oreille River, seven were classified as insectivores, feeding predominately on invertebrates, seven as insectivores-piscivores and five as ominvores (Table 2). In general, insectivores-piscivores accounted for the highest percent composition of catch during all years, followed closely by insectivore, and then omnivore (Figure 4).

Results of MANOVA comparing trophic structure revealed a significant year effect among years (Wilks Criterion = 0.441, P<0.001). Individual ANOVA tests indicated that abundance of insectivores-piscivores was not significantly different (P = 0.564) from year to year, but insectivores (P <0.001) and omnivores (P = 0.002) were significantly different (Figure 4a). Fisher's LSD determined that catch rates of insectivores were significantly higher in 1992 and 1999, than 1991 and 2000; showing no

apparent trend between pre- and post high winter water years. Catch rates of omnivores were significantly higher in 1991than both 1999 and 2000 (P<0.05), however no significant (P>0.05) relationship was determined between 1992 and years following higher winter lake levels.

Population Structure

     Largemouth bass —Size structure of largemouth bass sampled in the Pend Oreille River differed significantly ($KS_a = 7.60$, $P < 0.001$) among years. We found that larger size classes accounted for a higher abundance of the catch following 3-years of higher winter water levels (Figure 5). Largemouth bass collected in 1991 averaged 91 mm with lengths ranging from 26 to 503 mm, although most fish sampled were in the 41-50 mm size class. During 1992, a biomodal size distribution of largemouth bass was found with peaks at 61 – 70 and 181 – 190 mm, resulting in an average length of 116 mm. Overall however, only 5 % of the largemouth bass sampled in 1991 and 1992 were longer than 200 mm. In contrast, largemouth bass longer than 200 mm accounted for 17 and 22 % of the catch in 1999 and 2000, respectively.

     Similar to size structure, age structure of largemouth bass differed significantly ($\chi^2 = 746.39$, df = 15, $P < 0.001$) among years. We found a higher abundance of older individuals following higher winter water levels (Figure 6). Largemouth bass sampled in 1991 and 1992 consisted primarily of ages-0 and 1 fish, with fish ≥ age-2 accounting for less than 5 % of the catch. Largemouth bass ≥ age-2 accounted for 20 % and 46 % of the catch in 1999 and 2000, respectively.

Year-classes strength of largemouth bass was directly related to winter water levels. Year-classes of largemouth bass produced during the high winter water years of 1996, 1997 and 1998 were generally strong. In 1999, these years-classes (age-1, 2 and 3) accounted for 86 % of the catch, and 41 % of the catch in 2000 (age-2, 3 and 4). However, a disproportionately low number of age-0 largemouth bass were collected in 1999. This combined with virtual absence of age-1 fish in 2000 suggests recruitment failures in 1999 for largemouth bass.

Black crappie — Differences in size structure of black crappie were significant ($KS_a = 7.93$, $P < 0.001$) among years. Black crappie sampled prior to higher winter water levels (1991 and 1992) ranged in length from 39 to 266 mm, and averaged about 100 mm (Figure 7). Following higher winter water levels, average length of black crappie increased from 128 mm in 1999 to 140 mm in 2000. However, in all years, fish longer than 180 mm accounted for less than 3 % of the catch.

Overall, age structure of black crappie differed significantly ($\chi^2 = 565.60$, df = 12, $P < 0.001$) among years, except between 1991 and 1999 ($\chi^2 = 5.37$, df = 4, $P = 0.252$). During these years, age-1 fish dominated the catch, followed by age-2 fish (Figure 8). The oldest black crappie sampled during all years was age-4, with age-3 fish (1997 year-class)exceeding 4 % of the catch only in 2000. Catches of black crappie in 1999 and 2000 consisted primarily of the 1998 cohort, which accounted for over 80 % of the catch during both years. This cohort was produced during the last year of higher winter water levels.

Pumpkinseed — We found no significant ($KS_a = 1.09$, $P = 0.18$) difference in size structure of pumpkinseed among years. In all years, pumpkinseed averaged about

100 mm, with the majority of fish ranging between 70 to 140 mm in length (Figure 9). In all years, age-1 fish accounted for the highest proportion of the catch (Figure 10). However, age structure of pumpkinseed in 1992 differed significantly from 1999 ($\chi^2 =$ 271.94, $P < 0.001$) and 2000 ($\chi^2 = 251.73$, $P < 0.001$), in which a higher proportion of ages-3 and 4 fish were sampled following higher winter water levels. These fish represent cohorts established during high winter water years. Small sample sizes in 1991 (n = 58) precluded statistical comparisons of age structure with 1999 and 2000 data. In total, only 13 fish ≥ age-3 were collected in 1991.

Analysis of Year-Class Strength

CPUE of age-1 fish differed significantly by year for each selected warmwater species, however variation in abundance across years was not consistent among species (Figure 11). In general, catch rates of yearling largemouth bass and pumpkinseed were highest in 1992 and 1999, indicating strong year-classes in 1991 and 1998. However, catch rates of yearling pumpkinseed in 2000 were also high, whereas largemouth bass were significantly lower. CPUE of yearling black crappie were significantly lower in 2000 than in all other years. Because of significant year differences in abundance of age-1 fish, we were able to explore the influence of various environmental variables using a competing model approach.

Effects of spring temperature— Variation in mean monthly water temperatures during prespawning, spawning and early juvenile development periods were pronounced. The largest among-year differences in mean monthly water temperature were observed in

May and June, with the highest mean monthly temperatures generally recorded in 1998 and the lowest in 1999, except in April (Figure 12).

Analysis of variance using mean monthly spring temperatures as the predictor variable revealed a significant proportion of the variation (R^2) in yearling abundance was related to annual differences in spring water temperature, particularly during June (Table 3). Mean June temperatures accounted for 63 and 49 % of the variability in abundance of yearling largemouth bass and black crappie, respectively. The relationship between spring temperatures and yearling abundance of these species was positive, indicating warmer spring water temperatures were associated with stronger year-classes. A significant relationship also was detected between June temperatures and age-1 pumpkinseed abundance, although the coefficient of determination was considerably lower ($R^2 = 0.21$). No other monthly spring temperature was significant for pumpkinseed.

Effects of spring refill— Variation among years in timing of spring refill during spawning and early juvenile development periods was observed. The number of days from 1 January to reach full pool ranged from 146 d in 1998 to 171 d in 1999 (Figure 13). Daily fluctuations in water elevation were minimal; the main trend was a progressive increase.

Analysis of variance revealed a significant ($\alpha = 0.05$) relationship between timing of spring refill and yearling abundance for all species (Table 3). Parameter estimates (β) using spring refill in the model indicated a negative relationship, suggesting stronger year-classes were produced when spring refill was completed early. Based on coefficients of determination (R^2), timing of spring refill explained the largest percentage

of variation in largemouth bass ($R^2 = 0.44$) followed by black crappie ($R^2 = 0.37$), and the lowest in pumpkinseed ($R^2 = 0.22$).

Effects of growing season — Length of growing season, as determined by the number of degree days > 10 ^{o} C during the first year of life, was longest in 1998 (1416 d) followed by 1990 (1176 d), 1991 (1146 d) and 1999 (968 d; Figure 14). Analysis of variance using growing season as the predictor variable for yearling abundance was significant for largemouth bass and black crappie, but not for pumpkinseed (Table 3). Coefficients of determination (R^2) for largemouth bass and black crappie showed that 55 and 50 % of the variation in yearling abundance was attributed to length of growing season, respectively.

Effects of winter temperatures — Variation in mean monthly winter temperatures was largest in December, with smaller among-year variations in January and February (Figure 15). The coolest monthly water temperatures were reported in January, except during 1999-2000 when temperatures were coolest in February. Mean monthly temperatures during 1990-1991 were generally 1 to 3 ^{o}C cooler than in other years.

Analysis of variance using mean monthly winter temperature as the predictor variable revealed a significant proportion of the variation in yearly abundance of largemouth bass (February) and black crappie (January) was related to mean temperatures (Table 3). However, no significant relationships between yearling pumpkinseed abundance and mean monthly winter water temperatures were detected.

Effects of winter water elevation — Maximum winter drawdown for year-classes produced in 1990 and 1991 was 3.5 m; for year-classes produced in 1998, 2.1 m and in 1999, 2.8 m (Figure 16). Water levels remained stable once maximum drawdown

elevation was reached. When analysis of variance was used to describe the interaction between winter drawdown elevation and yearling abundance, the relationship was negative for all species (Table 3). However, correlation coefficients were only significant for pumpkinseed ($P = 0.029$). A strong 1991 year-class of largemouth bass produced under normal 3.5 m winter drawdown conditions contributed to a non-significant relationship.

Discussion

Extensive literature reviews by Ploskey (1982) and Fraser (1972) have demonstrated the importance of water levels on the stability of aquatic ecosystems, and especially with warmwater game fishes. Our 2-year survey examined the influence of higher lake levels in 1996, 1997 and 1998 in the Pend Oreille River on the fish community and population characteristics. We found that fish community structure changed little in the Pend Oreille River during the 3 years of the higher winter water levels, although population characteristics changed significantly. Overall, catch rates of most species following higher winter levels were similar to those under the 3.5 m drawdown. Yellow perch and northern pikeminnow were among the most prevalent species captured during all years. DuPont (1994) regarded these species as habitat generalist, and therefore may be more resilient to varying habitat conditions. Black crappie (increased), mountain whitefish (decreased), and suckers (decreased; represented mostly by largescale suckers) showed significant differences between pre- and post high winter water years although these differences may not be a direct result of higher winter water elevations.

Individual species ANOVA indicated that relative abundance of largemouth bass and pumpkinseed were significantly higher following the lake level experiment from those in 1991, but not 1992. Substantial increases in CPUE from 1991 to 1992 were attributed to high winter survival under unusually mild winter conditions and an early spring in 1992 (DuPont 1994). A number of factors influence the population abundance of various species annually and benefits of higher winter water elevations may be masked by other factors.

Abundance of insectivores and omnivores varied significantly from year to year, while the abundance of insectivores-piscivores did not. We found no evidence that insectivores changed as a result of higher winter water levels, as significant variation occurred between sampling periods (i.e pre-high winter water years 1991 and 1992; and post high winter water years 1999 and 2000). In contrast, omnivores were significantly higher in 1991 than 1999 and 2000, largely attributed to decreased abundance in catostomids (mainly largescale sucker). Reasons for the decrease are unclear, but because we found no significant difference in omnivore abundance between 1992 and years following higher winter water levels, we speculate that it may be related to natural variation in fish community structure, rather than winter water elevation.

We found evidence supporting the contention made by DuPont (1994) that the lack of suitable over-winter habitat was limiting the recruitment of warmwater fishes in the Pend Oreille River. A higher abundance of older age-classes observed in 1999 and 2000 suggests that winter survival improved during high water years. However, other environmental factors related to temperature and water levels fluctuations also appear to influence year-class formation.

Based on species responses to higher winter water levels, the largest change in size and age structure occurred in largemouth bass. Prior to higher winter water levels, age-0 and 1 fish accounted for over 95 % of the catch, resulting in low numbers of larger individuals in the fishery. Following higher winter water levels, however, we found a higher abundance of older individuals, and therefore a higher abundance of catchable sized largemouth bass. Year-classes established during higher winter water years were most prevalent in our samples, providing evidence that over-winter survival improved during high winter water years. For instance, the majority of fish collected in 1999 were ages-1, 2 and 3, corresponding with the experimental drawdown years of 1998, 1997 and 1996. These findings also are supported by angling reports of increased abundance of larger largemouth bass in the sport fishery (N. Horner, Idaho Department of Fish and Game, Coeur d' Alene, Personal Communication).In addition, we visited the weigh-in of local bass club tournaments held on the Pend Oreille River in fall 1999. Participants described improved catch rates of largemouth bass in 200 -300 mm (10 to 12 in) size range following the higher winter lake levels; they also observed increased abundance of smaller, juvenile bass following years of higher winter water levels.

Based on our regression analysis of age-1 fish abundance, water temperatures, timing of refill and length of the growing season appear to be important factors contributing to year-class strength of largemouth bass in the Pend Oreille River. Years with cooler spring temperatures, and thus shorter growing season, typically produced weak year-classes. Bowles (1985) found that water temperature affected over-winter survival of largemouth bass in the Coeur d' Alene Lake system by influencing the length and quality of the growing season. He found that fish less than 50 mm did not survive

long winters. The influence of water temperature may likely explain the disproportionately low number of young-of-the year collected in 1999. Spring water temperatures were 3-4 $^{\circ}$C cooler in 1999 than in 2000. Our CPUE data for largemouth bass was significantly higher in 1999 and 2000 than in 1991, but not 1992. Based on our age structure data, this was attributed to increased abundance of year-classes established during 1996, 1997, and 1998, years of higher winter water levels.

Increased abundance of black crappie following higher winter water levels was largely the result of a strong 1998 year-class that dominated the catch in 1999 and 2000. Abundance of older year-classes, including those produced during the high water years of 1996 and 1997 were negligible. The lack of older age classes following higher winter water levels suggests that recruitment of black crappie may be limited by factors other than suitable winter habitat.

Gabelhouse (1984) observed an inverse relationship between largemouth bass proportional stock density (PSD) and black crappie PSD, and postulated that black crappie densities were regulated by largemouth bass predation. McHugh (1990) reported a similar relationship when black and white crappie abundance increased following removal of largemouth less than 200 mm. While these studies were conducted in relatively small (< 30 ha) mid-western impoundments where interactions may be intensified, it is possible that interspecific interactions between largemouth bass and black crappie also may be occurring in the Pend Oreille River.

While size structure of pumpkinseed did not differ significantly among sampling years, we found a higher abundance of older individuals following higher winter lake levels. This discrepancy between size and age structure in pumpkinseeds may reflect a

trend towards intraspecific interactions that could result in slower growth rates at older ages, a characteristic of pumpkinseeds found in other northern water bodies (Scott and Crossman 1973). Nevertheless, a higher abundance of older pumpkinseed in the population suggests that winter survival increased during higher winter water years.

The influence of water temperature and water level fluctuations on early spring spawning success may also be affecting recruitment in the Pend Oreille River. During 1999, we collected relatively few age-0 warmwater fish, which may be attributed to an unusually cool spring combined with a late refill period. Based on our field observations, water temperatures recorded during spring 1999 were generally 3° C cooler than water temperatures during spring 2000. Spawning of largemouth bass may have occurred later in spring 1999, thereby contributing to a shortened growing season that would reduce the overall size of young-of-the-year going into their first winter. Also, water levels in the Pend Oreille River remained below full pool until early July, almost 3 weeks later than normal. Timing of hatch, length at first winter and stable water conditions all have been linked to year-class strength of largemouth bass in northern waters (Mitchell 1982; Bowles 1985; Rieman 1987).

We found a significant relationship between timing of spring refill and age-1 fish abundance. Increases in water level during the spring have been shown to adversely affect recruitment of warmwater fishes by increasing the incidence of nest abandonment, which may lead to increased egg and larvae predation. Increased water levels can also reduce water temperatures in the spring. Sharp decreases in water temperature can similarly adversely affect spawning success. Our field observations showed that when water levels increased, backwater temperatures decreased by approximately 3 $^{\circ}$ C. In

contrast, years in which water levels in the Pend Oreille River progressively increased, with little to no fluctuations and reached full pool by mid-May, produced strong year-classes.

Water levels at full pool also can improve spawning success by increasing structural complexity. Most of the structure in the Pend Oreille River is located along shoreline or at depths greater than 3 m. At full pool, predation should be less, as a result access to shoreline structure; Crowder and Cooper (1979) found a direct relationship with structural complexity; i.e. increases in structural complexity were associated with higher fish abundance.

The benefits of higher winter water elevations were mixed based on our regression analyses. We used age 1 fish abundance to "tease" the effects of the varying environmental conditions among the 4 years. Our statistical analyses clearly showed a significant "year" effect but because of the number of environmental factors that could contribute to year-class strength, it was difficult to interpret. Consequently, we used a competing models approach to separate these effects. Both pumpkinseed and black crappie revealed a significant relationship between winter water elevation and yearling abundance but not largemouth bass. Although not significant, we found that yearling largemouth bass abundance was inversely related to winter water elevation, indicating that stronger year-classes were produced under higher winter water levels. Since drawdown elevation alone was not significant for largemouth bass, the analyses indicated other environmental factors were contributing more to the abundance of age 1 largemouth bass during the 4 years of study. The power of our analysis was limited, however to the 4

years of data from 1991 and 1992, 1999 and 2000. Electrofishing effort was considerably

less in 1991 and 1992 and may have contributed to the outcome of the statistical analyses.

The competing models analyses showed that a number of environmental factors

significantly affected age-1 abundance of largemouth bass, and black crappie (Table 3).

Of those, spring water temperatures prior to and during the bass spawning season were

significant along with winter water temperatures in February. Also, winter drawdown

elevation was significant for black crappie and pumpkinseed.

Our results provided a generally clear understanding of the influence of

environmental factors on the warmwater fish community in the Pend Oreille River.

Evidence that the higher winter lake levels enhanced the warmwater fish community

were associated with community structure and higher population abundance of older and

larger warmwater fishes during years of higher lake levels. The competing models

analysis showed that overall water temperature effects contributed more to age-1 fish

abundance than higher water levels during the 4 years of study. The critical importance of

water temperature in the abundance of largemouth bass in Idaho has been clearly

demonstrated by Dillon (1991) and Bennett et al. (1991). We believe that drawdown

interacts with spring and winter conditions that ultimately determine the strength of the

year-class of warmwater fishes in the Pend Oreille River. For example, during years of

warmer spring water temperatures and longer growing seasons, larger age-0 fish enter the

winter. Warmer and shorter winters combine to offset the importance of higher winter

lake levels. However, when the opposite conditions prevail, and smaller age-0 fish enter

the winter, the importance of higher winter lake levels is realized resulting in higher over-

winter survival. Although our analyses demonstrate that multiple environmental factors

contribute to year-class strength of warmwater fishes in the Pend Oreille River, years of higher winter levels coincided with years of larger and older fish and stronger year-classes.

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Winter habitat requirements and overwintering survival of riverine fishes.
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Table 1. Habitat characteristics of littoral strata sampled in Pend Oreille River, Idaho.

Habitat Strata	Area Description	Length	Percent Composition
Stratum -1	Along the main river channel Avg. substrate size < 15 mm	75.5 km (shoreline)	60 %
Stratum -2	Along the main river channel Avg. substrate size > 15 mm	21.1 km (shoreline)	17 %
Stratum -3	Off river channel (sloughs) Avg. substrate size < 4 mm	27.0 km (shoreline)	22 %

Table 2. — Percent composition of fishes (by number) collected by electrofishing in the Pend Oreille River, Idaho before (1991-1992) and after (1999-2000) experimental drawdown. Age-0 fish were removed from the analysis.

Species	Tropic group[a]	Stratum 1				Stratum 2				Stratum 3				Total			
		Before		After		Before		After		Before		After		Before		After	
		1991	1992	1999	2000	1991	1992	1999	2000	1991	1992	1999	2000	1991	1992	1999	2000
Kokanee salmon	I	.5				.4				.1				.3			
Rainbow trout	I	5.2				2.2			.1	.4				2.8			
Cutthroat trout	I	1.0				1.9				.1				.9			
Lake trout	I-P											< .1				< .1	
Brown trout	I-P	.5	.2				.2		.4			.2	.2	.2	.1	.1	.2
Moutain whitefish	I	31.5	27.8	1.2	5.2	.7	4.5		.1	.5	.5			13.4	11.2	.3	1.1
Northern pikeminnow	I-P	23.4	23.9	36.2	37.2	54.5	44.8	63.5	63.7	5.4	2.1	2.4	1.2	24.2	20.3	22.8	23.6
Peamouth	I	5.8	.7	2.8	3.6	3.5	1.0	3.5	1.9	10.5		2.2	1.6	6.9	.5	2.6	2.1
Redside shiner	I	7.9	17.8	37.7	8.5	10.6	14.0	12.0	4.4	1.2	.2			6.2	9.8	11.5	2.9
Tench	O	1.1	.3	.3	2.1	.4	.3			2.9	5.2	2.0	4.0	1.6	2.3	1.2	2.7
Largescale sucker	O	10.1	9.1	1.9	1.4	23.2	16.1	4.1	7.7	8.5	.9	.5	1.8	12.6	7.6	1.6	3.1
Longnose sucker	O	1.0	.6	.4		.2	.2	.5		1.3	.7	.5	.1	.9	.5	.5	< .1
Bridgelip sucker	O						.2								< .1		
Brown bullhead	O	1.1	1.8	1.6	4.5		1.7			21.3	5.1	6.5	6.3	8.0	3.1	4.3	4.7
Largemouth bass	I-P	1.0	1.5	1.1	1.3	1.1	2.5	4.4	1.8	2.9	18.2	14.8	10.1	1.7	8.4	9.4	6.3
Smallmouth bass	I-P			.1				.5	2.1				.1			.1	.5
Black crappie	I-P	1.0	.5	3.6	11.3		1.7	2.7	.9	3.7	2.7	8.2	8.3	1.7	1.7	6.0	7.3
Pumpkinseed	I	.2	6.7	9.4	6.9	.2	5.3	6.4	8.0	6.5	43.2	37.7	41.3	2.4	21.0	24.6	26.1
Yellow perch	I-P	8.3	9.0	3.7	17.9	1.1	7.7	.5	7.8	34.6	21.1	24.9	24.9	16.0	13.5	14.9	19.4
Total number of fish		960	877	897	983	538	601	748	1,057	820	985	2,086	2,497	2,318	2,463	3,731	4,537

[a] Trophic groups diets. Insectivore (I): > 90 % invertebrates. Insectivore-piscivore (I-P): > 25 % fish, remainder invertebrates. Omnivores (O): 25 - 90 % plant detritus, < 10 % invertbrates.

Table 3.— Relationship between environmental variables and yearling abundance of largemouth bass, black crappie and pumpkinseed collected in the Pend Oreille River Idaho, in 1991, 1992, 1999 and 2000.

	Largemouth bass				Black crappie				Pumpkinseed			
	n	R^2	slope	P-value	n	R^2	slope	P-value	n	R^2	slope	P-value
Overall year effect	25	0.44	---	<0.001	25	0.45	---	< 0.001	25	0.20	---	0.002
Spring water temperatures												
April	25	0.01	0.162	0.722	25	0.10	0.842	0.130	25	0.01	-0.145	0.711
May	25	0.37	0.585	0.001	25	0.38	0.750	0.001	25	0.14	0.310	0.068
June	25	0.63	0.838	< 0.001	25	0.49	0.927	< 0.001	25	0.21	0.419	0.020
July	25	0.45	0.613	0.001	25	0.48	0.795	0.001	25	0.07	0.21	0.196
Spring refill	25	0.44	-0.091	0.003	25	0.37	-0.704	0.001	25	0.22	-0.0553	0.018
Growing season	25	0.55	0.006	< 0.001	25	0.5	0.007	0.0013	25	0.15	0.003	0.059
Winter water temperatures												
December	25	0.03	-0.036	0.0586	25	0.09	-0.01	0.452	25	0	-0.078	0.0739
January	25	0.00	0.056	0.924	25	0.03	-0.55	0.001	25	0.12	0.813	0.097
February	25	0.61	2.2	< 0.001	25	0.34	2.045	0.45	25	0.07	0.626	0.214
Drawdwon elevation	25	0.10	-0.842	0.132	25	0.07	-0.907	0.002	25	0.19	-1.026	0.029
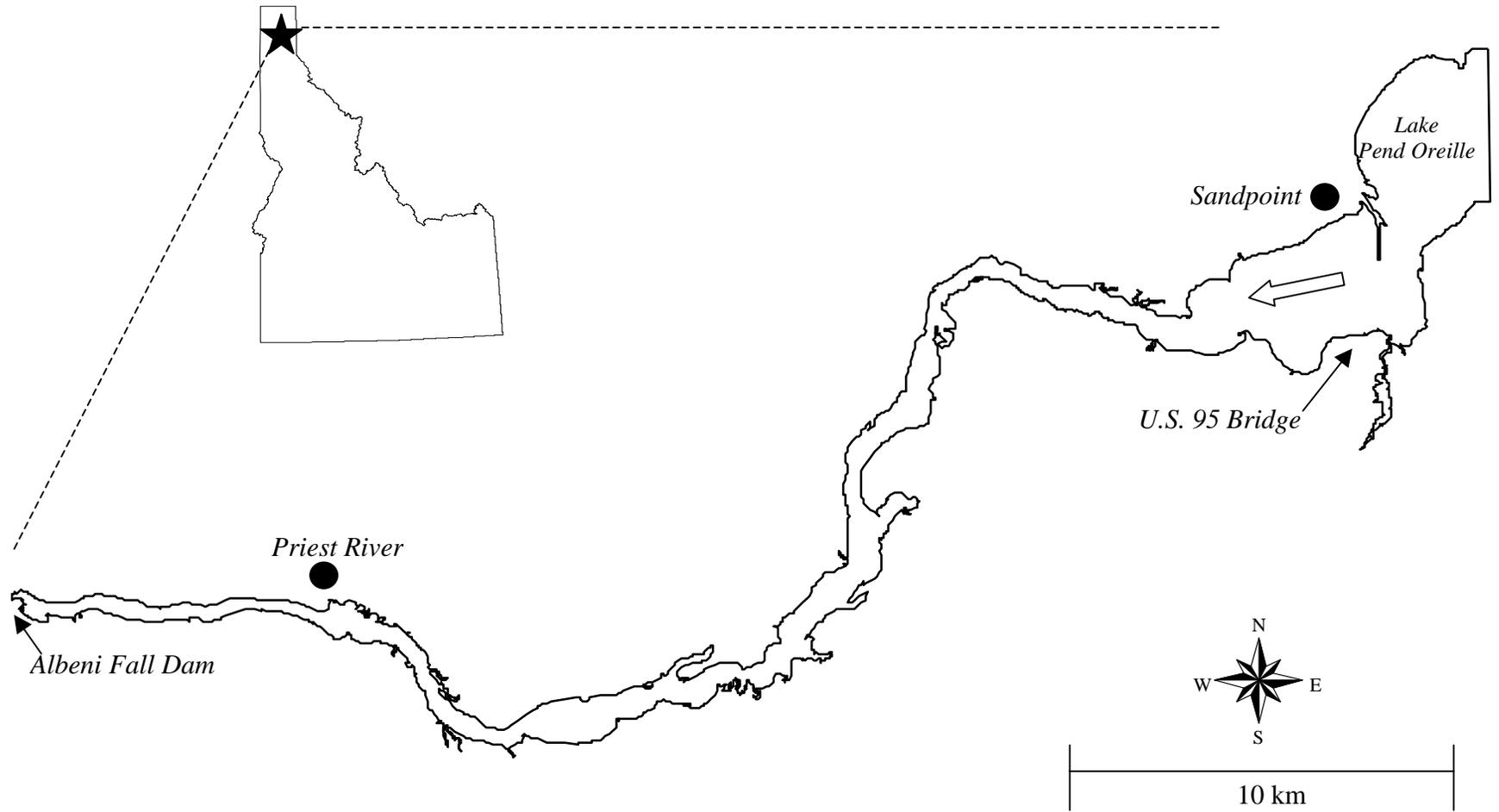
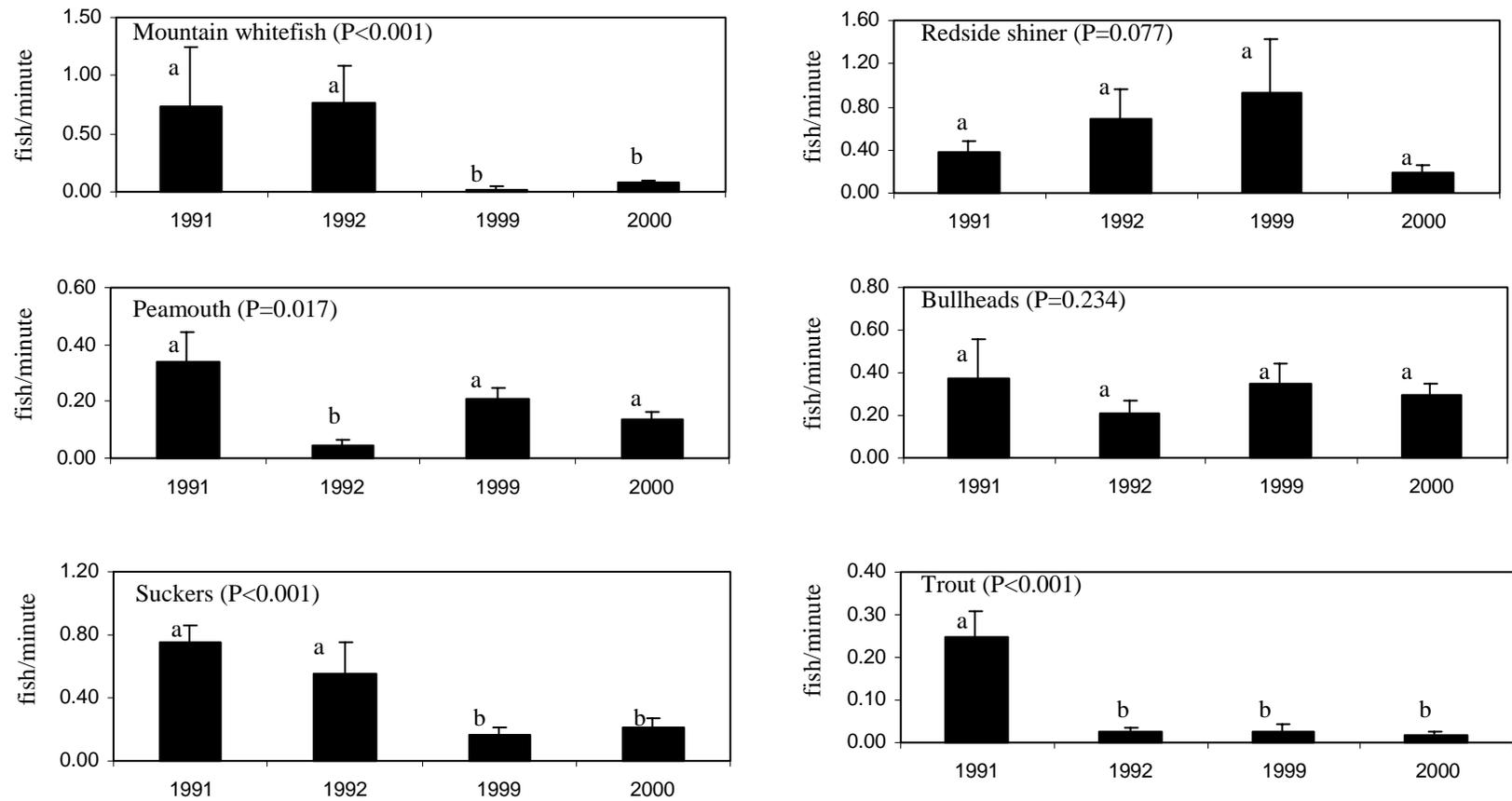Figure 1. — Study area on the Pend Oreille River, Idaho.
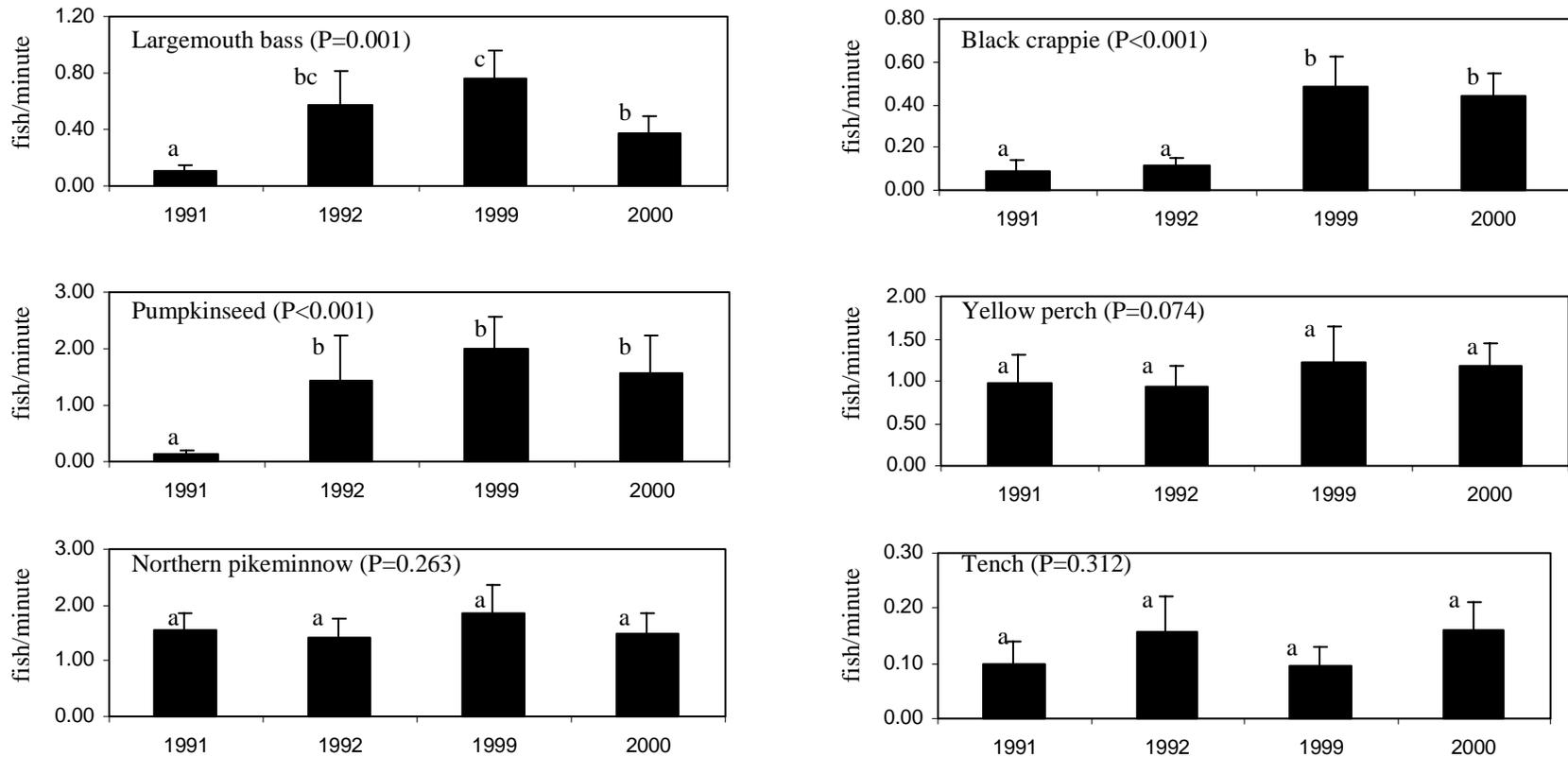
Figure 2. — Catch rates of fishes sampled by electrofishing from the Pend Oreille River before (1991-1992) and after (1999-2000) three years of higher winter water levels. Age-0 fish were not included in the analysis. Error bars represent standard error of mean CPUE. Significant differences (P < 0.05) are indicated by alphabetic superscript.
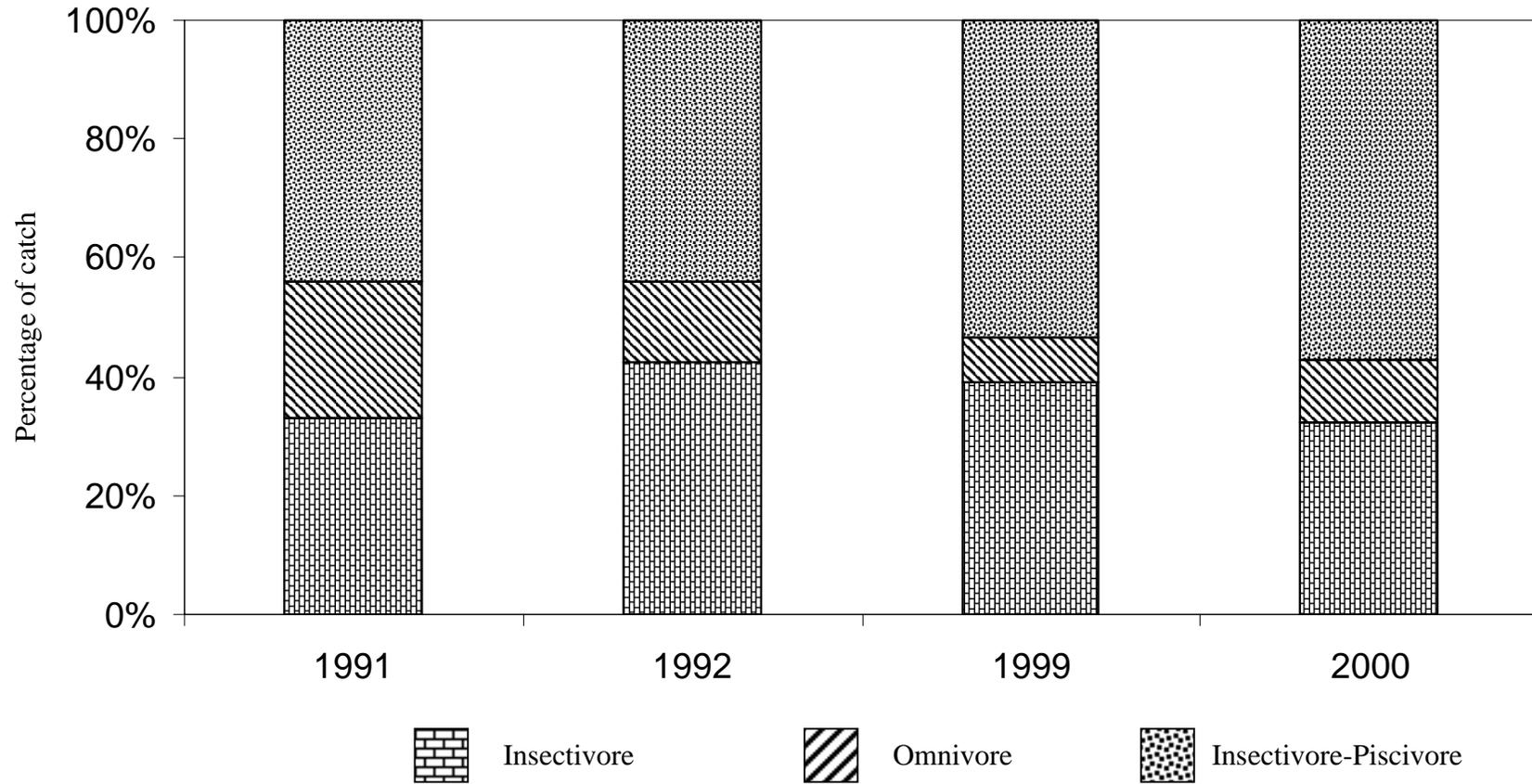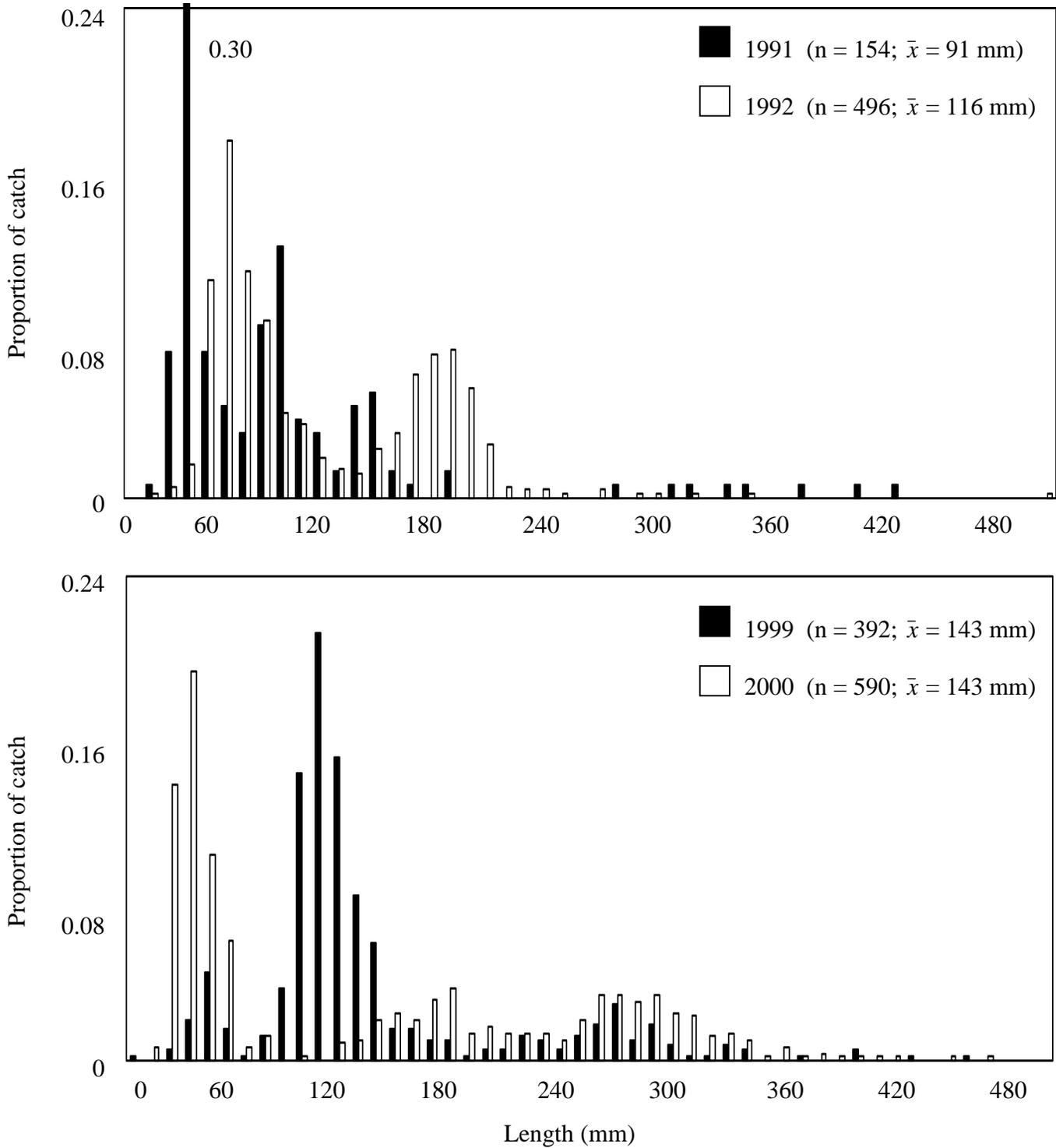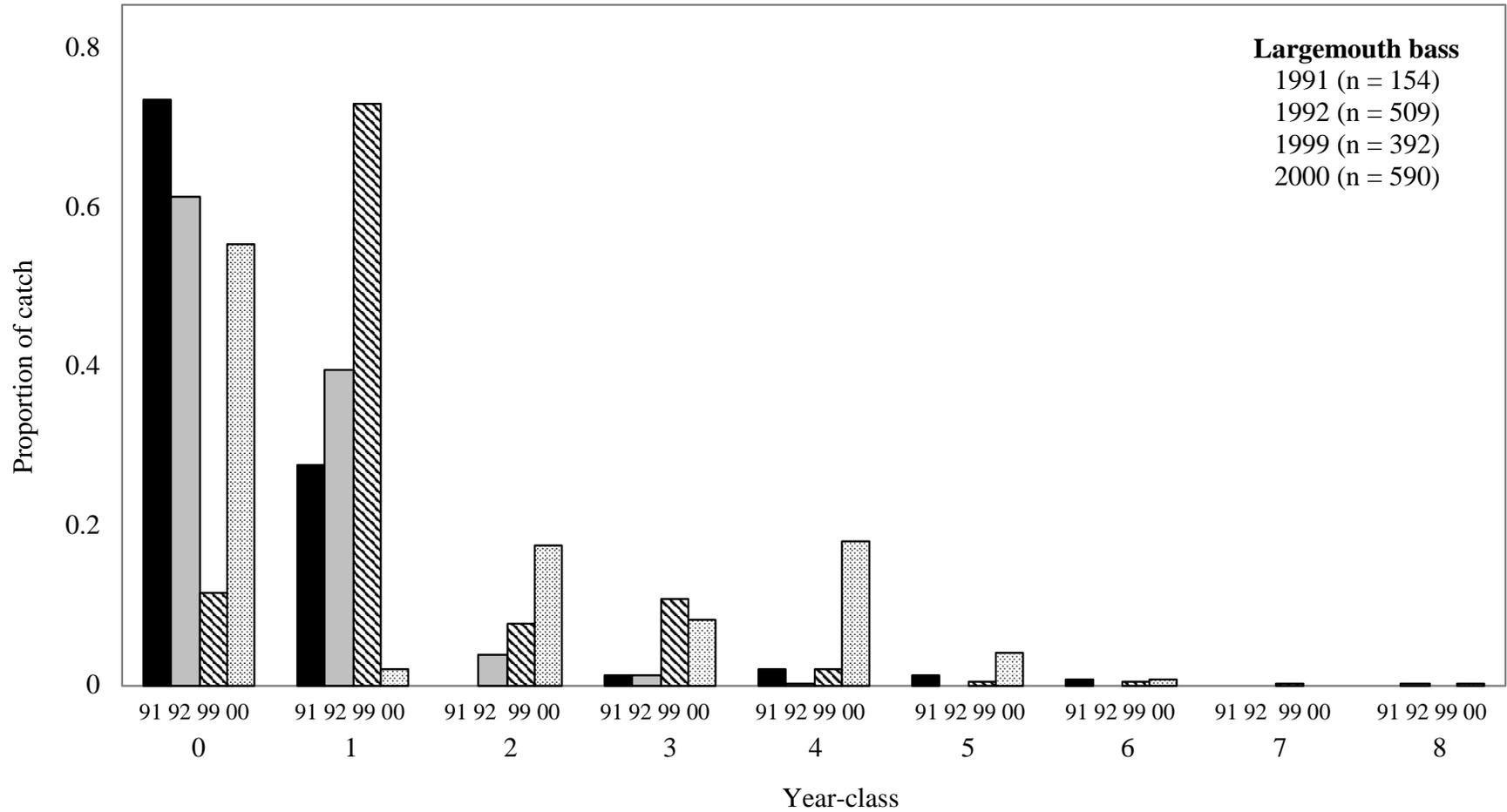
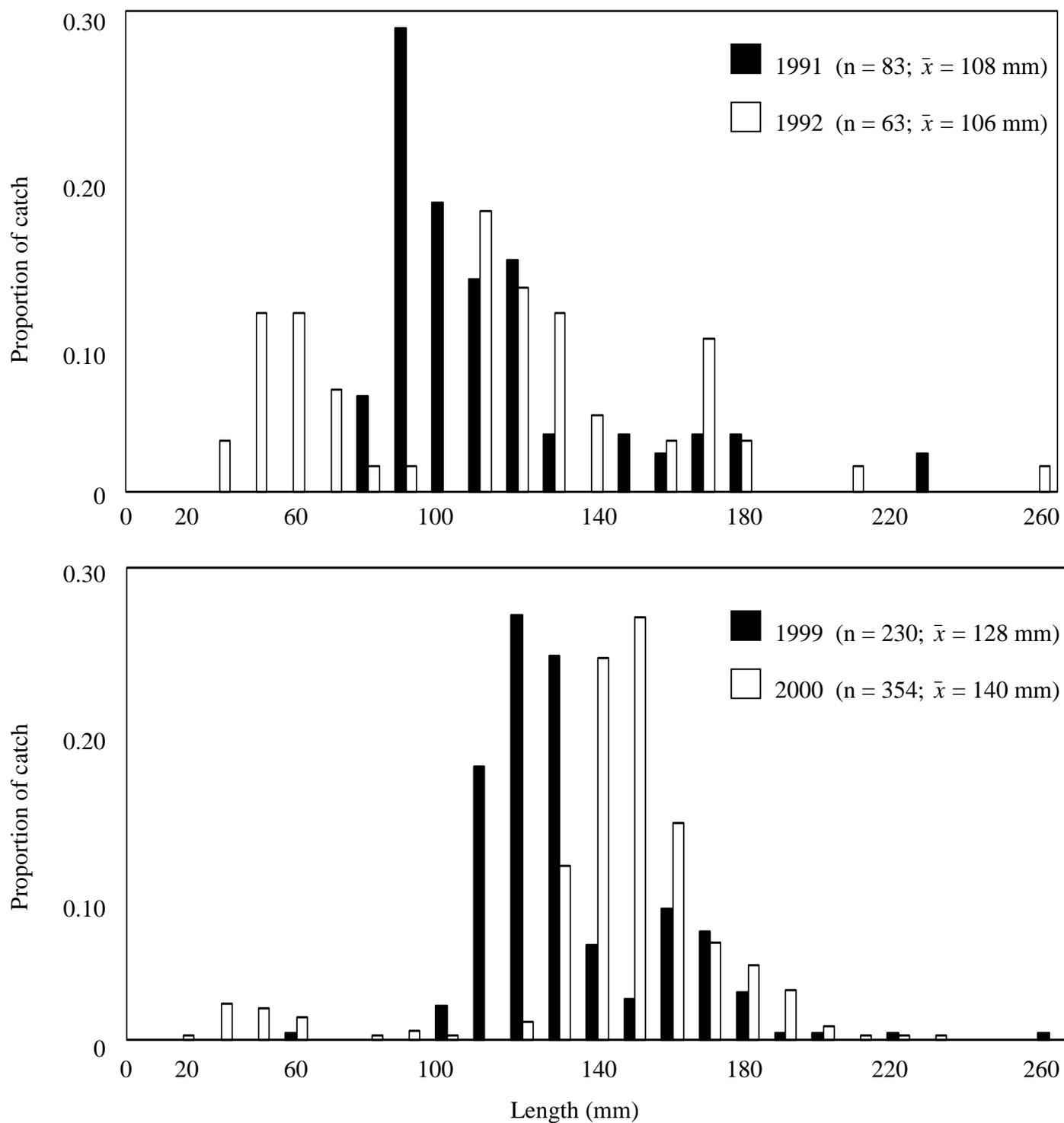Figure 3. — Catch rates of fishes sampled by electrofishing from the Pend Oreille River before (1991-1992) and after (1999-2000) three years of higher winter water levels. Age-0 fish were not included in the analysis. Error bars represent standard error of mean CPUE. Significant differences (P < 0.05) are indicated by alphabetic superscript.

Figure 4 — Percent composition of trophic groups collected in the Pend Oreille River, Idaho before (1991-1992) and after (1999-2000) three years of experimental drawdown.
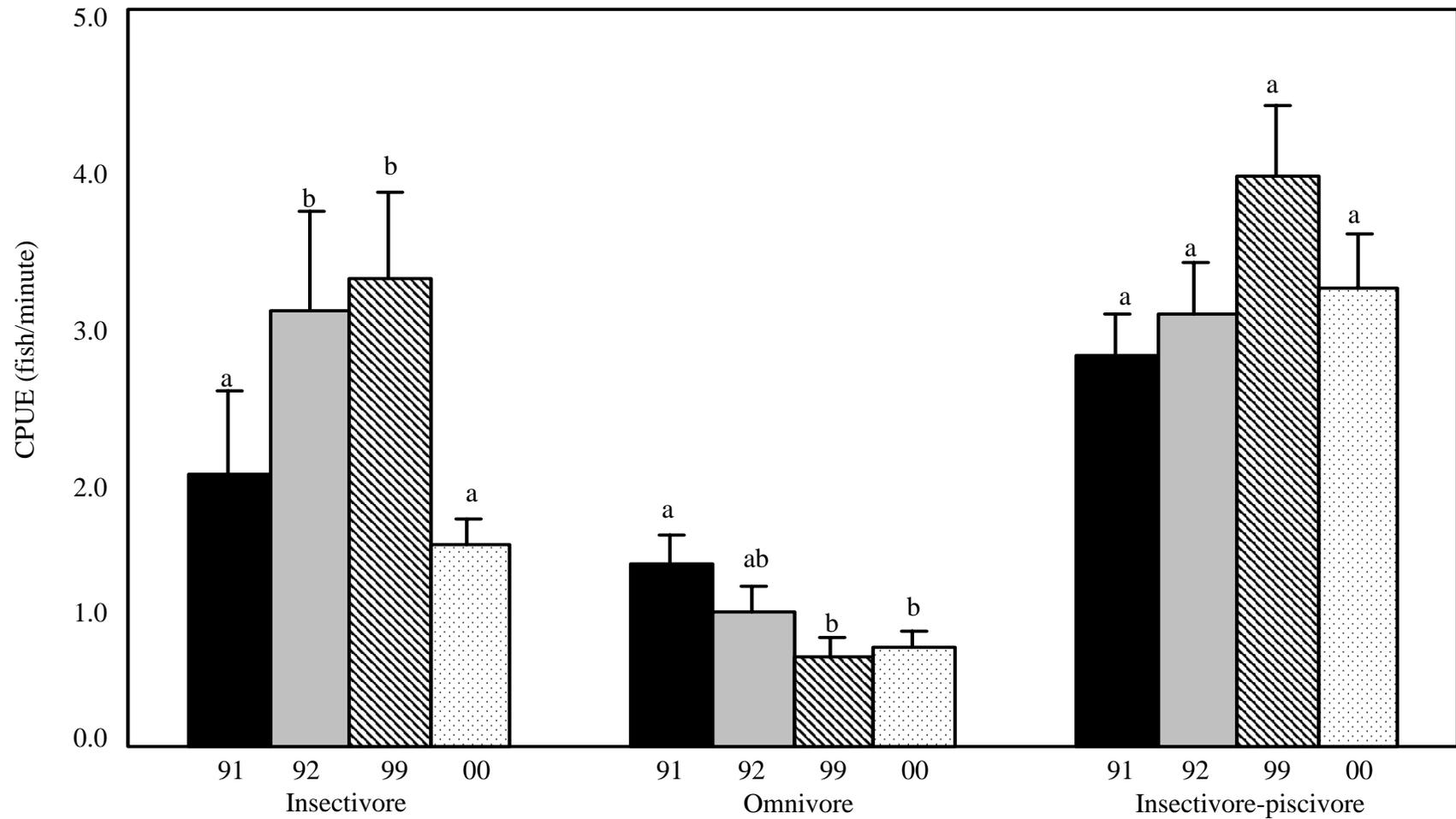
Figure 4a — CPUE of trophic groups (insectivores, omnivores and insectivores-picivores) collected from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of experimental drawdown. Error bar represent standard error of mean CPUE. Significant differences (P<0.05) are indicated by alphabetic superscripts.

Figure 5. — Length frequencies of largemouth bass collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.
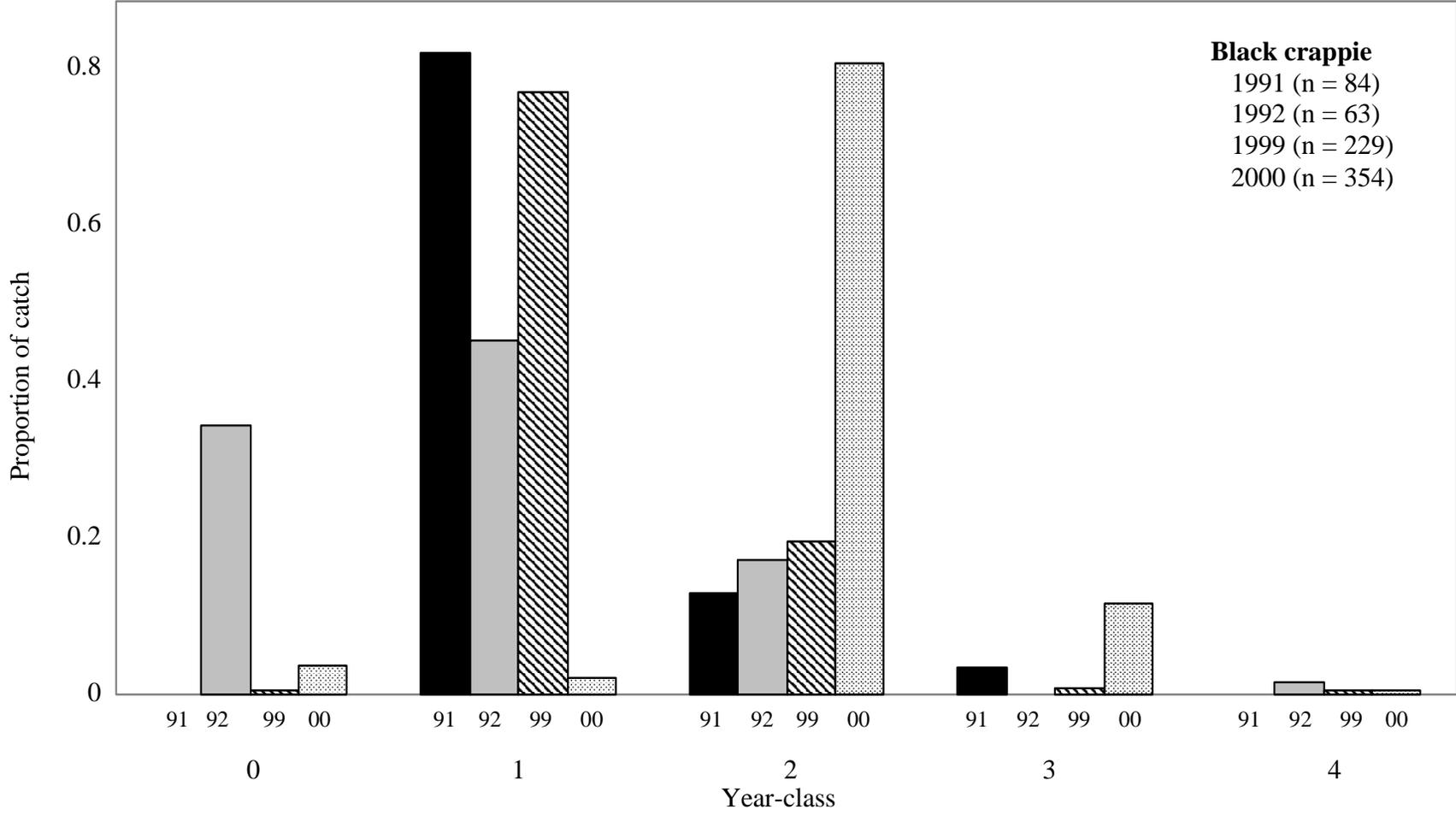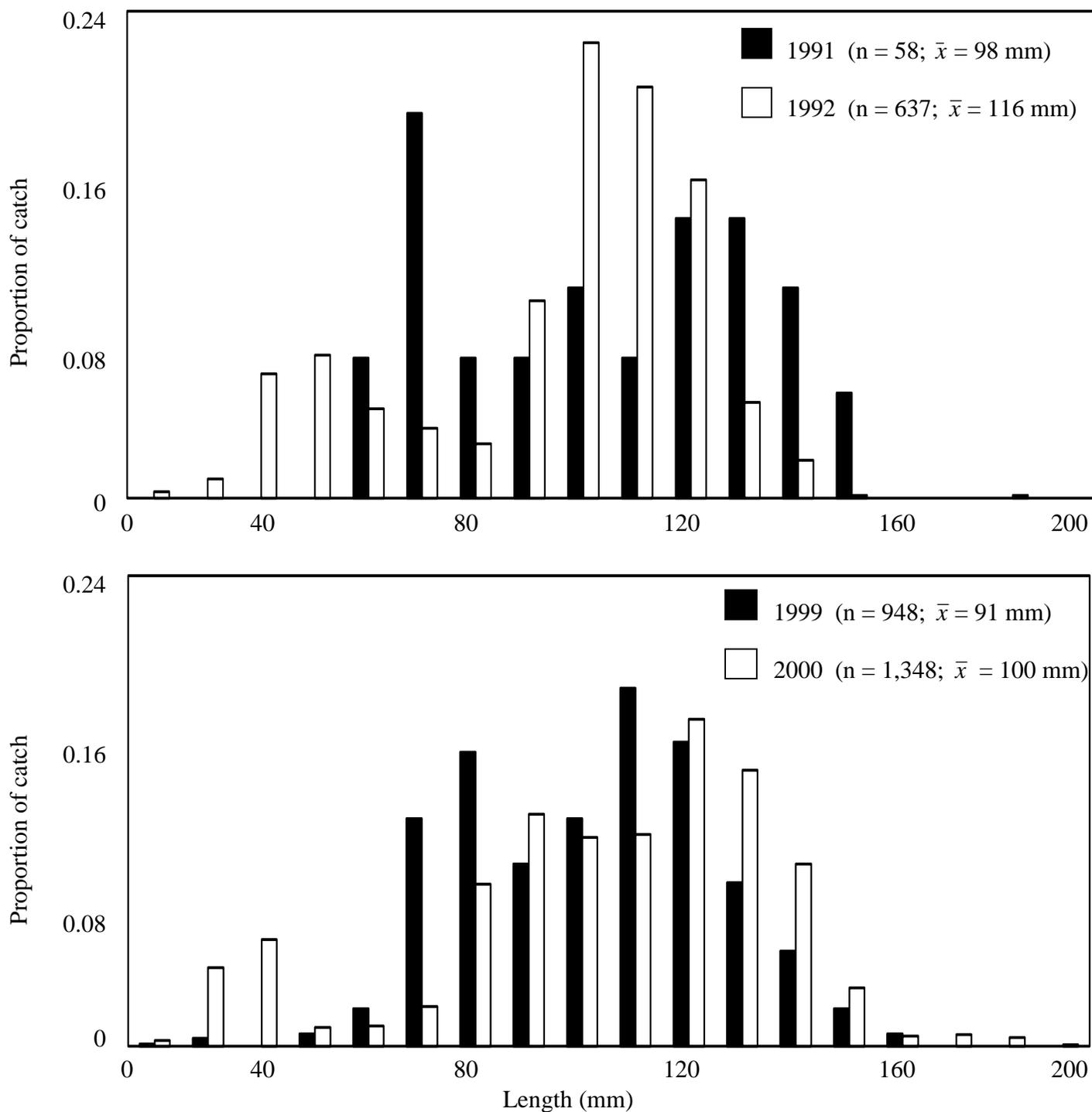
Figure 6. — Age structure of largemouth bass collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.

Figure 7. — Length frequencies of black crappie collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.
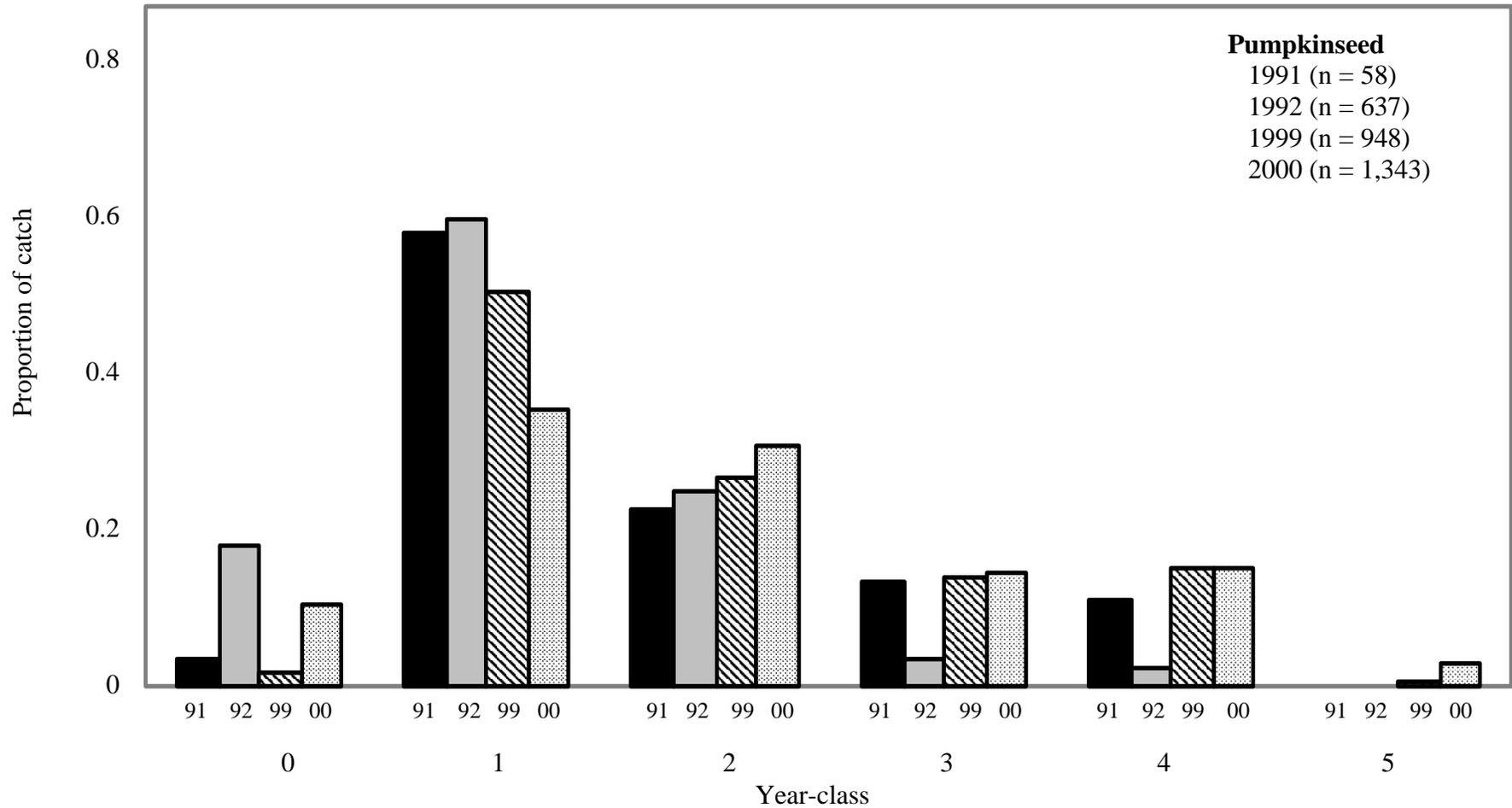
Figure 8. —— Age structure of black crappie collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.

Figure 9. — Length frequencies of pumpkinseed collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.
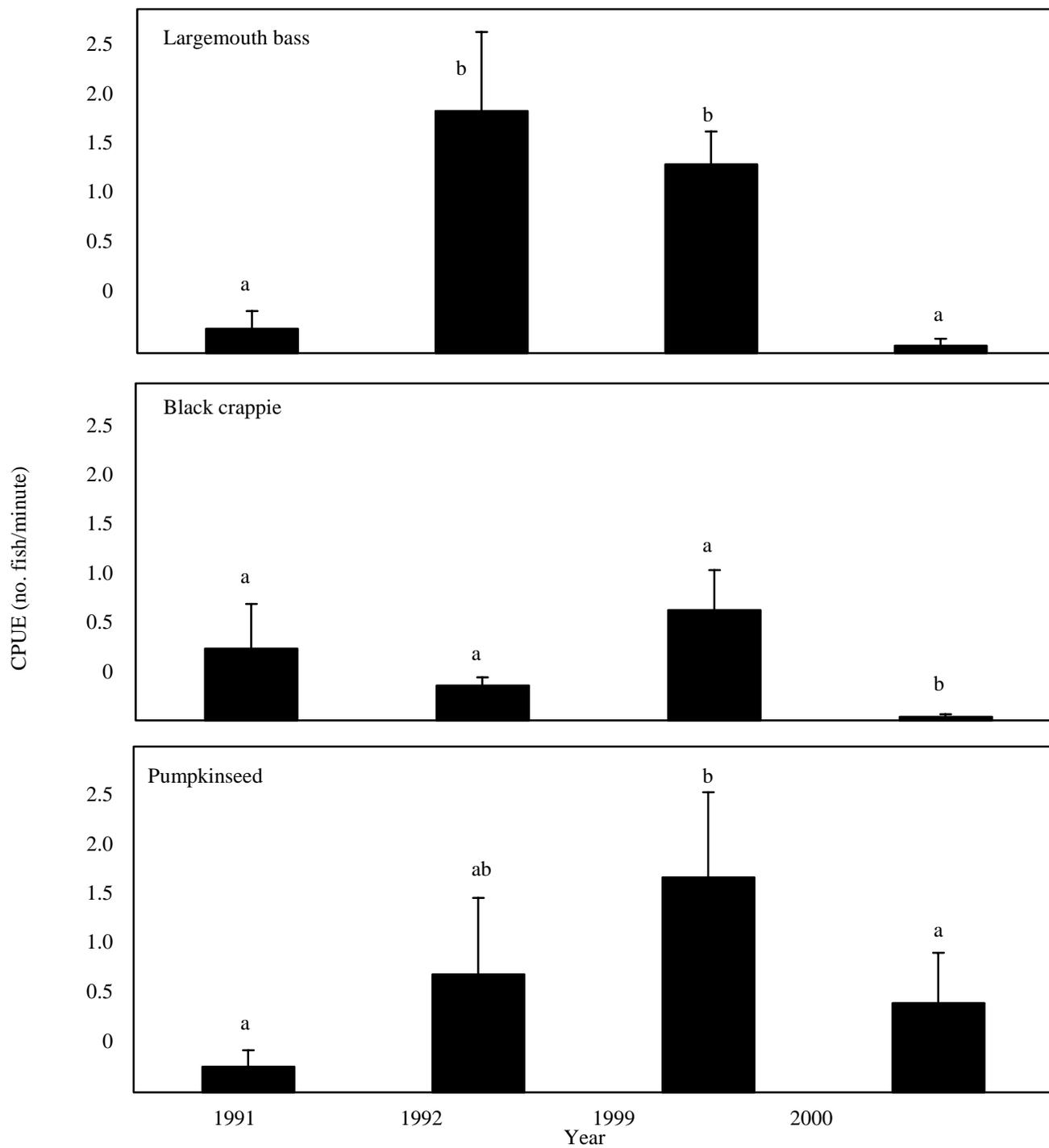
Figure 10. — Age structure of pumpkinseed collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.

Figure 11. CPUE of age-1 largemouth bass, black crappie, and pumpkinseed collected from in the Pend Oreille River, Idaho, in 1991, 1992, 1999 and 2000. Error bars represent standard error. Significant differences (P<0.05) are indicated by alphabetic superscripts.
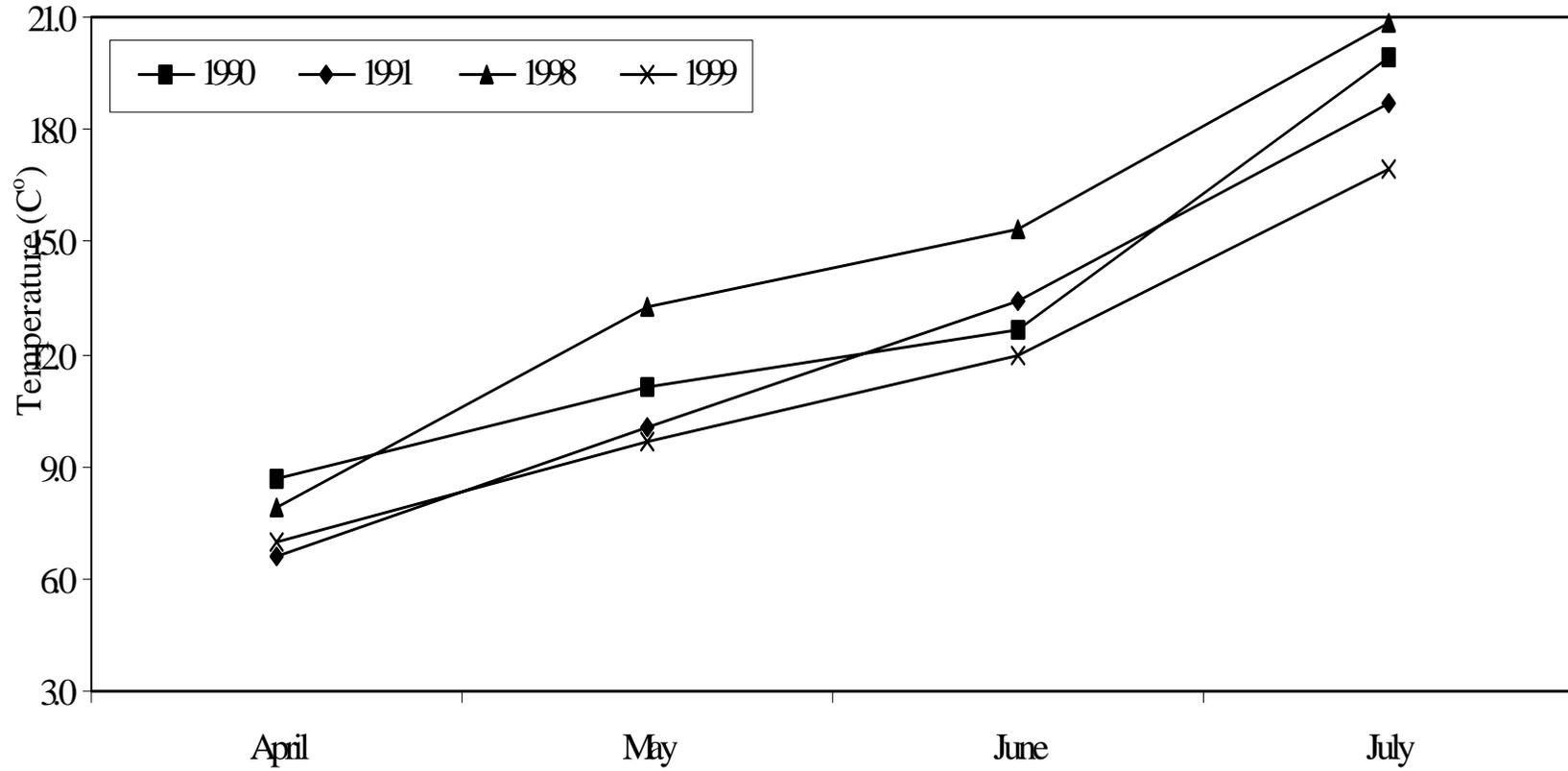
Figure 12.— Mean monthly temperatures during spring months associated with spawning activity and early juvenile development.
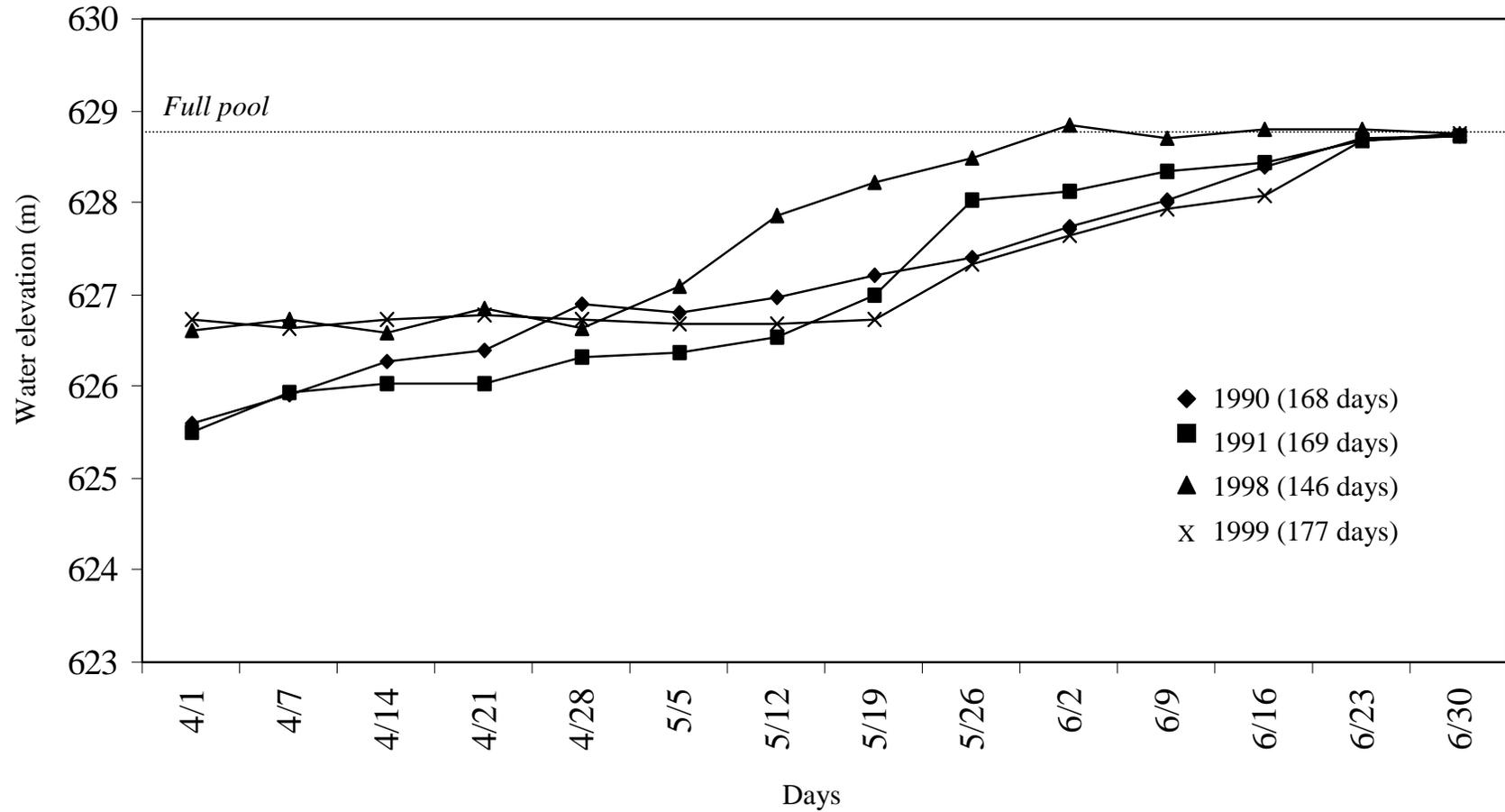
Figure 13.— Water level fluctuations during spawning and early juvenile development. Days refer to the number of days from January first to reach full pool.
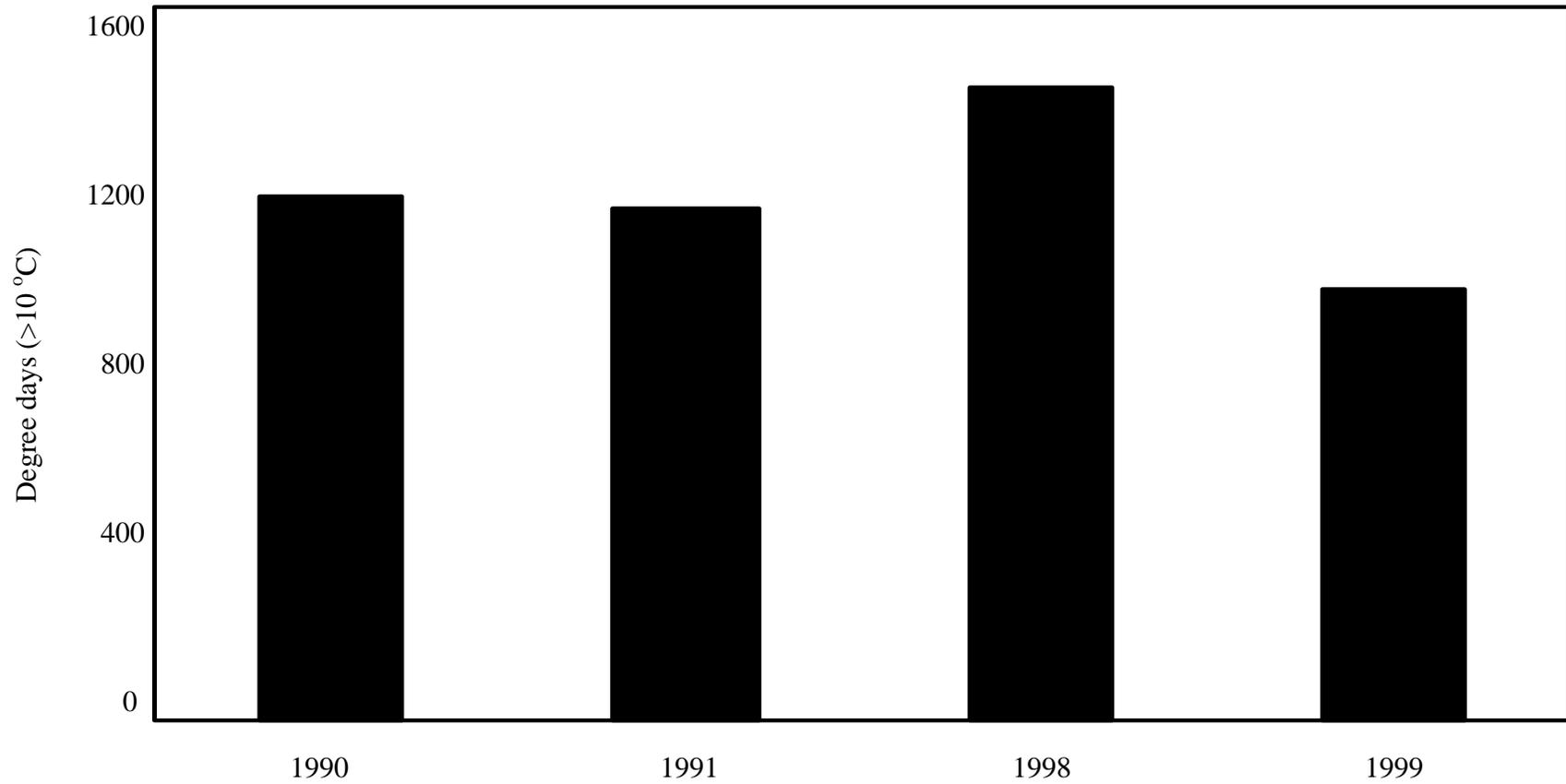
Figure 14.— Length of growing season (as determined by the number of degree-days $> 10\,^{\circ}$C) associated with the first year of life of age-1 fish.
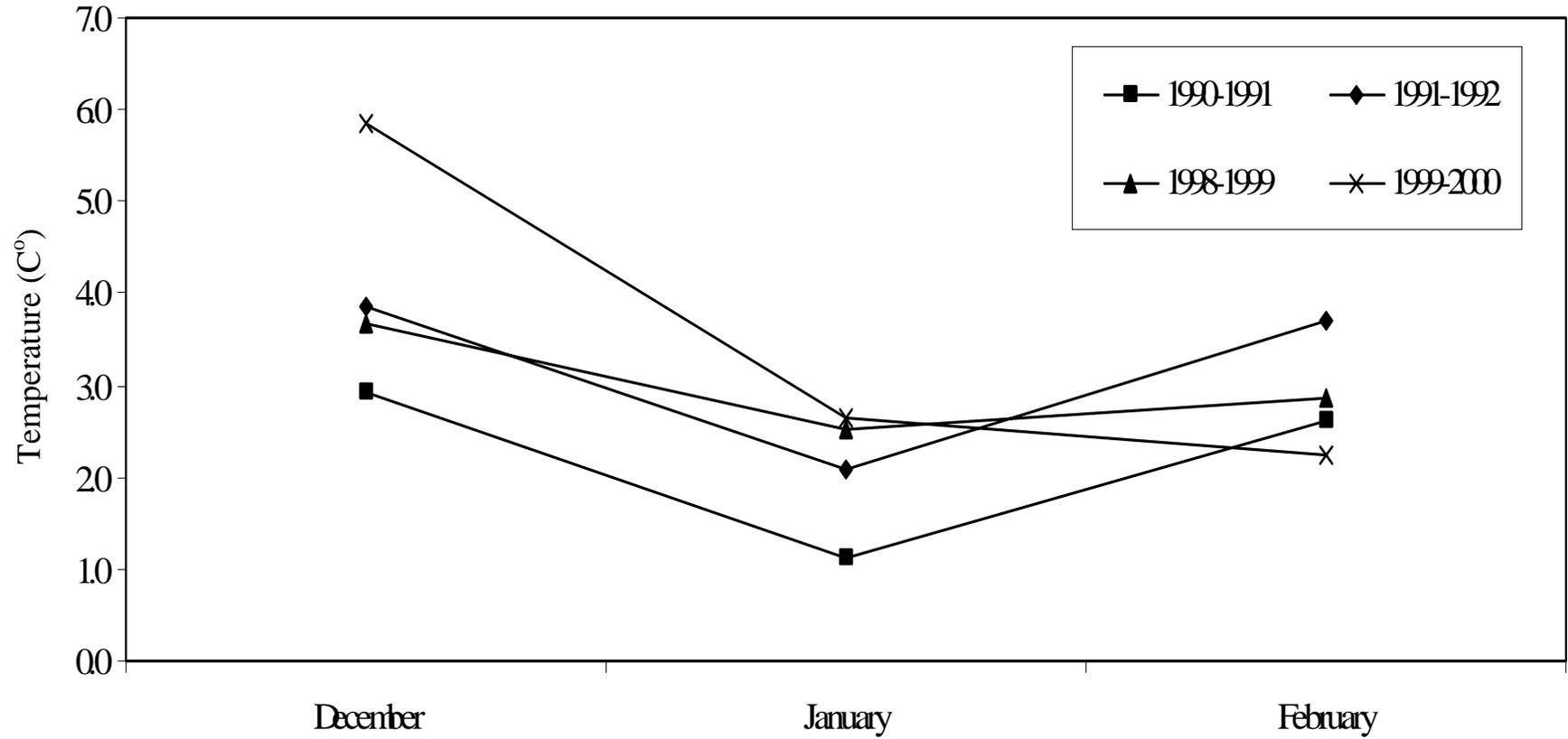
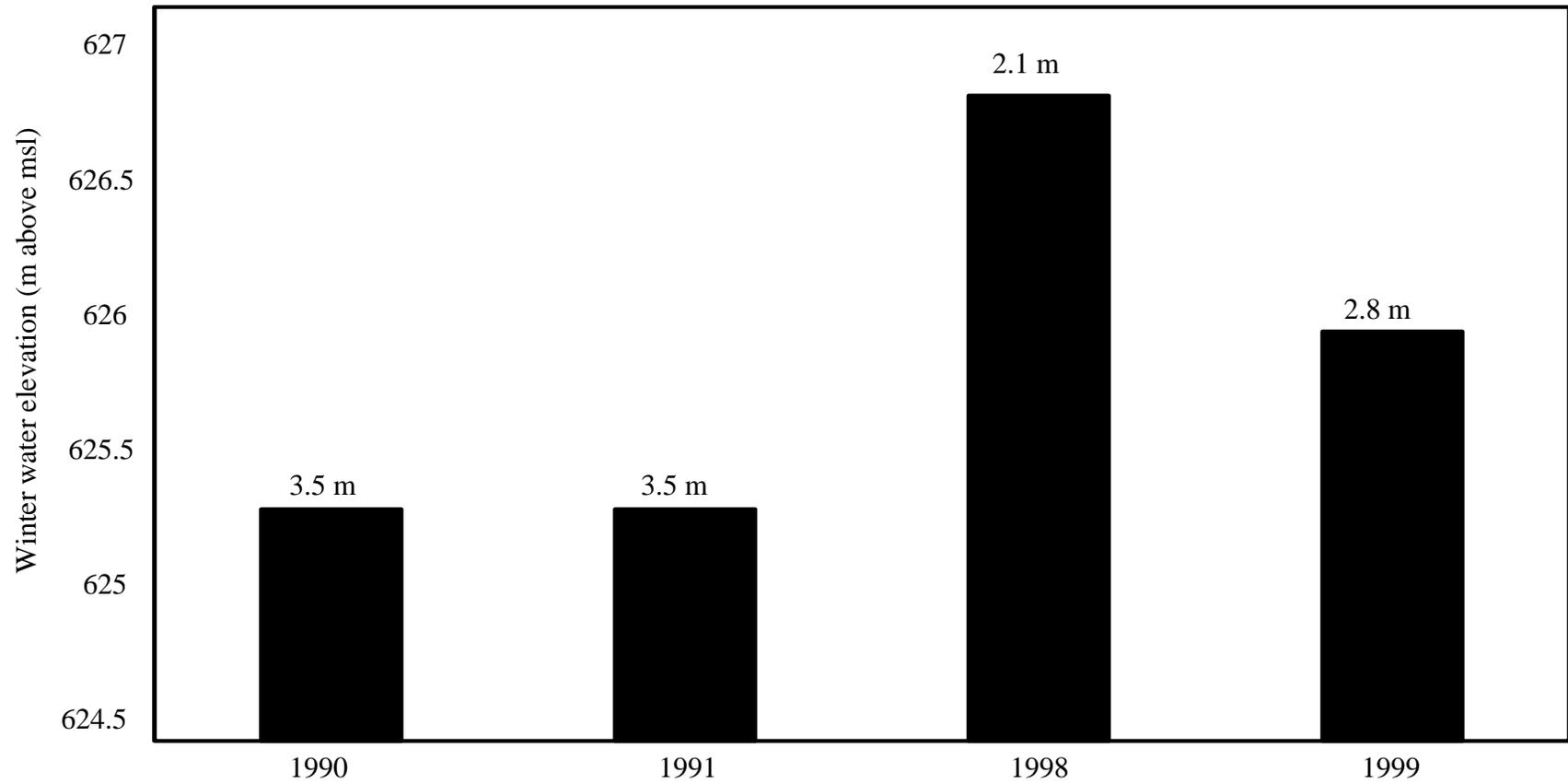Figure 15.— Mean monthly temperatures during months associated with first over-winter.

Figure 16.— Winter water elevation (m above msl) experienced with the first winter. Numbers indicate meters below full pool.

Appendix I

Fishes sampled from the Pend Oreille River, Idaho.

Kokanee salmon *(Oncorhynchus nerka)*
Rainbow trout   *(Oncorhynchus mykiss)*
Cutthroat trout   *(Oncorhynchus clarki)*
Lake trout   *(Salvelinus naymachus)*
Brown trout   *(Salvelinus trutta)*
Moutain whitefish   *(Prosopium williamsoni)*
Northern pikeminnow   *(Ptychocheilus oregonensis)*
Peamouth   *(Mylocheilus caurinus)*
Redside shinner *(Richardsonius balteatus)*
Tench *(Tinca tinca)*
Largescale sucker   *(Catostomus macrocheilus)*
Longnose sucker   *(Catostomus catostomus)*
Bridgelip sucker   *(Catostomus columbianus)*
Black bullhead   *(Ameiurus melas)*
Brown bullhead   *(Ameiurus nebulosis)*
Largemouth bass   *(Micropterus salmoides)*
Smallmouth bass   *(Micropterus dolomieui)*
Black crappie *(Pomoxis nigromaculatus)*
Pumkinseed   *(Lepomis gibbosus)*
Yellow perch   *(Perca flavescens)*

Movement and Habitat Selection of Adult Largemouth Bass Associated

with Winter Drawdown in the Pend Oreille River, Idaho

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Abstract

This paper characterizes movement and habitat selection of largemouth bass

Micropterus salmoides associated with winter drawdown, and loss of backwater

habitat in the 3,887 ha impounded section of the Pend Oreille River, Idaho. Twenty

adult largemouth bass (> 300 mm total length) were captured in a 30-km section of

reservoir, surgically implanted with radio transmitters, and monitored biweekly from

September 1999 to June 2000. Habitats available to largemouth bass under

drawdown conditions were separated into seven categories based on water depth,

velocity, presence of cover and orientation to the main river channel, and quantified

using Geographic Information System (GIS). In the fall, largemouth bass exhibited a

shift from backwater habitat to shoreline areas along the main river channel in

response to lowering water levels, however movement into over-wintering areas did

not occur until early November, when drawdown was near completion and water

temperatures were below $10\,^{\circ}$ C. Two primary over-wintering areas (combined area

102.1 ha) contained 95 % of the largemouth bass monitored (n=19) from November

to mid-March. Some fish traveled up to 16 km to winter in this area. Over-wintering

areas were protected from main river currents, but were located outside of traditional

backwater habitat, possibly to avoid cooler water temperatures in the back water

habitat. Aquatic vegetation in 1-3 m of depth was associated with 90.2 % of the

winter locations of largemouth bass, and was the most selected winter habitat. Our

analysis suggests that largemouth bass were selecting not only specific habitat

characteristics, but also a specific geographic area.

Introduction

Lowering water levels during winter is common in many dammed large river complexes to maximize power generation and prevent flooding. The implications of these practices, however, can adversely affect off-channel areas that function as essential over-wintering habitat for many riverine fishes (Greenbank 1956; Pitlo 1992; Sheehan et al. 1990; Raibley et al. 1997). Winter drawdowns can directly influence winter habitat through de-watering and exposure of off-channel areas, forcing fish to seek alternative winter habitat or over-winter in less suitable conditions associated with the main river channel (Pilto 1992). Indirect effects of winter drawdown are related to a reduction in water depth. Shallow backwaters are especially susceptible to oxygen depletion during periods of extensive snow and ice cover (Mathias and Barica 1980), and can often reach water temperatures near $0\,^{o}$ C. Large or untimely water level fluctuations during the winter may also trap fish in backwaters, and can lead to fish kills (Greenbank 1956). Winter survival of centrarchid fishes in riverine environments has been linked to the accessibility and quality of backwater habitat (Greenbank 1956; Carlson 1992; Pitlo 1992; Hatch 1991).

The Pend Oreille River, Idaho has been subjected to winter drawdown conditions that severally limit access to side channels and backwaters previously identified to be important winter habitat for centrarchid fishes. Recent concern over improving the warmwater sport fishery in the river has prompted a series of investigations designed to better understand the relation between drawdown conditions and over-winter survival. As a part of this research, a radio telemetry

study was conducted to evaluate the winter behavior and habitat selection of fish in response to winter drawdown conditions in the reservoir. Knowledge of winter habitat needs is important because it can be used to influence decisions concerning water level management and improving the warmwater sport fishery.

The specific objectives of this study were to:

1. Describe movement and habitat selection of largemouth bass associated with winter drawdown conditions in the Pend Oreille River, Idaho; and

2. Evaluate the role of winter water elevations in the selection of over-wintering habitat by largemouth bass.

Study Area

The Pend Oreille River begins at the outlet of Lake Pend Oreille, which is located in the northern Idaho at an elevation of 628.5 m (2061 ft) above mean sea level (Figure 1). Our study area was the upper portion of the river, extending from Albeni Falls Dam upstream 44.25 km to the U.S. Highway 95 bridge near the City of Sandpoint, Idaho. This section of river is operated as a run-of-the-river reservoir, with flows ranging seasonally from 617 to 2,044 m^3 (11,200-73,000 cfs). At full pool, the surface area is approximately 3,887 ha, the maximum depth is 48.5 m, and the average depth is 7.1 m (Dupont 1994). About 161 km of the shoreline, including sloughs and islands, has a gentle to moderate slope consisting mostly of fine sediments (< 4 mm), while about 16 km of shoreline is rocky, consisting of rip-rap (DuPont 1994). Aquatic macrophytes, mainly *Potamogeton spp.* and *Myriophyllum sibiricum* are abundant along the shoreline in many areas (Wagner 2000).

Six major backwaters occur in this section of the Pend Oreille River: Riley Creek Slough (Rkm 18.2), Hoodoo Creek Slough (Rkm 19.0), Tanner Creek Slough (Rkm 21.7), Cocolalla Slough (Rkm 23.2), Morton Slough (Rkm 25.4), and Gypsy Bay (Rkm 31.6; Figure 1). These areas are isolated from main river currents, have relatively shallow water depths (from 2 to 3.8 m), and contain heavy growths of aquatic macrophytes. Prevalent warmwater fishes, including pumpkinseed Lepomis gibbosus, largemouth bass, black crappie Pomoxis nigromaculatus, and yellow perch Perca flavescens, are typically found in high abundance in these adjacent areas (Dupont 1994). These areas were suspected to provide suitable winter habitat if winter water levels were increased.

Waters upstream of Albeni Falls Dam are evacuated annually from late fall to early spring for flood control and winter electrical generation (Dice 1983). During this study, drawdown began on 19 September and continued through 3 November 1999, at a mean rate of about 4.5 cm/day (Figure 2). Water levels were maintained at a target elevation of 625.8 m (2052 ft) from November to May, approximately 2.9 m lower than full pool elevation 628.5 m (2061 ft). Under this drawdown regime, Hoodoo Creek Slough, Gypsy Bay, and Riley Creek Slough were completely dewatered, and of the remaining three backwaters, only Morton Slough maintained water depths near 1.5 m. Spring refill began 5 May and reached full pool on 15 June 2000, at a mean rate of about 5.3 cm/day.

Methods

Data Collection

Winter movement patterns and habitat use of largemouth bass were determined throughout the study area using radio telemetry. Twenty adult largemouth bass were captured from 29 August through 19 October 1999 using boat electrofishing and angling (Table 1). Captured fish were anesthetized (MS-222), measured for total length (mm) and weight (g), and surgically implanted with a 17 by 40 mm (17 g dry weight) radio transmitter (model 5902, Advanced Telemetry Systems, Inc., Isanti, Minnesota) following similar techniques described by Ross and Kliner (1982), and Hart and Summerfelt (1975). Each transmitter was equipped with a braided wire antenna and coated with clear waterproof epoxy resin. Transmitters contained 3.0 V lithium batteries with a 300-d capacity, and each operated on a unique frequency between 151-152 MHz. Following surgery, largemouth bass were tagged with a serially numbered Floy [tm] tag for external identification, and returned to a holding tank until recovery, usually 10-20 minutes. Fish were released at the site of capture.

Each fish was contacted at least every 2 weeks through June of 2000, following a 7-day acclimation period (Guy et al. 1992). Radio-tagged fish were located using a boat equipped with a fixed signal receiver (model FM 1470, Advanced Telemetry System, Inc., Isanti, Minnesota), and a four-element 1.2 m yagi antenna. A hand-held directional antenna was used once in the general vicinity of a fish to determine its definitive location (< 2 m). Fish locations were recorded in Universal Transverse Mercator (UTM) coordinates using a global positing unit (GPS)

with an external antenna (Trimble Geoexplorer II). Date, time of day, water temperature ($^\circ$C), total depth (m), velocity (cm/sec), dissolved oxygen (DO; mg/L), turbidity (NTU), distance to nearest shore and cover type were also recorded at each contact point. Location files along with habitat parameters were downloaded to a computer, differentially corrected, and imported into ArcView v.3.2 (Environmental Systems Research Institute, ESRI) for analysis.

Habitats available to largemouth bass under winter drawdown conditions were determined from maps describing water depth, velocity, and presence or absence of aquatic macrophytes. Maps of water velocity and aquatic macrophytes were produced from field measurements collected during December 1999 and January 2000, while water depth was determined using a bathymetric contour map obtained from United States Geologic Survey (USGS 1996). All data collected on habitat variables were imported into ArcInfo v.7.2.1. and ArcView v.3.2. (ESRI) for spatial analysis.

Mean daily water elevations were obtained from the U.S. Army Corps of Engineers through readings at the Hope recording station on Lake Pend Oreille. Water temperature was recorded hourly at two permanent stations (main river channel and backwater; Figure 1) using three temperature loggers (model RIM 200, Ryan Instruments, Inc., Redmond, Washington) suspended at bottom, mid-depth, and surface positions.

Data Analysis

Minimum winter migration distance was calculated for each radio tagged fish as the linear distance from the location of initial capture to that of its preferred over-wintering area. Distance traveled was calculated using the Animal Movement extension in ArcView (ESRI 1997). This is a minimum distance of movement because fish were not monitored continuously.

Areas that remained wetted following the completion of winter drawdown and maintained water velocity < 1 cm/sec were deemed available to over-wintering largemouth bass as recommended by Winter and Ross (1982). Observations of use and availability were divided into seven habitat categories based on water depth, presence or absence of aquatic macrophytes, and orientation to the main river channel. These categories included: vegetated-shallow depth (0 - 1 m), open water-shallow depth, vegetated-medium depth (1 - 3 m), open water-medium depth, vegetated-deep depth (3 - 5 m), open water-deep depth, and backwaters (open water and vegetated, 0 - 1.5 m).

To determine the availability of each habitat category within the study area, a composite map was generated by logically overlaying the three habitat maps (water depth, velocity, and vegetation) and a shoreline reference map using the map-calculator command in ArcView v.3.2. (ESRI). Largemouth bass use of each habitat category was evaluated by overlaying a map of fish locations on the composite map delineating each habitat category. For each fish, the number of observations within each habitat category was then enumerated, and a chi-square test of independence ($\alpha = 0.05$) was used to test whether all fish were selecting similar habitat types.

Compositional analysis (Aebischer et al. 1993) was used to test whether largemouth bass selected over-wintering habitat categories in proportion to their availability. For this analysis, the number of observations within each habitat category was compared with the expected number given a random distribution of observations in each habitat category (H_o: use = availability). If a significant difference were detected, a pairwise t-test was used to rank the habitat types by relative use. All calculations were preformed using Resource Selection v.1 (Leban 1999), and only contacts made during the period between November and mid-March were used to determine winter habitat selection.

Results

Movement and Behavior

We radio tagged 20 adult largemouth bass within a 30-km section of the Pend Oreille River, in both backwater and main river habitats (Figure 3). A total of 381 locations were obtained from 19 largemouth bass from 2 October 1999 to 2 June 2000 (Table 1). The mean number of observations was 20/fish (range 14 - 26), and fish were tracked over an average of 246 d (range 170 - 276). No signals from one largemouth bass (no. 073) were ever received following release, and we assumed the radio tag was defective. We observed no emigration of fish outside the study area over the duration of this study.

Largemouth bass exhibited a shift from backwater habitat to shoreline areas along the main river channel coinciding with drawdown. Early attempts to capture largemouth bass were difficult, because larger fish appeared to be distributed over the study area. Consequently, only 10 largemouth bass were radio tagged prior to the initial drawdown in September. Of these, five were initially captured in backwater habitat. Following the onset of drawdown, these fish moved into deeper shoreline areas along the main river channel, but remained in the general vicinity of their original capture location. Further collections of largemouth bass for radio tagging also reflect this shift away from off-channel areas, as only three of the remaining 10 largemouth bass were captured in backwater habitat. By mid-October, when tagging was completed, all experimental fish were located outside of adjacent backwaters, but remained distributed throughout the study area. Movement towards over-wintering

areas and away from initial capture locations began in late-October as water temperatures in the main river channel decreased below $10\,^{\circ}$C, and winter drawdown was near completion.

On 4 November, 18 of 19 (95 %) largemouth bass were located in one of two primary wintering areas (PWA; Figure 4). The upper PWA (49.3 ha) was located along the shoreline immediately down-river of Gypsy Bay, while the lower PWA (52.9 ha) was located from the mouth of Morton Slough down-river to Tanner Creek Slough (Figure 4). Both areas were characterized as having zero water velocity, a gentle sloping bottom with a mean water column depth of 2 m and dense aquatic macrophtye growth. Of the 18 largemouth bass that wintered in these areas, all but one remained until early spring. In mid-January, one fish (no. 053) moved out of the upper PWA, and was located up-river 4.8 km along the south shoreline, where it remained until spring refill. The only experimental fish (no. 135) that over-wintered outside the PWA complex was located along the south shoreline at Rkm 13.5, where it remained for the duration of winter. Habitat characteristics where this fish over-wintered were similar to those found in the PWA.

Some fish traveled extensive distances to over-winter in the PWA (Table 1). One fish (no. 294) traveled from its initial capture site at the mouth of Priest River (Rkm 8.0), up-river at least 16 km. Two other fish (nos. 035 and 153) moved at least 10 km down-river, and traversed the main river channel before entering the lower PWA. Those fish initially captured near Morton and Cocolalla sloughs generally traveled under 2 km (Table 1). Although we were unable to follow the daily

movement of largemouth bass migrating to over-wintering areas, it appeared that most fish moved along the shoreline in the lowest water velocity.

Two general trends of largemouth movement occurred once in the over-wintering areas. One group (n = 9) remained relatively sedentary, especially once water temperature deceased below 6 $^{\circ}$C in December. These fish were repeatedly contacted in the lower PWA near the mouth of Morton Slough within an area less than 15 ha. Fish in the other group (n = 9) remained more active. For example, over a 3-day period in early January, at water temperatures approximately 3 $^{\circ}$C, fish no. 035 moved from the mouth of Morton Slough (lower PWA) up-river a minimum of 3.9 km to shoreline outside of Gypsy Bay (upper PWA). During this same 3-day period, another fish (no. 114) moved 5.1 km from outside of Morton Slough down-river to the mouth of Tanner Creek Slough. This pattern of movement between areas within PWA was observed throughout the winter, and did not appear to be affected by water temperature. However, movement was confined to areas protected from water velocity.

Temperature and dissolved oxygen (DO) profiles within the PWA indicated stratification did not occur during winter 1999-2000, as temperatures only differed from the top to the bottom by 0.1 to 0.5 $^{\circ}$C and dissolved oxygen consistently remained higher than 12 mg/l. By mid-December ice formed in backwaters and along shoreline areas of the upper and lower PWA, and remained until early March. Largemouth bass were frequently contacted under the ice, but remained in areas outside of defined backwaters. We found no indication of hypoxic conditions as a

result of ice cover along the main river or backwater habitat (measurements of DO taken under the ice ranged from 8.5 to 14.5 mg/l).

Movement away from the PWA complex began in mid-March when water temperatures in existing backwaters increased beyond those in the main river (Figure 2). On 13 March, we discovered three largemouth bass (nos. 193, 674, and 733) had moved from the lower PWA into Morton Slough. By 25 March, all the experimental fish that over-wintered in the upper and lower PWA were located in adjacent backwaters that remained accessible following drawdown. The majority of these fish (n = 15) were located in Morton Slough, however fish no. 773 was located in Cocolalla Slough, and fish no. 114 was located in Tanner Creek Slough. Fish no. 135 that wintered down-river from the PWA was also found in a shallow inlet near its over-wintering location. From March to April, mean water temperatures in backwaters increased from 7.5 to 15 ^{o} C, and remained about 3 ^{o} C warmer than the main river (Figure 5). During this period, all fish were close to shore in waters < 1 m in depth, and in no detectable cover. All experimental fish that moved into backwaters in March remained in these areas until spring refill in May.

During spring refill, tagged largemouth bass redistributed throughout the study area, but were typically located in reinundated backwaters. Of the 12 fish located following the completion of spring refill in June, nine had returned to areas where they were originally captured. For instance, largemouth bass no. 294 returned 16 km down-river to within a few meters of its original capture site. Similarly, fish no. 153 returned to its original capture site approximately 10 km up-river. The majority of fish initially captured near Morton Slough remained in the general area,

however, two largemouth bass (nos. 095 and 773) moved beyond the main river boundary via connecting culvert into the principal water body of Cocolalla Slough.

Winter Habitat Selection

A drawdown of 2.9 m in the Pend Oreille River in winter 1999 reduced the total surface areas by about 11.3 %, and exposed approximately 423 ha of shoreline. Under these conditions, the most frequently occurring habitat types available to largemouth bass were (1) open water-medium depth (1 – 3 m; 52.9 % of the available area), and (2) vegetated-medium depth (23.5 % of the available area; Table 2). Areas defined as vegetated-deep depth (3 - 5 m) accounted for the least amount of available habitat (1.4 %).

Largemouth bass selected proportionally similar habitat types ($\chi^2 = 53.54$, P = 0.49) during the winter, and were therefore pooled to determine habitat selection. Of the 225 fish contacts made from November to mid-March, 202 (90.2 %) were located in habitats defined as vegetated-medium depth (1 - 3 m), which was only 23.5 % of that available. In contrast, only 17 (7.6 %) contacts were made in open water-medium depth, despite this habitat accounted for 52.9 % of available habitat. Observations in areas defined as open water-shallow depth (0 - 1 m) and vegetated-shallow depth each accounted for 1 % of that used. Fish were not observed wintering in vegetated-deep depth (3 - 5 m), open water-deep depth (3 - 5 m) or backwaters, or outside areas defined as available (*i.e.* areas with water velocity > 1 m/sec).

Compositional analysis indicated that overall habitat use was clearly nonrandom ($\chi^2 = 128.9$; P < 0.0001). A pairwise comparison t-test indicated that

largemouth bass selected vegetated-medium depth habitat significantly higher than all other habitat types (P < 0.0001), and was therefore ranked 1 (i.e. most selected; Table 3). We found no significant difference between use of habitat types ranked 2 through 6, implying that these habitats are interchangeable, however open water-medium depth (ranked 2) received significantly higher use than backwater habitat (ranked 7).

Discussion

Results of this study clearly demonstrate the importance of specific wintering areas to largemouth bass in the Pend Oreille River. From the beginning of November to mid-March, 95 % of the largemouth bass monitored (n = 19) within a 30-km section of the reservoir were located in one of two small wintering areas (combine surface area 102.2 ha). These areas provided refuge from water velocity and maintained relatively stable and warmer water temperatures; both characteristics previously identified as suitable winter habitat (Sheehan et al. 1990; Pitlo 1992). However, primary over-wintering areas were located along the main river channel outside of existing backwaters. This is in contrast to previous studies that suggest off-channel areas typically provide suitable habitat and attract high densities of fish during the winter (Greenbank 1956; Sheehan et al. 1990; Pitlo 1992; Raibley et al. 1997). Possibly, largemouth bass over-winter along the shoreline of the Pend Oreille River because of the lack suitable backwater habitat under drawdown conditions.

Largemouth bass were probably not attracted to existing backwaters because of shallow water depths and unfavorable thermal conditions created by lower water levels. A drawdown of 2.9 m reduced the total surface of the Pend Oreille River by

approximately 11 %, exposing about 423 ha of shoreline. Most this area consisted of

shallow backwaters or sloughs located adjacent to the main river channel. Although

backwaters not completely dewatered remained accessible to fish, only Morton

Slough maintained water depths exceeding 1 m. Consequently, shallow backwaters

cooled more rapidly in the fall, and remained an average 3 ^{o} C cooler than the main

river channel until early January (Figure 2). Largemouth bass have been shown to

thermal regulate (Cherry et al. 1975; Crawshaw 1984; Cincotta and Struffer 1984),

and will seek areas providing the warmest available water to over-winter (Coutant

1975; Ross and Winter 1982; Sheehan et al. 1990; Pitlo 1992; Raibley et al. 1997).

Therefore, we believe warmer main channel areas with little to no water velocity

probably served as thermal refuge from cooler backwaters, and provided alternative

winter habitat under drawdown conditions.

The ability to find suitable winter habitat can be critical to the survival of

largemouth bass in riverine environments at northern latitudes. For instance, Pitlo

(1992) found that when low water levels denied access to suitable winter habitat in

the upper Mississipi River, radio-tagged largemouth bass suffered higher winter

mortality. Gent et al. (1995) also noted declines in largemouth bass populations in

the Mississippi River following destruction of backwater habitat due to

sedimentation. The fact that all radio tagged largemouth bass successfully over-

wintered outside of adjacent backwaters in the Pend Oreille River suggests that

essential habitat components were being met.

The high concentration of experimental fish, combined with the distance some

fish traveled to reach preferred over-wintering areas may however reflect a general

lack of suitable winter habitat under drawdown conditions. We found that within preferred over-wintering areas, radio tagged largemouth bass selected habitats containing aquatic vegetation in waters 1-3 m in depth. Based on our analysis of habitat availability, these habitat characteristics were present in other areas within the reservoir, but were unoccupied by experimental fish. In fact, several fish by-passed these areas when migrating to preferred winter locations. Measurements of water temperature, DO, and velocity taken from these areas throughout the winter indicate little difference from the PWA. This suggests that fish may be orienting to certain characteristics of over-wintering habitat that were not obvious from our research.

One possible reason for the strong affinity of largemouth bass to the specific over-wintering areas may be related to the overall size of the areas. While we found that other reservoir sections also contain preferred habitat, primary over-wintering areas contained the largest continuous surface area of aquatic vegetation. Other areas of preferred habitat were smaller, with more sparely distributed aquatic vegetation.

Another hypothesis to the apparent importance of these specific areas might be related to homing behavior. The ability of largemouth bass to return to particular over-wintering areas has been documented in previous studies (Carlson 1992; Pitlo 1992). While we are unable to determine whether largemouth bass return to the same wintering areas year after year, homing behavior and winter site fidelity may explain the strong allegiance to these particular locations.

Largemouth bass prefer habitats containing aquatic vegetation to open water. The strong association between largemouth bass and under water structure has been demonstrated (Johnson et al. 1988; Walters et al. 1991). Selection of aquatic

vegetation may be attributed to the lack of alternative shoreline cover (e.g. woody debris, boat docks) exposed following winter drawdown. Large beds of aquatic macrophytes, mainly *Potamogeton spp.* and *Myriophyllum sibiricum,* provided winter refuge throughout the winter. Increased habitat complexity has been shown to enhance over-winter survival of juvenile largemouth bass by providing shelter from predators (Miranda and Hubbard 1994), and may prevent fish from being washed down-stream (Carlson 1995).

Water temperature appeared to influence the movement of largemouth bass into and away from over-wintering areas. In the fall, largemouth bass exhibited a shift form backwater habitat into deeper shoreline areas coinciding with cooler water temperatures. Fish remained outside of shallow backwaters until early spring, when water temperatures warmed, and fish moved back into shoreline areas. Earlier studies have reported largemouth bass winter migrations that are characterized by fish shifting offshore during the winter and returning when water temperatures warm (Betsill et al. 1986; Woodward and Noble 1997). Access to warmer water temperatures in the spring may allow adult fish to begin spawning activity earlier, which may lead to a longer growth period, and ultimately improved survival of young-of the-year (Bowles 1985; Hatch 1991).

Although most radio-tagged largemouth bass did not leave the wintering areas, some fish continued to move within them. In contrast, largemouth bass were relatively sedentary during winter in other studies (Warden and Lorio 1975; Pitlo 1992), probably because decreased metabolic activity occurs at low temperatures (Johnson and Charlton 1960; Crawshaw 1984). The reason for sustained activity by

some fish is unclear. Largemouth bass have been shown to move under low water temperatures to avoid low DO levels (Sheehan et al. 1990; Railey et al. 1997; Gent et al. 1995). However, DO levels in both backwater and main river habitats remained high (> 8 mg/l) throughout the winter. Movement in response to predator-prey interactions is also unlikely, since feeding activity by largemouth bass is significantly reduced at water temperatures below 10 ^{o} C (Crawshaw 1984). Continued winter mobility may represent a mobile segment that exists within some largemouth bass populations (Woodward and Noble 1997), although this behavior has been most commonly observed in intermediate size classes (250-320 mm), and not during the winter.

Management Implication

From a fisheries management perspective, the high concentration of largemouth bass over-wintering in relatively small areas outside of traditional backwater habitat, suggest winter drawdown practices are limiting winter habitat. Future efforts to minimize winter drawdown in the Pend Oreille River would benefit largemouth bass and other warmwater games fishes that require off-channel habitats to successfully over-winter. However, with increased need for power production in the Pacific Northwest, maintaining higher winter water levels may not be a political option. In light of this, alternative management options that enhance suitable winter habitat under winter drawdown conditions should be considered.

One possible way of enhancing suitable over-wintering habitat is increasing the overall depth of adjacent backwaters and littoral areas through mechanical

dredging. Results of our study indicate that largemouth bass were not attracted to existing backwaters because of shallow water depths and unfavorable thermal conditions created by low water levels. Increasing the depths of these areas would promote warmer minimum temperatures and enhanced water temperature stability; both factors benefiting over-wintering fishes. However, a large-scale dredging operation is probably economically impractical for rehabilitating entire backwater complexes. One possible solution might be to rehabilitate backwaters by temporally damming, and isolating them from the main river channel. These areas could be then dewatered, allowed to dry, excavated, and then reconnected with the main river.

On a smaller scale, deepwater refuge could be created in known over-wintering areas to improve winter habitat conditions. For example, Gent et al. (1995) found that radio tagged largemouth bass over-winter in channels excavated to provide fish habitat in Brown's Lake, a sediment-filled backwater of the Upper Mississippi River. Creation of deepwater refuge in a few select areas may be more cost-effective than large-scale dredging, and still effectively enhance winter habitat.

Management of aquatic macrophytes also should be considered when enhancing suitable winter habitat. Our results indicate that largemouth bass preferred to winter in areas containing aquatic macrophyte growth rather than in open water. Lowering water levels during the winter, and exposing vast amounts of shoreline has been shown to significantly reduce aquatic marcophyte densities along littoral areas (Wagner 2000). A further reduction in winter drawdown would limited the extent of vegetated areas, and may thereby limit suitable winter habitat.

This study was designed to evaluate the winter behavior and habitat selection of adult largemouth bass, with little emphasis on younger age classes. As a result, we cannot confidently comment on whether smaller individuals exhibit similar winter behavior. Suitable winter habitat is especially critical to age-0 largemouth bass, because they are most susceptible to winter related mortality (Hatch 1991; Sheehan et al. 1990). Copland and Noble (1994), who monitored the displacement of tagged age-0 and age-1 largemouth bass in a reservoir, found little migration tendencies of fish away from their release sites over a five month period, even during a short period of low water levels. Hence, younger largemouth bass may not response to receding water levels by moving into deeper water, which may lead to higher winter mortality. Because recruitment of largemouth bass in northern waters is strongly based on over-winter survival of age-0 fish (Bowles 1985; Rieman 1987; Hatch 1991), we suggest that further investigation on winter behavior and habitat selection of these individuals is needed.

Of the 19 radio tagged bass tracked throughout the winter, two were harvested by anglers the following spring. At least three other fish were caught by anglers and released. It is possible that the five radio-tagged largemouth bass not detected after April were harvested and not reported. Spring angling effort particularly in backwater areas has increased in the Pend Oreille River in recent years (Larry Miller, Idaho Department of Fish and Game, personal communication). This is largely attributed to relatively high catch rates of largemouth bass in Morton and Cocolalla sloughs, presumably from high concentrations of fish. Increased angling pressure in

areas that attract largemouth bass in the spring could have deleterious effects on the

population and should be intensely monitored.

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Table 1. Summary of radio tagged largemouth bass in the Pend Oreille River, Idaho.

Fish code Number	Total Length (mm)	Weight (kg)	Study Dates[a]	Number of locations	Distance traveled[a] (km)
151.035	471	2.20	29 Aug 1999 - 16 Apr 2000	20	8.4
151.095	495	2.52	29 Aug 1999 - 2 Jun 2000	22	3.8
151.073	500	2.20	29 Aug 1999 - [b]	2	-
151.114	405	1.00	2 Sep 1999 - 31 May 2000	26	0.8
151.135	434	1.17	3 Sep 1999 - 31 May 2000	16	2.2
151.153	465	1.74	5 Sep 1999 - 2 Jun 2000	26	10.5
151.193	396	1.00	17 Sep 1999 - 16 Apr 2000[c]	19	1.5
151.173	393	0.80	17 Sep 1999 - 29 Apr 2000	18	1.3
151.253	412	1.05	18 Sep 1999 - 29 Apr 2000	20	1.2
151.233	400	1.03	18 Sep 1999 - 31 May 2000	21	1.3
151.273	372	0.77	2 Oct 1999 - 31 May 2000	20	1.5
151.315	398	0.97	3 Oct 1999 - 29 Apr 2000	18	1.0
151.294	485	1.79	3 Oct 1999 - 31 May 2000	19	15.9
151.693	356	0.69	7 Oct 1999 - 31 May 2000	21	1.3
151.674	365	0.69	7 Oct 1999 - 25 Mar 2000[c]	17	1.4
151.334	470	1.56	7 Oct 1999 - 31 May 2000	20	0.9
151.773	365	0.71	8 Oct 1999 - 2 Jun 2000	24	0.8
151.014	475	2.13	9 Oct 1999 - 2 Jun 2000	21	1.0
151.733	505	2.16	9 Oct 1999 - 31 May 2000	19	1.1
151.053	488	1.93	19 Oct 1999 - 13 Mar 2000	14	4.8

[a] From implantation of transmitter to wintering area.
[b] Signal was never received after release.
[c] Fish were harvested by anglers.

Table 2. Relative abundances (%) of habitats available to tagged largemouth bass during the winter period of November through mid-March, and percentages of observations within each habitat.

Habitat type	Abbreviation	Habitat Availability	Habitat Use
Vegetated-shallow depth (0 - 1 m)	VSD	5.3	1.2
Open water-shallow depth (0 - 1 m)	OWSD	5.9	1.0
Vegetated-medium depth (1 - 3 m)	VMD	23.5	90.2
Open water-medium depth (1 - 3 m)	OWMD	52.9	7.6
Vegetated-deep depth (3 - 5 m)	VDD	1.4	0.0
Open water-deep depth (3 – 5 m)	OWDD	3.7	0.0
Backwater	BW	7.3	0.0

Table 3. A ranking matrix for tagged largemouth bass based on comparing the proportions of use and availability of each habitat type. Signs (+ or -) indicate selection for and against a given habitat; triple sign (+++ or ---) indicate significant deviation from random at $P < 0.05$. See Table 2. for habitat abbreviations.

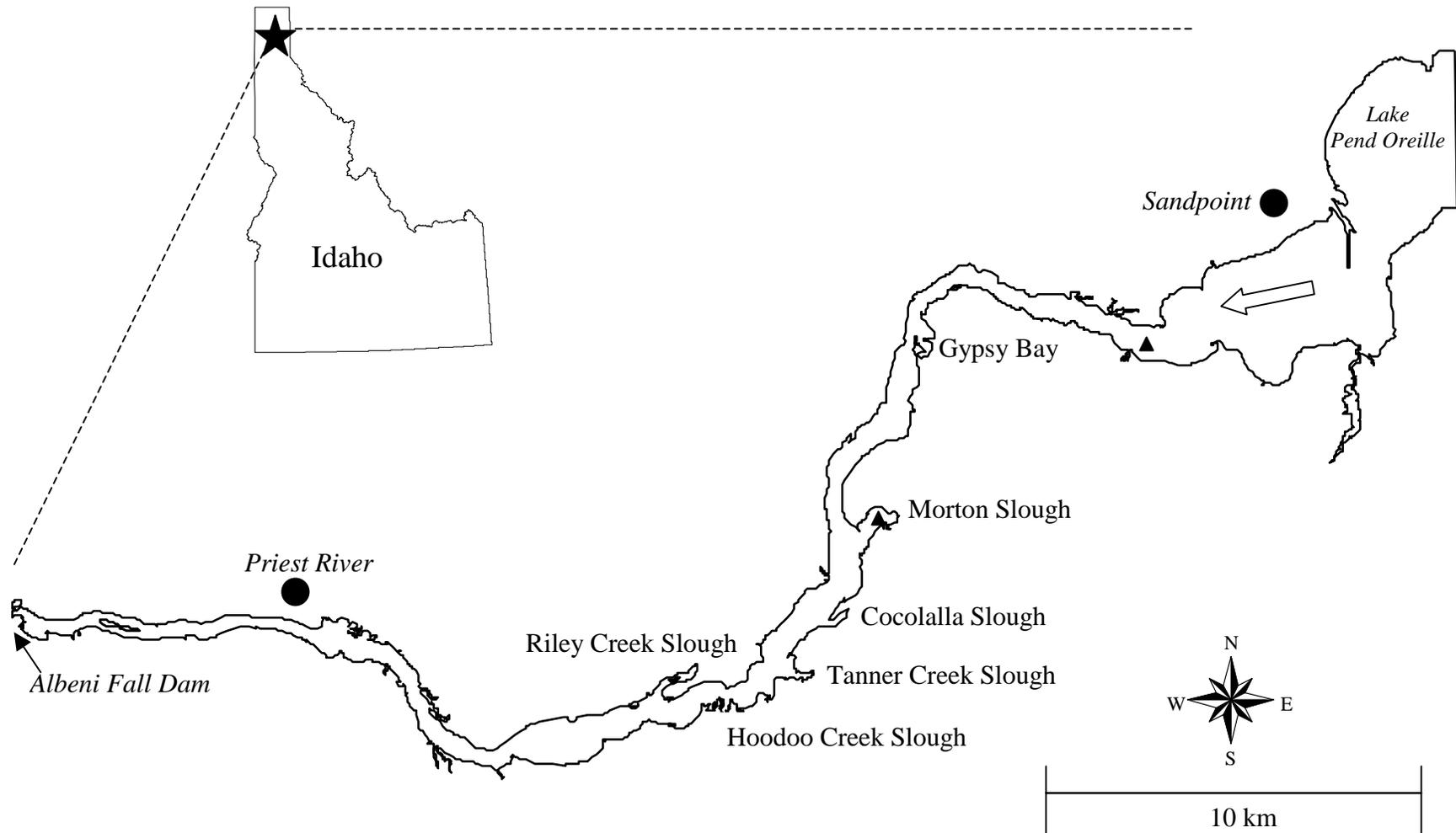| Habitat type	Habitat type							Rank
	VSD	OWSD	VMD	OWMD	VDD	OWDD	BW	
VSD		-	- - -	-	-	+	+	3
OWSD	-		- - -	-	-	+	+	4
VMD	+++	+++		+++	+++	+++	+++	1
OWMD	-	-	- - -		-	-	+++	2
VDD	-	-	- - -	-		+	+	5
OWDD	-	-	- - -	-	-		-	6
BW	-	-	- - -	- - -	-	-		7

Figure 1. Study area map of the Pend Oreille River including the six primary backwater areas. Triangles (▲) show the locations of the 2 temperature recording stations.
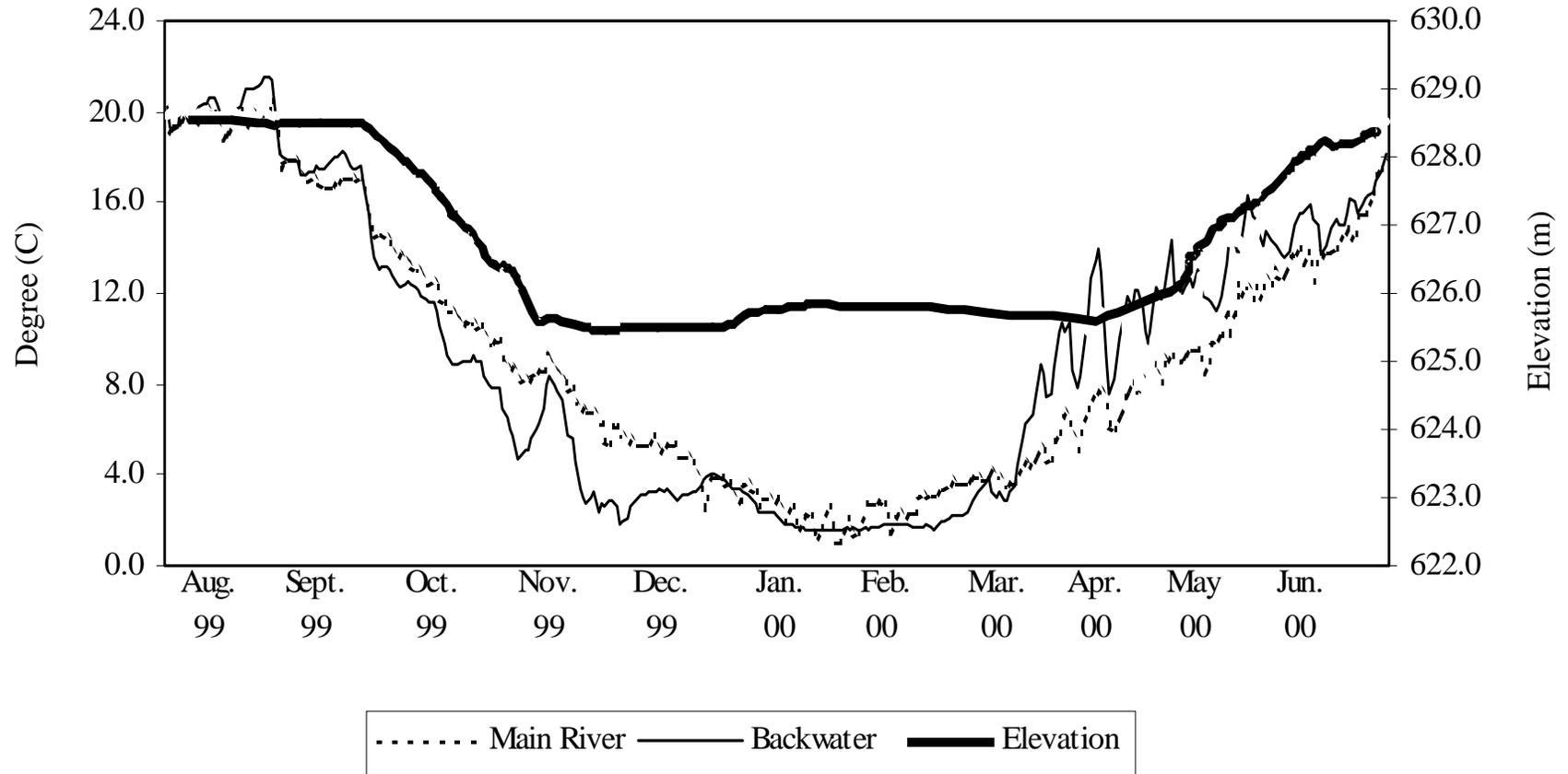
Figure 2. Mean daily water tempratures and water surface elevation from August 1999 to June 2000, in the Pend Oreille River, Idaho.
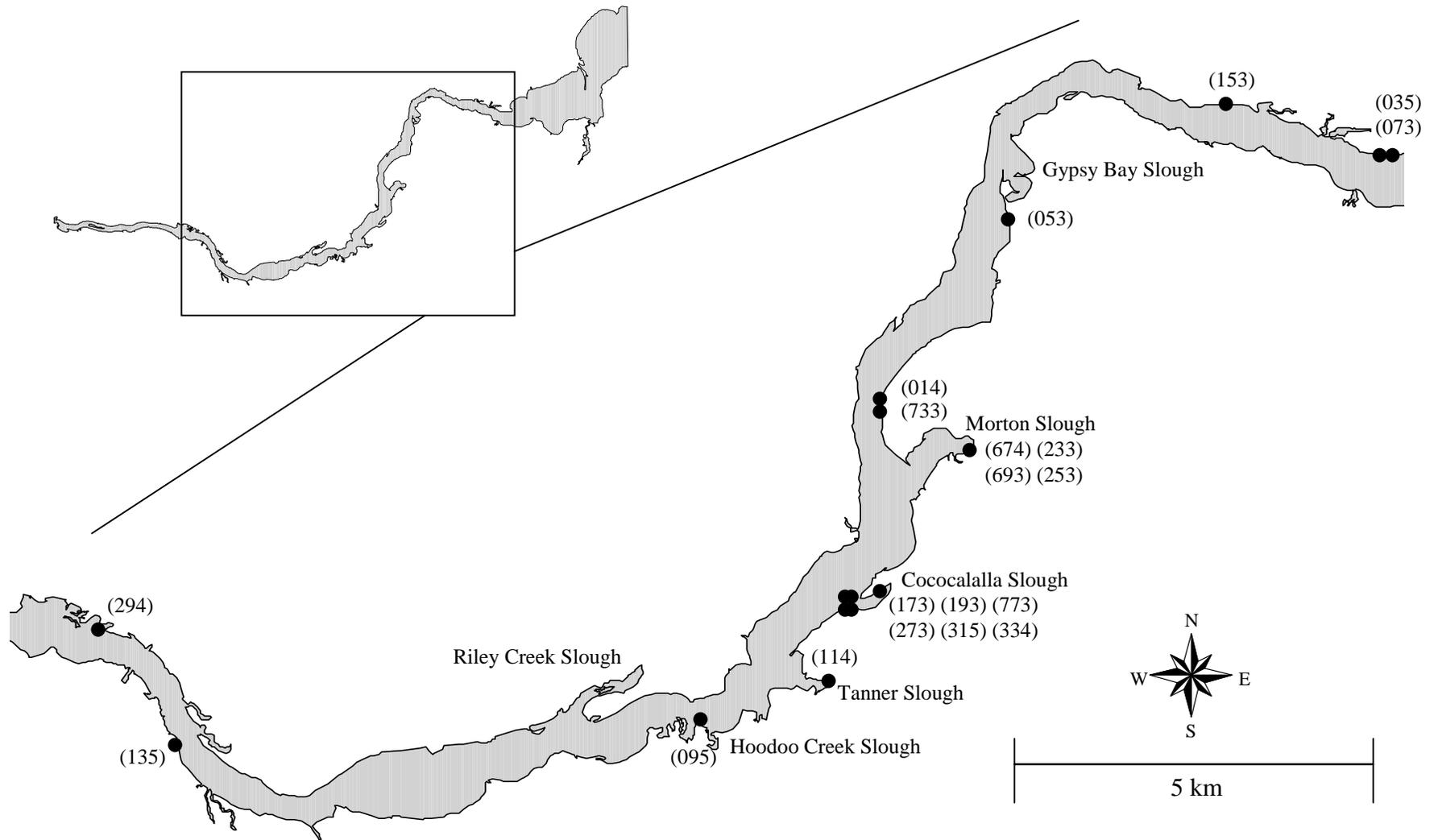
Figure 3. Initial capture locations of 20 radio tagged largemouth bass collected from August 29 to October 19, 1999 in the Pend Oreille River, Idaho. Parentheses contain codes of individual fish.
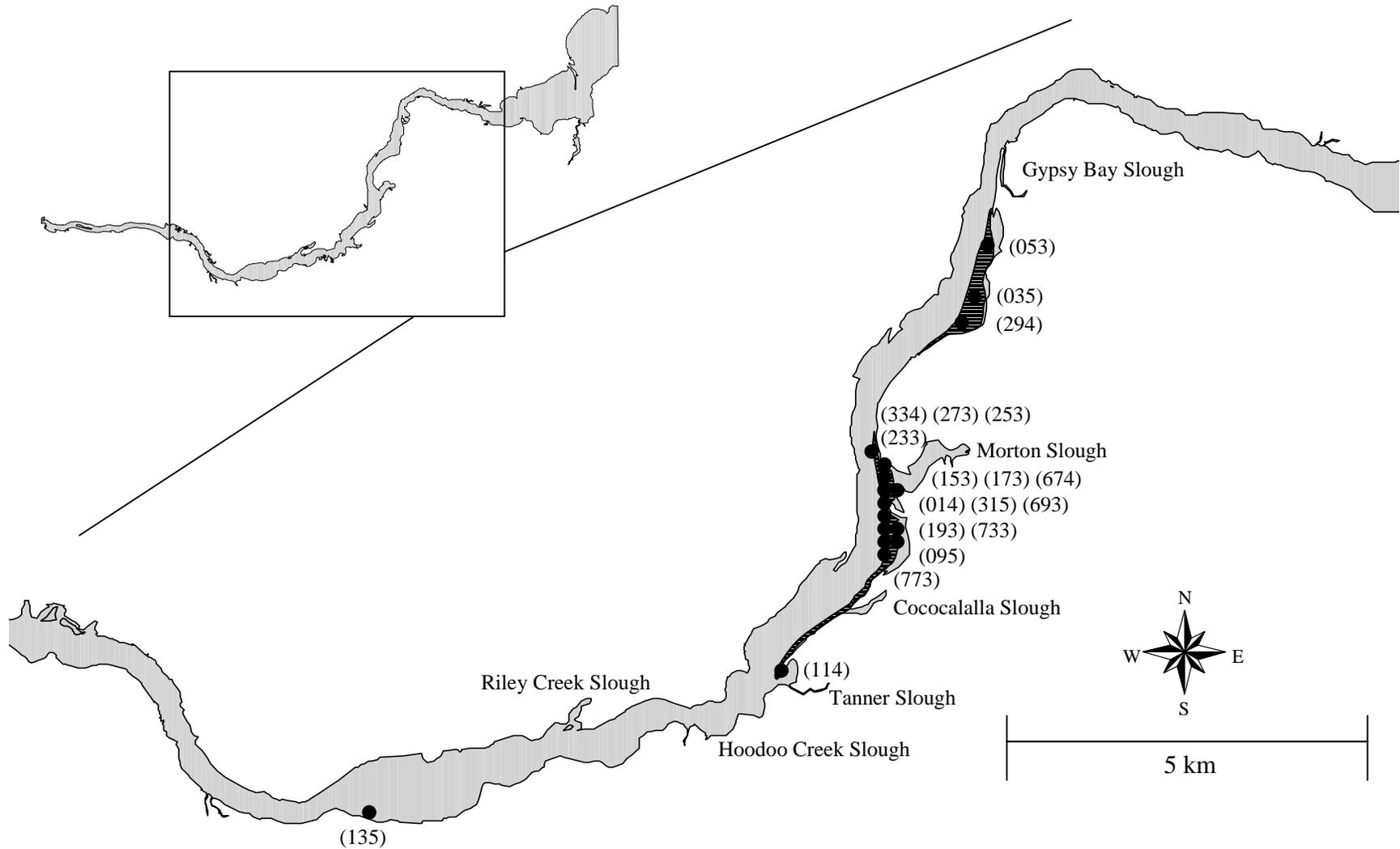
Figure 4. Locations of radio tagged largemouth bass in the Pend Oreille River, Idaho, on November 4, 2000 under 2.9 m winter drawdown conditions. Shaded areas indicate primary wintering areas (PWA) from November 1999 to March 2000.
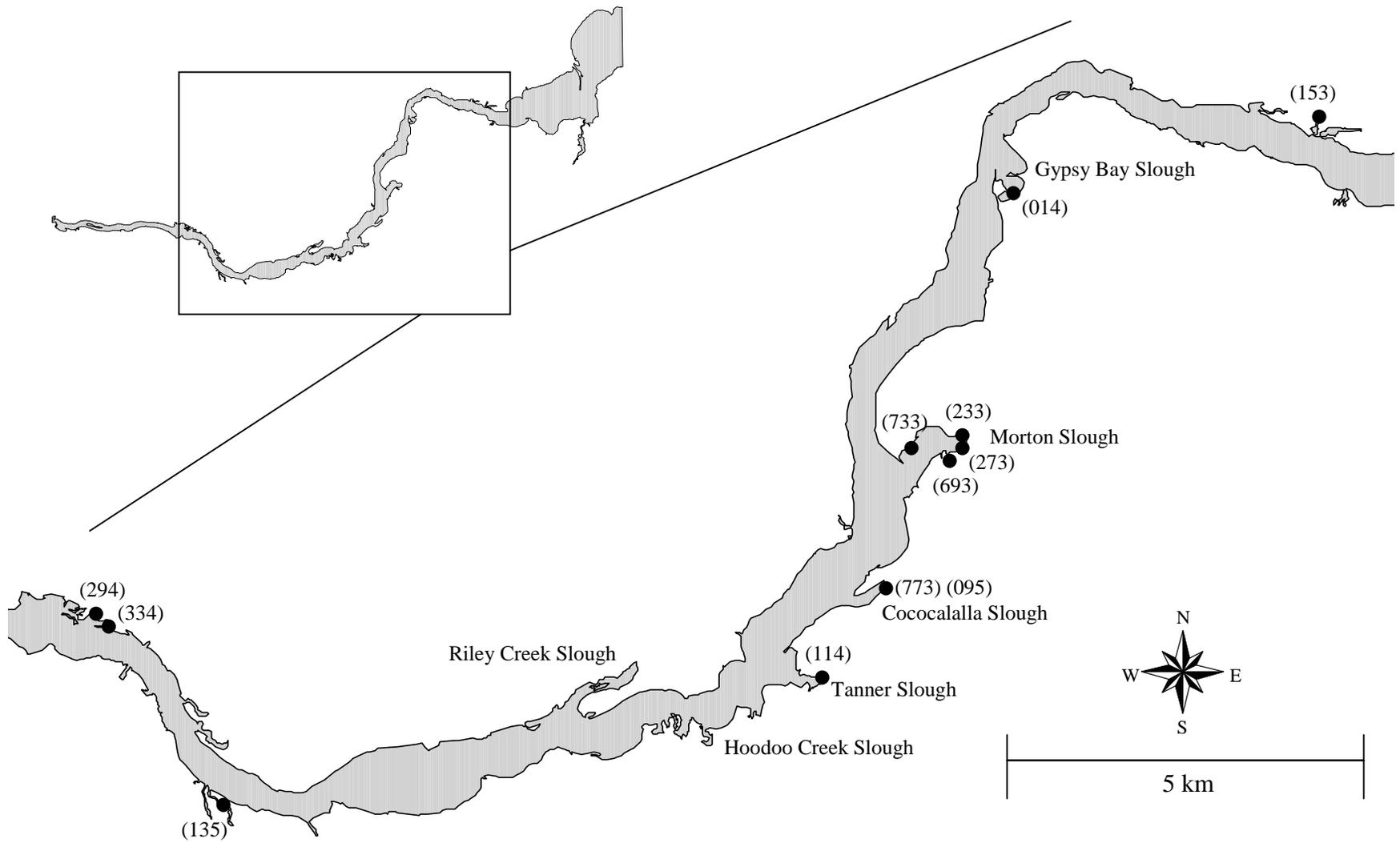
Figure 5. Locations of twelve radio tagged largemouth bass in the Pend Oreille River, Idaho, on 2 June, 2000.

Larval kokanee prey selection and growth

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December 2001

Abstract: We investigated how springtime zooplankton community changes at Lake Pend Oreille, Idaho, have affected larval kokanee <u>Oncorhynchus</u> <u>nerka</u> (20-36 mm TL) by first conducting prey selection trials at three relative cladoceran to copepod prey densities, and at three levels of kokanee stomach fullness. We then compared growth rates of larval kokanee fed either cladoceran or copepod prey. In prey selection trials, random feeding occurred when cladocerans were scarce, but cladocerans were selected when their relative abundance increased. Stomach fullness affected the total number of prey items ingested, but not prey selection. Kokanee growth was not associated with prey selection, as the copepod diet produced the greater growth. These laboratory results suggest that species relative abundance rather than absolute abundance affects larval kokanee prey selection, and that growth is influenced more by total zooplankton densities than by densities of preferred prey items.

Introduction

The springtime crustacean zooplankton community at Lake Pend Oreille, Idaho has changed following introduction of the omnivorous freshwater shrimp Mysis relicta (Rieman and Falter 1981). Prior to mysis introductions, cladoceran zooplankton such as Daphnia spp. and Bosmina longirostris would be nearly undetectable by sampling throughout winter, then increase in abundance starting around April (Stross 1954). By June, cladocerans were abundant and utilized by kokanee Oncorhynchus nerka as food, with Bosmina accounting for the majority of prey items in immature kokanee stomachs (Platts 1958; Stross 1954) Currently, zooplankton grazing by mysis suppresses cladoceran populations until mid-summer, when thermal stratification of the lake excludes mysis from the warm epilimnion and releases cladocerans from mysis predation (Chipps 1997).

With cladoceran zooplankton unavailable as food for newly emerged kokanee, the copepods Cyclops bicuspidatus and Diaptomus ashlandi have become the principal prey items (Clarke 1999; Rieman and Bowler 1980). In a stomach contents analysis conducted in late May and June, 1998, Bosmina, which were present at densities ranging from 0.05 to $1.91 \cdot L^{-1}$, represented less than 1 % of the biomass ingested (Clarke 1999). A net pen study conducted in June in Lake Pend Oreille demonstrated that newly emerged kokanee can survive and grow on a diet consisting primarily of Cyclops, even when Cyclops densities were much lower than those historically found in the lake (Clarke 1999). However, the study did not estimate the effect of a diet switch from cladocerans to copepods on the growth of newly emerged kokanee.

Previous research on the growth of young planktivorous fish fed either cladoceran or copepod prey has yielded somewhat ambiguous results, with some studies finding no growth differences (Mayer and Wahl 1997) whereas others recorded faster fish growth on copepods (Confer and Lake 1987) or cladocerans (Mills et al. 1989). Differences in digestibility (Sutela and Huusko 2000) and caloric

values (Schindler et. al. 1971) between zooplankton prey could explain faster growth from a particular diet. Additionally, Stockwell et. al. (1999) showed that adult kokanee can reduce the water content of Daphnia during ingestion, thereby allowing for more prey biomass to be packed into the stomach. If kokanee larvae were similarly able to "squeeze" water from cladocerans, but not from copepods, then a cladoceran meal might provide a higher biomass, and potentially a higher energy content.

Few studies have addressed the importance of prey type on larval salmonid prey selection, perhaps because salmonid species hatch at a relatively large size and would not be gape-limited by zooplankton prey items. We are aware of no such studies published on larval kokanee. However, Confer and O'Bryan (1989) reported that prey selection of post-larval (32-50 mm total length) rainbow trout Oncorhynchus mykiss changed as prey densities fluctuate, with smaller food items selected more readily at high prey densities. They postulate that such selection preferences should lead to greater growth efficiency. In prey selection trials with other fishes, factors such as zooplankton taxa, density, and behavior, and the degree of gut fullness affected selection (Confer and O'Bryan 1989; Confer et. al. 1990; Drenner et. al. 1978; Johnston and Mathias 1994; Mayer and Wahl 1997; Visser 1982).

This laboratory study investigates how springtime zooplankton community changes at Lake Pend Oreille have affected larval kokanee by first testing the importance of relative densities of cladocerans and copepods to prey selection, and then comparing growth rates of larval kokanee fed either cladoceran or copepod prey. If a selection preference were clearly evident, then we hypothesize a priori that the preferred item will produce the greatest growth.

Methods

Overview

Our experiments were conducted using swim-up larval kokanee obtained from the Cabinet

Gorge Hatchery (Cabinet Gorge, Idaho) and brought to the wet lab at the University of Idaho. Kokanee

eggs at the hatchery are maintained in batches, with groups of larvae emerging approximately weekly

from mid-February through April, enabling us to conduct multiple trials of our experiments in April

and May, 2001 using recently-hatched larvae. Larvae were not fed while at the hatchery. Following

transport from the hatchery, larvae were acclimated for 48 hrs, during which time they were fed a

mixture of cladoceran and copepod zooplankton. In growth experiments, larvae were placed in holding

containers and fed to satiation twice daily according to treatment group, with one group provided

cultured cladoceran prey, and a second group receiving copepod prey strained from Lake Pend Oreille.

Prey selection preferences were tested in a three by three factorial experiment, in which kokanee

having three levels of gut fullness received one of three manipulated densities of cladoceran and

copepod prey.

Ideally, cladocerans for the experiments would be <u>Bosmina</u>, the historically important early

season food source for larval kokanee. However, culturing of <u>Bosmina</u> proved difficult, so we used the

cladoceran <u>Ceriodaphnia dubia</u>. <u>Ceriodaphnia</u> cultures were maintained in 3.8 L plastic containers

using filtered Lake Pend Oreille water, with daily feedings consisting of a mixture of digested trout

chow, baker's yeast, and cultured <u>Chlamydomonas</u> algae. Copepods for these experiments were

collected once weekly from the upper 5 m of Lake Pend Oreille using a 80 μm mesh Wisconsin-style

plankton net with a 20 cm diameter mouth, and held in plastic containers in filtered lake water

Typically, the zooplankton community in the lake from April through June consists largely of <u>Cyclops</u>

and <u>Diaptomus</u> (Clarke 1999), but we subsampled our zooplankton collections to verify taxonomic composition.

<u>Growth Experiments</u>

Growth experiments consisted of three replicate trials using 50 uniformly sized kokanee larvae (22-26 mm TL) that were selected for each trial. In each trial, 10-2 L flow-through cylindrical plastic containers, perforated at the mouth, were stocked with two kokanee each, and randomly assigned to either the <u>Ceriodaphnia</u> or copepod treatment group. Containers were kept partially submerged in a water bath maintained at 10° C (a typical Lake Pend Oreille surface water temperature in early June, personal observation) using a ½ hp in-line chiller unit with water pumped from the bath into each container. Dissolved oxygen was monitored periodically using a Yellow Springs Instruments dissolved oxygen probe. Lighting was provided for 12 hours each day using two 40-watt fluorescent bulbs. We estimated the mean beginning dry weight of experimental fish by drying the remaining 30 individuals to a constant weight in a 65° C oven, and weighing them to the nearest 0.0001 g.

Kokanee were fed for 1 h each morning (between 0800 and 1000 hrs) and evening (between 1700 and 1900 hrs) by shutting off the water flow, then introducing the prey. Field studies found a maximum of about 50 prey items in larval kokanee stomachs following evening feeding (Clarke 1999, unpublished data), so we assumed that stocking at least 200 prey items into each plastic container would more than satiate two fish. After 1 h, prey were removed from containers, and water flow was restored. At the conclusion of the experiments, fish were euthanized in MS-222, and fish weights (nearest 0.0001 g) were obtained after drying to a constant weight in a 65° C oven. Instantaneous growth rates (G = % change in body weight·day^{-1}; Van Den Avyle 1993) were calculated for each fish. Growth rates were averaged for each container, and results from the three trials were pooled. An

ANOVA was used to test for significant differences between treatment groups (SAS Institute, Version 6.11). We also used Cohen's Effect Size ($d = (\mu_1 - \mu_2) / \sigma_\varepsilon$; Cohen 1977) to assess the practical significance of our results based on differences among treatment means, where μ_1 and μ_2 are treatment means, and σ_ε is the within groups population standard deviation from the ANOVA table. A d value of 0.2 denotes a small treatment effect, $d = 0.5$ is a medium effect, and $d > 0.8$ is a large effect.

Prey Selection Experiments

In prey selection trials, 6-2 L plastic containers were each stocked with one fish (22-36 mm TL) that had either an empty stomach, a full stomach, or a moderately full stomach. Fish having empty stomachs were starved for 24 hours, those with full stomachs were prefed to satiation with hatchery pellets 1 h prior to the experiment, while those having moderately full stomachs were prefed 3 hours prior. Each container then received live zooplankton, such that the number of zooplankton per liter in containers approximated either current springtime cladoceran to copepod ratios (2 cladocerans to 15 copepods· L^{-1}), those found before Mysis establishment (15 cladocerans to 20 copepods·L^{-1}), or an intermediate ratio (8 cladocerans to 17 copepods·L^{-1}). Hereafter, we refer to cladoceran to copepod ratios as prey ratio 1 (2:15), prey ratio 2 (8:17), and prey ratio 3 (15:20). Zooplankton were amassed in preparation for feeding using plastic transfer pipettes to separate and count individuals into 2 g water-filled vials. We avoided a potentially confounding factor in which some larvae received mostly Cyclops copepods, while others received mostly Diaptomus, by selecting Diaptomus as the only copepod prey. In addition, we attempted to select only adult zooplankton as prey. Kokanee larvae were allowed to feed for 10 min, then were euthanized and preserved in 10% formalin. Each larvae was weighed (mg wet weight), the stomach was removed by dissection, and prey items were identified.

Chesson's modified selectivity coefficient (s), which is an appropriate estimate of prey selection when predation reduces densities of individual prey types, was calculated for each fish (Chesson 1983). The coefficient is calculated as:

$$s_i = \frac{\ln((p_{i0} - r_i)/p_{i0})}{\sum\limits_{j=1}^{m} \ln((p_{j0} - r_j)/p_{j0})}$$

where r_i is the proportion of items of food type i in the predators diet, and p_{i0} is the proportion of food type i present in the environment at the beginning of the foraging bout. In a two-prey type experiment such as ours, the index value for one prey type will be equal to 1 - the value for the other type. Therefore, an ANOVA using copepod index values was used to investigate selection preferences.

Results

Growth

Four kokanee larvae died during growth experiments; three deaths occurred when fish escaped the holding containers through the water-flow perforations and were subsequently entrained in the chiller unit, while the fourth death was attributed to handling mortality. In each instance the container was maintained with one larvae thereafter. In designing this experiment, we were concerned that behavioral interactions between kokanee in individual containers might affect growth rates, thus we chose to use only two fish per container, and used as our treatment response the average growth per container. However, while observing fish activity during these experiments we saw surprisingly little interaction between individuals. Moreover, the coefficient of variation for ending kokanee weights (0.22) was similar to that for beginning weights (0.17), providing evidence that behavioral interactions between individuals in containers did not affect kokanee growth.

Kokanee fed copepod zooplankton grew faster than those fed Ceriodaphnia (Figure 1), although the difference was not statistically significant (F=1.75, p=0.1964). Cohen's Effect Size (*d*) was 0.10, indicating a small treatment effect. Instantaneous growth for larvae fed copepods averaged 1.61%·day^{-1} (range = -0.85 to 4.39%·day^{-1}), while those fed cladocerans averaged 0.92%·day^{-1} (range = -0.62 to 2.39%·day^{-1}). Zooplankton strained from Lake Pend Oreille, and fed to kokanee in the copepod treatment group, consisted entirely of copepods, with the majority (83%) being Cyclops.

Prey Selection

We found that selection was significantly influenced by prey ratio (F=3.32, p=0.0374; Figure 2). However, gut fullness alone did not significantly influence prey selection (F=0.59, p=0.5573), and no statistically significant interaction existed between gut fullness level and the ratio of cladocerans to copepods (F=1.05, p=0.3829). At the lowest Ceriodaphnia to Diaptomus ratio (prey ratio 1), kokanee selected Diaptomus (s=0.54) slightly more than would be expected from random feeding (s=0.5), but when Ceriodaphnia increased relative to Diaptomus, then Diaptomus selectivity coefficients declined to 0.44 for both prey ratios 2 and 3. No relationship existed between the size of larvae (range=0.036-0.40 mg) and selectivity index values (r=0.10, p=0.2038).

The total number of prey items ingested by kokanee increased significantly as zooplankton ratios increased (F=16.86, p<0.0001; Figure 3), and as stomach fullness increased (F=21.38, p<0.0001). The mean number of zooplankton ingested nearly doubled from prey ratio 1 (10.25 items/stomach) to prey ratio 3 (20.28 items/stomach), and declined by nearly half from an empty stomach (21.16 items/stomach) to a full stomach (11.95 items/stomach).

Discussion

Field studies have shown cladoceran zooplankton to be an important component in the diet of larval kokanee (Stross 1954; Northcote and Lorz 1966; Foerster 1968; Burgner 1991). In some instances kokanee larvae have actively selected cladocerans (Beattie and Clancy 1991), whereas in other instances they have not (Clarke 1999). Therefore, the effect of varied prey assemblages to larval kokanee prey selection is not well understood, and the effect of prey type on growth has been untested.

In these laboratory experiments, the relative density of cladoceran to copepod prey clearly affected feeding selection by larval kokanee, but no growth benefits were evident from feeding on the preferred prey, causing us to reject our a priori hypothesis that the preferred prey would produce the greatest growth . Our prey selection trials can be summarized as follows: Kokanee fed nearly randomly when Diaptomus were disproportionately abundant (i.e. prey ratio 1), but fed selectively on Ceriodaphnia when densities increased relative to Diaptomus. These laboratory results provide perspective for understanding a prey selection study of wild larval kokanee in Lake Pend Oreille that found little preferential feeding despite estimated cladoceran densities ($3 \cdot L^{-1}$) that appeared unusually high compared with prior year estimates (Clarke 1999). In that study, copepod density estimates were usually greater than $30 \cdot L^{-1}$, making cladocerans scarce relative to copepods. Therefore, results from these laboratory experiments are congruent with our field observations, and support a conclusion that relative prey densities are an important determinant in larval kokanee prey selection. In prey selection experiments with three-spined stickelback Gasterosteus aculeatus, relative abundance of the preferred prey type was found to be more important to prey selection than absolute abundance of any prey item (Visser 1982).

We did not attempt to relate larval kokanee prey selection to fluctuating total prey densities. Optimal foraging theory predicts that predators will feed more selectively as total food densities

increase, yet some evidence suggests that the theory may not apply to larval fishes. Juvenile larval walleye Stizostedion vitreum (>20mm TL) did not feed more selectively when prey densities increased by more than an order of magnitude (Mayer and Wahl 1997), and selection of preferred prey by young yellow perch Perca flavescens (22-62 mm TL) did not increase with increasing food densities (Confer et al. 1990). Furthermore, the diets of young fish in some feeding studies broadened to include less preferred prey types when prey densities increased (Johnston and Mathias 1994; Mills et al. 1987), a phenomenon referred to as "negative switching". Therefore, while we cannot rule out the possibility that increased total zooplankton densities, rather than changes in relative Ceriodaphnia densities, were responsible for the results we observed, there is ample evidence to support the latter conclusion.

As expected, the average total number of zooplankton ingested by kokanee larvae decreased as stomach fullness increased, but we saw no influence of stomach fullness on prey selection. Because Ceriodaphnia is generally considered to be an easily captured zooplankter (Drenner et. al. 1978), we anticipated that it would be strongly selected by satiated kokanee. Other studies have found strong correlates between selectivity and satiation (Bence and Murdoch 1986). However, it appears that prey size rather than evasiveness is the important determinant for prey selection by satiated fish, with smaller prey being preferred. Reported length estimates for Ceriodaphnia range from approximately 0.30-0.70 mm (Culver et al. 1985; McCauley 1984), while Diaptomus averages about 0.69 mm in June in Lake Pend Oreille (Clarke 1999). Therefore, we suspect that prey in our experiments were too similar in size for selection preferences by satiated fish to occur. As a result, we may still not fully understand the importance of Bosmina, the smallest of crustacean zooplankton, in the diet of nearly satiated wild fish.

Our growth results refute suppositions that cladoceran zooplankton provide an inherently better meal for larval kokanee than do copepods. Growth during these experiments was slightly faster from

fish fed copepods, a result that could be explained by differences in caloric values. In the literature, caloric values for copepods are generally about 10% higher than those of cladocerans (Comita and Schindler 1963; Schindler et al.1971). Cultured zooplankton are grown in a food-rich environment, and should have higher than normal caloric values (Confer and Lake 1987), so any bias from using lake-caught versus laboratory-reared zooplankton should have favored the Ceriodaphnia fed fish.

If a copepod diet provides better growth, why would kokanee select Ceriodaphnia in these experiments? Two potential explanations appear plausible. First, Ceriodaphnia may have been the more visible of the two prey types, possibly due to its eye pigmentation or presence of eggs, both of which would result in greater contrast for an otherwise relatively transparent organism. Studies have demonstrated that planktivorous fish feed selectively on cladocerans with more prominent eye pigments (Zaret and Kerfoot 1975), and on those with eggs (Mellors 1975), highlighting the importance of contrast to visual predators. Furthermore, Ceriodaphnia possesses a rounded body form that could increase its visibility to laterally searching predators. In a shallow water environment such as our experimental containers, lateral searches by kokanee would be the norm. Second, studies show that when detected, cladoceran zooplankton are more easily captured than copepods (Confer and Blades 1975).

Clarke and Bennett (in press) theorized that total zooplankton densities were more important than zooplankton species composition for predicting larval kokanee survival and growth. These laboratory studies support that hypothesis. For that reason, we believe that efforts to correlate larval kokanee cohort mortality with food abundance should focus on total zooplankton densities or biomass, rather than cladoceran densities or biomass.

Acknowledgments

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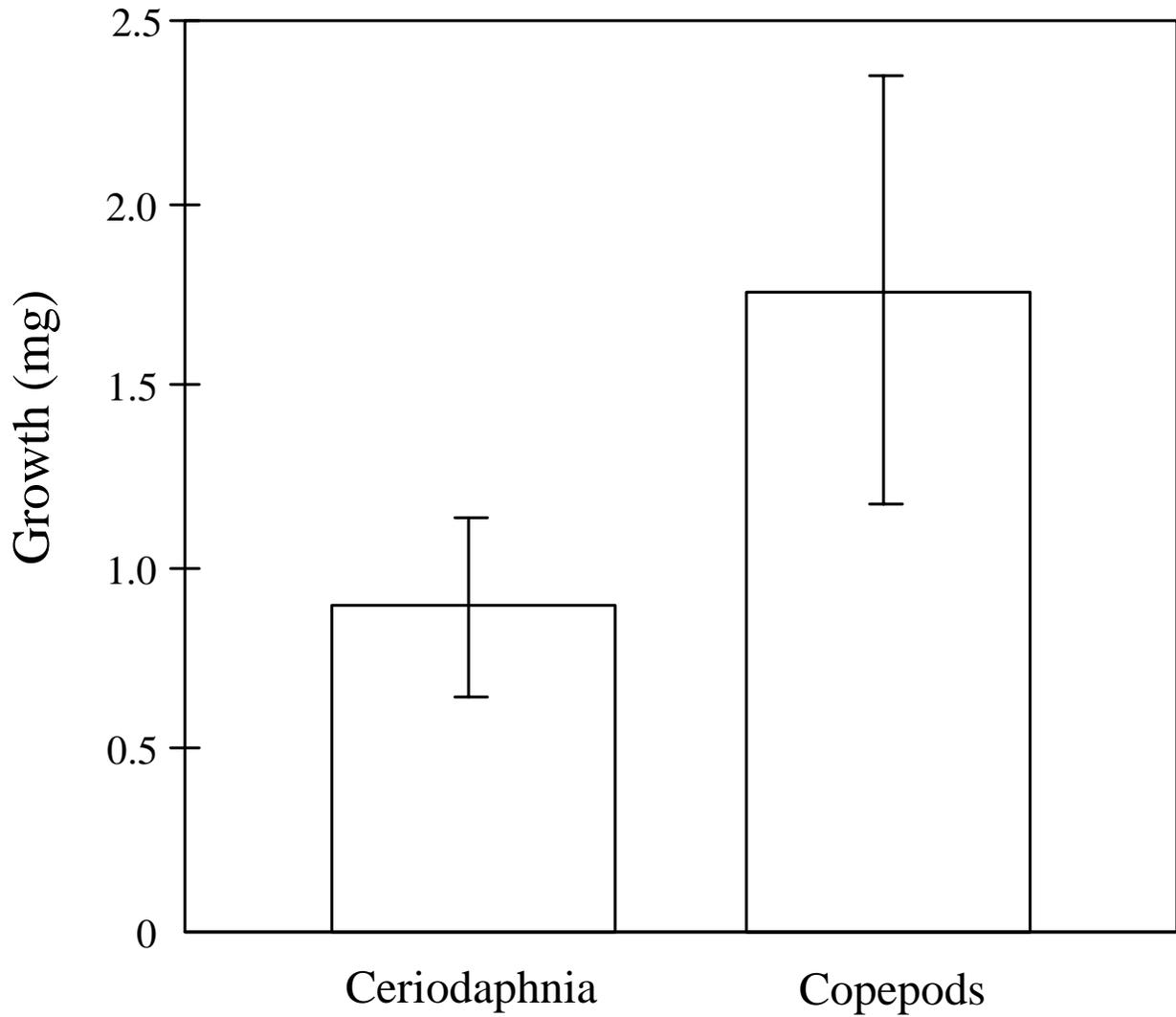versus visibility selection. Ecology 56:232-237.

Figure 1. Mean kokanee growth (ending weight - beginning weight) fed either <u>Ceriodaphnia</u> or a

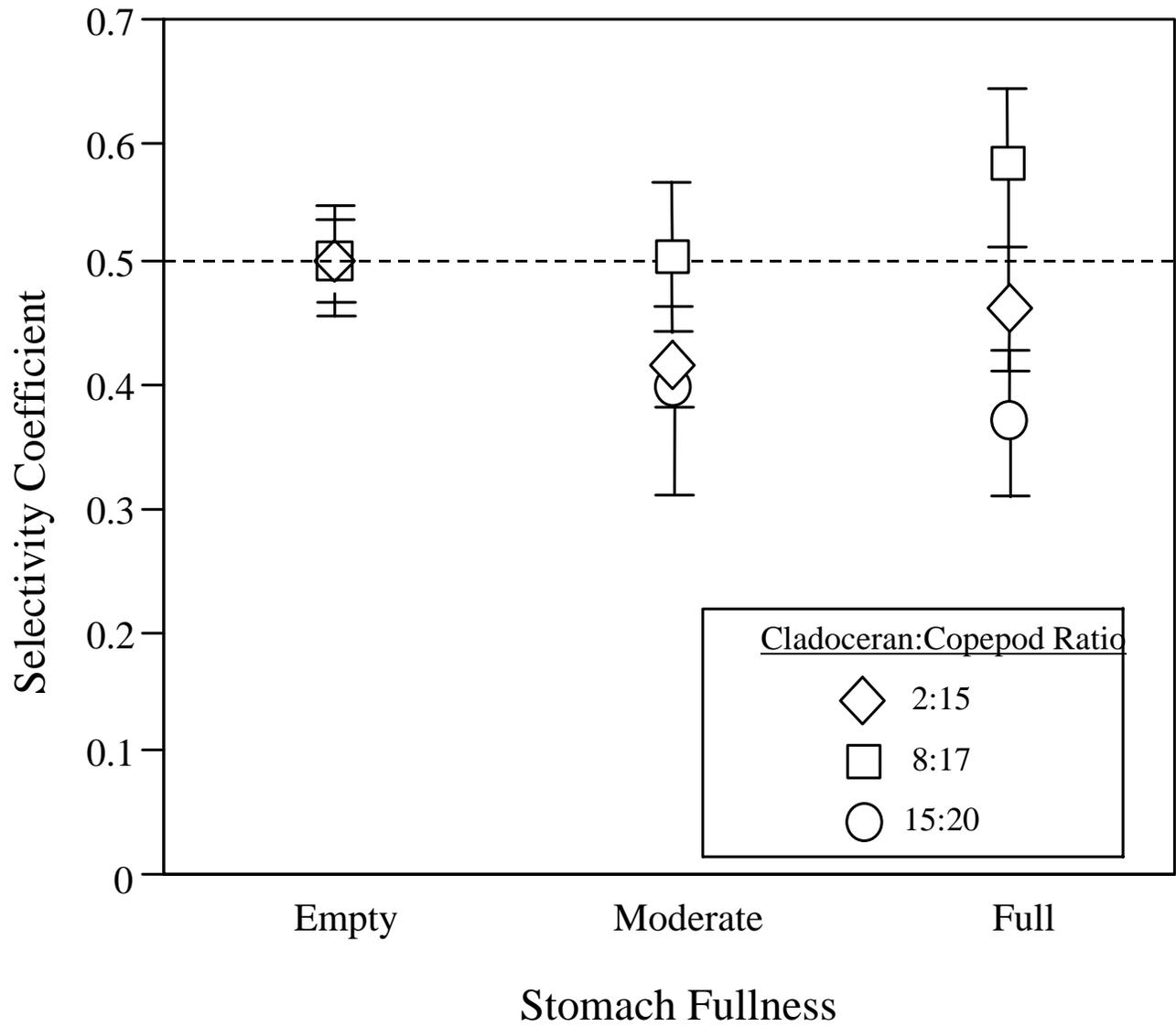mixed copepod diet for ten days. Vertical lines represent one standard error.

Figure 2. Chesson's selectivity coefficient (α) for kokanee feeding on <u>Diaptomus</u> at one of three relative prey ratios, and at three levels of gut fullness. Dashed line represents random feeding, vertical lines represent one standard error.
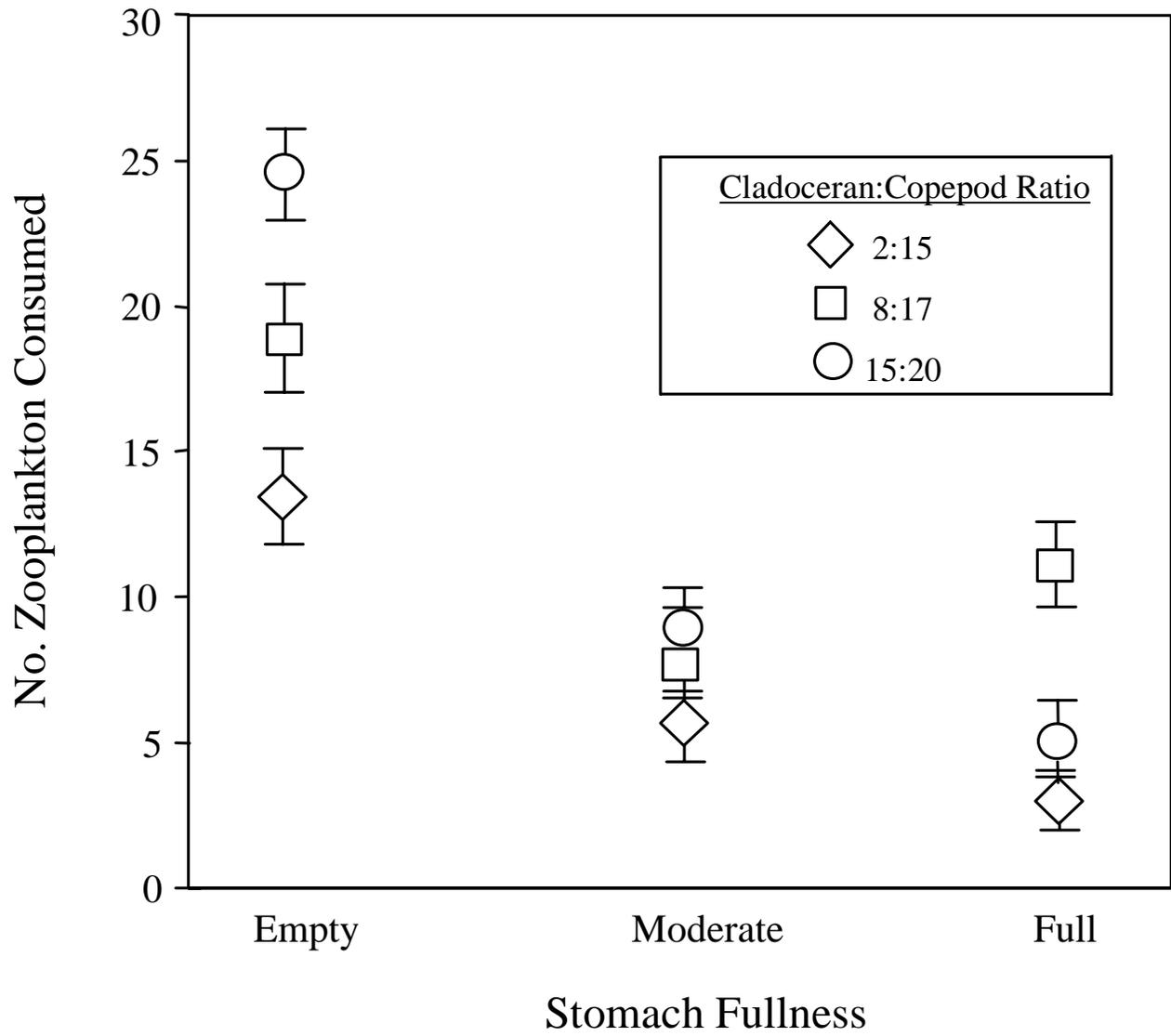
Figure 3. Mean total number of prey items ingested by kokanee feeding at one of three relative prey ratios, and at three levels of gut fullness. Vertical bars represent one standard error.