Lake Pend Oreille Fishery Recovery Project

Final Report
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FISHERY RESEARCH

LAKE PEND OREILLE FISHERY RECOVERY PROJECT

COMPLETION REPORT
October 1, 1996 – December 31, 2001

Prepared by:

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IDFG Report Number 02-56
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CHAPTER 1: LAKE LEVEL CHANGES AND THEIR EFFECT ON KOKANEE SURVIVAL

ABSTRACT

The winter elevation of Lake Pend Oreille, Idaho was changed in an attempt to enhance shoreline spawning areas for kokanee. Winter lake elevations were kept 1.2 m higher than full drawdown for three years (winters of 1996-97, 1997-98, and 1998-99) and 0.6 m higher than full drawdown for the next two years (1999-00 and 2000-01). Kokanee egg-to-fry survival increased more than 150% (from a mean of 3.2% to 8.1%) during the years of elevated lake levels (excluding 1997) ($p = 0.06$). The only year not showing a substantial improvement was 1997, a year with the highest spring flows on record. Egg-to-fry survival was positively correlated to the amount of change in elevation of the lake ($r^2 = 0.85$). During years of elevated water levels, kokanee utilized the shallow, newly inundated gravel and had a modal spawning depth of 1.2 m. During a full drawdown year, kokanee spawned at deeper depths with a modal spawning depth of 4.0 m. Egg-to-fry survival rates did not correlate well to warmer water conditions, the number of hatchery kokanee stocked, or the abundance of opossum shrimp in the lake. These findings lead to the conclusion that lake level manipulations can be used to recover the kokanee population in Lake Pend Oreille.

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INTRODUCTION

Lake Pend Oreille historically provided the largest sport fishery in Idaho. From 1952 until 1966, it produced an angler harvest that averaged one million kokanee annually. Kokanee attracted most of the fishing effort and was an extremely popular fishery. At its peak in 1953, total fishing effort was 522,700 hours and harvest was 1.3 million kokanee (Jeppson 1954). To put this into perspective, on a single day in 1953, 863 fishermen were fishing the Bayview section of the lake (approximately the southern third of the lake). This sport fishery was extremely important to local communities based on the amount of angler participation.

Harvest of kokanee began a prolonged, steady decline in the mid-1960s. By this time, Cabinet Gorge Dam had been built (1952), which blocked kokanee from spawning in the Clark Fork River and caused the population to be largely dependent on shoreline spawning. Kokanee need areas of gravel that are relatively free from silt and sand (<30%) to have good survival as the eggs incubate. Shoreline spawning success was also influenced by the operation of Albeni Falls Dam (Maiolie and Elam 1993). In 1966, the dam began a pattern of operation that lowered lake levels 3.5 m (11.5 feet) each fall. Drawdowns were finished immediately before kokanee began spawning on the shorelines. These consistently deep drawdowns reduced the amount of gravel available for kokanee spawning along the lake's shorelines (Fredericks et al. 1995).

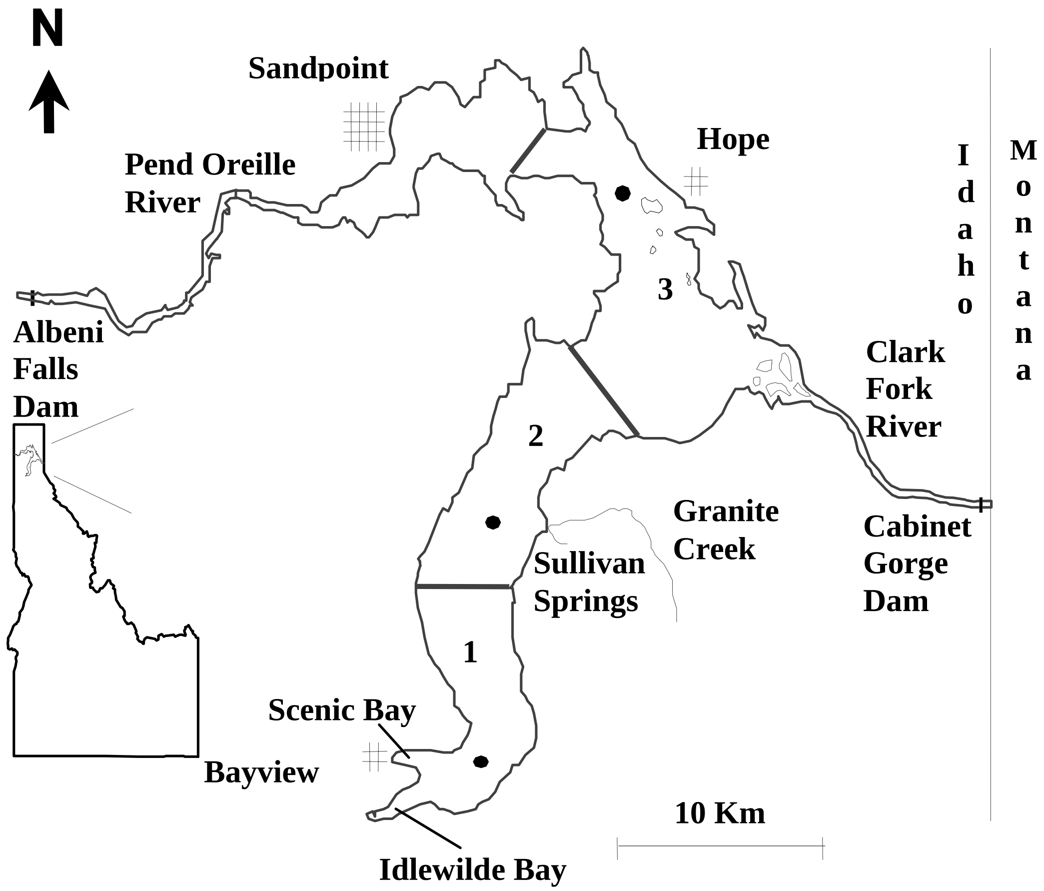
Idaho Department of Fish and Game recognized the need to change lake levels to enhance kokanee spawning in 1991. In 1996, the U.S. Army Corps of Engineers changed the drawdown of the lake as recommended by the Northwest Power Planning Council. These changes were made on a temporary basis to determine whether an altered drawdown of the lake could be used to recover the impacted kokanee population. In this chapter, we examined the effects on kokanee recruitment of a higher winter pool level that provided enhanced spawning areas on the shoreline.

STUDY AREA

Lake Pend Oreille is located in the northern panhandle of Idaho (Figure 1.1). It is the state’s largest lake and has a surface area of 38,300 ha, a mean depth of 164 m, and a maximum depth of 351 m. Summer pool elevation of Lake Pend Oreille is 628.7 m. Pelagic habitat used by kokanee is considered to be 22,546 ha (Bowler 1978). The Clark Fork River is the largest tributary to the lake. Outflow from the lake forms the Pend Oreille River.

Lake Pend Oreille is a temperate, oligotrophic lake. The average summer water temperature (May to October) is approximately 9°C in the upper 45 m of water (Rieman 1977; Bowles et al. 1987, 1988, 1989). Thermal stratification typically occurs from late June to September. Operation of Albeni Falls Dam on the Pend Oreille River keeps the lake level high and stable at about 628.7 m from July through September, followed by lower lake levels of 625.1 m during fall and winter. This was typical dam operation between 1966 and 1996, although the minimum elevation varied between years (Figure 1.2).

A wide diversity of fish species is present in Lake Pend Oreille. Kokanee migrated downstream from Flathead Lake in the early 1930s and were well established by the 1940s. Other game fish include: Gerrard rainbow trout *Oncorhynchus mykiss*, bull trout *Salvelinus confluentus,* westslope cutthroat trout *Oncorhynchus clarki lewisi*, lake whitefish *Coregonus clupeaformis,* mountain whitefish *Prosopium williamsoni*, and lake trout *Salvelinus namaycush*, in addition to several other cool and warm water species.



Section	Area (hectares)
1	6,386
2	7,776
3	8,384

Figure 1.1. Map of Lake Pend Oreille, Idaho, showing prominent landmarks and the three lake sections used in sampling. Inserted table shows the amount of kokanee habitat in each lake section.

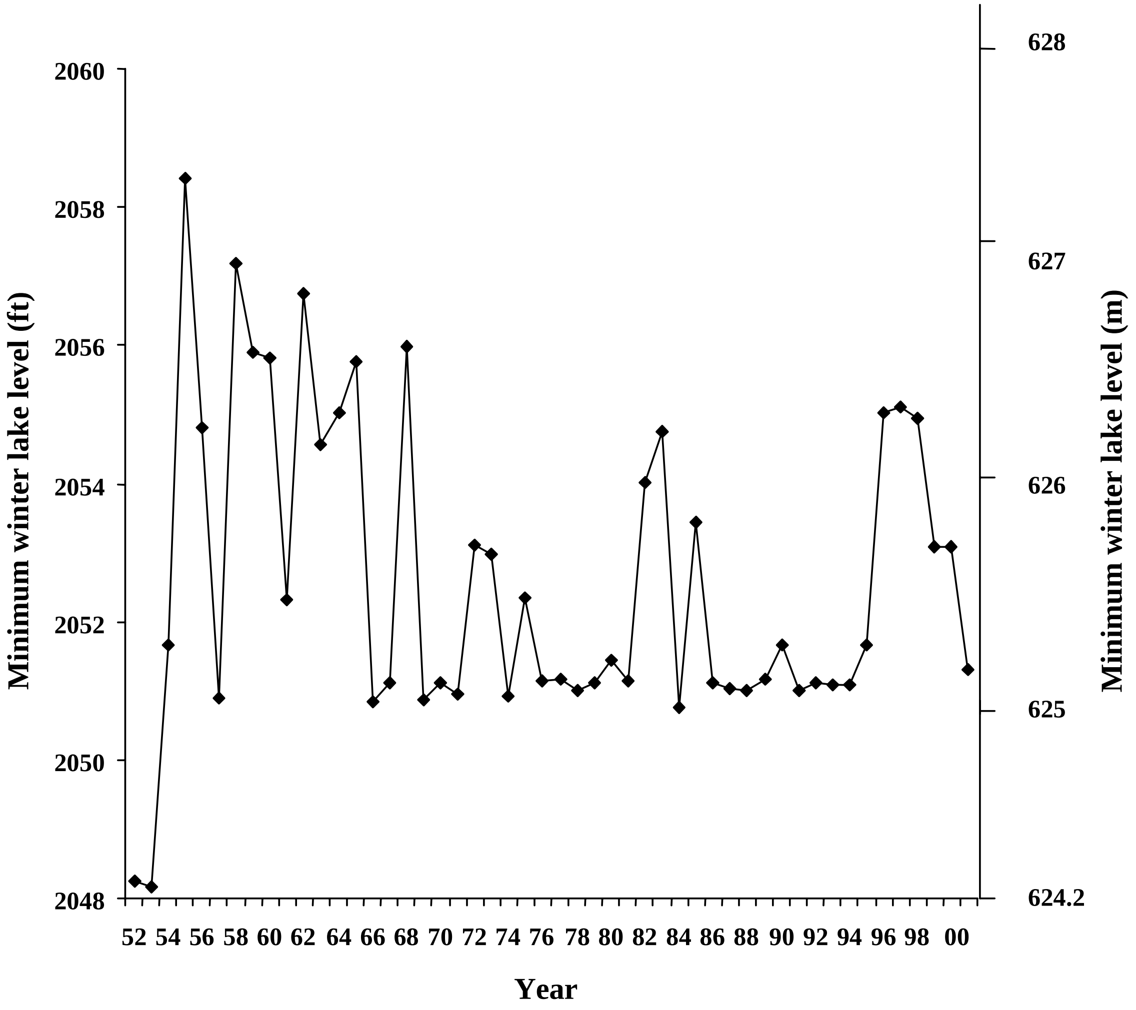


Figure 1.2. Minimum lake levels of Lake Pend Oreille, Idaho, 1952-2001. Data provided by the U.S. Army Corps of Engineers at Albeni Falls Dam. Note the pattern of lower lake levels after 1966.

METHODS

The overall approach of this study was to change the winter elevation of Lake Pend Oreille and then monitor the resulting changes in the kokanee population. The most sensitive variable was the survival rate between naturally spawned eggs and wild (non-hatchery) fry. This wild egg-to-fry survival was estimated three ways: 1) taking the hydroacoustic estimate of fry for each section of the lake and multiplying it times the percent of wild fry in each section based on the midwater trawl catch, and then dividing by the potential wild egg deposition (wild PED) as estimated by midwater trawling; 2) estimating the abundance of fry, and the percentage that were wild, in each section of the lake by a separate collection using a smaller, fine mesh, fry net, and then dividing by the potential wild PED as estimated by midwater trawling; and 3) taking the hydroacoustic estimate of fry for each section of the lake and multiplying it times the percent of wild fry in each section based on the percent of wild kokanee fry collected with the fry net, and then dividing by the potential wild PED as estimated by midwater trawling. The former method was calculated for each year of the study and the latter two methods were calculated from 1999 to 2001.

Lake Level Changes

Since consistent drawdowns to 625.1 m (2051 ft above mean sea level) were implicated in the declines of kokanee (Maiolie and Elam 1993), the lake level experiment was designed to determine if higher minimum lake levels would benefit the population. Thus, the test was to compare kokanee survival during years of full drawdown to their survival when the lake level was held higher. This test, therefore, took an adaptive management approach. The identified limiting factors of the system were examined and changed to see if the survival rate of kokanee fry would improve.

Lake Pend Oreille was drawn down to nearly its full extent in 1994 and 1995: 625.4 m and 625.3 m, respectively. Kokanee survival during these years served as baseline data for this experiment. However, the drawdown in fall of 1995 was somewhat unusual in that the lake was lowered to 625.3 m on November 24, then raised to 626.5 m on December 5. Kokanee, therefore, could spawn at a higher lake elevation in the second half of the spawning season. Lake levels remained above 626.4 m for the remainder of the winter.

During the first three winters of elevated lake levels (1996-97, 1997-98, and 1998-99), the winter lake elevation was held above 626.4 m (2055 ft), which was 1.2 m higher than most previous years in the last three decades (Figure 1.3). During the next two winters (1999-00 and 2000-01), the winter lake level was held above 625.8 m (2053 feet) or 0.6 m higher than most previous years. The original study design was for the lake to be at its low pool level (625.1 m) in 1999 and 2000, but it was held higher due to legal action over lake levels.

During this study, as in most years since 1966, the lake was lowered to its winter pool level prior to the peak of the kokanee-spawning season. This was to minimize the damage to redds caused by dropping the lake level after eggs were laid. We compared our estimates of kokanee fry survival and abundance under each of these drawdown regimes. At the onset of the experiment, we defined a >26% increase in egg-to-fry survival as one of the criteria for a successful test (Maiolie 1996).

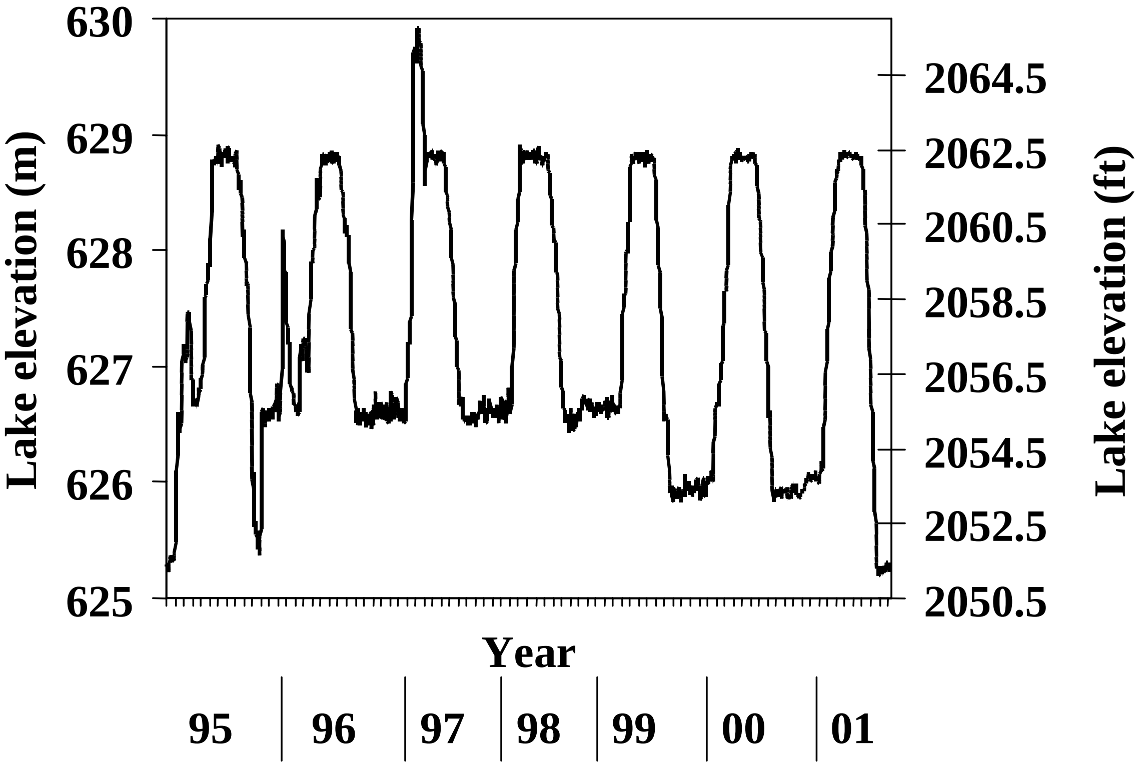


Figure 1.3. Monthly average water level of Lake Pend Oreille, Idaho, 1995-2001.

Hydroacoustics

We conducted hydroacoustic surveys on Lake Pend Oreille between mid-August and mid-September in 1995-2001. Transect selection was determined by a stratified-random or a stratified uniform approach (Figure 1.4). All hydroacoustic surveys were conducted at night and took approximately four consecutive nights to complete. A Simrad EY500 portable scientific echo sounder set to ping at 1.0 s intervals was used for the surveys. The echo sounder was calibrated annually for signal attenuation to the sides of the acoustic axis using Simrad's Lobe program. In addition, calibration of the echo sounder was checked using a 23 mm copper calibration sphere before the start of the surveys and gains adjusted to achieve the correct target strengths. Data collected during the surveys were analyzed using Simrad EP500 software version 5.2 (Figure 1.5).

The mean target strengths of at least 300 kokanee were "trace tracked" annually to separate age classes of kokanee. To be considered a fish in the trace track, the fish had to be detected (pinged) at least twice, not move more than 30 cm vertically between detections, and not missed by more than one ping during the tracking. A bar graph of target strengths versus frequency was drawn each year (Figure 1.6). We used the low points on the graph to define the breaks between fry and all other age classes of fish (older age classes could not be separated on the basis of target strengths). Density estimates of kokanee fry and older age classes were averaged within lake sections and multiplied by the area of each section (Figure 1.1) to obtain population estimates. Abundance of each older age class of kokanee was estimated based on its percent frequency within trawl samples for each section of the lake.

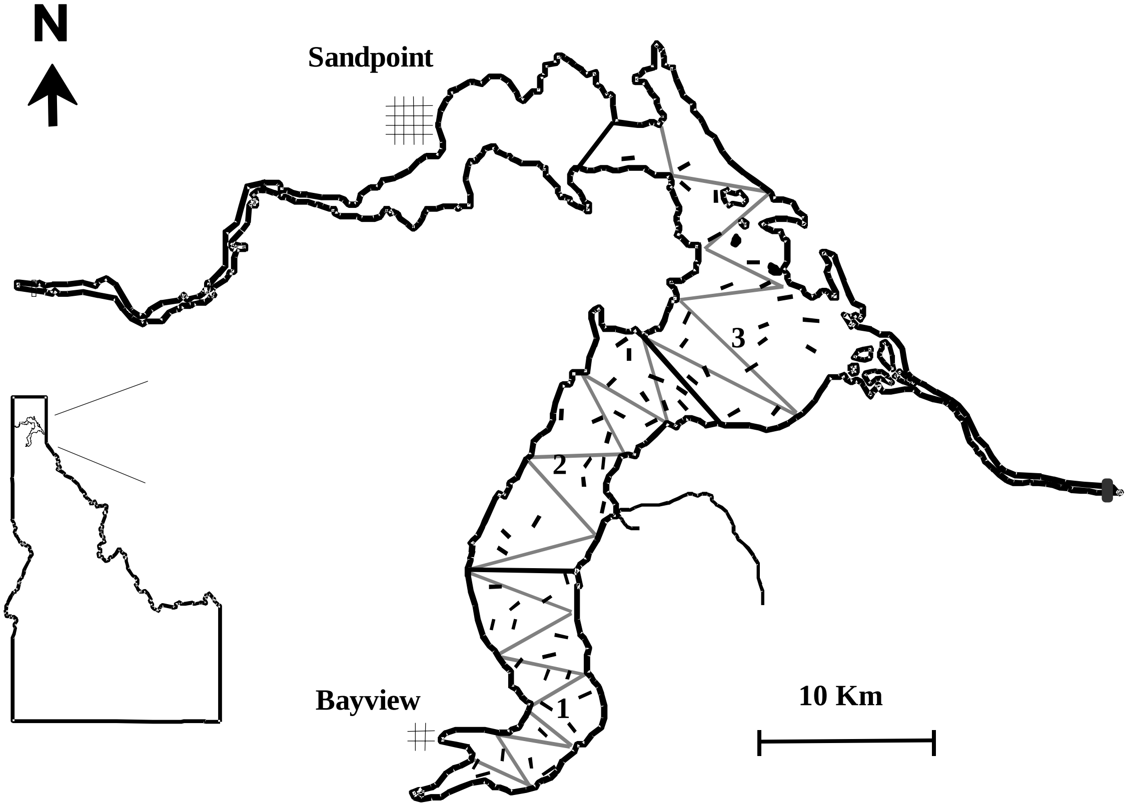
To estimate the abundance of hatchery and wild fry, we took the total estimate of fry in each section of the lake based on hydroacoustics and multiplied it by the proportion of each type of fry collected in the midwater trawl samples for that section. Section totals were summed to get lake-wide abundance estimates of hatchery and wild fry. Fry in the trawl samples had their otoliths sent to Washington Department of Fisheries and Wildlife to determine how many fry had the cold-brand mark of a hatchery fish (see Hatchery Fry Marking for more details on otolith analysis).

Wild egg-to-fry survival rates were determined by subtracting the annual hatchery egg takes from the annual potential egg deposition, as determined by the trawl data (see Midwater Trawling in Methods section). The wild PED was then divided into the estimates of wild fry based on hydroacoustic data from the following year to determine egg-to-fry survival rates for wild kokanee.

In 1995 and 1996, 12 transects were randomly chosen in each of three lake sections, totaling 36 transects per year. Each transect took approximately 15 minutes, with an average boat speed of 1.5 m/s. In both years, sampling sites were located using Global Positioning System (GPS), and a compass bearing for the direction of each transect was randomly chosen. A total of 785 fish were trace tracked in 1995 and 1,765 fish in 1996 to delineate the size distribution of kokanee fry and older age classes of fish.

In 1997, 1998 and 1999, 20 transect locations were randomly chosen in each of three lake sections, totaling 60 transects per year (Figure 1.4). Sampling sites were located using GPS, and a compass bearing for the direction of each transect was randomly chosen at each site. The boat speed was approximately 1.4 m/s (boat speed does not affect the calculations of fish density). Each transect was 10 minutes in length. A total of 1,231 fish were trace tracked in 1997, 308 in 1998, and 496 in 1999.

In 2000 and 2001, 21 transects were completed throughout the lake with eight transects in section one, six in section two, and seven in section three. We used a uniformly spaced, zigzag pattern on the lake going from shoreline to shoreline (Figure 1.4). Transect length ranged from 3.36 km to 9.46 km. Sampling sites were located using GPS. Approximately 1245 fish were trace tracked in 2000 and 880 fish in 2001. The boat speed was approximately 1.4 m/s.



Section	Area (hectares)
1	6,386
2	7,776
3	8,384

▬ 1999 Hydroacoustic transects

> 2000 Hydroacoustic transects

Figure 1.4. The location of the hydroacoustic transects used to assess the kokanee population in Lake Pend Oreille, Idaho during 1999 and 2000.

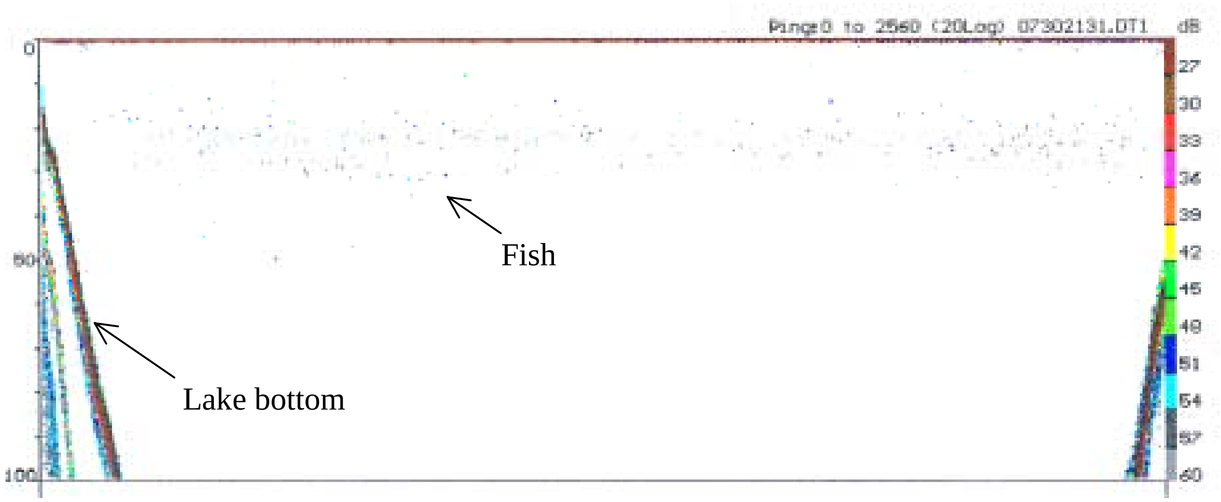


Figure 1.5. Example of an echogram collected during hydroacoustic surveys on Lake Pend Oreille, Idaho, July 2001. Scale of depth is in meters. Horizontal distance across the echogram was approximately 3.9 km.

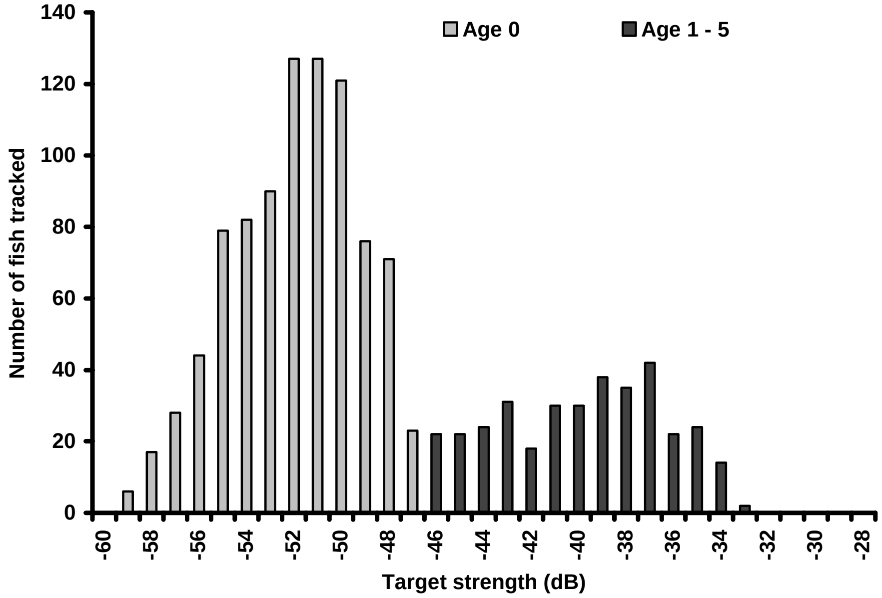


Figure 1.6. Example of target strengths of pelagic fish used to determine population estimates of kokanee in Lake Pend Oreille, Idaho. Data was collected in 2000.

Fry Netting

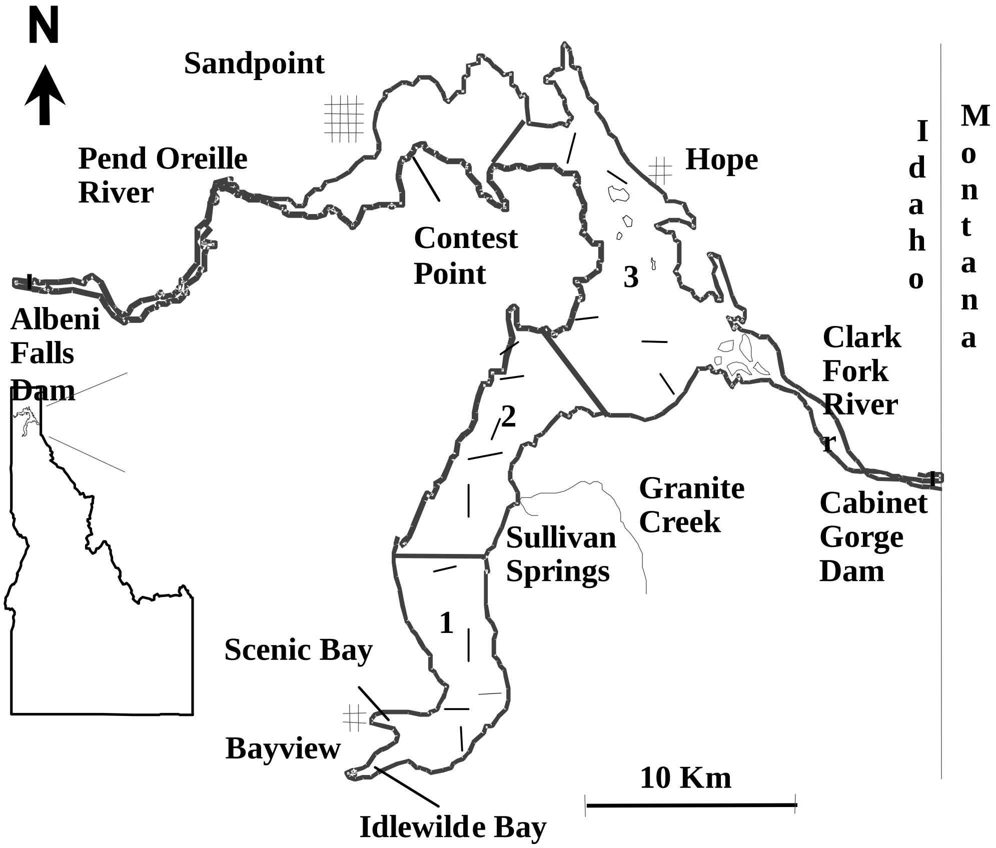
We designed and constructed a small mesh net as a second method to estimate kokanee fry abundance. Sampling with the fry net began on Lake Pend Oreille in 1999 and has continued annually thereafter. Net hauls were made during the same new moon period as that year's midwater trawling. Five transects in each lake section were chosen randomly by a stratified random sampling technique, totaling 15 transects during 1999 (Figure 1.7). The number of net hauls was increased to 10 in each lake section during 2000 and 2001.

The fry net was 1.27 m by 1.57 m across the mouth (2 m^2) and 5.5 m in length. Bar mesh size for the net was 0.8 mm by 1.6 mm. The sampling bucket, on the cod end of the net, contained panels of 1 mm mesh.

Stepwise oblique tows were made through the layer of kokanee seen on the boat's echo sounder. Fry net depths ranged from 13 m to 41 m. The fry net was towed for three minutes at each "step" (a step corresponded to a 15 m length of cable) until the entire kokanee layer had been sampled. The average boat speed was 1.5 m/s. A Kahlsico digital flowmeter model 005WE138 was secured to the fry net's mouth approximately one third of the way between the net frame and the center of the mouth.

All kokanee caught in the fry net were immediately frozen on dry ice. Upon return to the dock, the fry were stored in a freezer for later analysis. The fish were later thawed and measured for length and weight. Total length of each fry was rounded down to the nearest whole mm. In 1999 only, wild and hatchery fry in the fry net were determined based on the percent of hatchery and wild fry in each centimeter length group as determined by otolith analysis of kokanee fry caught in the mid-water trawling. Beginning in 2000, otoliths were removed from the fry caught in the fry net and sent to Washington Department of Fish and Wildlife for analysis. We randomly selected 30 fry from each section to have their otoliths analyzed. In 2001, we randomly selected 33 fry from both sections 1 and 2 and 34 fry from section 3 for otolith analysis.

Density of fry (fish/ha) in the kokanee layer was calculated for each net tow based on the volume of water sampled by the net [boat speed (m/s) x time (s) x the area of the net mouth (m^2)] as it passed through the kokanee layer, multiplied by the thickness of the kokanee layer (m), and multiplied by 10,000 to convert estimates to fish/ha. Flowmeter readings were not used since they recorded the distance obtained while raising and lowering the fry net. Density estimates were averaged per section and expanded by the area of the section. Estimates of fry within each section were summed to determine the lake-wide population estimate of fry.



Section	Area (hectares)
1	6386
2	7776
3	8384

Figure 1.7. Map of Lake Pend Oreille, Idaho, showing fry trawl transects. Five transects were randomly chosen in each lake section in 1999.

Hatchery Fry Marking

All kokanee fry released from the Cabinet Gorge Fish Hatchery since 1997 were marked by "cold branding" their otoliths (Volk et al. 1990). Cold branding provided researchers with a method to separate hatchery and wild kokanee throughout their lifecycles by noting the dark banding pattern on the otoliths of the hatchery fry (Figure 1.8). A total of 8.25, 17.71, and 12.21 million kokanee fry were stocked in 1999, 2000, and 2001 respectively. This included a 1999 total of 1.12 million early spawning variety and 7.13 million late spawning kokanee, as well as a 2000 total of 16.00 million late spawning variety and an additional 1.71 million late spawning kokanee released late in May. During 2001, all 12.21 million were late spawners.

Personnel from the Cabinet Gorge Fish Hatchery and the Clark Fork Hatchery reared and marked all of the kokanee fry. Fry within an individual raceway were from eggs collected within ten days of each other. Thermal treatments were initiated five to ten days after the fry entered their respective raceways. Each year the fry are treated to create a unique banding pattern on their otoliths. In 1999 (brood year 1998), fry of Lake Pend Oreille origin received four 24 h cool water events scheduled over nine days with one day between the first two and last two events, and three days between the second and third events. In 2000 (brood year 1999), fry of Lake Pend Oreille origin received four dark (coldwater) brands as the rearing water was systematically raised and lowered 6-9°F, alternated in 24 to 48 hour time periods. In 2001 (brood year 2000), fry received a banding pattern of four dark rings in an 11-day period. There were three days between the first two and last two events and only one day between the second and third events.

Each year, fry from each raceway were sacrificed to verify the thermal marking. These fry were sent to the Washington Department of Fish and Wildlife Otolith Laboratory in Olympia, Washington. Recognizable otolith marks were verified on all thermally treated individuals. There were no examples of thermally treated individuals not exhibiting their respective mark patterns.

To determine the banding pattern, the Washington Department of Fish and Wildlife personnel removed one sagitta from each specimen vial and oriented it on a glass plate. The otoliths were then surrounded with a preformed rubber mold. Rubber molds were then filled with clear fiberglass resin and were cured in an oven for one hour. The resulting blocks of resin containing the otoliths were cut into groups of four otoliths per block for sectioning and polishing. Blocks of four otoliths were lapped on a rotating disc of 500 grit carborundum paper until the nucleus of each otolith was clearly visible. The otoliths were then polished using a rotating polishing cloth saturated with one micron deagglomerated alpha alumina and water slurry. After lapping and polishing, the otoliths were examined with a compound microscope at 200x and/or 400x magnification. Patterns within the otolith were compared to those on reference samples taken from the hatchery fry during rearing. For accuracy, two independent readers examined each otolith. Differences between the readers were settled by reexamining the otolith.

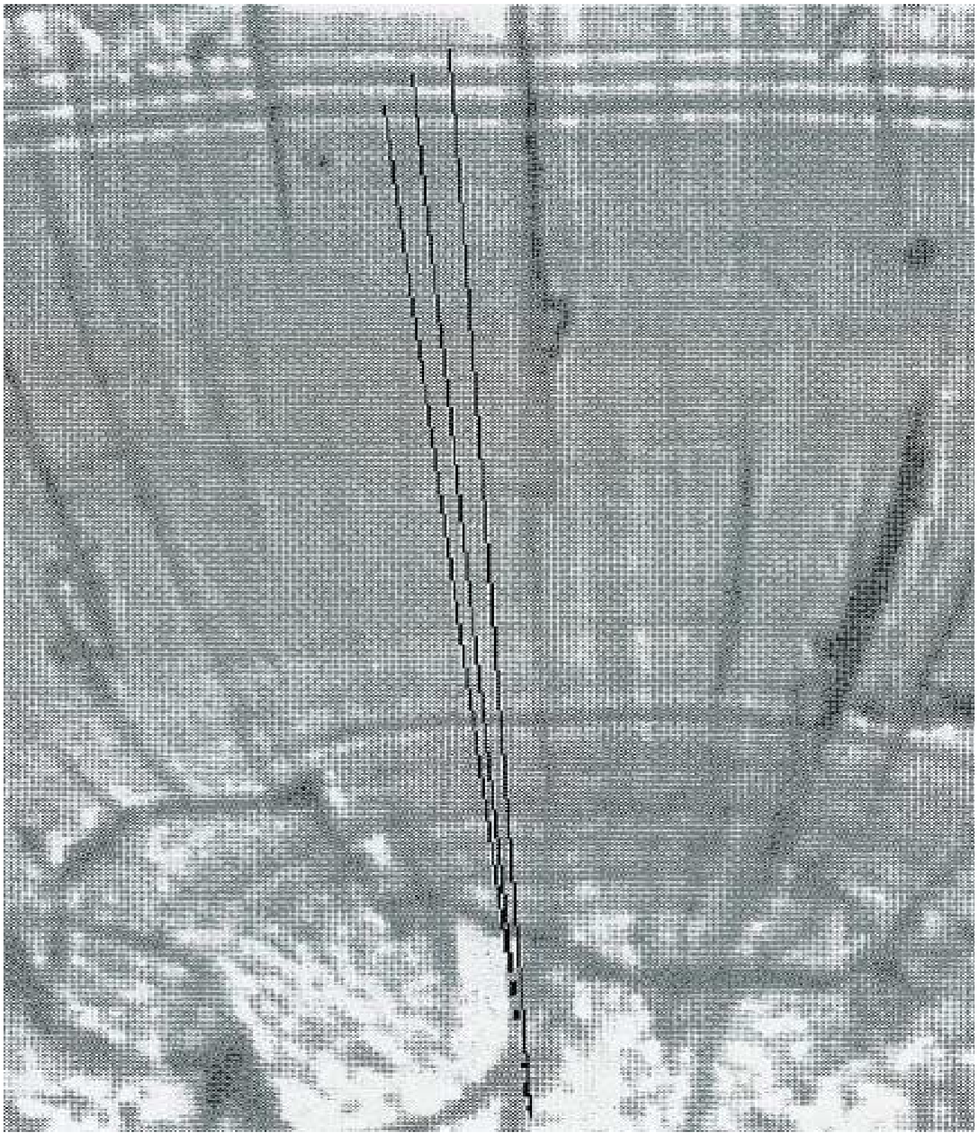


Figure 1.8. Example of cold-water branding on otolith. There were three 48-hour warm water events. The first two events were followed by 48 hours of ambient (cold) water and the final event by a return to ambient water. Overlay lines originate in the otolith core and terminate at the cold-water events. Notice the three white spaces created by the warm water events. Shown at 400X.

Midwater Trawling

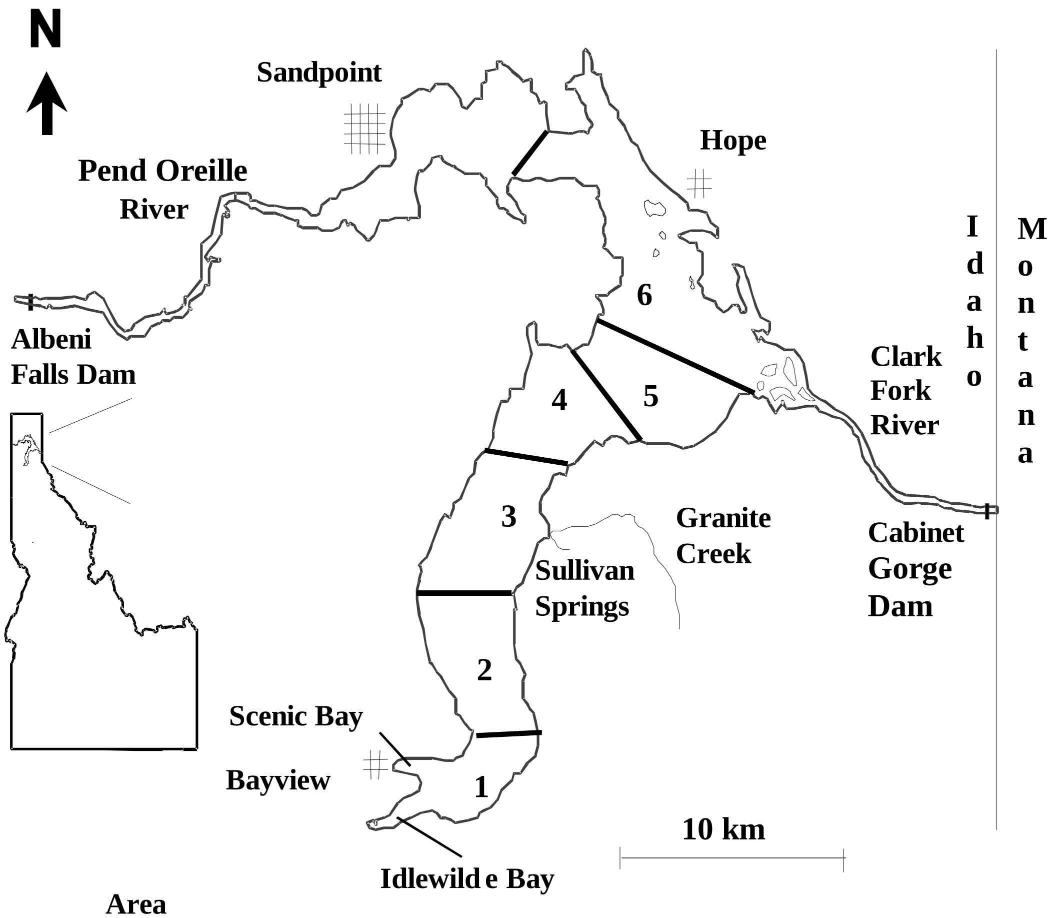
We conducted standardized midwater trawling in Lake Pend Oreille on August 22-29, 1995; September 8-12, 1996; September 29 to October 4, 1997; August 17-24, 1998; September 7-10, 1999; August 28 to September 1, 2000; and August 13-16, 2001. In addition, trawling was conducted by similar methodology during 1994 under a different project proposal (Maiolie et al. 1994). Trawling dates were during the dark phase of the moon, which optimized the capture efficiency of the trawl (Bowler et al. 1979).

The locations of the individual sampling transects changed in some years. In 1994 and 1995, the lake was divided into six sections (Figure 1.9), and a stratified systematic sampling scheme was used to estimate kokanee abundance and density. Six transects were systematically selected within each section, and one haul was made along each transect. The same transect locations were used in kokanee population monitoring on Lake Pend Oreille since 1977 (Bowler et al. 1979; Bowles et al. 1988, 1989; Paragamian and Ellis 1994). During 1996 and all later years, sections 1 and 2, 3 and 4, 5 and 6 were combined to stratify the lake into three sections to improve the precision of our estimates based on the advice of a statistician. Twelve randomly selected locations were chosen within each section for a total of 36 trawls (Figure 1.10).

Rieman (1992) described the midwater trawl and sampling procedure in detail. The net was 13.7 m long with a 3 m x 3 m mouth. Mesh sizes (stretch measure) graduated from 32, 25, 19, and 13 mm in the body of the net to 6 mm in the cod end. The trawl net was towed at a speed of 1.5 m/s by an 8.5 m boat. We determined the vertical distribution of kokanee by using a Raytheon Model V850 depth sounder with a 20° hull-mounted transducer. In 1998, we switched to using a Furuno Model FCV-582 depth sounder with a 10° transom mounted transducer. A step-wise oblique tow was conducted along each transect which sampled the entire vertical distribution of kokanee.

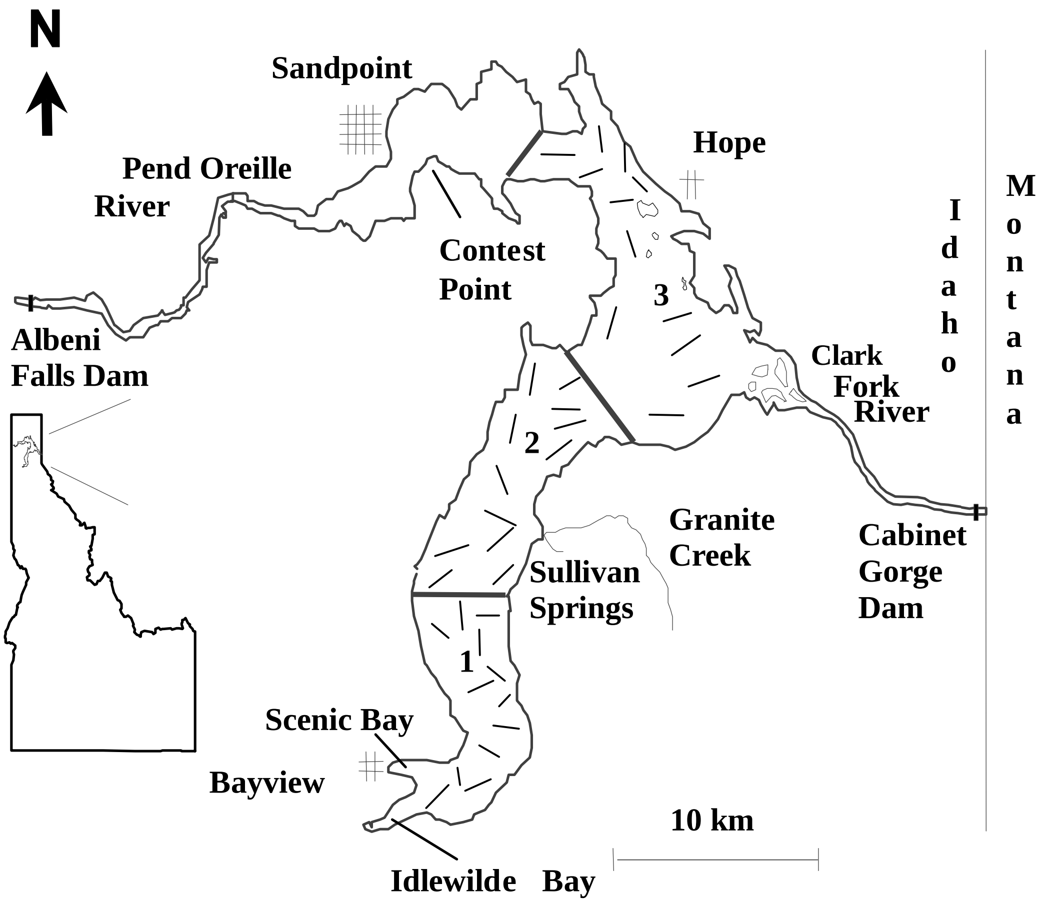
Fish from each trawl sample were counted and placed on ice until morning when they were transferred to a freezer. Lengths and weights of individual kokanee were recorded, and all fish over 170 mm were checked for maturity. Scales were taken from 10 fish in each 10 mm size interval for aging (Figure 1.11). Beginning in 1997, otoliths (317 pairs) were removed from kokanee fry and sent to the Washington Department of Fish and Wildlife Otolith Analysis Laboratory to determine if the fry were of hatchery or wild origin. In 1998, 200 pairs of otoliths were removed from age-0 and age-1 kokanee; in 1999, 205 pairs of otoliths were removed from age-0, age-1, and age-2 kokanee; in 2000, 291 pairs of otoliths were removed from age-0, age-1, age-2, and age-3 kokanee, and in 2001, 242 pairs of otoliths were sent for analysis from all age classes of kokanee.

Potential egg deposition was calculated by using percent maturity within each 1 cm length group. Percent maturity was multiplied by the population estimate within each length group and then summed. To obtain the population estimate for mature females, we then divided the total mature population by two. The number of mature females in the lake was then multiplied by the mean fecundity seen at the Granite Creek spawning station to estimate PED. We then subtracted the number of eggs collected by hatchery personnel at the Cabinet Gorge Hatchery and Granite Creek egg-take stations to determine the number of eggs spawned by wild fish (wild PED).



Section	Area (hectares)
1	3166
2	3220
3	3739
4	4037
5	3373
6	5011

Figure 1.9. Map of Lake Pend Oreille, Idaho, showing prominent landmarks and the six lake sections used in 1995.



Lake Sections (hectares)

1	6386
2	7776
3	8384

╱ Trawl Transect

Figure 1.10. Map of Lake Pend Oreille, Idaho, showing the location of transects used for midwater trawling in 1999 on Lake Pend Oreille.

Figure 1.11. Example of a kokanee scale (age-4). Arrows indicate the location of annuli.

Limnology

We measured water temperature, dissolved oxygen, and water clarity (Secchi transparency) monthly from January through December 1997 to 2001. Data were collected at three standardized locations, representing the southern, middle, and northern sections of the lake (Figure 1.1). Sample dates were approximately the middle of each month. We used a Yellow Springs Instrument Company model 57 meter to measure temperature and dissolved oxygen from the surface to a depth of 59 m. The meter was calibrated before each survey using the “water saturated air” method suggested by the manufacturer. Water clarity was monitored at each station using a 20 cm diameter Secchi disk during each survey.

RESULTS

Hydroacoustics

Population estimates of kokanee fry made by hydroacoustics ranged from 3.708 million (1998) to 14.141 million (2000) (Table 1.1). The highest densities of fry were generally found in the northern third of the lake (Section 3), closer to where the hatchery fry are stocked. Ninety percent confidence limits on these estimates ranged from 8.6 to 15.7%

The hydroacoustic estimates of wild fry derived using the percent composition of wild fry in the midwater trawl net ranged from 1.019 million fry (1998) to 5.231 million fry (2000) (Table 1.2 and Figure 1.12). Wild fry were distributed differently across the lake sections in different years. During 2000, wild fry abundance was highest in the middle of the lake; however, in 1996 they were higher in the north end, and in 1995 they were highest in the south end.

Abundance estimates of kokanee ages 1 to 5 ranged from 2.218 to 7.327 million (Table 1.3). The northern section of the lake (section 3) generally had the highest population estimate of kokanee.

Table 1.1. Hydroacoustic population estimates (millions) of kokanee fry in three sections of Lake Pend Oreille, Idaho, from 1995 through 2001.

Year	Southern Section (1)	Middle Section (2)	Northern Section (3)	Total for Lake	90% C.I.
2001	2.384	4.857	3.806	11.047	±10.2%
2000	2.489	5.951	5.701	14.141	±11.5%
1999	1.234	2.128	2.661	6.023	±8.6%
1998	0.755	0.926	2.027	3.708	±11.8%
1997	1.126	1.700	3.264	6.090	±9.9%
1996	1.412	2.592	2.936	6.940	±15.7%
1995	1.691	2.268	3.251	7.210	±9.0%

Table 1.2 Hydroacoustic population estimates of wild kokanee fry (millions) in Lake Pend Oreille, Idaho, 1995 to 2001 by lake section. Fry estimates (Table 1.1) were partitioned into wild fry based on otolith analysis of fry caught by midwater trawling (Table 1.6).

Year	Section 1	Section 2	Section 3	Total Wild Fry Abundance
2001	1.355	1.541	0.837	3.733
2000	1.326	2.342	1.563	5.231
1999	0.805	0.940	0.828	2.573
1998	0.318	0.218	0.483	1.019
1997	0.714	0.538	1.323	2.575
1996	0.841	0.886	0.934	2.661
1995	1.305	1.235	0.600	3.140

Table 1.3. Hydroacoustic population estimates (millions) of kokanee ages 1-5 in three sections of Lake Pend Oreille, Idaho, from 1995 through 2001.

Year	Section 1	Section 2	Section 3	Total for Lake	90% C.I.
2001	0.980	1.479	2.443	4.902	±9.5%
2000	0.871	1.032	1.935	3.838	±14.2%
1999	0.762	0.240	1.817	2.819	±17.8%
1998	0.933	0.823	3.272	5.028	±16.7%
1997	1.234	1.316	3.211	5.761	±15.8%
1996	2.208	2.384	2.736	7.328	±18.6%
1995	2.951	1.171	2.746	6.868	±11.8%

Fry Netting

Density estimates of kokanee fry made with the fry net were closely correlated to fry density estimates based on hydroacoustics ($r^2 = 0.88$) (Figure 1.13 and Table 1.4). Fry densities in the hydroacoustic estimates were 1.33 times the estimates in the fry net. Lower estimates with the fry net were likely due to net avoidance by the fry. Whole lake population estimates using the two sampling methods showed a slightly better correlation than did the lake section estimates ($r^2 = 0.90$), probably due to the larger sample size in the whole lake estimates. Close correlation between the two sampling methods helps to corroborate the accuracy of either method.

Kokanee fry collected with the fry net ranged from 12% wild (northern section in 2001) to 88% wild (southern section in 2001) (Figure 1.14). Highest percentages of wild fry were found in the southern section of the lake where most of the shoreline spawning occurs. These percentages of wild fry provide a second method to partition the hydroacoustic estimates. This yielded population estimates of wild fry of 3.937 million in 1999, 7.822 million in 2000, and 3.537 in 2001 (Table 1.5). Wild fry survival rates were therefore 9.1% in 1999, 14.9% in 2000, and 6.2% in 2001 based on this methodology.

Sizes of the fry showed a bimodal distribution with the wild fry being smaller than the hatchery fry (Figure 1.15). Wild fry generally ranged in size from 24 to 80 mm, with a mean of about 40 mm and the majority of them smaller than 60 mm.

Table 1.4. Population estimates (millions) of all kokanee fry in Lake Pend Oreille, Idaho 1999 to 2001 based on fry netting.

Lake Section	1999	2000	2001
Southern	1.220	2.271	1.962
Middle	1.529	4.548	3.409
Northern	2.085	3.693	3.432
Total	4.834	10.513	8.804

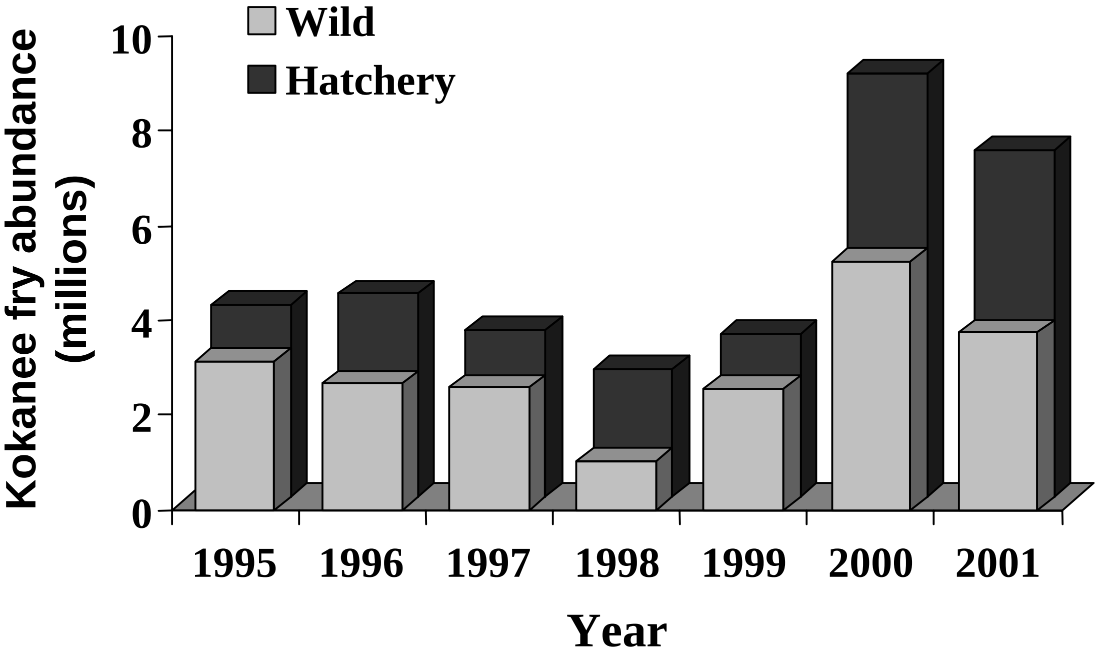


Figure 1.12. Population estimates of kokanee fry based on hydroacoustic surveys in Lake Pend Oreille, Idaho, 1995 to 2001. Estimates were partitioned into hatchery and wild components based on the composition of the mid-water trawl catch.

Table 1. 5. Hydroacoustic/fry net estimates of wild kokanee fry (millions) in Lake Pend Oreille, Idaho 1999 to 2001. Population estimate was based on hydroacoustic fry abundance (Table 1.0) and partitioned into the percent of wild fry based on the otolith analysis of the catch in a fry net. Wild potential egg deposition (PED) (millions) was estimated by midwater trawling.

Lake Section	**1999**		**2000**		**2001**	
	Percent Wild	**Estimate**	**Percent Wild**	**Estimate**	**Percent Wild**	**Estimate**
Southern	81%	1.000	73%	1.817	88%	1.727
Middle	78%	1.660	53%	3.154	41%	1.398
Northern	48%	1.277	50%	2.851	12%	0.412
Total of wild fry		3.937		7.822		3.537
Wild PED previous year		43.185		52.41		56.67
Wild egg-to-fry survival		9.1%		14.9%		6.2%

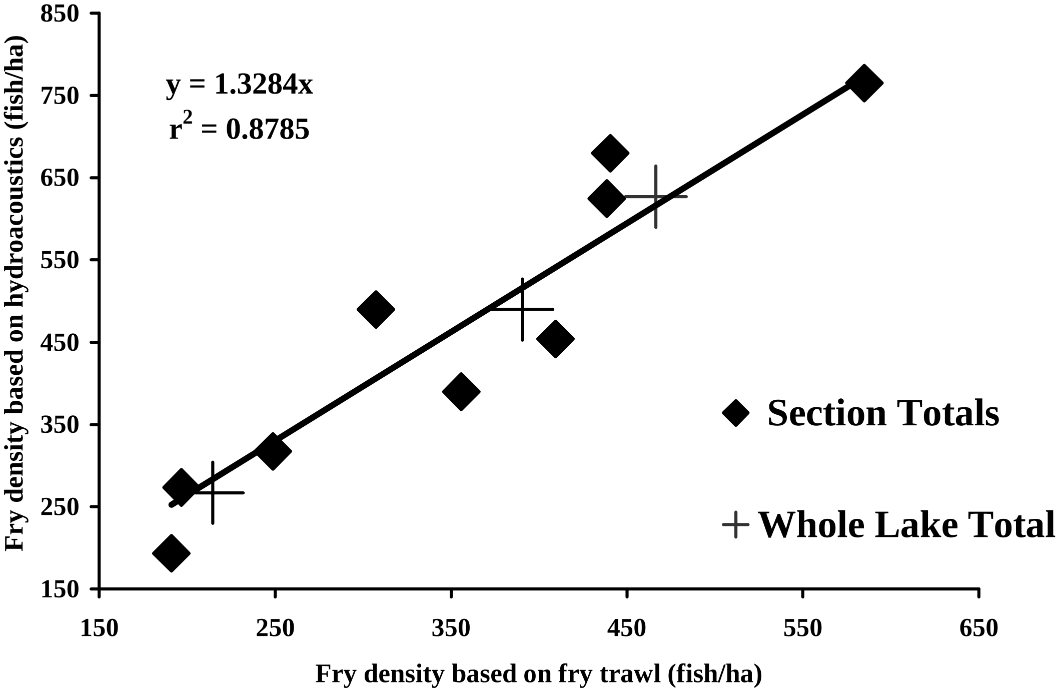


Figure 1.13. Comparison of kokanee fry density estimates made by hydroacoustics and fry netting in Lake Pend Oreille 1999, 2000, and 2001. Correlation and equation were based on section totals. Density estimates for each lake section (diamonds) used five to ten fry trawls and six to eight hydroacoustic transects. Whole lake density estimates (+) were based on 15 to 30 fry trawls and 20 to 60 hydroacoustic transects.

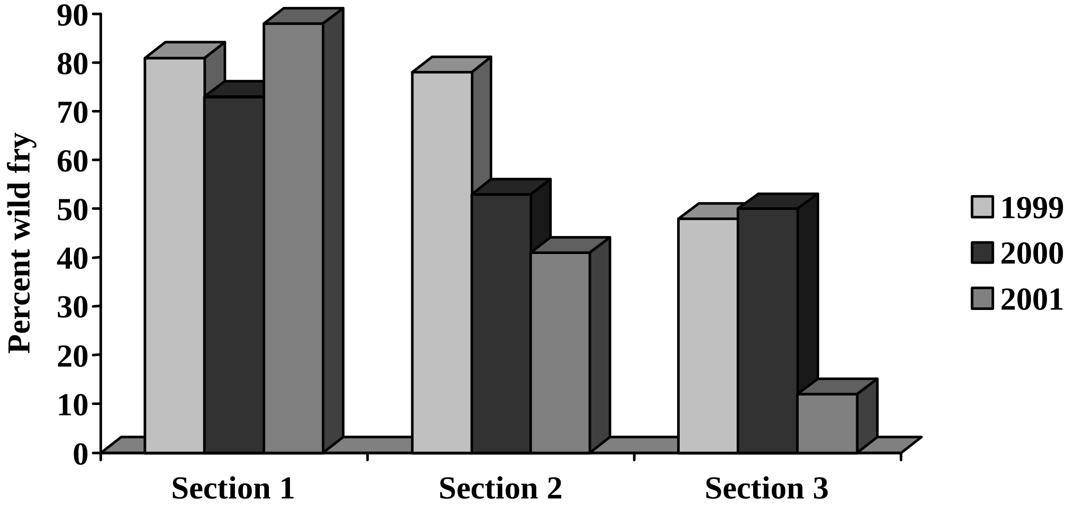


Figure 1.14. Percentage of wild fry collected in a fry net in each section of Lake Pend Oreille, Idaho, 1999, 2000, and 2001.

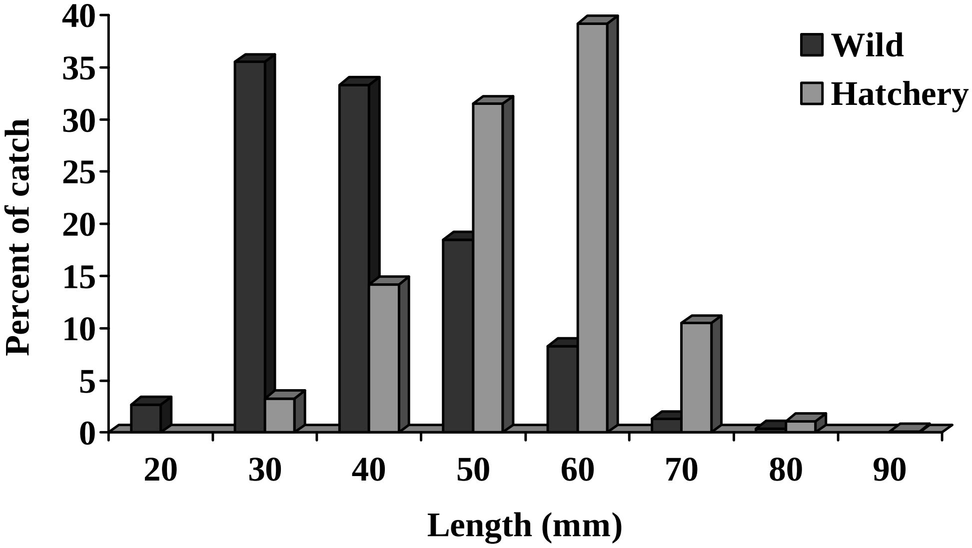


Figure 1.15. Length frequency of wild and hatchery kokanee fry collected in Lake Pend Oreille, Idaho, August 2000 with a fry net.

Midwater Trawling

Wild kokanee fry comprised 18% to 77% of the fry caught in individual sections of Lake Pend Oreille (Table 1.6) with the midwater trawl. Section 1 (southern section) consistently had the highest percentage of wild fry. These percentages were used to partition the hydroacoustic estimate into an abundance estimate of wild fry (Table 1.2).

The population estimate of mature female kokanee ranged from 33,404 females in 1997 to 599,000 females in 1994 (Fredericks et al. 1995) (Table 1.7). Wild PED was estimated to range from 10.65 million eggs in 1997 to 229.4 million eggs in 1994 (Idaho Department of Fish and Game files).

Table 1.6. The percent of wild kokanee fry in three sections of Lake Pend Oreille, Idaho based on their collection in a midwater trawl and examination of their otoliths for hatchery banding patterns.

Year	Section 1	Section 2	Section 3
2001	56.83	31.73	21.99
2000	53.29	39.35	27.42
1999	65.22	44.16	31.13
1998	42.11	23.53	23.81
1997	63.41	31.65	40.52
1996	59.52	34.20	31.82
1995	77.19	54.45	18.46

Wild Fry Survival

Based on hydroacoustic estimates of fry abundance partitioned by the percent that were wild in the midwater trawl, survival rates from wild kokanee eggs to wild fry varied from a low of 1.4% to a high of 10.0% (Table 1.7 and Figure 1.16). Survival rates showed dramatic improvement during four out of five years when lake levels were raised (Figure 1.16). Mean survival was 3.15% before lake levels changed in 1995 and 1996 (n = 2). After lake levels changed in 1998 to 2001, wild fry survival averaged 8.05% (n = 4). The increase in survival rate was statistically significant at the probability level of p = 0.059 (5.9% probability that the observed changes were due to random chance). Data from 1997 was not used in this comparison since it was a flood year with the highest spring flow on record for the Pend Oreille River (McGrane 1999). Survival remained low during 1997 (eggs laid in 1996) (1.8%).

Wild egg-to-fry survival was positively correlated to the increase in winter lake elevation during this study (r^2 = 0.85, 1997 data excluded) (Figure 1.17). For example, wild fry survival was estimated at 9.6% in 1998 (eggs that were laid in 1997) when the lake was held at an elevation of 626.4 m or 1.3 m above the lake's minimum pool level. Survival was also high (10%) in 2000, a year that lake levels were held 0.6 m higher than normal. Wild fry survival was also inversely correlated to the number of mature female kokanee in the lake (Figure 1.18). When the lake was drawn down to its low pool elevation, fry survival was 1.4 % and 4.9% as the abundance of mature female kokanee went from 599,000 to 152,000, respectively. Better survival rates were estimated in years when the lake was held higher during the winter. Survival rates in these years varied from 6.0% to 10.0%.

An additional calculation of wild egg-to-fry survival was based on the number of wild kokanee fry in the hydroacoustic estimates, partitioned into wild fry based on the proportion of wild fry in the fry net, and dividing by the wild PED estimates made by trawling. Egg-to-fry survival rates were 9.1% in 1999, 14.9% in 2000, and 6.2% in 2001.

Table 1.7. Comparison of minimum lake level to number of mature females (as determined by midwater trawling), mean fecundity, hatchery egg take, potential egg deposition (PED), wild fry abundance the following year (by hydroacoustics), and percent survival of kokanee fry in Lake Pend Oreille, Idaho, 1995-2001.

Year Class of Eggs[a]	Minimum Lake Level (ft) (m)	Number of Females	Eggs Per Female	PED (millions)	Hatchery Egg Take (millions)	Wild PED (millions)	Wild Fry Abundance Following Year (millions)	Percent Survival (eggs to fry the next year)
2001	2051.3 625.2	33,563	481	16.14	7.68	8.46	—	—
2000	2053.1 625.8	167,794	417	69.97	13.30	56.67	3.733	6.6
1999	2053.1 625.8	197,358	379	74.79	22.38	52.41	5.231	10.0
1998	2054.9 626.3	156,580	333	52.14	8.96	43.18	2.573	6.0
1997	2055.1 626.4	33,404	335	11.19	0.54	10.65	1.019	9.6
1996	2055.0 626.4	413,720	353	146.04	4.49	141.55	2.575	1.8
1995	2051.7 625.4	151,650	444	67.33	12.89	54.44	2.661	4.9
1994	2051.1 625.2	599,000	411	246	16.6	229.4	3.140	1.4

[a] Year class of eggs is defined as the year the eggs were laid.

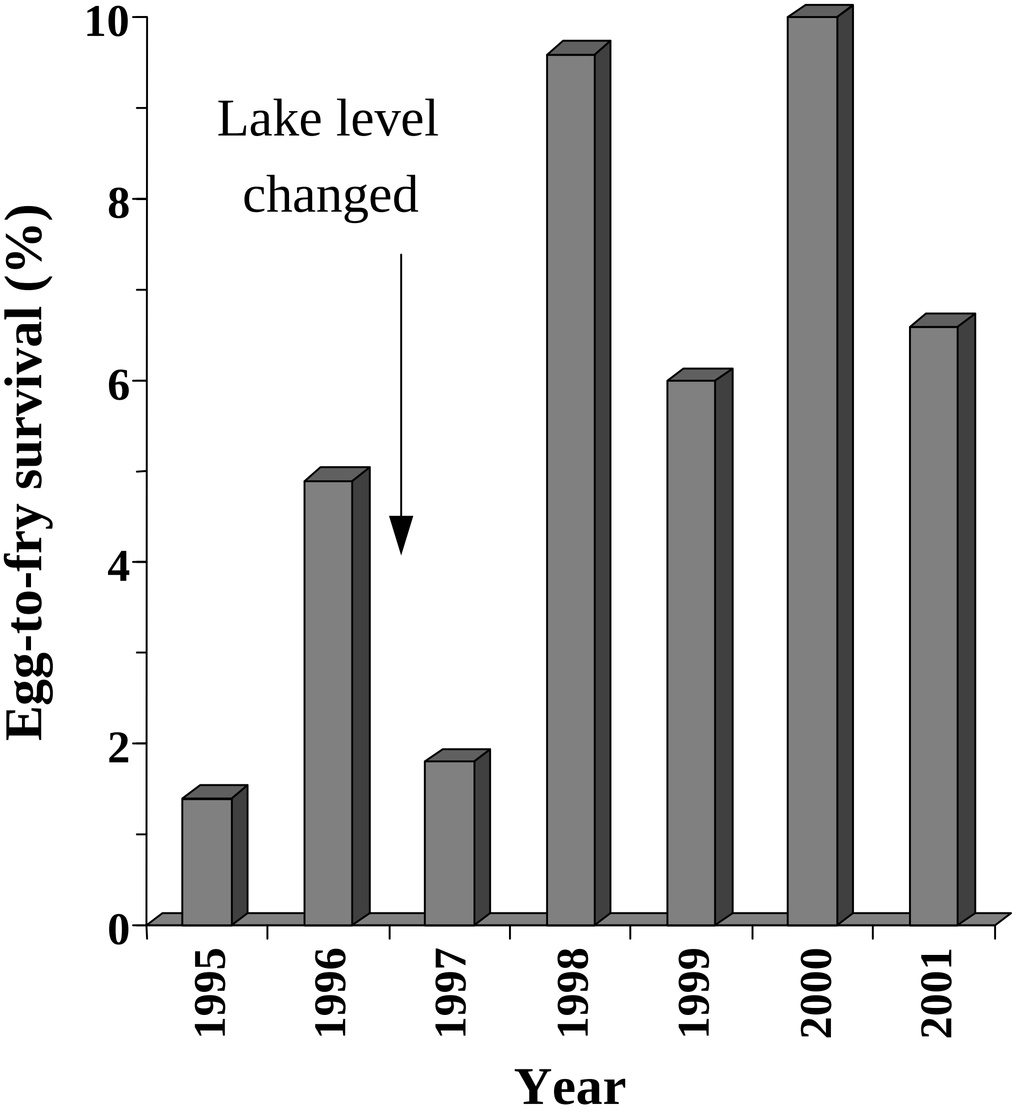


Figure 1.16. Survival of wild kokanee eggs to fry in the fall of their first year of life in Lake Pend Oreille, Idaho. Survival was based on potential wild egg deposition estimates made by trawling and wild fry abundance estimated by hydroacoustics. Winter lake levels were changed in each year after 1996. Year on the x axis is the year the fry were sampled.

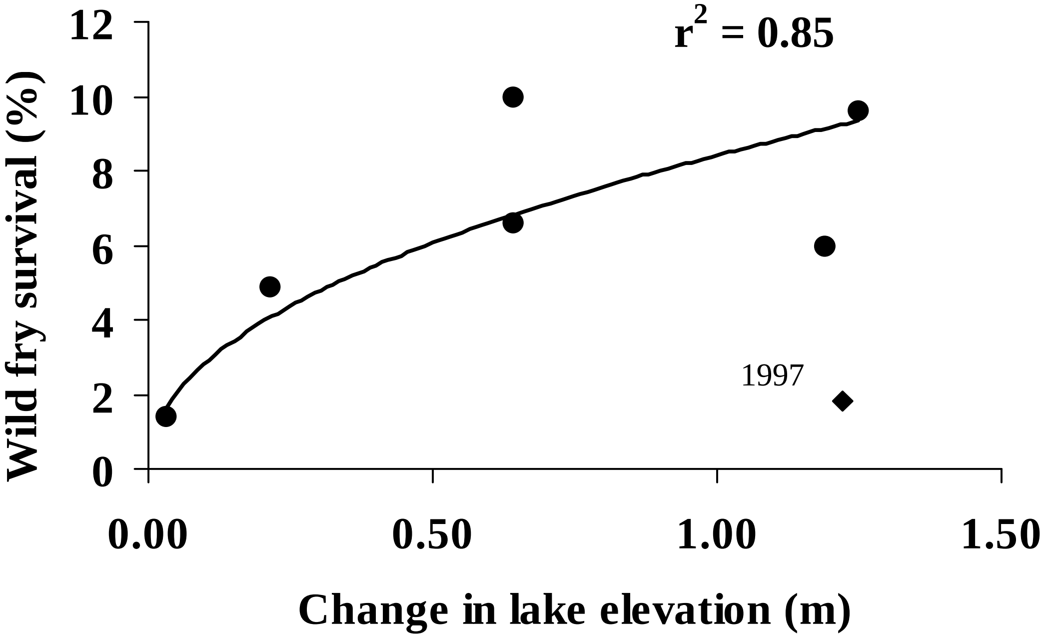


Figure 1.17. Correlation between wild fry survival (Table 1.7) and the change in lake elevation above low pool level (elevation 625.1 m, 2051 ft). Data from the flood year of 1997 was omitted from the correlation.

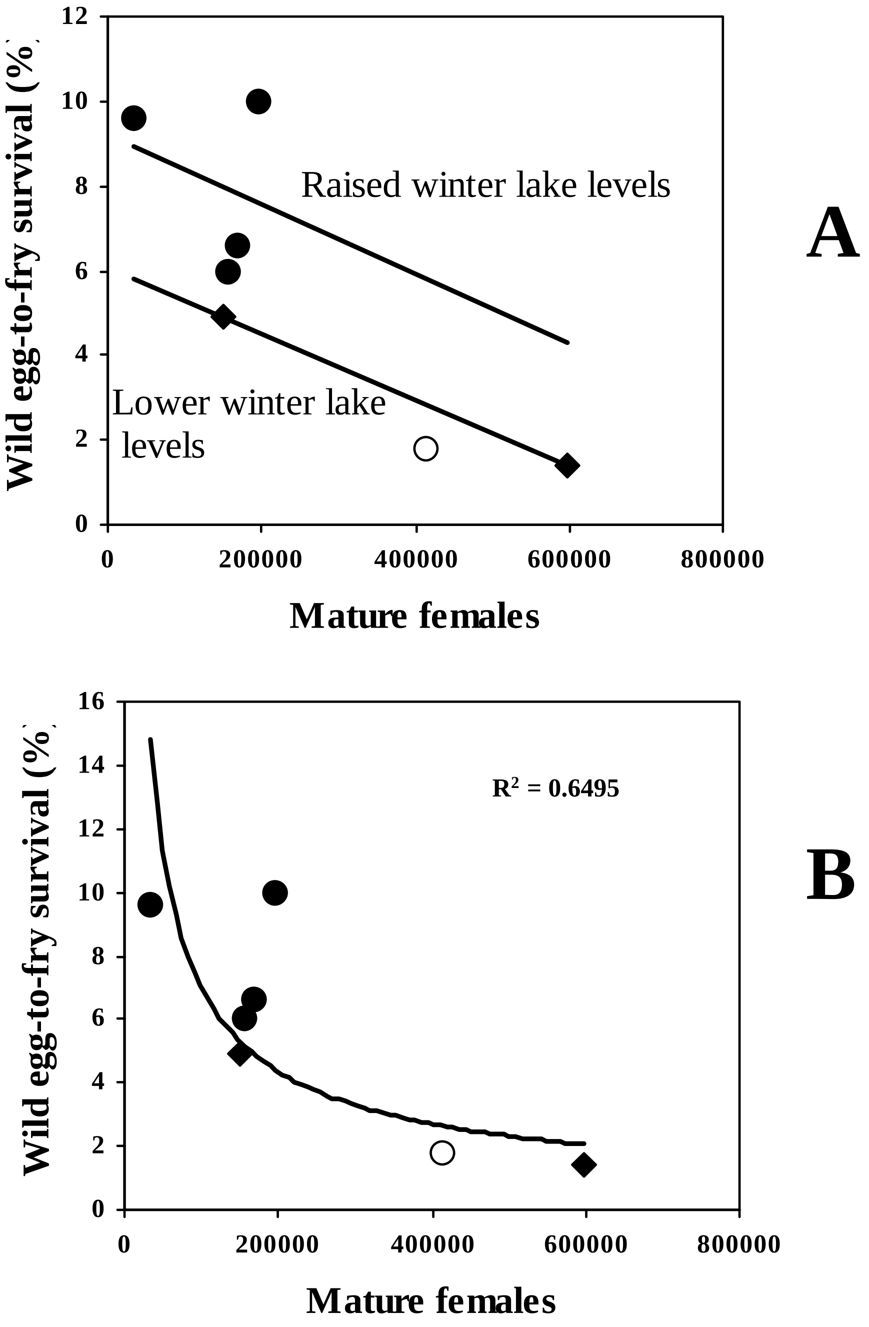


Figure 1.18. Survival of kokanee from wild spawned eggs to fry in Lake Pend Oreille, Idaho. A.) Lower line (diamonds) is the survival trend when lake is lowered to its minimum pool level during the fall drawdown (n = 2). Upper line (dots) is the survival trend when lake elevation is raised during winter (n = 4). Lines were extended beyond the range of points for clarity. Flood year of 1997 (open circle) was omitted from correlations. B.) Relationship between the number of female kokanee and wild egg-to-fry survival data. Line was fitted by power regression.

Depth of Kokanee Spawning

We found that the modal depth of kokanee spawning was at 1.2 m during the spawning season of 1997 during a year in which the lake level was 1.2 m above minimum pool (Figure 1.19). Thus, the most frequently used area for spawning was the old water line at elevation 625.1 (2051 ft). Scenic Bay contained 37% of the redds based on area during that year (Figure 1.20).

During 1999, the peak depth of kokanee spawning was again 1.2 m (Figure 1.19). The lake's minimum elevation that winter was 625.8, making the peak depth utilized by kokanee at elevation 624.6 (0.5 m below the old water line at minimum pool). Thirty-eight percent of all redds by area were located in Scenic Bay (Figure 1.20).

We noted much deeper spawning in 2001 with a modal spawning depth of 4.0 m (Figure 1.19). The lake was drawn down to an elevation of 625.1 m (2051 ft); thus, the peak of spawning occurred at an elevation of 621.1. Most of the spawning activity occurred in Scenic Bay (70% of the total area of all redds) (Figure 1.20).

Limnology

The lowest and highest Secchi depths obtained during the four-year analysis occurred in 1997 and 2000 respectively (Table 1.8). In May of 1997, we measured a Secchi depth of 0.7 m at the north end and a depth of 19.5 m in the southern section during March of 2000. Overall, the northern section of the lake had considerably lower water transparencies than the middle and southern sections between 1997 and 2000. The mean Secchi depth from April to October was not well correlated to the survival rates of wild kokanee fry (r^2 = 0.50).

Surface water temperature ranged from 2.9°C to 25.2°C between 1997 and 2000. The maximum water temperature for *Mysis* shrimp feeding is thought to be 14°C (Martinez and Bergersen 1991). Throughout the study, the maximum depth reached by 14°C water was generally between depths of 15 and 23 m, but timing and duration of this warm water at these depths varied considerably from year to year (Figure 1.21 and 1.22). Lake Pend Oreille maintained 14°C temperatures at the surface, 10 m depth, and 15 m depth for more days in 1999 than any other year (Table 1.9). Mid-June water temperatures between 1997 and 2000 rose above an eight-year range of temperatures (from 1985 to 1992) in 1999 between 5 m and 10 m depths and in 2000 between 20 m and 50 m depth (Figure 1.23). Days of water temperature over 14°C at the 10 m depth and 15 m depth were weakly correlated to the survival rates of wild kokanee fry (r^2 = 0.50 and 0.22, respectively) (Figure 1.24).

Each year of analysis, the dissolved oxygen concentrations were similar among all three stations. At each station in 1997, we measured oxygen concentrations between 13.5 mg/l and 14.0 mg/l in May and 8.2 mg/l to 8.3 mg/l in September. The values in May 1997 represent oxygen saturation levels over 130% when adjusted for water temperature and elevation. At each station in 1998, we obtained oxygen concentrations between 12.0 mg/l to 12.6 mg/l in May and 7.8 mg/l to 8.0 mg/l in September. At each station in 1999, we obtained oxygen concentrations between 11.2 mg/l and 11.6 mg/l in May and 8.3 mg/l to 8.6 mg/l in September. In 2000, we measured oxygen concentrations of 11.9 mg/l to 12.0 mg/l in April and 8.3 mg/l to 8.6 mg/l in September. As expected, dissolved oxygen readings declined as water temperature increased. All measurements of dissolved oxygen were sufficient for good kokanee growth and survival, with the exception that gas supersaturation in May of 1997 could potentially be lethal.

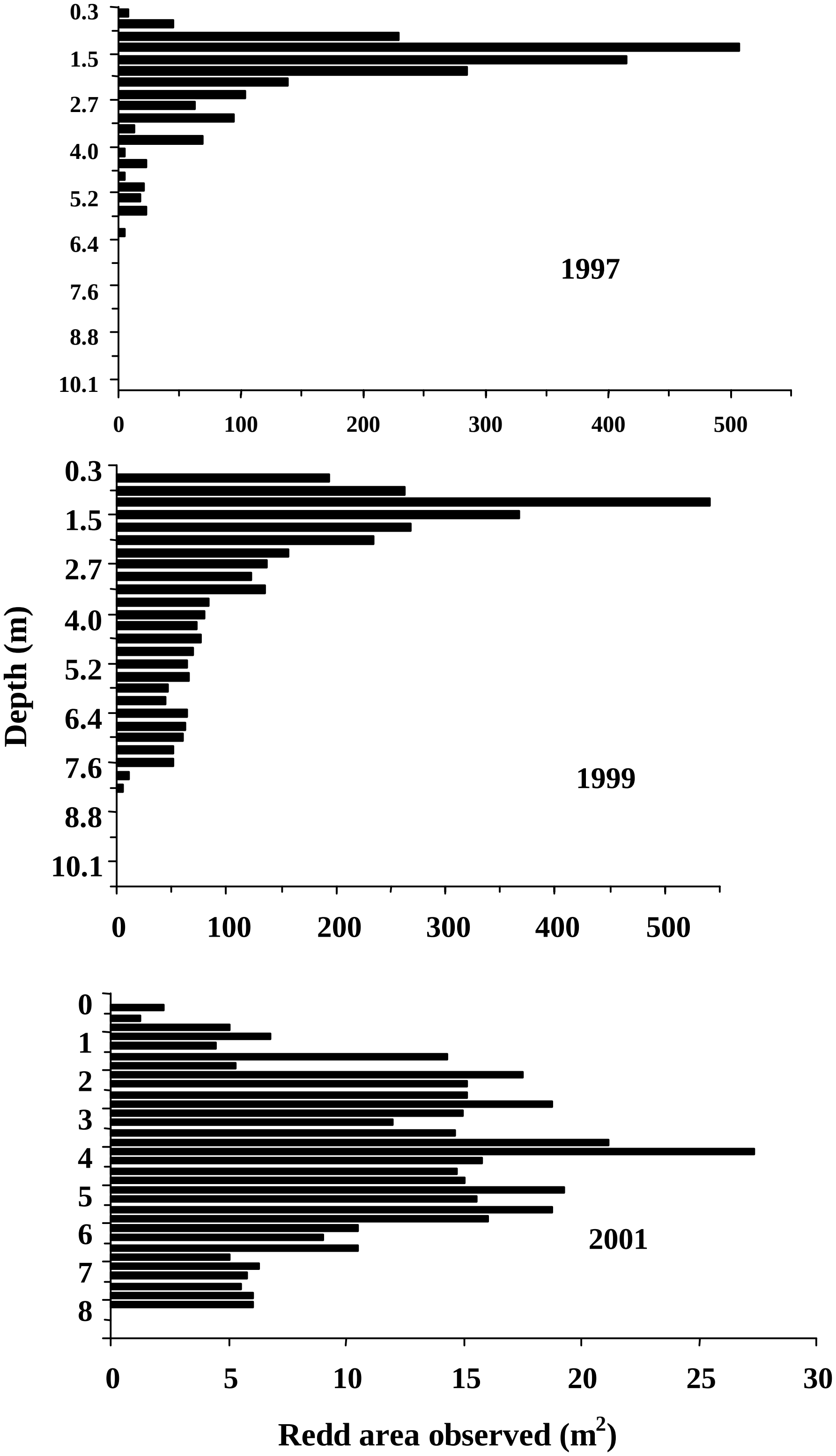


Figure 1.19. Depths of kokanee spawning on the shorelines of Lake Pend Oreille, Idaho. The lake's winter pool level was 1.2 m above minimum pool in 1997, 0.6 m above minimum pool in 1999, and at the minimum pool level in 2001.

Table 1.8. Secchi transparencies (m) at three locations in Lake Pend Oreille, Idaho in 1953, 1974, 1997, 1998, 1999, & 2000. Mean transparency is for April through October.

Southern station	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**	**Mean**
1953	—	—	—	11.9	8.0	3.7	6.1	11.6	8.5	12.8	—	—	8.9
1974	—	—	—	8.8	7.6	3.7	3.9	9.2	9.1	9.3	—	—	7.4
1997	—	—	—	12.5	4.0	2.7	6.5	8.2	9.0	6.2	7.5	8.7	7.0
1998	16.5	17.0	13.5	9.0	6.0	4.0	5.5	11.0	9.5	7.7	8.5	10.0	7.5
1999	—	—	—	5.9	7.0	2.7	5.6	7.3	8.3	7.5	8.8	11.5	6.3
2000	11.5	—	19.5	5.5	5.9	7.2	9.4	11.4	9.5	8.0	10.0	13.5	8.1
Mid-lake station													
1953	—	—	—	—	—	3.7	6.1	10.7	12.2	12.2	—	—	—
1974	—	—	—	—	5.5	2.3	4.7	9.8	9.4	11.6	—	—	—
1997	—	—	—	16.5	5.2	2.0	5.0	7.9	6.8	8.0	9.0	10.0	7.3
1998	16.5	17.2	13.5	9.0	4.5	3.5	6.0	11.5	10.0	7.0	—	—	7.3
1999	—	—	—	13.3	5.5	2.5	6.5	6.9	7.0	7.5	8.0	13.1	7.0
2000	16.0	—	19.0	10.8	7.0	6.2	9.4	10.0	9.1	10.2	—	—	9.0
Northern station													
1953	—	—	—	3.0	3.7	0.9	6.4	9.4	11.0	10.4	—	—	6.4
1974	—	—	—	4.0	0.9	0.4	2.8	9.4	10.2	11.6	—	—	5.6
1997	—	—	—	5.3	0.7	1.0	4.0	8.5	5.8	5.5	6.2	7.9	4.4
1998	7.7	9.5	7.0	5.5	3.2	1.2	4.1	10.0	7.5	6.5	—	—	5.4
1999	—	—	—	5.9	4.0	2.8	5.0	6.0	7.5	7.5	8.0	7.1	5.5
2000	8.2	—	8.6	5.7	4.2	6.0	9.2	11.0	8.7	8.0	8.2	—	7.5
Total lake mean													
1953	—	—	—	—	—	2.77	6.20	10.57	10.57	11.80	—	—	—
1974	—	—	—	—	4.67	2.13	3.80	9.47	9.57	10.83	—	—	—
1997	—	—	—	11.43	3.30	1.90	5.17	8.20	7.20	6.57	7.5	8.8	6.23
1998	13.5	14.5	11.3	7.83	4.57	2.90	5.20	10.83	9.00	7.08	—	—	6.77
1999	—	—	—	8.37	5.50	2.67	5.70	6.73	7.60	7.50	8.2	10.5	6.29
2000	11.9	—	15.7	7.33	5.70	6.50	9.33	10.80	9.10	8.73	—	—	8.21

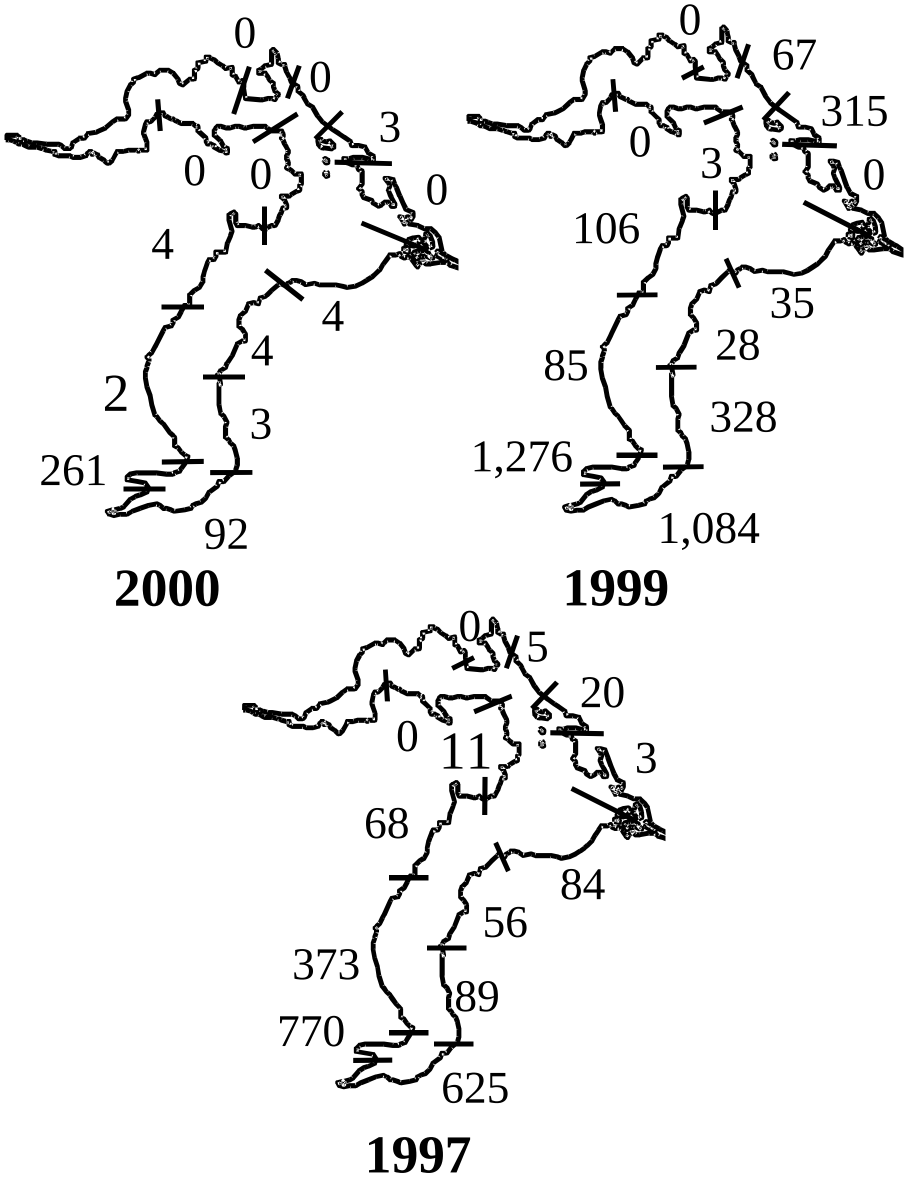


Figure 1.20. Map of Lake Pend Oreille showing area (m^2) of kokanee redds surveyed in each of the 14 survey sections in three different years.

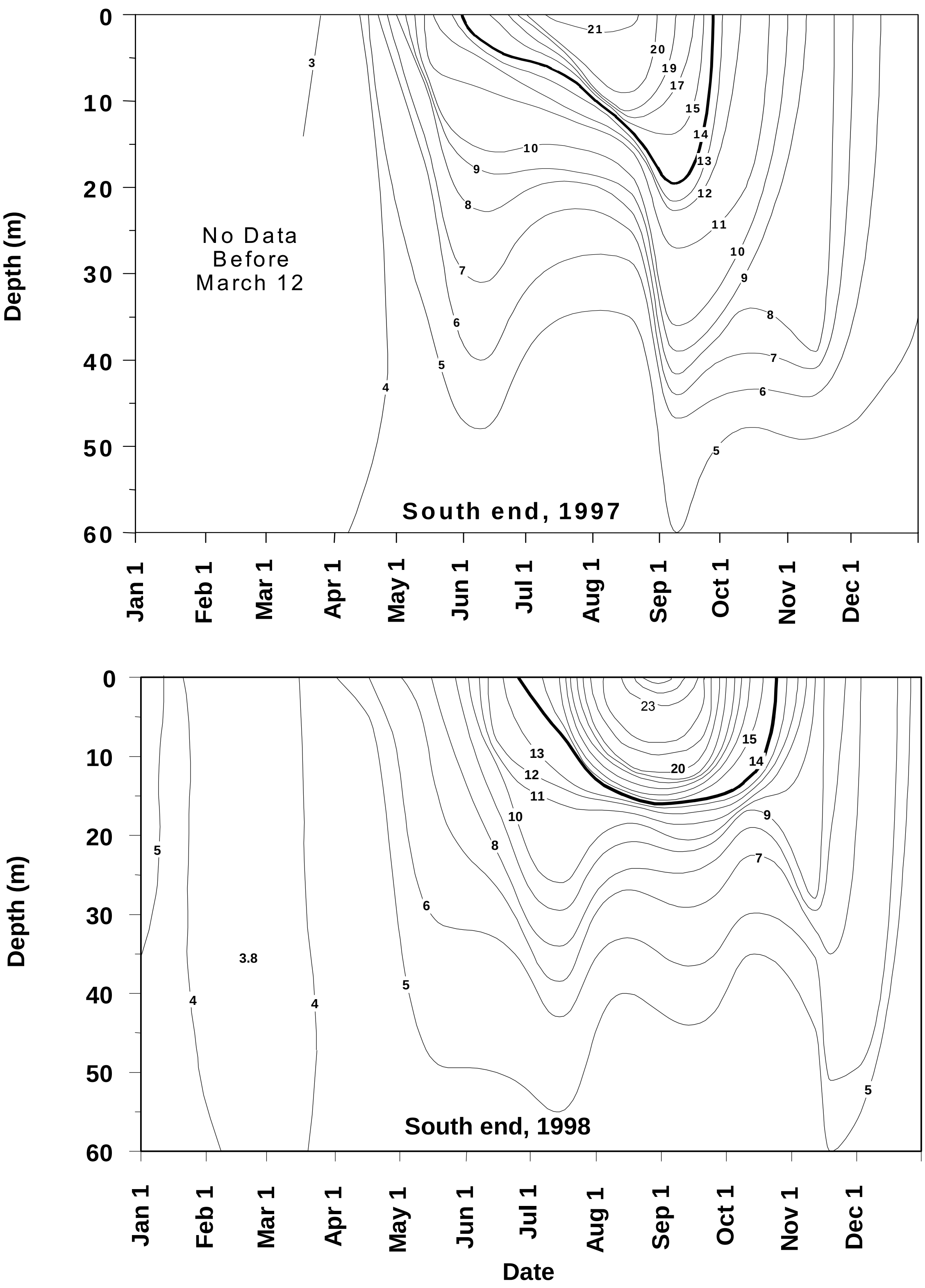


Figure 1.21. Isopleths of water temperature (°C) in Lake Pend Oreille, Idaho, 1997-1998.

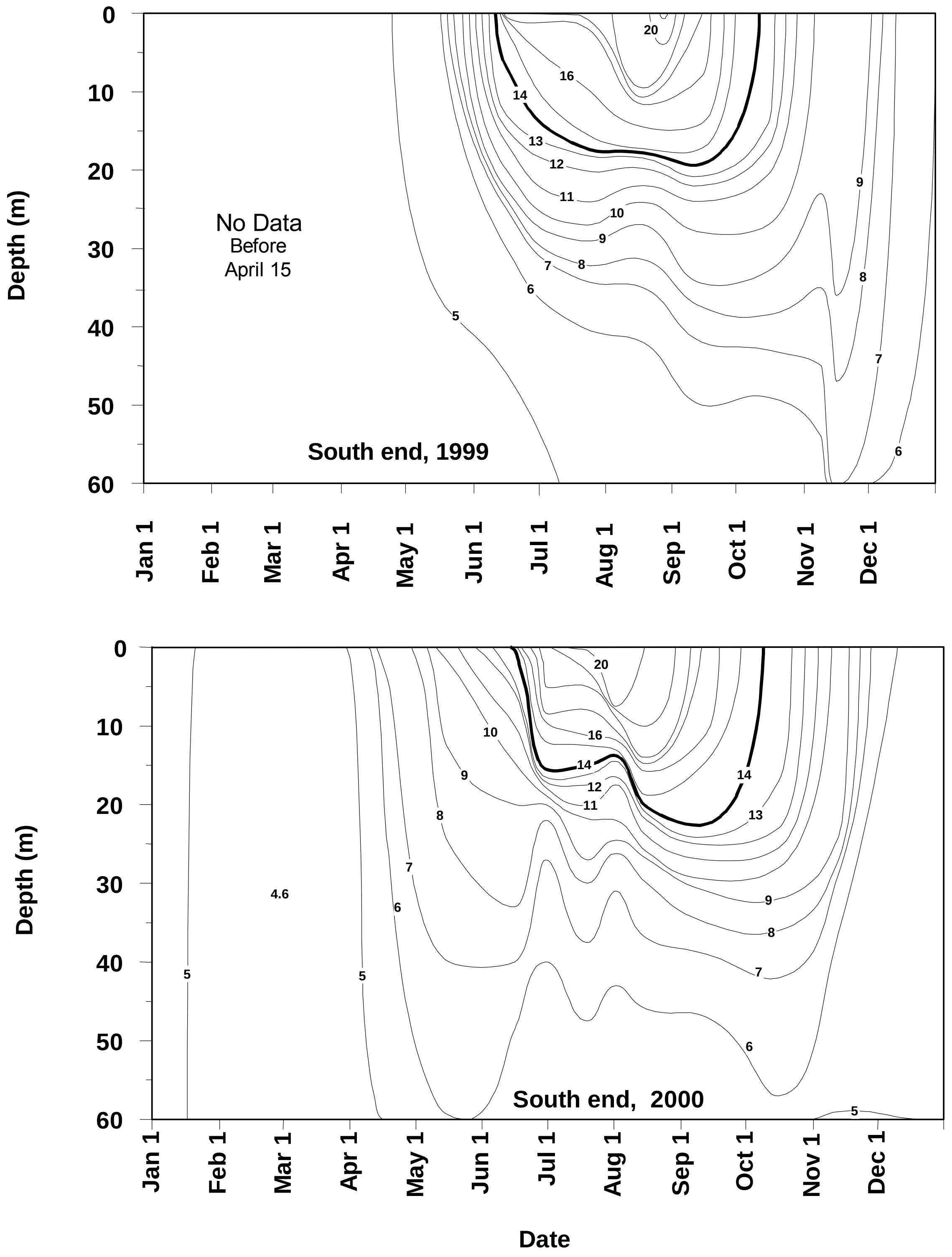


Figure 1.22. Isopleths of water temperature (°C) in Lake Pend Oreille, Idaho, 1999-2000.

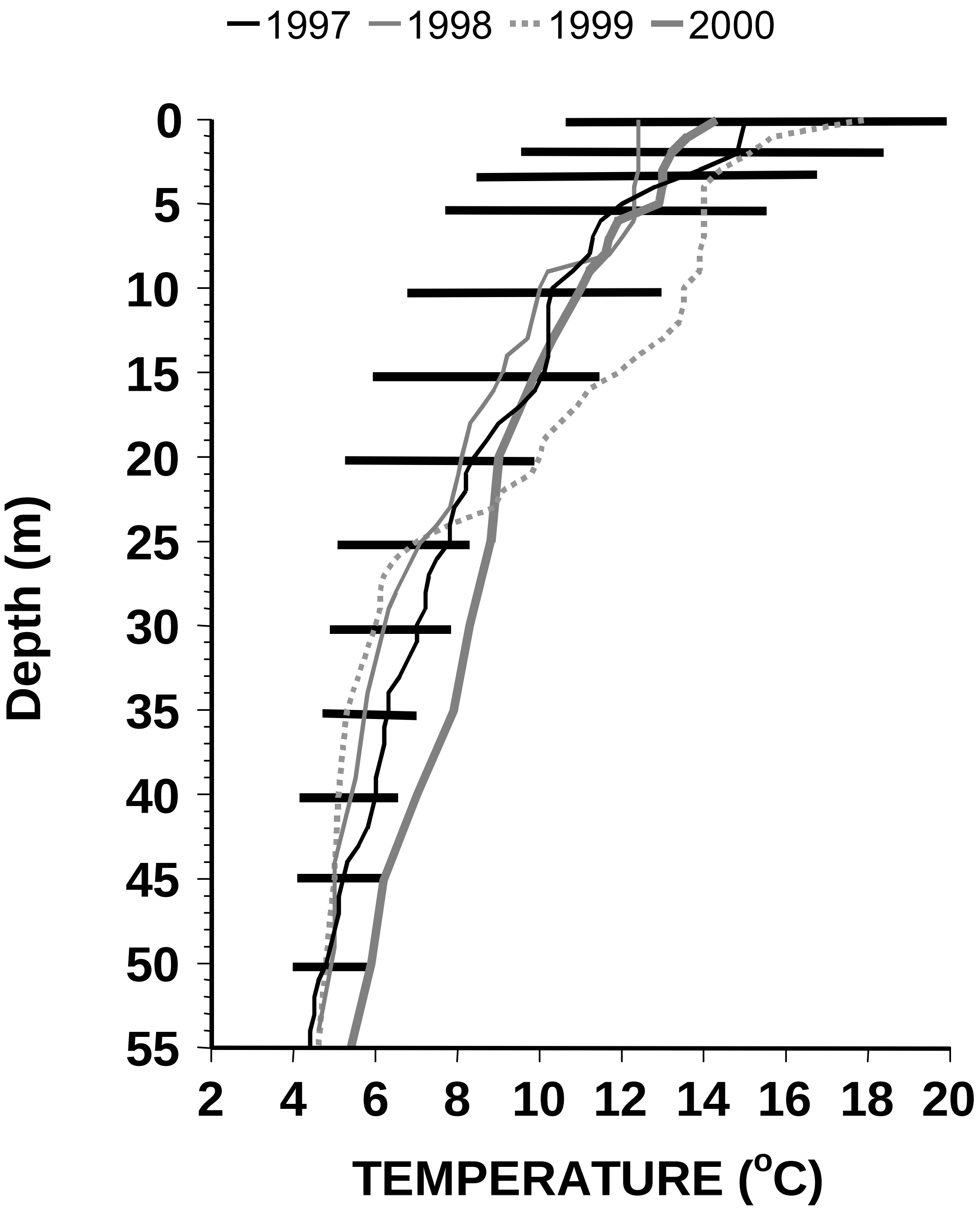


Figure 1.23. Mid-June temperature for 1997-2000 in the southern section of Lake Pend Oreille, Idaho. Horizontal black lines represent an eight-year range of June temperatures (1985-1992) at specific depths.

Table 1.9. Dates and number of days with water temperatures exceeding 14°C at the surface, at 10 m depth, and at 15 m on the south end of Lake Pend Oreille, Idaho, each year from 1997 to 2001.

	14°C at Surface		14°C at 10 m		14°C at 15 m	
Year	Dates	# Days	Dates	# Days	Dates	# Days
1997	6-1 to 9-29	121	8-1 to 9-20	51	8-27 to 9-15	20
1998	6-25 to 10-25	123	7-21 to 10-16	88	8-22 to 9-25	35
1999	6-11 to 10-11	123	6-21 to 10-5	107	7-4 to 9-30	89
2000	6-14 to 10-9	118	6-25 to 10-3	101	6-28 to 9-25	85
2001	6-24 to 10-15	114	7-28 to 10-6	71	8-7 to 10-2	57

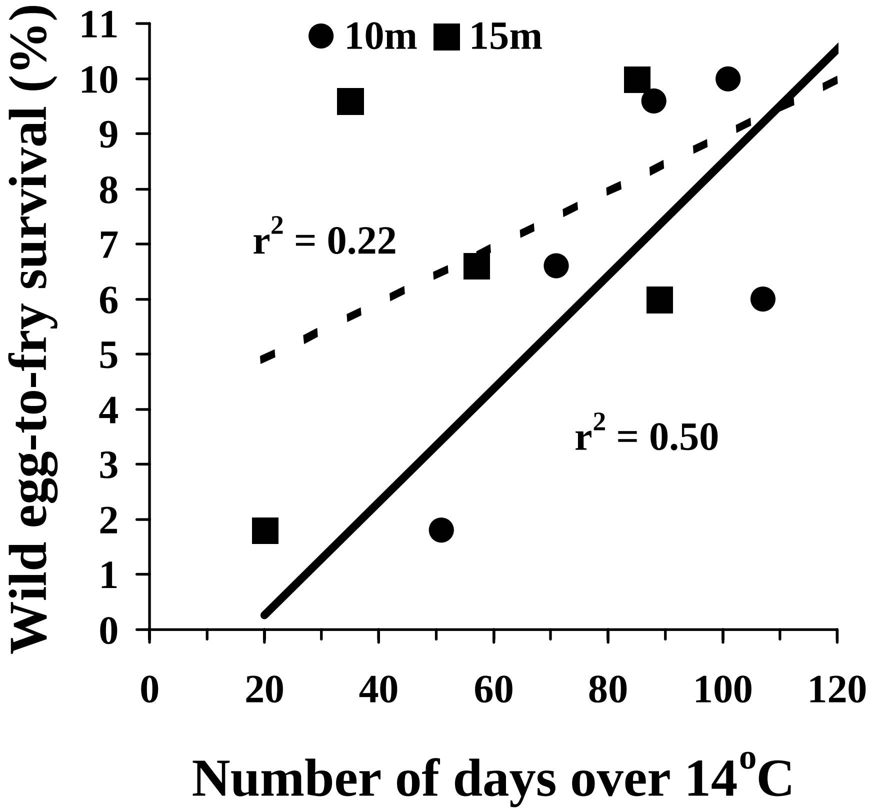


Figure 1.24. The relationship between the number of days during summer that the water temperature was over 14°C and the survival rate of wild kokanee fry in Lake Pend Oreille, Idaho. Two regressions are shown: one for the top 10 m of water (dots with the solid line), and one for the top 15 m of water (squares with the dashed line).

Hatchery Kokanee Stocking

The number of kokanee stocked annually by Cabinet Gorge and Clark Fork Fish hatcheries was regressed against wild egg-to-fry survival (Figure 1.25). The correlation was very weak (r^2 = 0.012) with good wild egg-to-fry survival rates occurring in years of both high or low hatchery stockings.

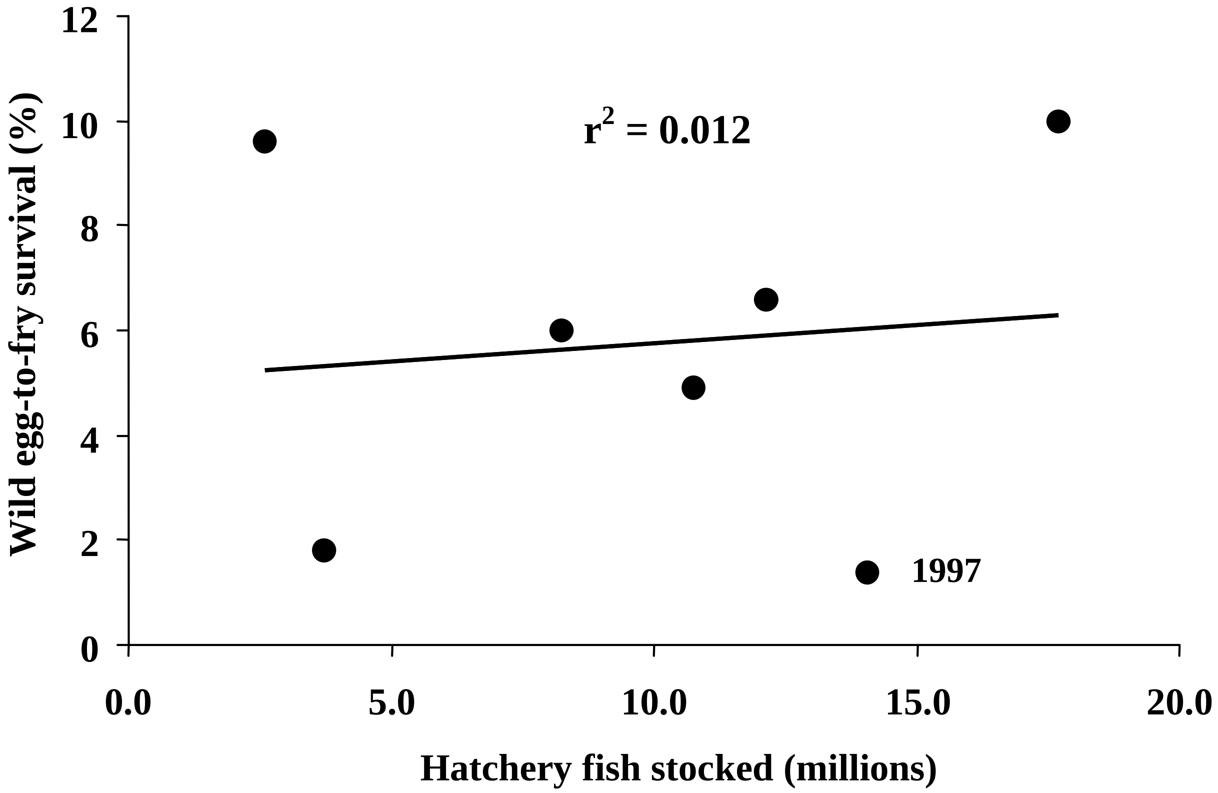


Figure 1.25. Relationship between the number of kokanee fry stocked in Lake Pend Oreille, Idaho and the egg-to-fry survival rate of wild-spawned kokanee from 1995 to 2001. The point for the flood year of 1997 was marked for clarity.

DISCUSSION

Winter elevations of Lake Pend Oreille were changed between 1996 and 2000 to see if survival of wild kokanee eggs would be enhanced. In the original proposal, an enhancement of 26% was the criteria for a successful test (Maiolie 1996). During this study, kokanee survival improved 157% (from a mean of 3.2% in 1995 and 1996 to a mean of 8.1% in 1998, 1999, 2000, and 2001) during the years with a raised winter lake elevation (Figure 1.16). Improvements of this magnitude were much better than anticipated and should be considered a success. Increases in survival of this magnitude could be sufficient to recover the kokanee population if it can be boosted out of the current predator trap that is causing high mortality on older age classes of kokanee (Chapter 3).

This study took an adaptive management approach; an identified limiting factor for this ecosystem was changed, and the results were monitored. The large increases in survival therefore constitute a "success" and can be considered positive advancement for future management. This approach was appropriate because it changed a factor in the ecosystem and then monitored the function of the entire ecosystem for an indication of improvement to kokanee survival. The study should not be viewed as a controlled experiment. Large lakes have no true control. We compared kokanee survival to past years knowing that they are not true controls. Many variables can change annually on any large lake system. We examined several of those variables in this chapter. Warmer water temperatures, Secchi depths, and the number of kokanee fry stocked into the lake were also not well correlated to kokanee egg-to-fry survival and were not thought to influence the outcome of the test. One variable that was correlated to kokanee survival was the number of adult kokanee in the population. Kokanee have been declining in Lake Pend Oreille for the past three decades. Their decline continued during this test. Lower year classes of adults could be expected to produce good survival rates. This is consistent with the original hypothesis that spawning areas are in limited supply. When the population declines, there is less superimposition of redds and egg-to-fry survival improves. In this study, the lake levels changed and kokanee survival improved. Other variables did not (and likely never will) remain constant throughout the test. The importance of other factors can be examined in the future by continued monitoring while changing lake levels.

Our expectation was to see two separate relationships as in Figure 1.18A. Kokanee egg-to-fry survival would remain high, even at high adult densities, under enhanced spawning conditions provided by effective lake level management. Varying the winter lake level enhances kokanee spawning in many widely separated areas of the lake. Thus, kokanee survival can be enhanced two ways. Egg survival is improved in individual redds, because gravel is clean and is of suitable size so that eggs can be buried where they are less likely to be preyed upon. Secondly, spawning takes place in expanded areas of the lake, which minimizes superimposition of redds and spreads the fry out where it would be more difficult for predators to effectively feed on a large segment of the population. Evidence for this was documented in the distribution of kokanee spawning. During the years of higher water levels, more kokanee spawn in areas outside of Scenic Bay. However, when the lake was drawn down to minimum pool, most of the kokanee spawning occurred within this one location. If shoreline spawning areas were in poor condition, egg-to-fry survival would be lower, especially at high adult densities where superimposition of redds would become more pronounced (lower line in Figure 1.18A). A second explanation for an increase in egg-to-fry survival was that adult kokanee density was driving the survival rates as seen in Figure 1.18B. This should be examined by determining wild fry survival when the number of spawning females is high and the winter lake levels have been raised to improve shoreline gravel (1.2 m higher than the previous year).

One past hypothesis for kokanee declines in Lake Pend Oreille was that opossum shrimp were delaying springtime zooplankton production, thereby causing high mortality of kokanee fry due to starvation. However, results of this lake level experiment tend to disprove this hypothesis. Egg-to-fry survival rates of 6-10% were estimated by hydroacoustics partitioned by the percent of wild fish in the trawl. Egg-to-fry survival rates were estimated as high as 14.9% in 2000 based on hydroacoustic estimates of fry abundance partitioned by the percent of wild kokanee in the fry net. These survival rates were considered to be very high and not show the impacts of intense competition for food resources. Secondly, kokanee survival increased markedly after lake levels changed. We would not have expected to see this response if opossum shrimp had truly reduced the carrying capacity of kokanee fry in the lake.

Winter lake levels were raised 0.6 and 1.2 m during this study. Kokanee survival under both of these levels was high compared to years of full drawdown. This indicated that either elevation change was sufficient to enhance spawning during years when the kokanee population was low, ranging from 33,000 to 197,000 mature female kokanee. The trend line in the regression of Figure 1.17 would indicate that 1.2 m increases in winter lake level would give a higher probability of better egg-to-fry survival. This is also consistent with the recommendations in Chapter 4. We would expect that raising the lake 1.2 m would show a more pronounced affect with a stronger adult population.

The fry net yielded higher density estimates of wild kokanee than the trawl net because the small mesh size prevented even the smallest wild fry from escaping. Using the hydroacoustic estimate of fry partitioned by the percent of wild fry in the fry net yielded possibly the most realistic estimate of wild egg-to-fry survival (6-15% in years of raised lake levels). These rates were considered high for a kokanee population. For comparison, in Sullivan Springs Creek, after stream improvements and limiting the spawning run to 10,000 kokanee, egg-to-emergent fry survival was calculated at 6.1% (Whitt 1958). This survival rate would be expected to drop considerably if the time period were extended to fall fry. Survival rates in our current lake level study, therefore, indicated excellent kokanee survival. The wild egg-to-fry survival rate for kokanee in Lake Pend Oreille was estimated at 1.3% in 1978 (Rieman and Bowler 1980) and 1.5% in 1990 (Paragamian et al. 1991). These studies were based on trawling and may not be directly comparable to the much higher survival rates estimated in the current study.

CONCLUSIONS

We found that the egg-to-fry survival of wild kokanee was markedly improved during the years of higher winter water levels. The major improvement in survival was of a magnitude sufficient to lead to increases in the kokanee population. Therefore, our conclusion is that lake level changes should continue as a means of recovering the kokanee population in Lake Pend Oreille.

RECOMMENDATIONS

1. In this study, winter lake elevations were raised and improved kokanee fry survival was documented (Figure 1.17). We therefore recommend periodically raising lake levels by 0.6 m (2 ft) to 1.2 m (4 ft) as an attempt to recover the kokanee population. This will

allow kokanee to spawn on gravel that has been washed and resorted by wave action. Highest pool levels should coincide with the strongest year classes of adult kokanee. (See Chapter 4 for additional recommendations on lake level changes.) Lake levels were lowered in 2001 to resort gravel on potential spawning areas (U.S. Army Corps of Engineers elevation records). We then recommend the lake be held higher in the winter of 2002-2003 when good year classes of adult kokanee are anticipated.

2. Kokanee in Lake Pend Oreille should be monitored annually by hydroacoustics, fry netting, and trawling similar to the approach used in this study. This time-series information would be invaluable in determining the continued response of kokanee to changes in lake level and to document their response to other environmental variables.

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CHAPTER 2: OPOSSUM SHRIMP INVESTIGATIONS

ABSTRACT

We monitored the opossum shrimp *Mysis relicta* population in Lake Pend Oreille from 1997 to 2001. Our goal was to determine if shrimp were influencing the outcome of the lake level tests (Chapter 1) or preventing the recovery of the kokanee population in the lake. We netted shrimp with a 1 m hoop net and a high-speed Miller sampler. Immature and adult shrimp densities ranged from 252 shrimp/m^2 in 1997 to 426 shrimp/m^2 in 1998 based on hoop net sampling. Shrimp densities were not well correlated to the egg-to-fry survival rate of naturally–produced kokanee ($r^2 = 0.03$), indicating they were not influencing the outcome of the lake level test. High survival rates of kokanee (9.6% from eggs to fry) were noted in 1998 when shrimp densities reached their highest point during this study (426 shrimp/m^2). Shrimp abundance estimates since 1973 indicated the population peaked in 1980; however, it has continued to decline to the present date. With these findings, we concluded that opossum shrimp are not currently limiting the kokanee population.

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INTRODUCTION

During the 1960s and 1970s, opossum shrimp *Mysis relicta* were introduced in lakes and reservoirs throughout the western United States, Canada, and Scandinavia to enhance the food base for sport fisheries (Lansenby et al. 1986). Several hundred lakes were stocked with opossum shrimp (Northcote 1991). Years later, shrimp were documented to have negatively impacted zooplankton populations in many of the lakes where they were introduced, which may have directly or indirectly affected the sport fish populations. However, opossum shrimp introductions were labeled a qualified success in some lentic ecosystems. Factors influencing the success included the shape of the lake, current conditions, nutrient status of the lake, temperature of the water, and presence of fish species that feed on opossum shrimp (Northcote 1991; Rieman and Falter 1981).

In an effort to increase food availability for juvenile kokanee *Oncorhynchus nerka*, Idaho Department of Fish and Game (IDFG) introduced opossum shrimp to Lake Pend Oreille from 1966 to 1970. Opossum shrimp established themselves in the lake after nine to ten years (Bowles et al. 1991). Starting in the mid-1960s, the number of kokanee harvested by anglers began a steady decline. In 2000, the kokanee fishery was closed due to low numbers of fish. In the early 1980s, kokanee declines were blamed on the establishment of opossum shrimp, which were thought to compete with the kokanee for food.

It was hypothesized that kokanee declines after 1975 were due to the introduction of opossum shrimp to Lake Pend Oreille, resulting in a reduction of the availability of food for newly emerged kokanee fry (Bowler and Rieman 1981). Egg-to-fry survival was estimated at 1.21% in 1978, suggesting that lack of food was causing poor survival of young kokanee, therefore resulting in poor recruitment to adults (Rieman and Bowler 1980). Older age classes of kokanee had good survival rates and did not appear to have been impacted by the introduction of the opossum shrimp.

The purpose of our investigation of opossum shrimp in Lake Pend Oreille was twofold. First, we evaluated whether or not dramatic changes in shrimp abundance influenced the outcome of the lake level experiment. Second, we further investigated the hypothesis that shrimp were limiting the kokanee population and keeping it from recovering to previous levels. Researchers at the University of Idaho conducted part of this work. Their results are included in their entirety as Chapter 2B.

METHODS

To better understand the influences of opossum shrimp abundance on the lake level experiment, *Mysis relicta* were sampled annually from 1997 to 2001. Shrimp avoid light through a diel vertical migration from the deep waters they inhabit during daylight hours to the epilimnion they inhabit at night. This migration is due not only to light levels and temperature, but also the need to curtail predation and take advantage of food intake opportunities (Gal et al. 1999). Due to this behavior, our opossum shrimp sampling occurred at night when the shrimp are closer to the surface of the lake. All sampling was conducted during the dark phases of the moon in June. This has been the standard sampling date for most of the previous work on shrimp and for all of our sampling since 1997. Vertical net tows and Miller sampling techniques were used to collect the shrimp (methods described below). The purpose of this dual sampling was to allow us to convert the older data sets, collected with the Miller sampler, into density estimates consistent with vertical net tows.

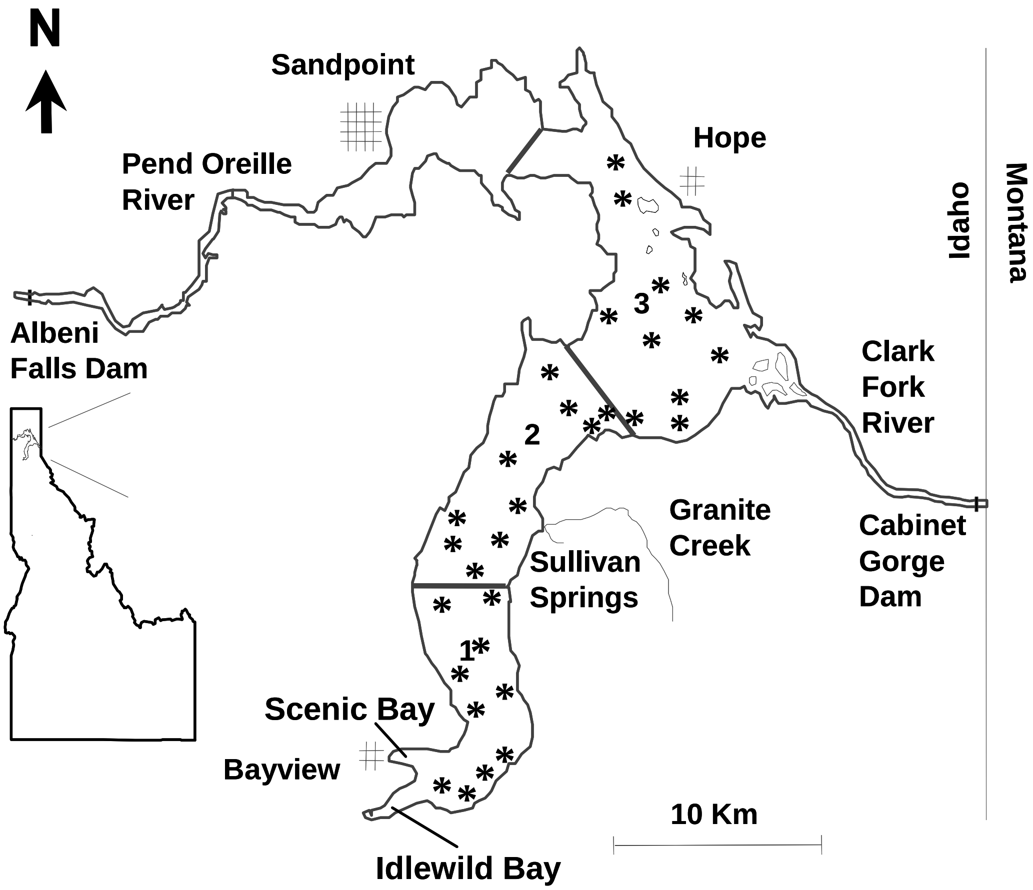
Opossum shrimp were measured from the tip of the rostrum to the end of the telson, excluding setae. They were classified into five categories according to maturity and gender: young-of-year, immature males and females, and mature males and females. These data were used annually to determine the opossum shrimp length frequency distribution (Figure 2.2). Young-of-year are generally less than 10 mm in length and have indistinguishable sex characteristics. Immature males are distinguishable by the presence of two thumb-like appendages located at the base of the legs on the eighth thoracic segment, by the elongation of the pleopod on the fourth abdominal segment, and by the infinitesimal development of the conical process, located on the distal end of the third segment of the antennular peduncle. In mature males, the conical process becomes more visible and setiferous. In mature breeding males, the fourth pleopod extends past the end of the telson. Female opossum shrimp are discernable by the formation of a brood pouch located on the underside of the seventh and eight thoracic segments. The brood pouch is small and light colored in immature females; however, mature brooding females exhibit brood pouches filled with, or recently emptied of, eggs, embryos, or larvae (Gregg 1976; Pennak 1978).

Vertical Net Tows

The vertical tow technique was used annually from 1997 to 2001 and during previous opossum shrimp sampling in 1995 and 1996 (Chipps 1997). Shrimp were collected using a hoop net that was 1 m in diameter and equipped with a flowmeter. Net mesh and cod-end bucket mesh measured 1000 um and 500 um, respectively. We lowered the net to a depth of 45.7 m (150 feet) and raised it at a rate of 0.5 to 0.7 m/s using an electric winch. Collected opossum shrimp were immediately placed in denatured ethanol for preservation. Eight sampling sites were randomly selected from each of the three sections of the lake in 1997, 1998, and 1999. Ten sampling sites were randomly selected from each lake section in 2000 and 2001 (Figure 2.1). Global positioning system (GPS) coordinates were used to locate each sampling site.

Miller Sampler

During 1999, we collected shrimp at 12 sites (four sites in each of the three sections) with the Miller sampler concurrently with the vertical tow nets by using a second boat. In 2000, 12 additional sites were sampled with both gear types (10 in the northern section and 2 in the middle section). The Miller sampler had a 104 mm diameter opening (0.00849 m^2) and 500 um mesh. The Miller sampler was lowered to 45.7 m and towed at 1.7 m/s. It was then raised 3 m at 10 s intervals until it reached the surface. A General Oceanics, Inc. flowmeter was positioned over the side of the boat at the beginning of each transect to measure the horizontal towing distance. Densities of shrimp collected by the two methods were compared by linear regression analysis to develop a conversion equation. The mean densities of opossum shrimp collected by the Miller sampler and the vertical tow were compared statistically with a student's t-test.



Section	Area (hectares)
1	6386
2	7776
3	8384

*** - Mysis sampling locations**

Figure 2.1. Map of Lake Pend Oreille, Idaho showing the opossum shrimp sampling locations used in June 2001.

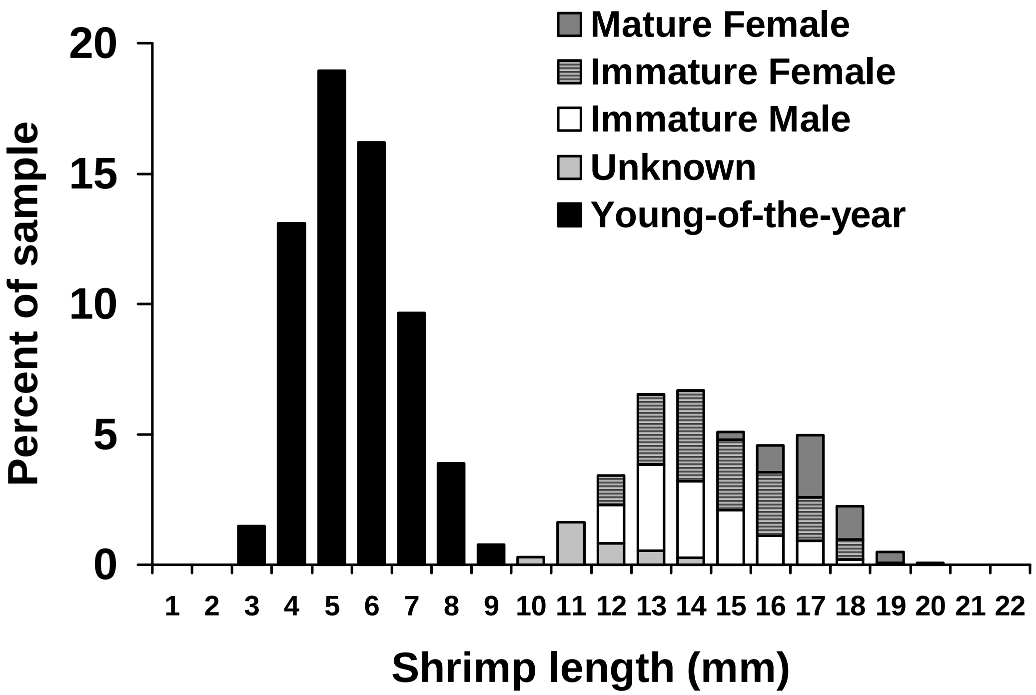


Figure 2.2. Opossum shrimp length frequency distribution during June 2001, on Lake Pend Oreille, Idaho.

RESULTS

Between 1997 and 2001, we estimated a mean density of all age classes of shrimp at 689 shrimp/m^2, with a range from 510 to 880 shrimp/m^2 (Figure 2.3). These estimates were lower than density estimates made in the early 1980s (Figure 2.3). From 1980 to 1985, the mean density of all age classes of opossum shrimp was 1,440 shrimp/m^2. Population estimates peaked during 1980 and showed a generally downward trend that continued through 2001 (Figure 2.3).

Our estimates of immature and adult shrimp (excluding young-of-the-year shrimp) peaked in 1998, one year after the 1997 flood, with a mean of 426 opossum shrimp/m^2, (Figure 2.4). From 1998 through 2001, immature and adult shrimp densities declined to 225 opossum shrimp/m^2.

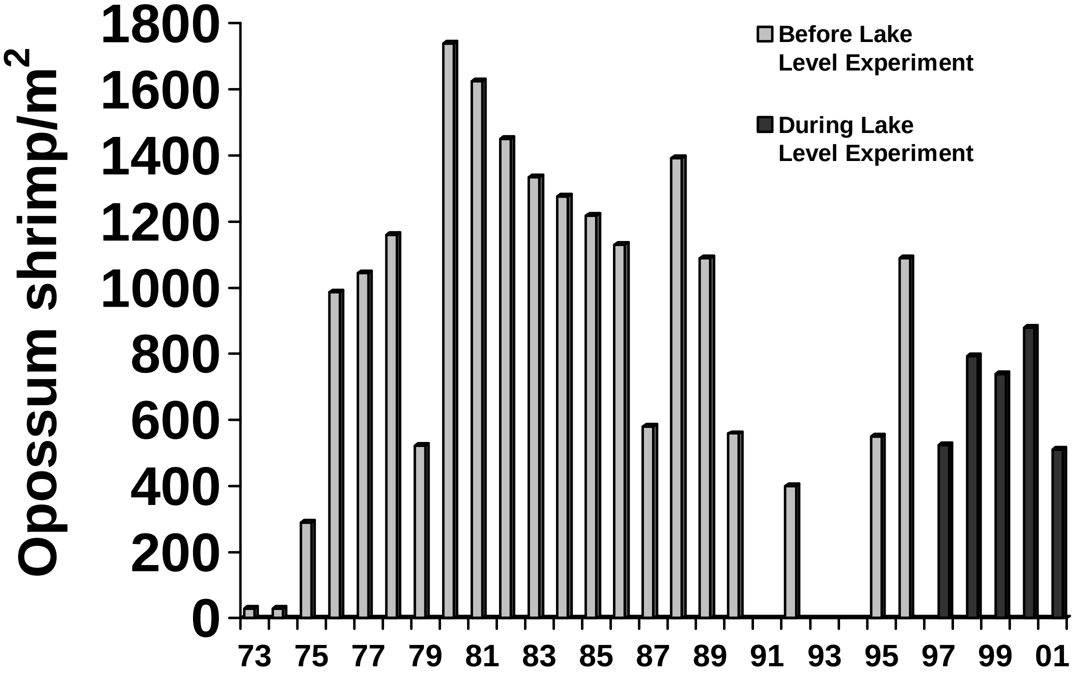


Figure 2.3. Annual mean density of opossum shrimp in Lake Pend Oreille, Idaho 1973-2001. Data collected before 1989 were obtained from Bowles et al. (1991), and data from 1995 and 1996 were from Chipps (1997). Shrimp densities from 1992 and earlier were converted from Miller sampler estimates to vertical net tow estimates by using the equation presented in Figure 2.7A. Gaps in the bar chart indicate no data were collected that year.

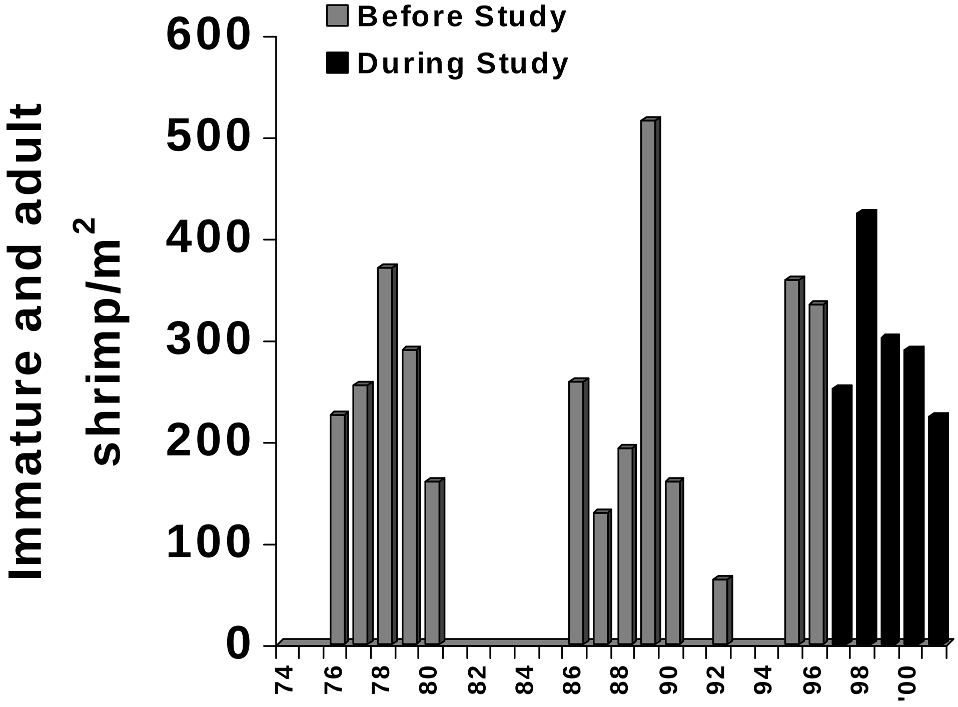


Figure 2.4. Density of immature and adult opossum shrimp/m^2 in Lake Pend Oreille, Idaho 1974-2001. Data collected before 1995 were converted from Miller sampler estimates to vertical net tow estimates by the equation in Figure 2.6B. Data from 1976-1980 are from Bowler and Rieman (1981) and data from 1986 to 1992 were from Paragamian and Ellis (1994). Gaps in the bar chart indicate no data were collected, or the young-of-the-year fraction could not be determined.

Trends in opossum shrimp densities within the three lake sections varied between 1997 and 2001 (Figure 2.5). With the exception of 1998, the opossum shrimp densities were generally less in the northern lake section. Young-of-the-year densities were consistently higher in the southern and middle sections of Lake Pend Oreille. Immature and adult shrimp densities were generally highest in the northern section of the lake (Table. 2.1). Shrimp densities declined to the lowest densities on record in the northern section during the flood year of 1997, but rebounded to the highest densities on record the following year (Figure 2.5).

Comparisons between 1999 Miller sampler and vertical tow data indicated a strong correlation of determination (r^2 = .82); however, a significantly higher (p = .0001) density of opossum shrimp was captured when using the Miller sampler (Figure 2.6).

Densities of immature and adult shrimp between 1995 and 2001 were poorly correlated with that year's estimate of survival rate for wild spawn kokanee eggs to wild kokanee fry (r^2 = 0.09) (Figure 2.7).

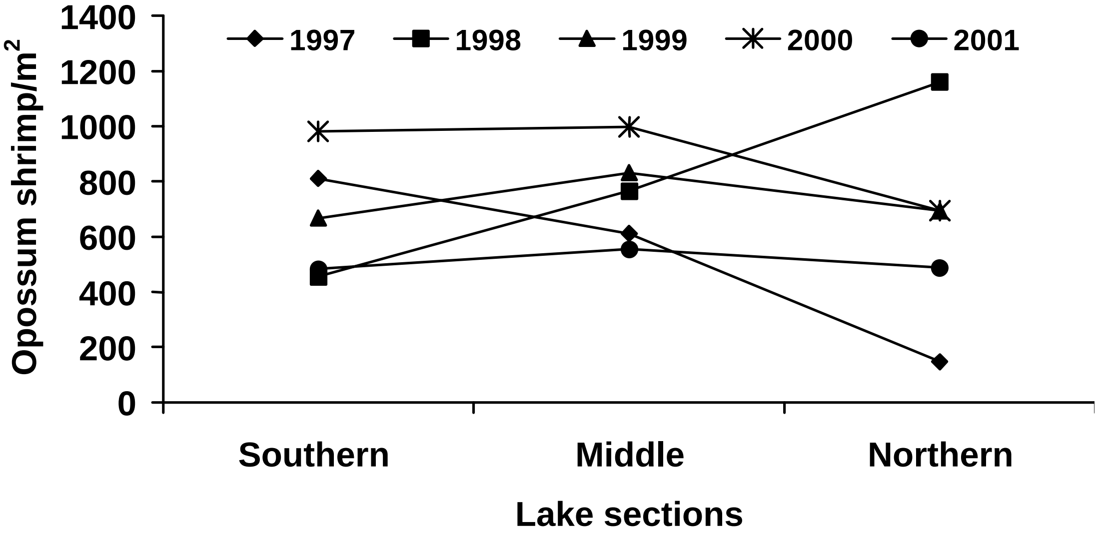


Figure 2.5. Mean density of all age classes of opossum shrimp/m^2 per lake section, Lake Pend Oreille, Idaho 1997-2001.

Table 2.1. Yearly mean density (shrimp/m^2) comparisons of young-of-the-year and immature/adult opossum shrimp per lake section in Lake Pend Oreille, Idaho, 1997-2001.

Lake Section and Life Stage	1997	1998	1999	2000	2001
Southern Section:					
Young-of-the-year	431.5	306.5	432.0	696.3	330.0
Immature and adult	379.8	148.6	234.6	283.5	155.2
Middle Section:					
Young-of-the-year	338.9	565.8	594.3	659.0	333.9
Immature and adult	273.4	198.9	237.1	338.2	221.1
Northern Section:					
Young-of-the-year	44.0	230.3	293.5	449.0	205.2
Immature and adult	102.4	929.8	412.3	245.2	281.5

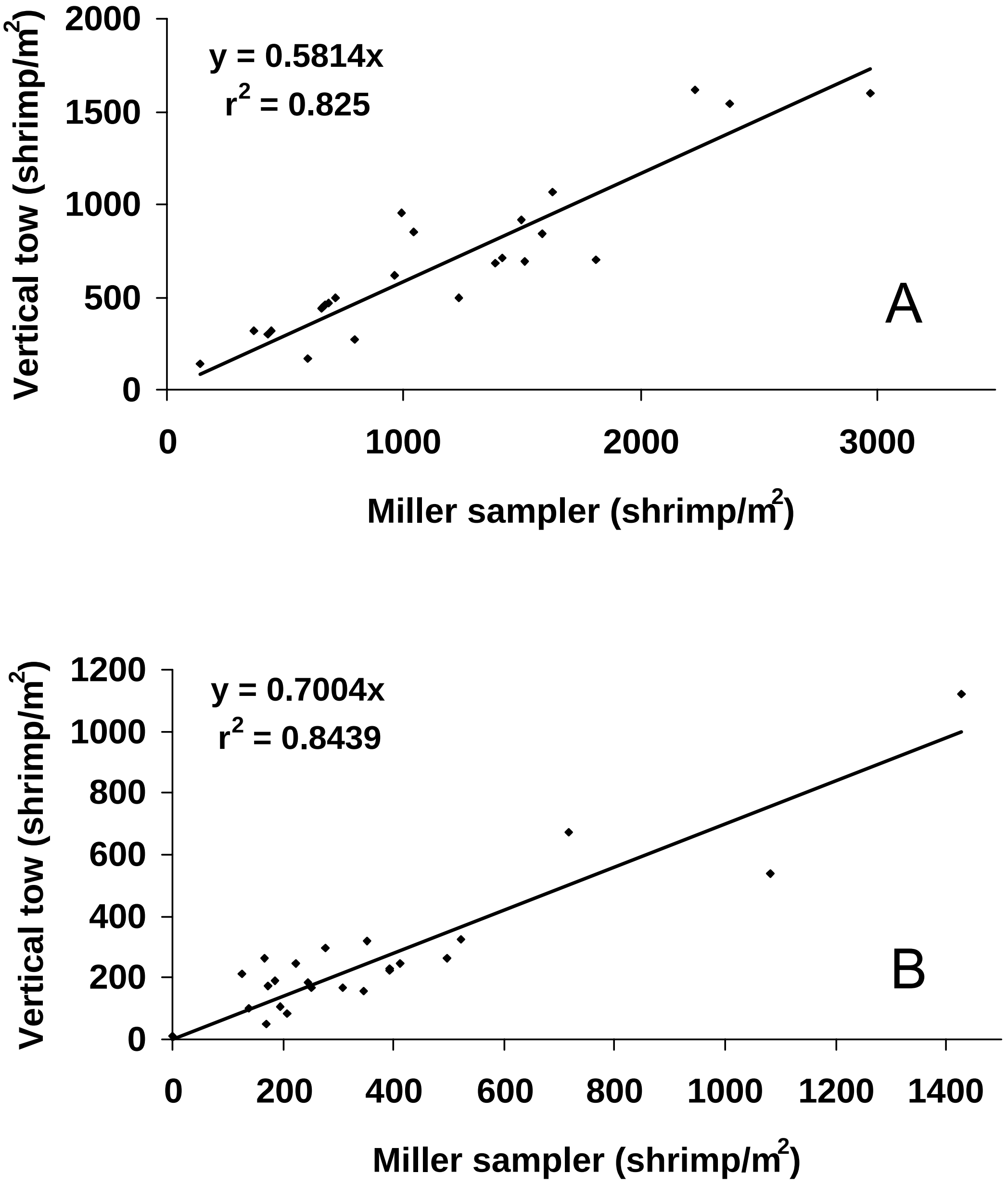


Figure 2.6. Comparison of shrimp density estimates collected with a Miller sampler and vertical net tows in Lake Pend Oreille, Idaho 1999 and 2000. Figure A is a linear regression utilizing all shrimp and Figure B uses only adult and immature shrimp (excludes young-of-the-year shrimp). The y-intercepts were set at zero.

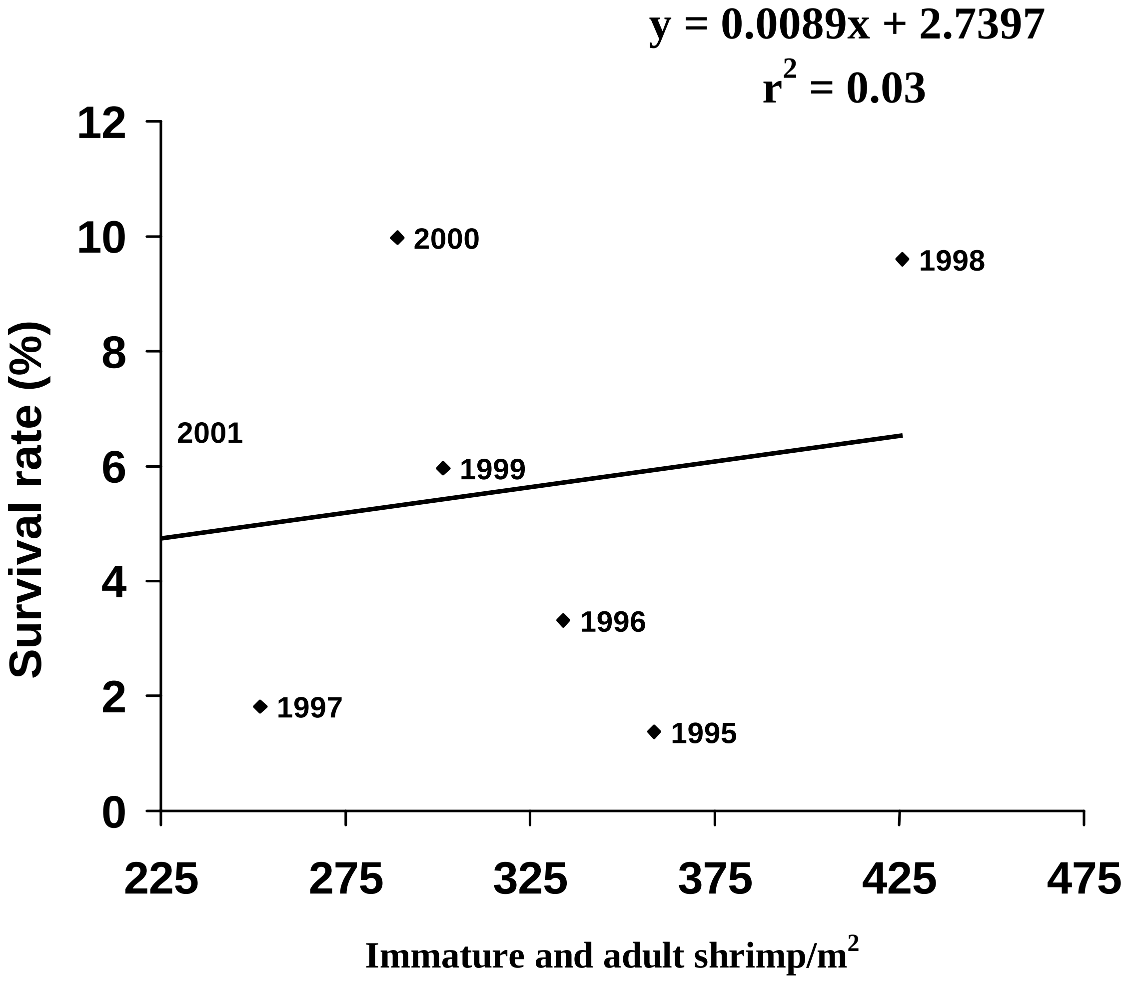


Figure 2.7. Correlation between mean opossum shrimp densities and the survival rate from kokanee eggs to fry in Lake Pend Oreille, Idaho 1995-2001.

DISCUSSION

We found little correlation between kokanee egg-to-fry survival and immature/adult shrimp abundance (Figure 2.7). These life stages of shrimp would be most likely to compete with kokanee if food were a limiting factor. Chipps (1997) found that young-of-the-year shrimp exert little predation mortality on crustacean zooplankton and do not become potential competitors with kokanee until they reach a length of >8 mm. Excellent kokanee survival was found in 1998 when the shrimp population was high and also in 2000 when the shrimp population was lower. Conversely, poor kokanee survival was seen in 1997 when the shrimp population was low and in 1995 when the shrimp population was relatively high. The fact that the kokanee population responded dramatically to lake level changes (Chapter 1) regardless of shrimp abundance demonstrated that shrimp were not limiting the survival of kokanee fry.

The original hypothesis was that newly emerged kokanee fry were starving shortly after emergence because opossum shrimp had delayed the bloom of cladocern zooplankton by approximately one month in some years (Rieman and Bowler 1980). However, the blooms of copepods had not been delayed. Clark (1999) found that the most important item in the diet of newly emerged kokanee in May to June 1998 was the copepod *Cyclops bicuspidatus thomasi* (Chapter 2B), which was also the most abundant prey item in the lake at that time. This food habits study demonstrated that kokanee fry are not dependent on a diet of cladocerns, and in fact, the study shows that kokanee are feeding on the more common types of plankton that were still readily available after the establishment of opossum shrimp.

Net pen experiments also demonstrated that kokanee survival was not being impacted by food availability due to competition with opossum shrimp. Clark (1999) (Chapter 2B) placed newly emerged kokanee fry in net pens in Lake Pend Oreille in 1998. One set of net pens had a large enough mesh to allow kokanee to feed on the ambient levels of zooplankton without the addition of supplemental food to the pen. The other set of pens held newly emerged kokanee fry that were allowed to feed on the ambient food, but were also given additional zooplankton. Kokanee mortality did not occur in either pen. In fact, kokanee growth was not significantly different between the two pens despite the supplemental feeding.

Rieman (1981) obtained results similar to those mentioned above. In Rieman's experiment, button-up fry were placed in net pens from early April to early July. The fry were not given additional food and had to rely on ambient zooplankton. Rieman's net pen tests also showed "negligible" mortality of kokanee held at ambient zooplankton levels in Lake Pend Oreille. The first four experiments had 97% survival; the next five experiments had 100% survival. Rieman stated "the potential for mortality of juvenile kokanee due directly to starvation appears to be low."

It was not hypothesized that opossum shrimp were impacting kokanee older than the fry stage. Kokanee older than fry continued to survive well until the mid-1990s. Based on trawl data obtained from 1977 to 1998 (excluding the flood year of 1997) in Lake Pend Oreille, survival rates of kokanee from age-0 to age-1 averaged 52%; age-1 to age-2 averaged 80%, and age-2 to age-3 averaged 79%. This compares favorably with Coeur d'Alene Lake from 1991 to 1999 (excluding the flood year of 1996). During this time, survival averaged 49%, 82%, and 62%, respectively, for the same year classes (Fredericks and Horner 2001). Coeur d'Alene Lake does not contain opossum shrimp; however, kokanee predators in the form of chinook salmon are present there, and the lake provides a popular kokanee fishery. The same trawling gear was used in Spirit Lake between 1989 and 2000 (data was not collected in 1992 and 1996). The mean survival rate from age-1 to age-2 was 56%, and a mean survival rate from age-2 to age-3 was 40% (Fredericks and Horner 2001). Spirit Lake does not contain opossum shrimp or major kokanee predators, and it provides a very popular fishery for kokanee. These data indicate good kokanee survival in Lake Pend Oreille after the fry stage, in spite of the presence of opossum shrimp.

The history of kokanee declines in Lake Pend Oreille also sheds some doubt on the hypothesis that opossum shrimp were limiting the kokanee population. Bowles et al. (1991) illustrates the decline in angler's catch of kokanee in comparison to the densities of opossum shrimp in Lake Pend Oreille. Kokanee catch had declined 64% between 1964-1974, from 22 fish/ha in 1964 to 8 fish/ha, respectively. By 1974, shrimp densities in the lake were still exceedingly low. By 1976, when shrimp abundance first increased to over 1,000 shrimp/m^2, kokanee harvest had already declined to approximately 6 fish/ha. This large decline in kokanee harvest in the decades before the establishment of opossum shrimp must have been caused by some factors other than the introduction of opossum shrimp.

Between 1952 and 1966, Maiolie and Elam (1993) found a strong inverse relationship ($r^2 = -0.71$) between the drawdown of Lake Pend Oreille after November 15, when kokanee spawning begins in earnest, and the harvest of kokanee five years later. This negative trend was highly significant ($p = 0.005$). These results implicated lake level management in the early declines of the kokanee stock.

In Chapter 1 of this report, we discussed how lake level management continued to impact the kokanee populations after 1966 by making much of the spawning gravel unavailable to shoreline spawning kokanee. After 1966, the lake was drawn down to its minimum pool level during most years. Fredericks et al. (1995) found that only 35,460 m^2 of suitable spawning gravels were below the water line when the lake was held at its minimum pool elevation of 625.1 m. When the lake is maintained at a winter level of 626.7 m, 231,134 m^2 of gravel remains available for spawning. Reduction in the amount of suitable spawning areas would have limited the kokanee populations to a low level that would be in balance with this amount of spawning habitat and would have contributed to the kokanee declines between 1966 and 1996. Changes in the winter lake level from 1995 to 2000 were positively correlated with kokanee egg-to-fry survival (see Chapter 1). This finding also suggests that lake levels, not opossum shrimp, were limiting the kokanee population.

Although competition with shrimp did not appear to be limiting the kokanee population throughout this study, it is possible that competition could be an important factor if the kokanee population expands toward a "recovered" level. In this study, the density of kokanee was so low that food was not a limiting factor. Standing stocks of kokanee in 1977 and 1978 were 13-17 kg/ha. Rieman and Bowler (1980) concluded that those densities of kokanee "did not have a significant cropping effect on available food," and "density-dependent interactions related to food do not appear to be important." During those years, immature and adult shrimp densities were similar to current opossum shrimp densities. Rieman and Bowler (1980) did document a decline in the mean length of Daphnia in certain areas of the lake, which suggested significant cropping pressure at the relatively high density of 30 to 40 kg/ha. We estimated that the lake contained 4 kg/ha of kokanee in 1999 and 6 kg/ha of kokanee in 2000. We, therefore, expect that kokanee standing stocks could increase by at least several fold before food limitations occur.

CONCLUSIONS

We conclude that opossum shrimp are not currently limiting the kokanee population or causing the ongoing declines in kokanee abundance. We also find that changes in opossum shrimp abundance did not nullify the outcome of the lake level experiment. Shrimp population was both high and low during years of higher winter lake levels, and shrimp abundance did not correlate with kokanee survival. A review of the history of shrimp sampling also shows that shrimp did not cause the early declines in the kokanee population from 1966 to 1975, which was before they became well established in the lake.

RECOMMENDATIONS

1. We recommend continuing efforts to recover the kokanee population through lake level changes and other management actions. Our findings do not support the conclusion that the kokanee population is being limited by opossum shrimp.

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CHAPTER 3: KOKANEE PREDATION

ABSTRACT

We examined the predator and prey (kokanee) relationship in Lake Pend Oreille to determine if it is in balance. Hydroacoustics surveys were conducted to estimate the population of large pelagic fish over 415 mm (-33 dB) that were likely to be predators (rainbow trout, lake trout or bull trout). Midwater trawling and hydroacoustics were used to estimate kokanee production, yield, and survival rates. Rough estimates of large pelagic fish remained relatively stable at 13,000 to 17,000 fish between 1998 and 2001, which indicated no large decline due to the liberalized sport fish regulation changes in 2000. Kokanee biomass declined from 344 metric tons in 1995 to 149 metric tons in 2001, illustrating a continuing decline in the kokanee population. Kokanee survival rates between age-1 and age-2 fish dropped substantially from 79% in 1996 to 27% in 2001, which were attributed to predation. Even with the declines in the kokanee biomass, kokanee yield (the weight of all kokanee that died between years) remained high at 314 metric tons. Based on linear modeling of the empirical data, yield would need to decline by 24% to balance with kokanee production. The imbalance between the kokanee prey base and predators appeared to have arisen in 1997 when high spring run-off caused abrupt declines in kokanee abundance. After this time, dispensatory mortality appeared to cause a further decline in the kokanee population.

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INTRODUCTION

When the Lake Pend Oreille Project was originally designed in 1994 and 1995, there was speculation that predation may be causing declines in the kokanee population. Survival rates of all age classes of kokanee had been monitored for 18 years prior to the implementation of the project. These data indicated good survival rates of kokanee older than fry; however, the population was still declining. The Northwest Power Planning Council addressed the possibility that predation may be causing the declines in the kokanee population by requesting investigations into the uncertainties related to predator abundance and predation levels in Lake Pend Oreille.

Idaho Department of Fish and Game and the University of Idaho collaborated to conduct studies on predation in Lake Pend Oreille. The kokanee population was closely monitored by Idaho Department of Fish and Game, with research emphasis on kokanee survival rates between age classes, kokanee production rates, and kokanee yield. The University of Idaho focused their research efforts on estimating predator abundance, determining predator food habits, and using a bioenergetic model to approximate the number of kokanee consumed by predators. The University of Idaho studies are included in their entirety at the end of this chapter (Chapter 3B).

METHODS

Surveys for Large Pelagic Fish

We conducted hydroacoustic surveys of Lake Pend Oreille each year between 1995 and 2001, within two weeks of the annual mid-water trawling. Survey methods were described in detail in Chapter 1. An analysis method called "trace tracking" was used to identify the predators. To be considered a pelagic predator, the fish must have a target strength larger than -33 dB (a size equal to a 415 mm salmonid [Love 1971]), must be detected (pinged) at least twice, not move more than 30 cm vertically between detections, and not be missed by more than 1 ping during the tracking. In addition, the fish must be located in a minimum water column depth of 70 meters and be at least 10 meters from the bottom. Hydroacoustic transects were not used in areas where the majority of the lake bottom was within 70 meters of the surface. This phase of our investigation only included the open, pelagic region of the lake. Future investigations will include analysis in the littoral areas; which will likely contain a more diverse species community and require additional methods of sampling.

Kokanee Population Estimates and Survival Rates

The catch of our annual midwater trawling (see Chapter 1) was used to determine the percent frequency of each age class of kokanee between age-1 and age-5 for each section of the lake. Hydroacoustic estimates were multiplied by this percentage to estimate year class abundance. Age-0 kokanee were estimated directly from the echograms. We estimated annual survival rates for each year class of kokanee by dividing a year class by its abundance the previous year. By closely monitoring changes among and between age classes, we were able to estimate the effect predation may have on the kokanee population in Lake Pend Oreille.

Population estimates based on trawling were calculated directly from the catch in the mid-water trawl sampling. Fish numbers within each age group and within each transect (haul) were divided by the volume of water filtered by the net within the kokanee layer, to calculate age-specific density estimates (fish/m^3). These density estimates were multiplied by the thickness of the kokanee layer in meters, and multiplied by 10,000 to calculate density estimates in fish/ha for each age class of kokanee. Average density was calculated for each lake section and multiplied by the area of the section to estimate kokanee abundance within each section. Section estimates were summed to estimate a whole-lake population abundance. The area of each section was calculated for the 91.5 m contour; however, the northern section was calculated from the 36.6 m contour because of shallower water. The 91.5 m contour was used because it represents the pelagic area of lake where kokanee are found during late summer (Bowler 1978). For consistency, these same areas have been used each year since 1978. Ninety percent confidence intervals were calculated on the kokanee abundance estimates (Scheaffer et al. 1979). Survival rates were calculated by dividing the abundance estimate of each age class of kokanee by its abundance the previous year.

We conducted standardized midwater trawling in Lake Pend Oreille on August 22-29, 1995; September 8-12, 1996; September 29 to October 4, 1997; August 17-24, 1998; September 7-10, 1999; August 28 to September 1, 2000; and August 13-16, 2001. In addition, trawling was conducted by similar methodology during 1994 under a different project proposal (Maiolie et al. 1994). Trawling dates were during the dark phase of the moon, which optimized the capture efficiency of the trawl (Bowler et al. 1979).

Biomass, Production, Yield

We calculated the biomass, production, and yield of the kokanee population in Lake Pend Oreille to look for evidence of high predation. Biomass is the total weight of kokanee within Lake Pend Oreille. It was calculated by multiplying the population estimate of each year class of kokanee times the mean weight of kokanee in that year class.

Production was defined as the growth in weight of the kokanee population regardless of whether the fish was alive or dead at the end of the year (Ricker 1975). To determine production of an age class of kokanee between two years, we use a three-step equation for each age class of kokanee. First, we subtracted the mean weight per fish of each kokanee year class of the previous year from the current year’s mean weight of each age class (to get the increase in weight). Second, we averaged the population estimates between the two years. Lastly, we multiplied the increase in mean weight by the average population estimate for each age class. We then summed the results for all of the year classes to determine the production for the entire population. These calculations assume a linear rate of mortality throughout the year.

Yield refers to the total biomass lost from the population due to all forms of mortality (Ricker 1975). To determine annual yield for each age class, we calculated the mean weight per fish between the current and previous year. We then subtracted the population estimate of the current year from the previous year to get the number of fish that died. Lastly, we multiplied the mean weight times the number that died to estimated the yield for each age class. Results were summed across all year classes to estimate yield for the population. Again, calculations assume a linear rate of mortality throughout the year.

Bioenergetic Modeling

From 1997 through 1999, researchers from the University of Idaho estimated the rate of predation on the kokanee populations in Lake Pend Oreille (Chapter 3B, Vidergar 2000). To estimate the population abundance of rainbow trout, bull trout, and lake trout, a mark-and-recapture tagging program was established. Volunteer anglers used spaghetti tags to mark fish if they were over ≥406 mm fork length during the two-year study. Tag number, fork length, species, approximate location of catch, depth of catch, date of catch, and name of angler were recorded before each fish was released. Recapture efforts for rainbow trout was performed during November of 1998, August 20 to November 4, 1998 for bull trout and April 25 to May 1, 1999 for lake trout.

In addition to the tagging effort, University of Idaho researchers also collected fish with monofilament gillnets during the daylight hours of November 1-4, 1998 and electrofished from June to November of 1998. To identify food items in the stomachs of rainbow trout, bull trout, lake trout ≥406 mm, and northern pikeminnow ≥100 mm, stomach samples were collected using lavage techniques. To estimate how many kokanee were consumed by rainbow trout, bull trout, and lake trout ≥406 mm, University of Idaho researchers utilized the computer model *Fish Bioenergetics 3.0* (Chapter 3B).

RESULTS

Surveys for Large Pelagic Fish

We calculated relatively stable estimates of large pelagic fish using hydroacoustic surveys. Estimates ranged from 13,000 to 17,000 annually (Table 3.1). All of these fish were in the open water of the lake where water depths were greater than 70 m and were more than 10 m above the lake's bottom. The highest abundance estimates were located in the northern section of the lake (section 3) and were 1.5 to 5 times higher than the other sections. The species of these fish is unknown; however, we believe they were not kokanee because of their large size (>-33 dB, 415 mm). Depth distribution of many of these fish was deeper than is typical for kokanee, and they were in water <10°C, which was commonly colder than the preferred kokanee temperature for kokanee (Figure 3.1).

Table 3.1. Abundance of large pelagic fish determined by hydroacoustic surveys in Lake Pend Oreille, Idaho, 1998-2001.

Year	Section 1	Section 2	Section 3	Lake Total
2001	1,130	638	11,527	13,295
2000	2,023	3,156	10,310	15,489
1999	2,426	2,039	11,297	15,762
1998	4,930	5,070	7,294	17,294

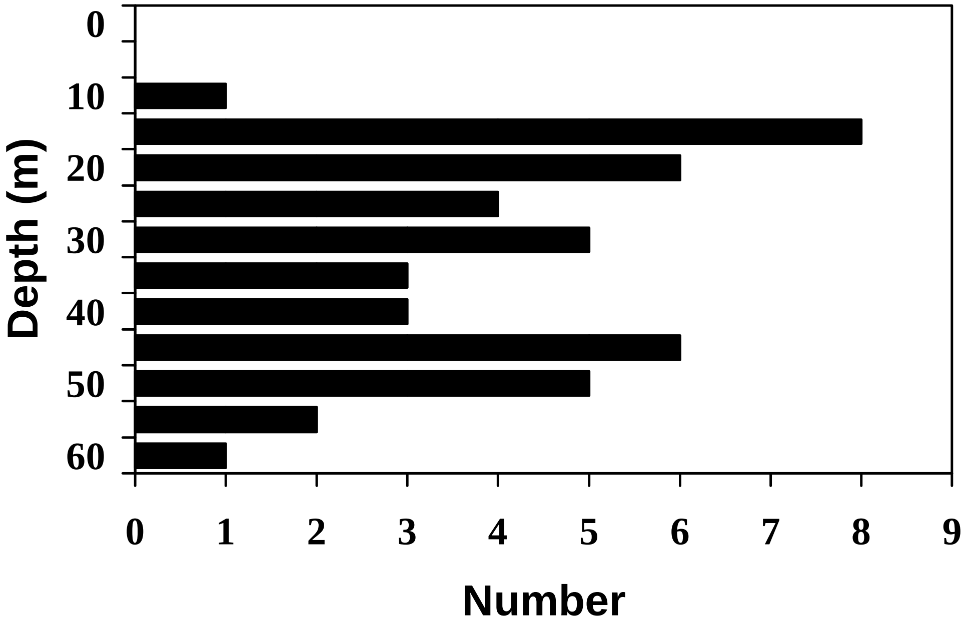

Figure 3.1. Depth distribution of fish larger than –33 dB (415 mm) in Lake Pend Oreille, Idaho in hydroacoustic surveys conducted between 1998 and 2001.

Kokanee Population Estimates and Survival Rates

Population estimates of kokanee based on hydroacoustics, and partitioned by the percent frequency in the trawl catch, indicated the highest population of age-1 to age-5 kokanee occurred in 1996, with an estimated 7.328 million kokanee (Table 3.2). A general declining trend in kokanee abundance occurred after 1996, with the lowest population estimate occurring in 1999, with an estimated 2.819 million kokanee (90% CI: ± 17.8%). Population estimates then increased between 1999 and 2001 to 4.902 million (90% CI: ± 9.5%). Throughout the five-year study, we consistently observed higher kokanee populations in the northern section (Section 3) of Lake Pend Oreille (Table 3.2). The percent frequencies of each age class of kokanee in each section of the lake, as determined by midwater trawling, are presented in Table 3.3. These were multiplied by the hydroacoustic estimates of age-1 to age-5 kokanee to estimate kokanee abundance in each age class (Table 3.4).

Estimates of each age class of kokanee based volumetrically on the trawl catch are presented in Table 3.5. Age-4 kokanee were found to be very low in 1997 (40,000) and 2001 (30,000). Fry abundance was estimated to be very low in the flood year of 1997 (2.23 million) and the following year (0.72 million).

We calculated the survival rates between each age class of kokanee both in the trawl catch and based on the hydroacoustic estimate to look for the impacts of predation. From 1996 to 1999, we observed a steady decline in the percent survival of age-1 to age-2 kokanee, as survival dropped from 79% to 18%, respectively (Table 3.6 and Figure 3.2). A slight increase in survival was observed in 2000 and 2001 as survival increased to 22% and 27%, respectively.

Survival rate from age-2 to age-3 (Figure 3.3) and from age-3 to age-4, showed declines in the flood year of 1997, rebounded in 1998, 1999, and 2000, and then sharply declined in 2001.

Table 3.2. Hydroacoustic population estimates (millions) of kokanee ages 1-5 in three sections of Lake Pend Oreille, Idaho from 1995 through 2001.

Year	Section 1	Section 2	Section 3	Total for Lake	90 % C.I.
2001	0.980	1.479	2.443	4.902	± 9.5%
2000	0.871	1.032	1.935	3.838	± 14.2%
1999	0.762	0.240	1.817	2.819	± 17.8%
1998	0.933	0.823	3.272	5.028	± 16.7%
1997	1.234	1.316	3.211	5.761	± 15.8%
1996	2.208	2.384	2.736	7.328	± 18.6%
1995	2.951	1.171	2.746	6.868	± 11.8%

Table 3.3. Percent of each age class of kokanee in each section of Lake Pend Oreille, Idaho as determined by trawling, 1995-2001.

	Percent Frequency				
Year/Section	Age-1	Age-2	Age-3	Age-4	Age-5
2001					
Section 1	75.93	19.79	0.54	2.32	1.42
Section 2	70.94	27.51	0.39	0.91	0.26
Section 3	89.67	9.65	0.00	0.37	0.31
2000					
Section 1	57.71	10.43	13.64	17.85	0.37
Section 2	77.88	6.48	10.74	4.62	0.28
Section 3	94.32	2.00	2.10	1.58	0.00
1999					
Section 1	8.52	14.48	25.43	47.29	4.28
Section 2	15.25	18.25	27.74	34.99	3.77
Section 3	43.00	14.02	17.52	22.94	2.52
1998					
Section 1	2.68	20.59	63.57	13.16	[a]
Section 2	45.31	18.57	32.39	3.73	[a]
Section 3	56.32	14.56	27.07	2.05	[a]
1997					
Section 1	29.29	37.69	29.25	3.77	[a]
Section 2	34.06	41.02	19.85	5.07	[a]
Section 3	65.47	26.80	7.64	0.09	[a]
1996					
Section 1	24.20	47.51	16.81	11.48	[a]
Section 2	33.77	54.25	6.95	5.03	[a]
Section 3	66.49	24.63	4.94	3.94	[a]
1995					
Section 1	23.69	43.20	29.78	3.33	[a]
Section 2	73.61	10.76	7.43	8.20	[a]
Section 3	81.61	10.71	2.99	4.69	[a]

[a] Age-5 data was unavailable.

Table 3.4. Hydroacoustic population estimate of each age class of kokanee in each section of Lake Pend Oreille, Idaho partitioned by trawling age class percentages, 1995-2001.

Year/Section	**Age-1**	**Age-2**	**Age-3**	**Age-4**	**Age-5**
2001					
Section 1	0.744	0.194	0.005	0.023	0.014
Section 2	1.049	0.407	0.006	0.013	0.004
Section 3	2.191	0.236	0	0.009	0.007
Total	3.984	0.837	0.011	0.045	0.025
2000					
Section 1	0.503	0.091	0.119	0.155	0.003
Section 2	0.804	0.067	0.111	0.047	0.003
Section 3	1.825	0.039	0.041	0.030	0.000
Total	3.132	0.197	0.271	0.232	0.006
1999					
Section 1	0.065	0.110	0.194	0.360	0.033
Section 2	0.037	0.044	0.066	0.084	0.009
Section 3	0.781	0.255	0.318	0.417	0.046
Total	0.883	0.409	0.578	0.861	0.088
1998					
Section 1	0.025	0.192	0.593	0.123	[a]
Section 2	0.373	0.153	0.267	0.030	[a]
Section 3	1.843	0.476	0.886	0.067	[a]
Total	2.241	0.821	1.746	0.220	
1997					
Section 1	0.361	0.465	0.361	0.047	[a]
Section 2	0.448	0.540	0.261	0.067	[a]
Section 3	2.102	0.861	0.245	0.003	[a]
Total	2.911	1.866	0.867	0.117	
1996					
Section 1	0.534	1.049	0.371	0.254	[a]
Section 2	0.805	1.294	0.165	0.120	[a]
Section 3	1.819	0.674	0.135	0.108	[a]
Total	3.158	3.017	0.671	0.482	
1995					
Section 1	0.699	1.275	0.879	0.098	[a]
Section 2	0.862	0.126	0.087	0.096	[a]
Section 3	2.241	0.294	0.082	0.129	[a]
Total	**3.802**	**1.695**	**1.048**	**0.323**	

[a] Age-5 data was unavailable.

Table 3.5. Population estimates (millions) of kokanee, by age-class, in Lake Pend Oreille, Idaho, 1995-2001. Estimates were obtained by midwater trawling.

Year	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5	Total	Density fish/ha	Standing Stock kg/ha
2001	5.43	3.69	0.63	0.01	0.03	0.02	9.81	435	5.36
2000	8.37	2.50	0.17	0.24	0.22	0.01	11.51	510	6.20
1999	3.80	0.23	0.14	0.20	0.29	0.03	4.69	209	3.87
1998	0.72	0.89	0.33	0.73	0.10	0	2.77	123	4.60
1997	2.23	1.15	0.77	0.38	0.04	0	4.57	203	4.20
1996	5.42	3.57	3.14	0.67	0.48	0	13.28	589	16.22
1995	4.62	3.10	1.17	0.69	0.21	0.03	9.82	434	10.92

Table 3.6. Survival rates (%) between kokanee year classes estimated by midwater trawling and hydroacoustics, 1996-2001. Year refers to the year the older age class in the survival estimate was collected.

	Age Class							
Year	0 to 1		1 to 2		2 to 3		3 to 4	
	Trawl	Acoustics	Trawl	Acoustics	Trawl	Acoustics	Trawl	Acoustics
2001	44	28	25	27	3	6	13	17
2000	66	52	74	22	168	66	107	40
1999	32	24	16	18	61	71	40	49
1998	40	37	29	28	95	94	25	26
1997	21	42	22	59	12	29	6	17
1996	77	44	101	79	57	40	70	46
1995	46	—	307	—	99	—	21	—
1994	12	—	47	—	76	—	38	—
1993	32	—	98	—	256	—	92	—
1992	67	—	94	—	63	—	83	—
1991	25	—	111	—	53	—	82	—
1990	35	—	124	—	27	—	44	—
1989	16	—	72	—	88	—	97	—
1988	47	—	65	—	45	—	81	—
1987	47	—	73	—	63	—	77	—
1986	64	—	66	—	43	—	[a]	—
1985	39	—	70	—	[a]	—	[a]	—
1984	70	—	53	—	[a]	—	[a]	—
1983	59	—	18	—	[a]	—	[a]	—
1982	119	—	47	—	[a]	—	[a]	—
1981	80	—	79	—	[a]	—	[a]	—
1980	50	—	73	—	[a]	—	[a]	—

[a] Unable to calculate survival rate since age-3 and -4 kokanee were not separated prior to 1986.

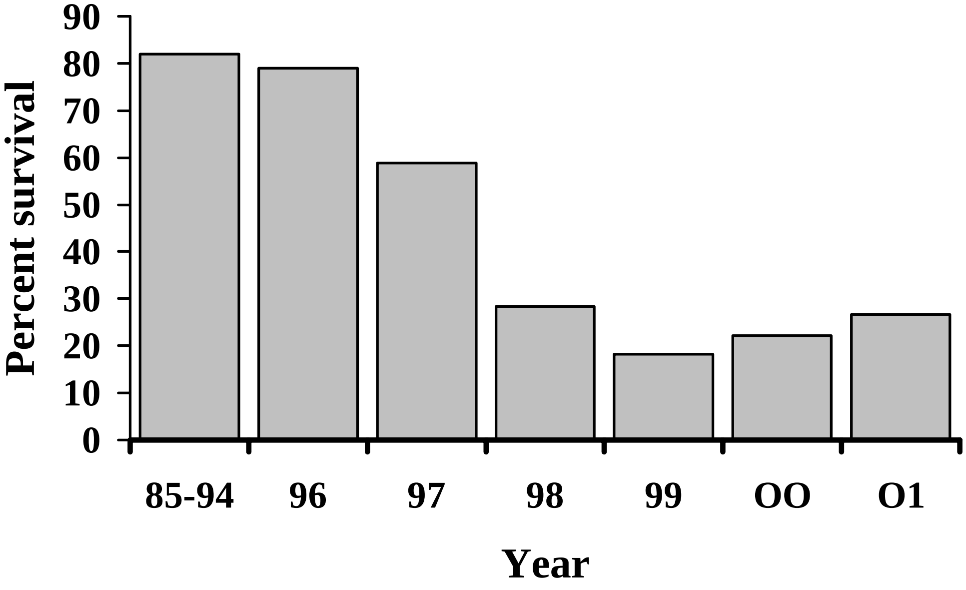

Figure 3.2. Percent survival of age-1 to age-2 kokanee in Lake Pend Oreille, Idaho from 1985 to 2001. Data from 1996 to 2001 was based on hydroacoustic surveys that were partitioned into age classes based on the percent frequency of trawl catches. Data from 1985 to 1994 was based on midwater trawling.

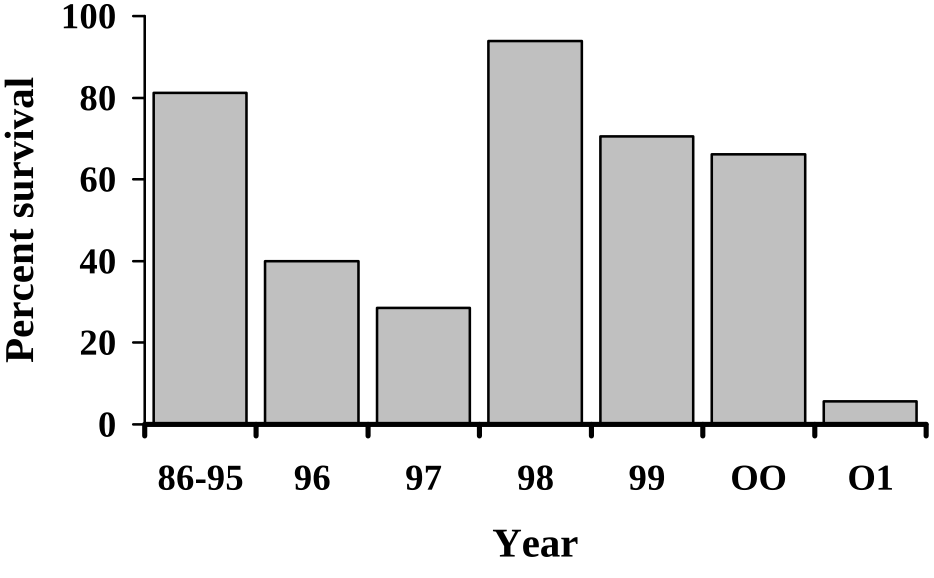

Figure 3.3. Percent survival of kokanee from age-2 to age-3 in Lake Pend Oreille, Idaho from 1985 to 2001. Data from 1996 to 2001 was based on hydroacoustic surveys that were partitioned into age classes based on the percent frequency in trawl catches. Data from 1986 to 1995 was based on midwater trawling.

Biomass, Production, Yield

The biomass of kokanee in Lake Pend Oreille declined 58% from 1996 to 2001 (Table 3.7). We also observed a decline in kokanee production during the study, from 278.4 t in 1996 to 250.1 t in 2001. In 1997, the occurrence of a 100-year flood increased the yield over the previous year by 22% to 354.3 t (Table 3.7). In 1998, yield dropped back to 208.5 t and then started a gradual increase to where it has now surpassed the 1996 yield of 274.7 t. In 2001, yield reached the high for a normal water year of 313.5 t. In 1997, 1999, 2000, and 2001, yield was higher than production, which resulted in a decline of kokanee biomass (Figure 3.4).

We plotted production and yield against biomass to determine the relationship (Figure 3.4). Yield negatively correlated with changes in biomass, whereas production was positively correlated to biomass. The two trend lines crossed at a point where biomass equals about 300 t.

Table 3.7. Biomass, production and yield (metric tons) of kokanee in Lake Pend Oreille, Idaho 1996-2001.

Year	Biomass	Production	Yield
2001	148.2	250.1	313.5
2000	169.9	194.2	284.1
1999	249.0	256.0	271.4
1998	253.2	230.3	208.5
1997	228.7	220.7	354.3
1996	352.6	278.4	274.7
1995	343.6		

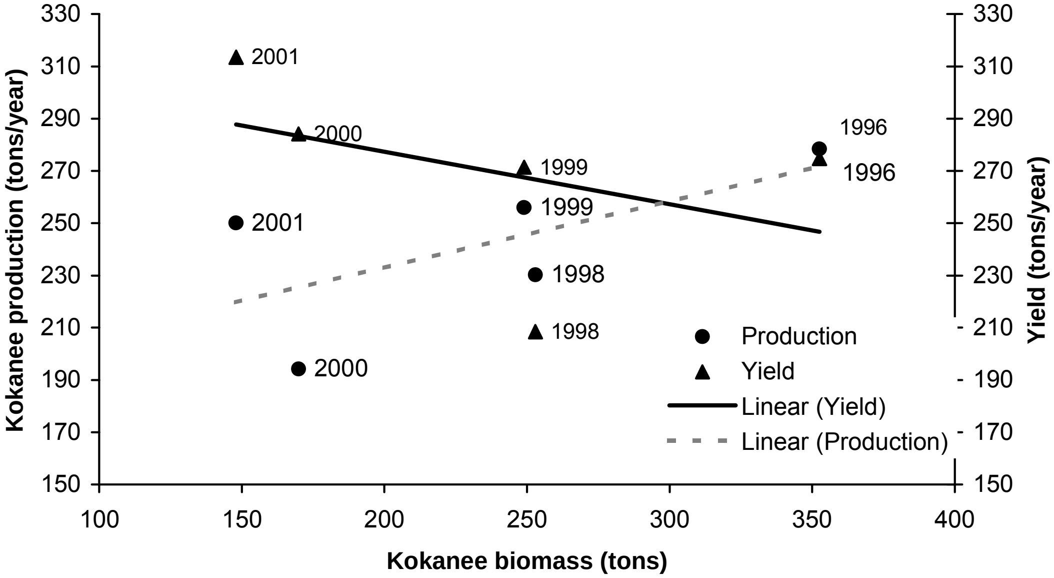

Figure 3.4. Kokanee biomass, production, and yield (metric tons) for Lake Pend Oreille, Idaho 1996-2001, excluding 1997 due to 100-year flood.

Bioenergetic Modeling

From April 1997 to April 1999, researchers from the University of Idaho studied the bioenergetics of Lake Pend Oreille (Chapter 3B, Vidergar 2000). During the study, they estimated that there were over 14,000 rainbow trout (0.64/ha), 12,000 bull trout (0.54/ha), and 1,700 lake trout (0.08/ha) present in Lake Pend Oreille. The predator population, therefore, consisted of 51% rainbow trout, 43% bull trout, and 6% lake trout. Kokanee were the primary food item of rainbow trout, bull trout, and lake trout, comprising 77%, 66%, and 87% of their diet by weight, respectively.

Bioenergetic modeling was used to determine that collectively these three predators consumed more than 153.5 t (tonnes) of kokanee in 1998. We estimated that kokanee production was 230.3 t in 1998. Predators, therefore, consumed 67% of the annual production that year, and kokanee biomass dropped by 25 t from 1997 to 1998 (Table 3.7).

DISCUSSION

Predation levels on kokanee in Lake Pend Oreille appeared to be too high considering the depressed levels of the kokanee population. Survival rates of kokanee from eggs-to-fry have improved substantially during the lake level study (Chapter 1); however, survival from age-1 to age-2 greatly declined (Figure 3.2). Low survival of kokanee from age-1 to age-4 prevented kokanee from recovering after the flood during 1997. Very high abundance of fry in 2000 and 2001 may help this situation. These strong year classes of kokanee may satiate the predators and still remain numerically strong, allowing a good year class to reach maturity. However, a reduction in predation levels is still warranted in anticipation of future weak year classes of kokanee.

The kokanee population in the lake had been declining for over three decades. When it reached a low level in 1985, we began heavily supporting the population with hatchery stocking. This appeared to stop the downward trend in kokanee abundance and likely sustained a substantial predator population. Most age classes of kokanee had relatively poor survival during the 1997 flood year (Table 3.6). Age-1 to -2 kokanee survival dropped to 59%, age-2 to -3 survival dropped to 29%, and age-3 to -4 survival dropped to 17%. The biomass of the population dropped 124 t, a decline of 35%. Instead of recovering after the 1997 flood year, kokanee survival continued to decline between age-1 and age-2. These two-year classes were the size groups of kokanee most often found in the stomachs of the lake’s predators (Chapter 3B). It appears a “bottleneck” has developed in the kokanee population; numerically strong year classes of kokanee were reduced in number between age-1 and age-2. Because of low abundance of older age classes of kokanee, predators may be focusing their foraging efforts on this age group. These findings also suggest that age-1 to -2 survival could be used as an index of kokanee predation. Survival rates of age 1 to age 2 kokanee below 50% appear indicative of an out-of-balance population.

We analyzed the echograms for the presence of fish larger than kokanee, which were likely to be rainbow trout, bull trout, or possibly lake trout (all of which are kokanee predators). Our estimates remained relatively stable each year with a predator population estimate of 13,000 to 17,000 fish, but we caution that they should only be considered rough estimates due to the wide variability between transects. These estimates were similar to predator population estimates for rainbow trout or bull trout made by mark-and-recapture techniques (Chapter 3B). It was interesting to note that the estimates of large pelagic fish did not decline substantially during 2000 or 2001 (Table 3.1) when fishing regulations changed to liberalize the harvest of rainbow trout and lake trout. (Kokanee yield increased between 2000 and 2001, indicating a possible increase in predation levels [Table 3.7].) Large pelagic fish were often found at depths greater than 30 m where water temperatures were below 10°C. We suspect that some of these fish may be bull trout or lake trout, although the species is currently unknown and can only be hypothesized. A project was proposed for 2002 that would help to identify these fish. Our current work would indicate that it is feasible to conduct annual population estimates of large fish in the pelagic region of Lake Pend Oreille. This information would be invaluable in our ongoing efforts to balance predators and prey.

Our graphs of kokanee production and yield (Figure 3.4) can be used as an empirical model to balance predator and prey. We interpret these findings to mean that predator and prey would be balanced if the kokanee population biomass were increased to 300 t (at the current abundance of predators). The figure could also be interpreted as indicating predator and prey would balance if predators were reduced to the point where kokanee yield was lowered by 70 t or 27% (at the current abundance of kokanee).

CONCLUSIONS

We conclude that predation levels in Lake Pend Oreille are too high for the current kokanee prey base. The predation problems were likely caused by low abundance of kokanee, not a recent expansion of the predator populations. Predation appears to be affecting the kokanee survival rate especially between the age-1 and -2.

RECOMMENDATIONS

1. We strongly recommend developing management strategies that would reduce predation levels in Lake Pend Oreille.
2. Hydroacoustic survey methods should be developed to provide annual estimates of rainbow trout, bull trout, and lake trout.
3. We also recommend continued efforts to restore kokanee spawning habitat as an important method to balance predator and prey.

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CHAPTER 4: SHORELINE SPAWNING SUBSTRATES

ABSTRACT

Idaho Department of Fish and Game recommended changes to the winter lake level of Lake Pend Oreille in an effort to provide more suitable spawning gravel on the shorelines. We monitored the shoreline gravel to determine if its quality declined during our study and to evaluate the effect of wave action on the existing shoreline substrates. Of primary interest was the quality of the gravel between the elevations of 625.1 m (2051 ft) and 626.1 m (2054 ft), since this was the substrate inundated by raising winter lake levels. We observed a gradual increase of cobble and a reduction in gravel at most sample locations. After five years of raised lake levels, many areas that previously contained gravel became unsuitable for kokanee spawning. We also monitored the effect of wave action at five beaches. A trench was filled with crushed white limestone from the waterline to a depth of 2 m. The disturbance of the limestone was monitored in February, March, and May of 2000. We found that gravel in water less than 1 m deep was likely to be displaced by wave action, which indicated the potential for poor survival of kokanee eggs at shallow depths. Two other studies examined the effects of wave action on shoreline substrate. Colored gravel was placed at various elevations at five different sites. The movement of the gravel was measured after a period of time to determine both horizontal and vertical movement caused by the combination of lake level changes and wave action. The gravel movement was highly variable among sample locations, but some distinct patterns were observed. Gravel was typically displaced from its point of origin and accumulated within narrow horizontal bands along the shoreline. These bands were generally just above the current waterline and resulted largely from periods of high wind and wave activity. Based on the results of these experiments, we conclude that lake level management was highly influential in determining the quantity and quality of shoreline gravel that was available for spawning kokanee.

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INTRODUCTION

This study examined the effects of changing lake levels on the quality of shoreline gravel usable for kokanee spawning. Studies by Rowan et al. (1992) showed that the distribution of fine sediment along the shoreline was determined by wave action and shoreline slope. Our work recognized that wave action also influences the distribution of shoreline gravel that is important for kokanee spawning. Previous studies in 1994 found that most of the shoreline gravel was left above the waterline when the lake was drawn down during the fall (Fredericks et al. 1995). Beginning in 1996, the winter elevation was kept higher to inundate additional shoreline spawning areas. We then monitored the quality of the gravels over a period of seven years. Our original intent was to determine if siltation was gradually destroying the quality of these shoreline areas or if they were remaining productive spawning areas.

METHODS

Gravel Sampling

We sampled five shoreline sites at the following locations: in Garfield Bay; near the mouth of Trestle Creek; north of the mouth of North Gold Creek; at Hope; and within Ellisport Bay (Figure 4.1). Each site was first surveyed in 1992, which established a baseline of conditions that existed during years of full drawdown of the lake level (Maiolie and Elam 1993). Each of these sites was a historical location for kokanee spawning (Jeppson 1960). Sampling was conducted annually from 1998 to 2001 during July and August. At that time, the lake was at its summer, full-pool level.

All gravel samples were collected while Scuba diving. We tied a rope to the shoreline at each transect location and stretched it out into the lake perpendicular to the shore. Two scuba divers swam parallel to the rope and visually identified bands of similar substrate composition. Flagging was tied to the rope to mark the distance between the top and the bottom of each substrate band. Two random samples of substrate were collected from each substrate band. Divers scooped approximately two liters of substrate into a container and sealed it underwater to eliminate the loss of fine material during transport to the surface. A different methodology was used at Garfield Bay. At this location, divers collected a sample every 1.2 m along the transect that extended from the 625 m elevation (just below the low pool level) to an elevation of 628.6 m (near the full pool level reached during summer). Data from 1992 has been included in our analysis to serve as a baseline comparison of substrate composition before the onset of the lake level experiment.

Each sample was individually bagged, labeled, and oven dried. We then screened the substrate through soil sieves (63.5 mm, 31.75 mm, 16.00 mm, 9.50 mm, 6.35 mm, 2.00 mm, and 0.84 mm). The substrate retained on each screen was weighed and calculated as a percent (by weight) of the total sample. We defined “cobble” as substrates that were 31.75 mm or greater, “gravel” as substrates between 31.75 to 6.35 mm, and “fines” as the substrates smaller than 6.35 mm.

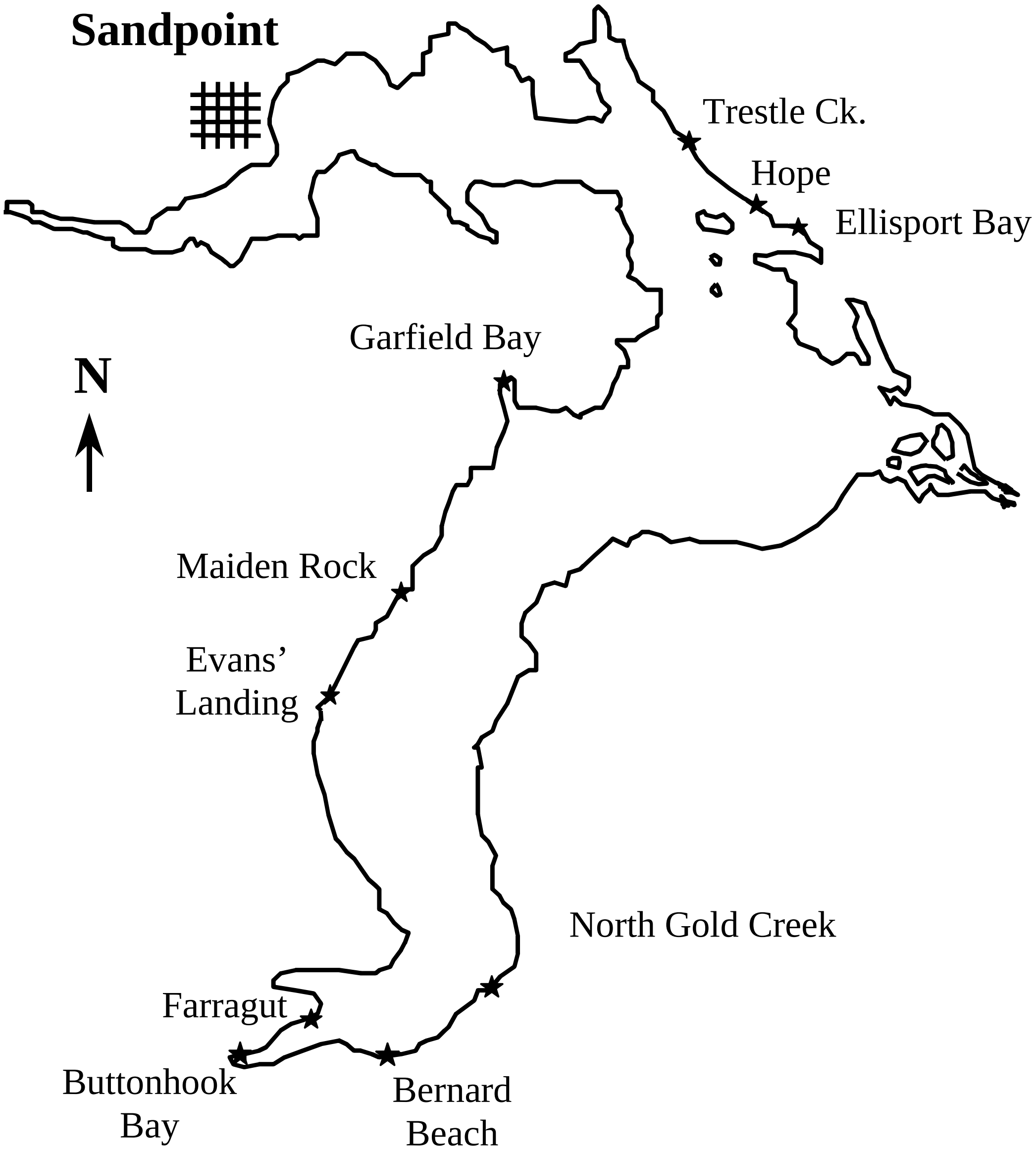

Figure 4.1. Map of Lake Pend Oreille illustrating locations where gravel sampling and experiments occurred.

White Line Studies

Between November 17, 1999 and December 14, 1999, white gravel was placed at five lakeshore locations to determine the depth that wave action and its associated scouring would affect shoreline gravel. Kokanee eggs spend the entire winter in the gravel, and their survival would be unlikely if the gravel was moved and the eggs became dislodged. Crushed white limestone with a mean size of 20 mm was placed at Bernard Beach, Maiden Rock, Hope, Buttonhook Bay, and near the Farragut State Park boat ramp (Figure 4.1). This size of gravel was selected to represent spawning substrate used by kokanee. A trench approximately 8 cm deep and 13 cm wide was excavated from the shoreline at each sampling site and filled with the white gravel. The gravel strip was perpendicular to the shoreline and ran from the waterline to a depth of about 2 m. The top and bottom of each white line was marked with a large rock painted with fluorescent orange paint to establish the original position of the line.

Each site was inspected on February 23, March 20, and May 1, 2000 to monitor the effects of wave action on the white gravel. The depth from the water surface to the top of the white gravel was measured during each inspection. Photos were taken in February and March. The final inspection in May occurred after the lake level had risen 0.7 m. We measured the depth of disturbance as well as the depth to which the white line was destroyed. In addition, the portion of the lines which were disturbed or destroyed were excavated by hand to determine if the gravel had been completely dislodged or if it had been covered by the surrounding substrates.

Colored Gravel Movement

The movement of shoreline gravel was monitored through the use of brightly painted gravel placed on potential spawning beaches at Evan’s Landing, Bernard Beach, Trestle Creek, Maiden Rock, and Ellisport Bay (Figure 4.1).

In September 2000 while the lake level was near full pool, we placed about 18 L of fluorescent yellow gravel at an elevation of 627.55 m and 18 L of fluorescent orange gravel at 626.64 m at the Bernard Beach, Evan’s Landing, and Trestle Creek sample locations (Figure 4.1). As the lake was lowered during September and November, the colored gravel was dispersed by wave action. We allowed the lake to reach its low winter elevation and returned to measure the vertical and horizontal movement of the colored gravel in November.

We conducted an additional study beginning in February 2001 after the lake level had dropped to its final winter level of 625.7 m. At specific locations on the shorelines of Bernard Beach, Maiden Rock, and Ellisport Bay, we placed approximately 10 L of fluorescent green gravel 15 cm above the waterline and 10 L of silver gravel 30 cm below the waterline. We returned to these sites monthly to document gravel movements throughout the winter.

During these studies, lake elevations were obtained on a daily basis from the U.S. Army Corps of Engineers. The vertical movement of each gravel piece was measured using a surveyor’s transit and stadia rod. The horizontal distance that gravel moved was measured with a 61 m measuring tape. Only visibly exposed pieces of colored gravel were measured, and each was removed to eliminate the possibility of measuring it twice.

RESULTS

Gravel Sampling

Ellisport Bay

From 1998 to 2001, during the second to fifth winters of higher water levels, we observed a gradual increase in the percent of cobble substrate and a decrease in the percent of gravel and fines between the elevations of 624.7 and 627.7 m (Figure 4.2). At 625.1 to 625.7 m, the percent of cobble in our samples increased from 47.8% in 1999 to 94.5% in 2001 (Figure 4.3). This was an increase of 75.5% from the 1992 value. The percent of gravel progressively declined from 26.4% in 1998 to 5.4% in 2001. This was a 31% decrease since 1992. We observed an increase in the percent of fines from 6.5% in 1998 to 30.8% in 1999, with a decline to 0.1% in 2001.

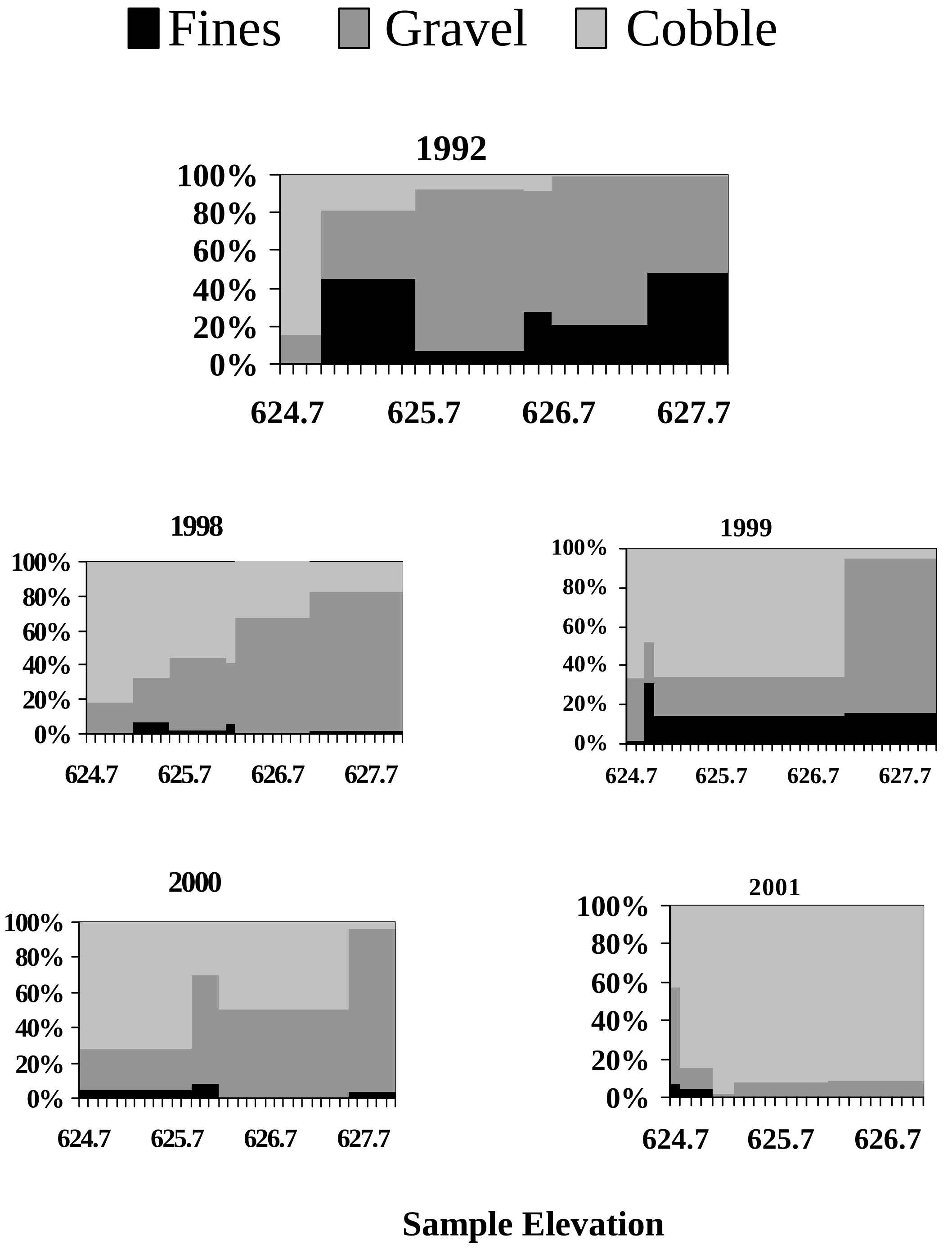

Figure 4.2. Comparison of substrate composition between 624.7 and 627.7 m at Ellisport Bay, 1992, 1998-2001 Lake Pend Oreille, Idaho.

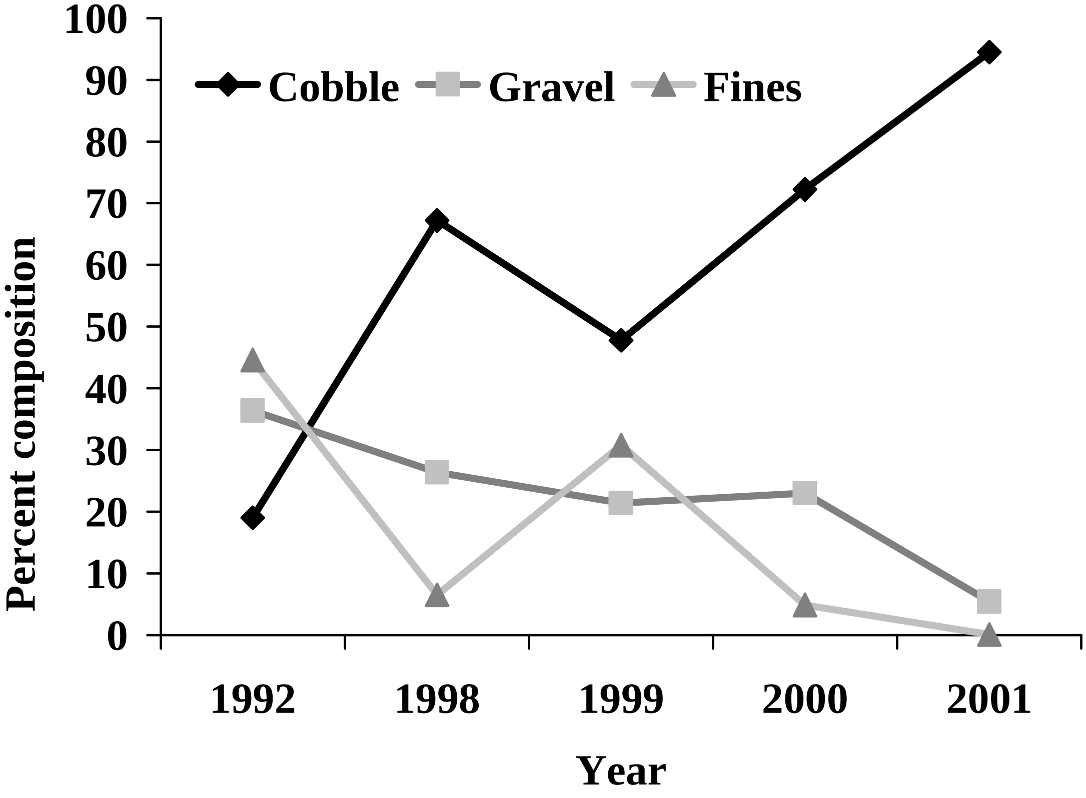

Figure 4.3. Comparison of substrate composition between 625.1 and 625.7 m at Ellisport Bay, 1992, 1998-2001 Lake Pend Oreille, Idaho.

Trestle Creek

The substrate composition on the Trestle Creek shoreline showed a general decline in the amount of potential spawning gravel during this study (Figure 4.4). Between the elevations of 625 m and 626 m, the percent of gravel declined from 43% in 1992 to 18% in 1998 to 24% in 1999 to 4% in 2000 to 17% in 2001 (Figure 4.5). The percent of cobble increased from 59.9% in 1998 to 93.2% in 2000 and then declined to 47% in 2001. The percent of fines decreased from 22.2% in 1998 to 2.5% in 2000, but then increased to 35.8% in 2001.

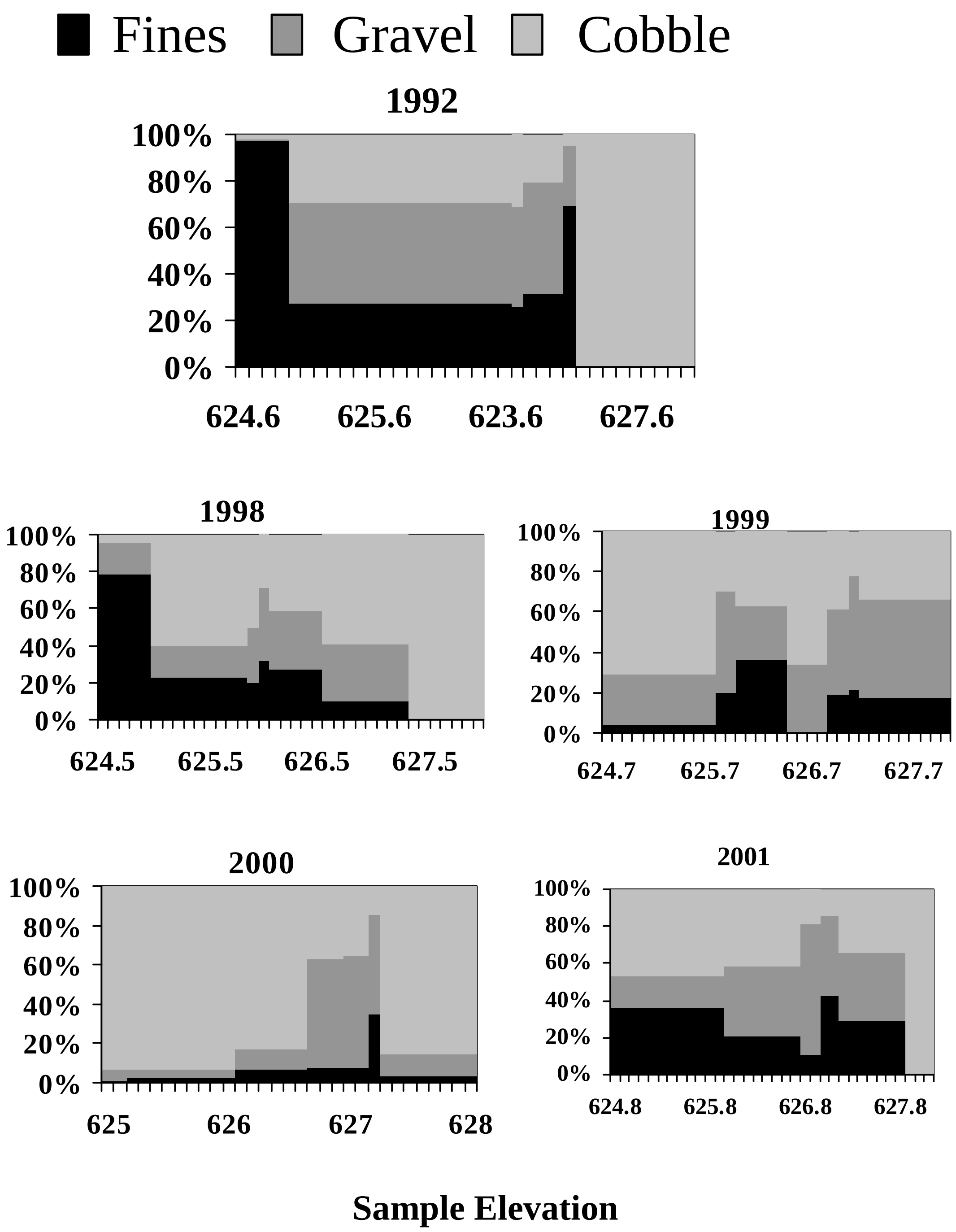

Figure 4.4. Comparison of substrate composition between 624.7 and 627.7 m at Trestle Creek, 1992, 1998-2001 Lake Pend Oreille, Idaho.

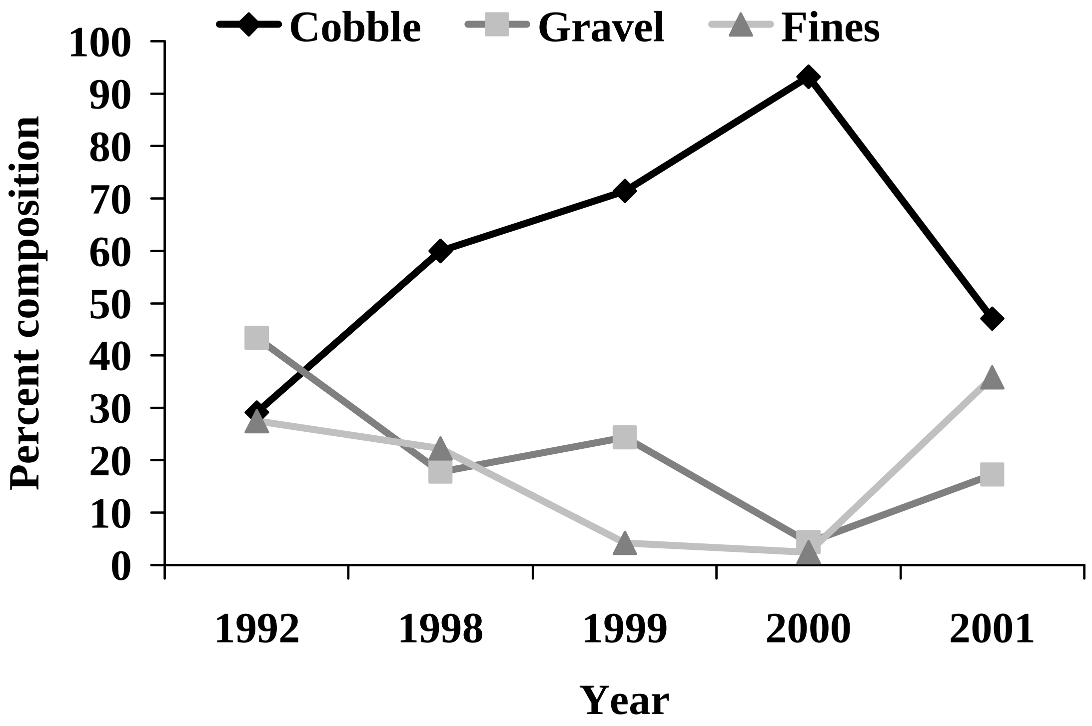

Figure 4.5. Comparison of substrate composition between 625.1 and 625.7 m at Trestle Creek, 1992, 1998-2001 Lake Pend Oreille, Idaho.

Garfield Bay

Between the study elevations, the lowest amount of gravel and the greatest quantity of cobble was observed in 1998 (Figure 4.6). From 625.1 to 625.7 m, gravel increased from 3.3% in 1998 to 12.9% in 2001; however, this is still below the 1992 value of 14.6% (Figure 4.7). Fines increased from 4.1% in 1998 to 18% in 1999, and then dropped to 5.6% in 2001. The percent of cobble was highest in 1998 with 92.62% and gradually decreased to a low point of 75.43% in 2000. This value was still 15% higher than 1992 (Figure 4.7).

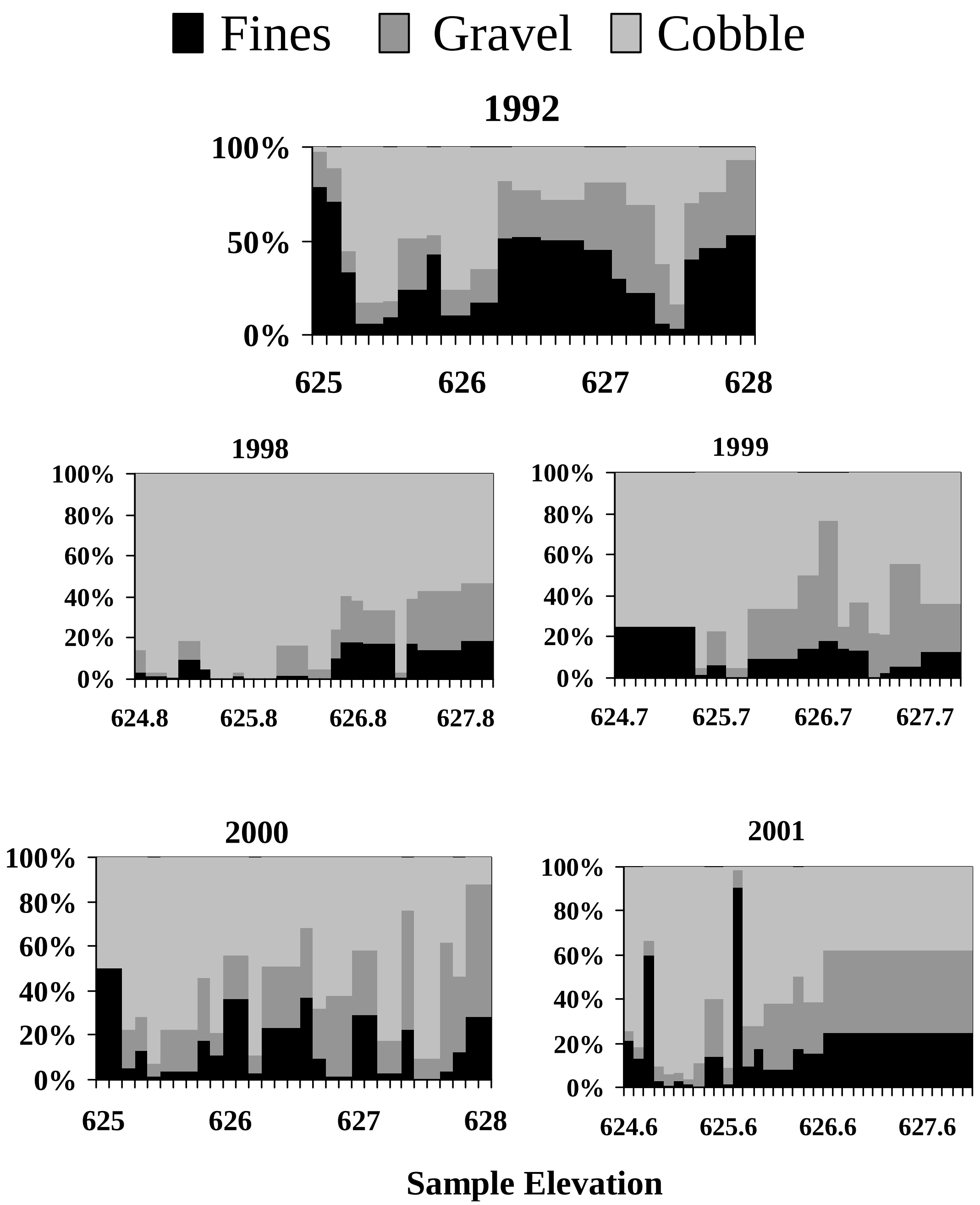

Figure 4.6. Comparison of substrate composition between 624.7 and 627.7 m at Garfield Bay, 1992, 1998-2001 Lake Pend Oreille, Idaho.

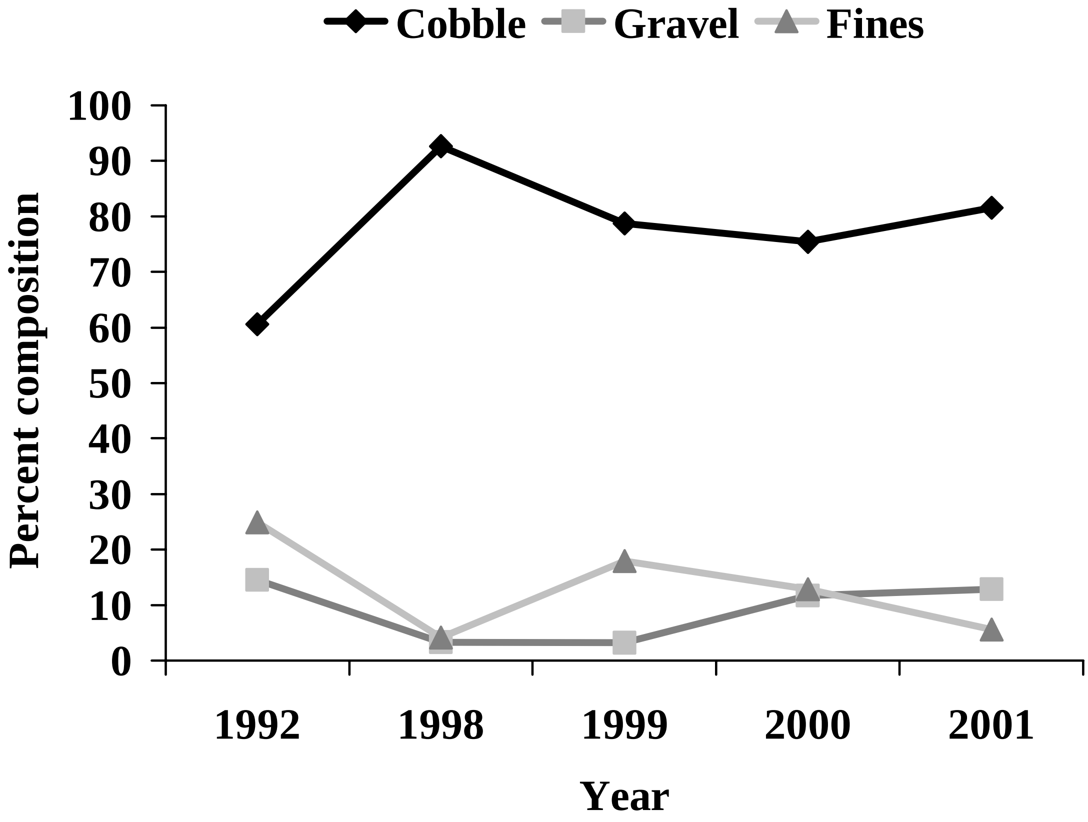

Figure 4.7. Comparison of substrate composition between 625.1 and 625.7 m at Garfield Bay, 1992, 1998-2001 Lake Pend Oreille, Idaho.

Hope

We observed an increase in gravel in a narrow band between 626.5 m and 627.3 m during years of higher winter lake levels, with a net decrease at other elevations (Figure 4.8). Between 625.1 to 625.7 m, we observed an increase in cobble from 89.2% to 100% in 2000 and 2001 (Figure 4.9). The percent of gravel and fines decreased from 2.25% and 8.55%, respectively, in 1998 to 0% in both 2000 and 2001.

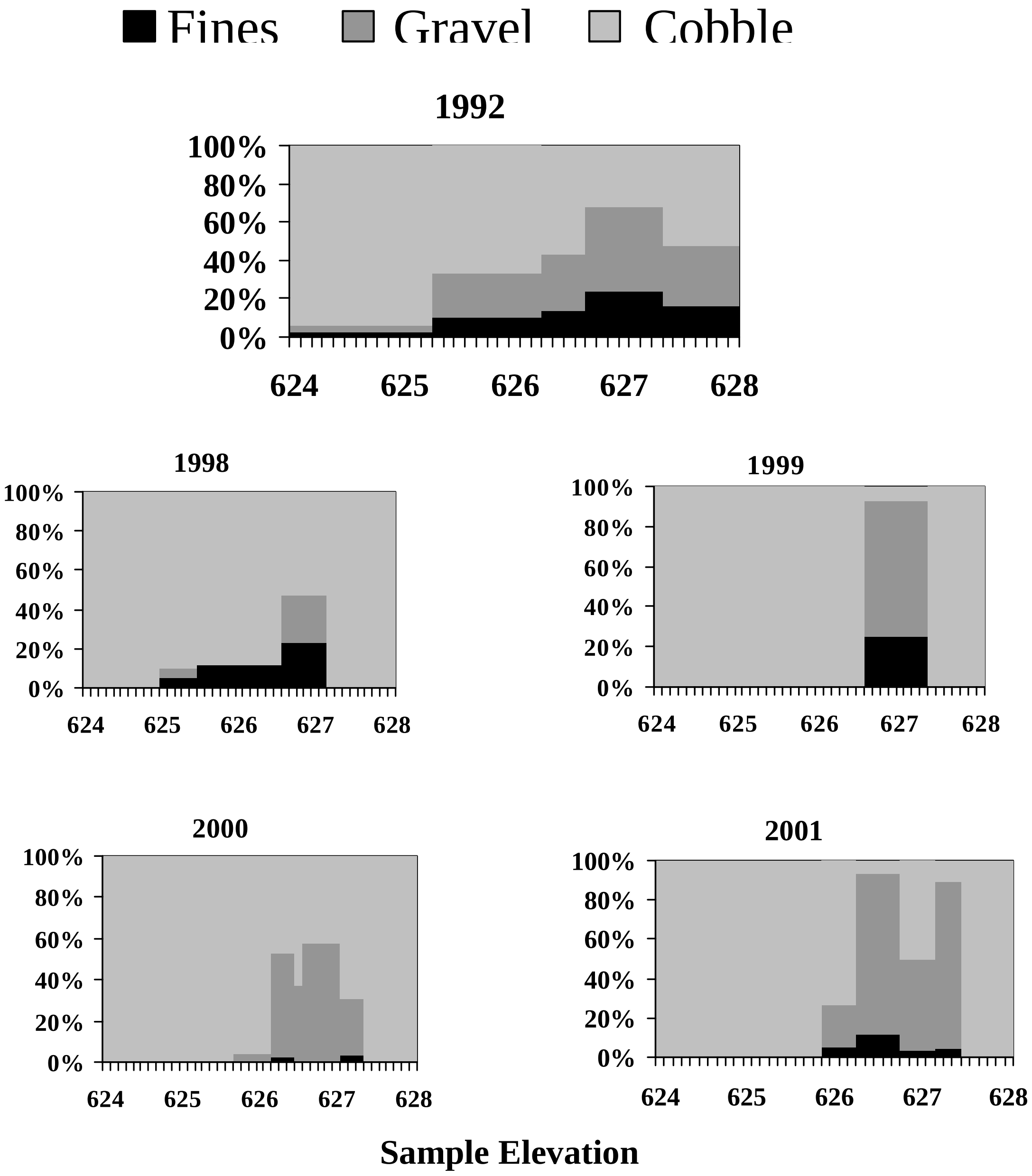

Figure 4.8. Comparison of substrate composition between 624.7 and 627.7 m at Hope, 1992, 1998-2001 Lake Pend Oreille, Idaho.

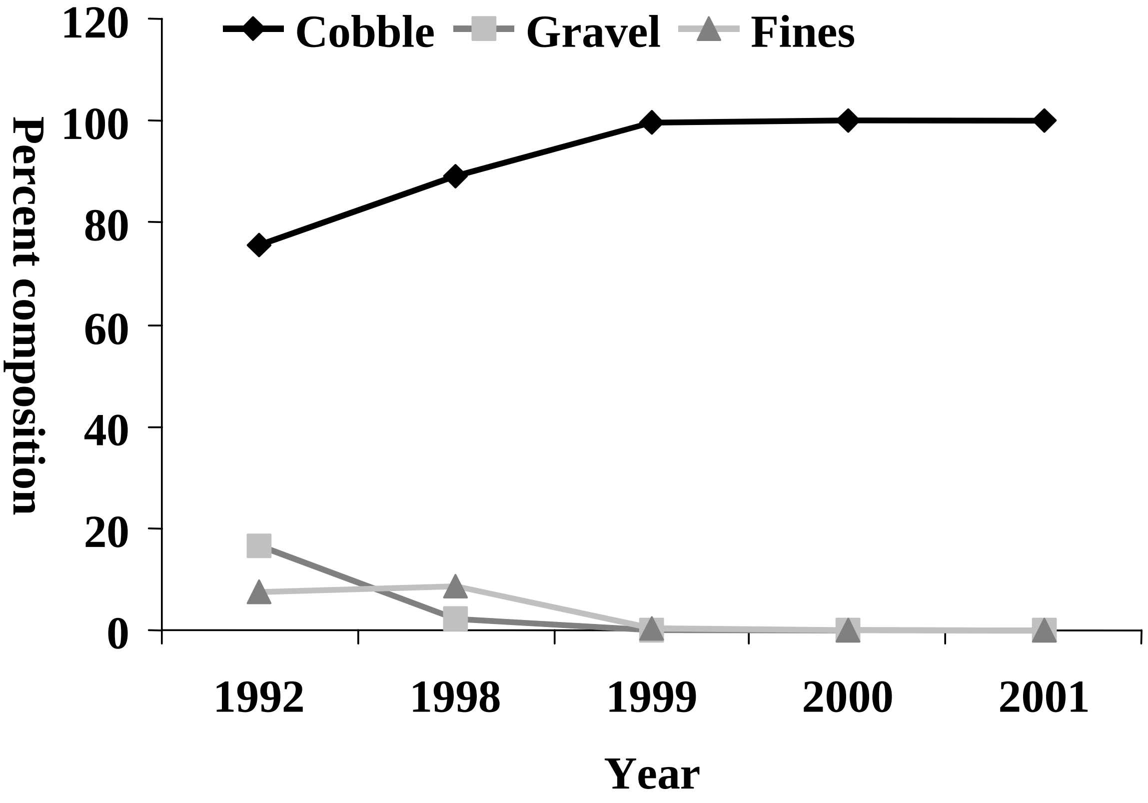

Figure 4.9. Comparison of substrate composition between 625.1 and 625.7 m at Hope, 1992, 1998-2001 Lake Pend Oreille, Idaho.

North Gold Creek

The substrate composition at this sampling location was highly variable between years (Figure 4.10). During the study, the creek channel changed course several times and cut across the transect area. Between 625.1 and 625.7 m, we observed a steady decrease in cobble from 19.5% in 1998 to 0% in 2000, with a rapid increase to 52.8% in 2001(Figure 4.11). On the contrary, gravel increased from 26.4% in 1998 to 44.8% in 2000, with a drop to 32.3% in 2001. The percent of fines also increased between 1998 and 1999 from 54.1% to 67.3%, respectively, but then dropped in 2001 to 14.9%. The final 2001 values for cobble, gravel, and fines were very similar to the prestudy 1992 values of 56.3%, 36.3%, and 7.4%, respectively (Figure 4.11).

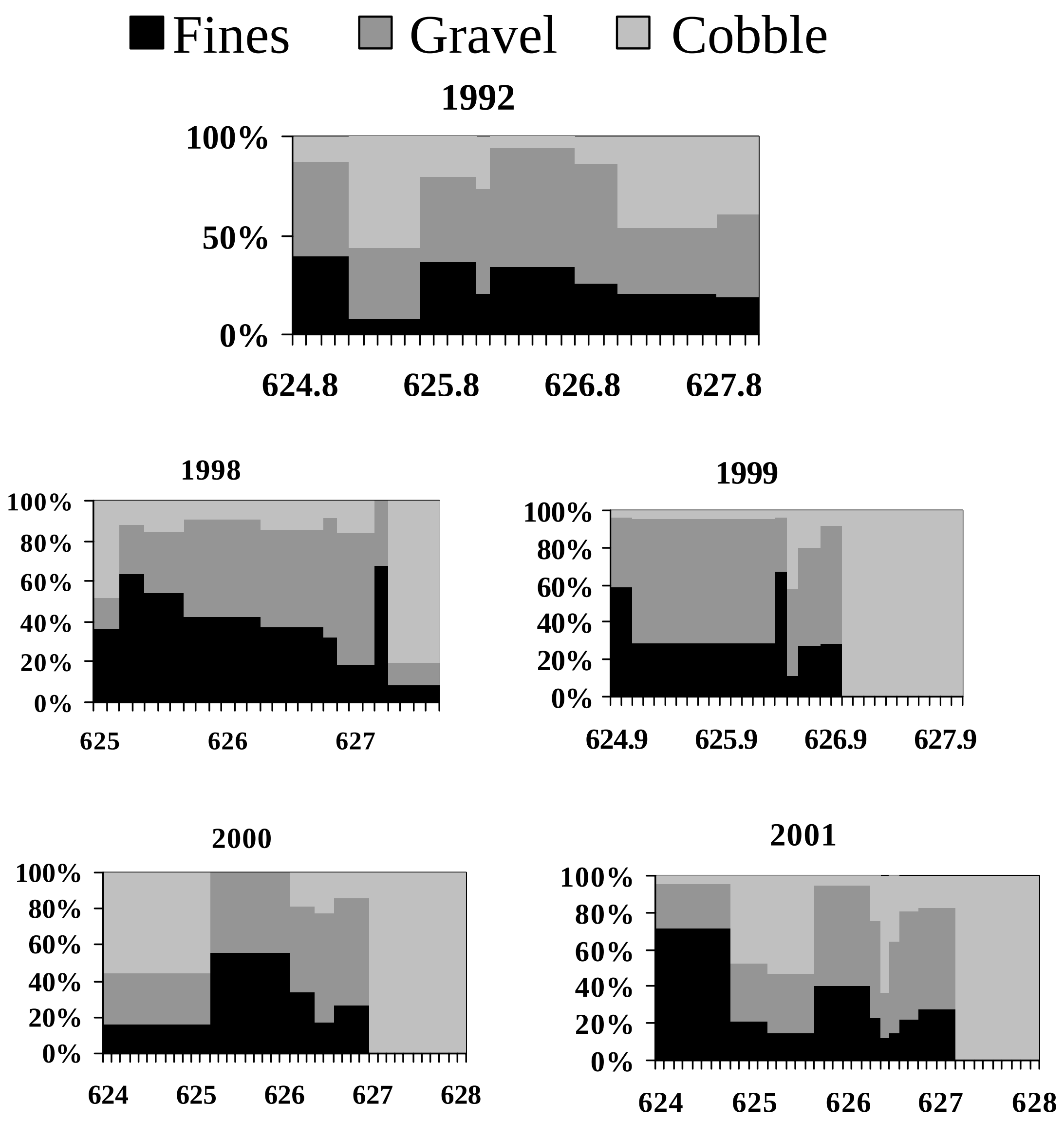

Figure 4.10. Comparison of substrate composition between 624.7 and 627.7 m at North Gold Creek, 1992, 1998-2001 Lake Pend Oreille, Idaho.

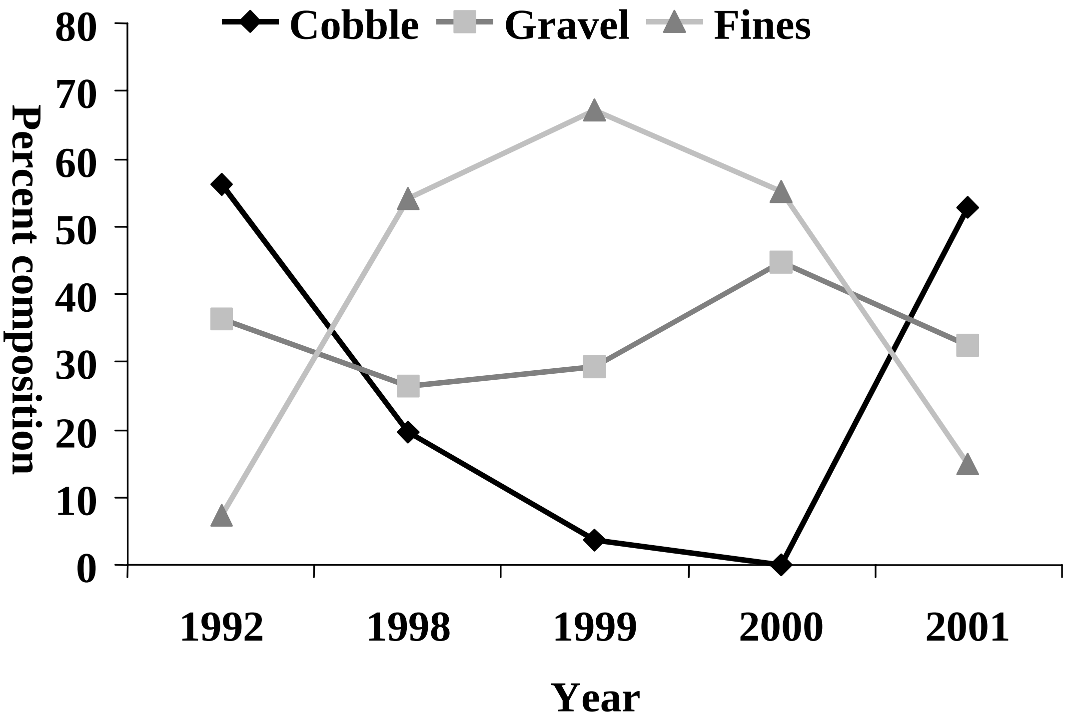

Figure 4.11. Comparison of substrate composition between 625.1 and 625.7 m at North Gold Creek, 1992, 1998-2001 Lake Pend Oreille, Idaho.

Table 4.1. The location, date, and depth (m) to which white gravel placed on the shoreline in Lake Pend Oreille, Idaho was disturbed by wave action.

Site of White Line Placement	Date of Initial Placement	Date of Inspection February 23, 2000	 March 20, 2000	 May 01, 2000
Farragut State Park	11-17-99	0.46	0.73	0.88
Bernard Beach	11-18-99	0.67	0.70	0.67
Maiden Rock	11-18-99	1.13	1.40	1.43
Hope	12-09-99	0.55	Not determined	0.49
Buttonhook Bay	12-14-99	0.00	0.02	0.08

White Line Study

White gravel placed on the shorelines gave a clear indication of the depth to which wave action affected gravel-sized rocks. At deeper depths, the gravel stayed in place and was easily observable throughout the winter. However, the white rocks were clearly displaced to varying depths at the shallow end of the lines (Table 4.1 and Figure 4.12).

The Maiden Rock location showed gravel disturbance to the deepest depth (1.43 m). This site is located along the western side of the lake and exposed to southern winds. The Buttonhook Bay site showed the least amount of gravel displacement. It was sheltered from wind and wave action from every direction and showed only 8 cm of disturbance during the winter. The depth of wave action was intermediate at the other sites. Gravel at the Farragut site was displaced to a water depth of 0.88 m, Bernard Beach to a depth of 0.67 m, and the site at Hope to a depth of 0.49 m (Table 4.1). An indication of the speed with which the shoreline gravel can be displaced is given by an observation made at the Hope site within 24 hours of placement. Upon returning to the site the following morning, two members of the crew estimated that wave action from a storm the previous night had already displaced the line to a depth of about 0.5 m. The depth of disturbance did not change appreciably for the remainder of the winter.

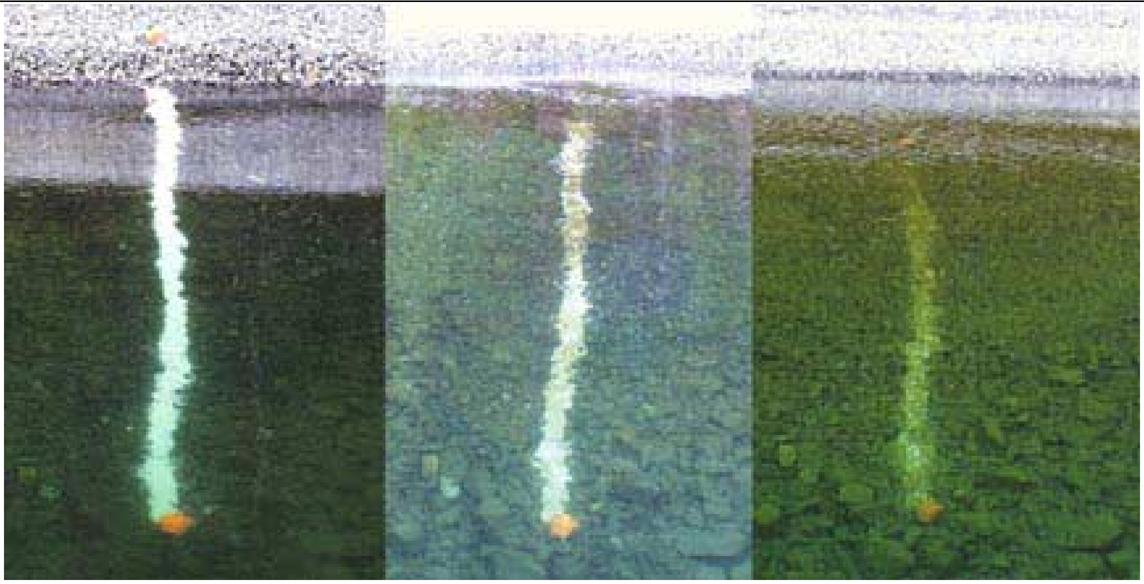

Figure 4.12. White gravel line constructed at Bernard Beach on Lake Pend Oreille, Idaho. First photo taken immediately after construction on November 18, 1999. Middle photo taken on January 20, 2000, and last photo taken on March 30, 2000. In the last photograph the orange rock at the top of the gravel line had moved.

Colored Gravel Movement

Bernard Beach

The majority of the yellow gravel was deposited in a narrow band between 20 and 50 cm above the spot of original placement (Figure 4.13); however, some yellow gravel was spotted more than 1 m above the original placement site. The mean elevational change for yellow gravel was 0.47 m above original placement (or +0.47 m). Very few pieces had moved below placement. The yellow gravel traveled as much as 11 m horizontally. The orange gravel moved greater than 12 m horizontally in a narrow band slightly above placement, and vertically from 0.76 m below placement (-0.76 m) to 0.52 m above placement (+0.52 m). The mean elevation change for orange gravel was +0.28 m (Table 4.2).

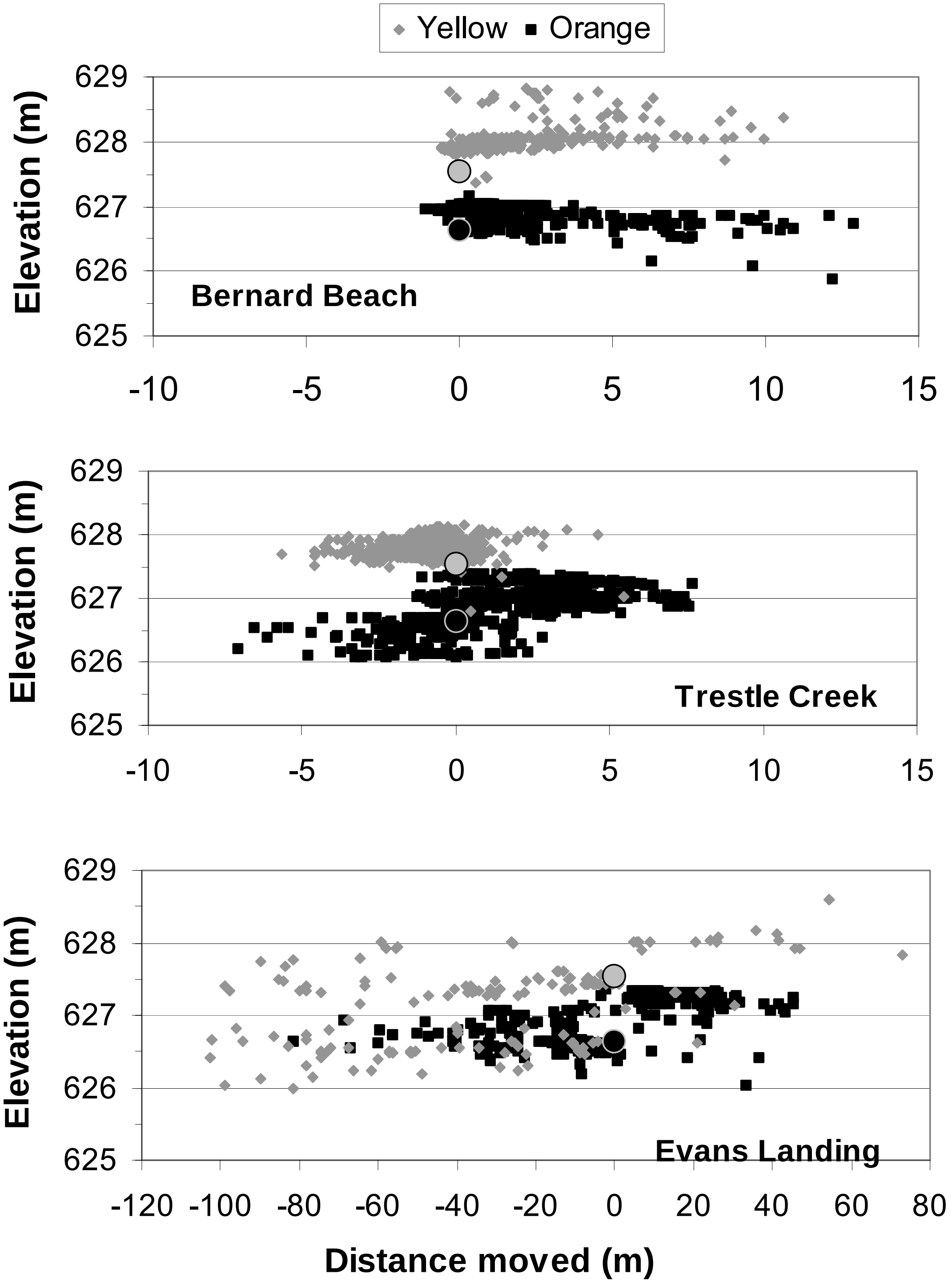

Figure 4.13. Movement of orange and yellow gravel placed at Bernard Beach, Trestle Creek, and Evans Landing on Lake Pend Oreille, Idaho during the fall drawdown period from September 2000 to November 2000. Shaded circles mark the points of initial placement of gravel.

Table 4.2. Selected statistics on the distribution patterns for colored gravel placed at various locations around Lake Pend Oreille, Idaho during the fall drawdown period, 2000. At the time of placement, the lake surface was at 628.6 m above mean sea level (full pool). Yellow gravel was placed at 627.58 m and orange gravel placed at 626.67 m. The lake was allowed to drop to winter pool (625.8) before gravel movements were measured.

Site, group, # recovered	% moving up	% staying at elev.*	% moving down	Max elev. Increase (m)	Max elev. Decrease (m)	Mean elev. change (m)	Mean horizontal change	Maximum horizontal movement	Total horizontal spread
Bernard Beach, yellow, n = 344	98.84	0.87	0.29	1.28	0.18	+ 0.47	+ 1.80	10.58	11.19
Evans Landing, yellow, n = 159	15.72	25.16	59.12	1.04	1.55	- 0.42	- 31.58	102.71	175.58
Trestle Creek, yellow, n = 1,746	38.49	61.34	0.17	0.60	0.74	+ 0.16	- 0.51	5.7	11.20
Bernard Beach, orange, n = 741	82.00	17.30	0.70	0.52	0.76	+ 0.28	+ 1.45	12.86	13.99
Evans Landing, orange, n = 334	57.8	35.3	6.9	0.85	0.61	+ 0.29	- 2.14	81.38	126.64
Trestle Creek, orange, n = 1,742	26.6	66.7	6.7	0.75	0.57	+ 0.12	+ 0.5	7.7	14.8

* - Remained within 0.15m (up or down) of original placement elevation

Trestle Creek

Yellow gravel was observed to travel vertically as much as 0.74 m and spread horizontally across a range of approximately 11 m (Table 4.2). The vertical movement of the orange gravel was between +0.75 and -0.57 m in two distinct bands, one above placement and the other below, with a 15 m range of horizontal movement. These two bands are on opposite sides of the point of origin as can be seen in Figure 4.13, indicating that they were formed by separate storm events with wave activity moving in opposite directions.

Evan’s Landing

We observed the most sporadic spreading of the yellow gravel at this site (Figure 4.13). Yellow gravel showed a range of horizontal movement of approximately 176 m and vertical movement as great as +1.04 m and -1.55 m (Table 4.2). The orange gravel was also highly disturbed at this site, with a range of horizontal movement of approximately 126 m and vertical movement from +0.85 to –0.61 m.

Bernard Beach

Fluorescent green and silver gravel showed the most extreme movement at this site due to exposure to northern winds. At this location, silver gravel moved up to 234 m horizontally and vertically between +1.01 m and -0.91 m (Table 4.3). The green gravel spread approximately

170 m horizontally, and vertically from +0.64 to -1.34 m. Both colors were deposited in three distinct bands, as can be seen in Figure 4.14.

Table 4.3. Selected statistics on the distribution patterns for colored gravel placed at various locations around Lake Pend Oreille, Idaho during the winter low water period, February 7 to April 5, 2001. At the time of placement, the lake was at winter low pool (625.8 m above mean sea level). Green gravel was placed 0.15 m above the waterline, and silver gravel was placed 0.3 m below the waterline. Wave action was allowed to redistribute the gravel for approximately two months before movements were measured.

Site, group, # recovered	% moving up	% staying at elev.*	% moving down	Max elev. Increase (m)	Max elev. Decrease (m)	Mean elev. change (m)	Mean horizontal change	Maximum horizontal movement	Total horizontal spread
Bernard Beach, green, n = 119	16.0	16.8	67.2	+0.64	-1.34	-0.38	+69.72	166.72	169.77
Maiden Rock, green, n = 220	10.5	52.7	36.8	+0.58	-0.70	-0.12	+29.42	73.45	111.97
Ellisport Bay, green, n = 143	14.7	20.3	65.0	+0.33	-0.37	-0.14	+ 9.38	31.09	31.09
Bernard Beach, silver, n = 139	58.3	10.0	31.7	+1.01	-0.91	+0.12	+82.51	172.51	234.20
Maiden Rock, silver, n = 275	85.4	14.6	0	+1.04	-0.03	+0.35	+27.07	72.82	80.44
Ellisport Bay, silver, n = 40	25.0	75.0	0	+0.25	0	+0.12	+0.10	0.76	1.22

* - Remained within 0.15m (up or down) of original placement elevation.

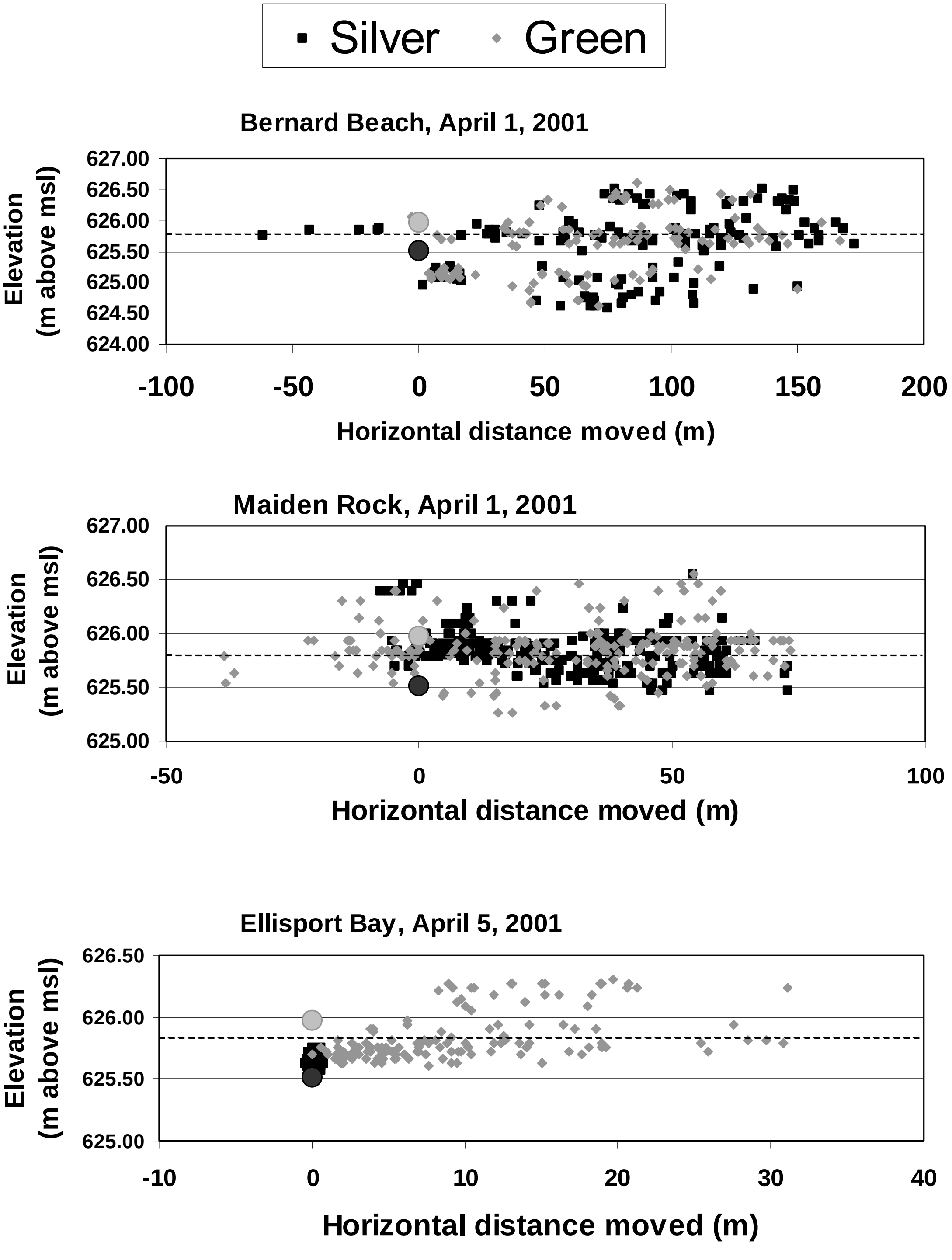

Figure 4.14. Movement of green and silver gravel placed at Bernard Beach, Maiden Rock, and Ellisport Bay on Lake Pend Oreille, Idaho during the winter low-water period from February 7 to April 5, 2001. Shaded circles mark points of original placement of gravel, and dashed lines represent the waterline at the time of placement.

Maiden Rock

A maximum horizontal movement of about 73 m was observed at this location for both green and silver gravel (Figure 4.14). Green gravel moved vertically 0.58 m up and 0.7 m down from the original location of deposition, with a mean change of -0.12 m. Silver gravel was measured to move +1.04 m to –0.03 m vertically, with a mean change of +0.35 m and a total horizontal spread of over 80 m (Table 4.3). The majority of gravel was deposited at or just above the waterline.

Ellisport Bay

This location was the least affected by waves during this study. The fluorescent green gravel exhibited a maximum horizontal movement of 31 m. Vertical movement of 0.3 m up and 0.5 m down the shoreline was also noted (Table 4.3). The silver gravel did not move a measurable distance horizontally and only 0.1 m vertically (Figure 4.14).

A great deal of variability was noted in movements among the various sites, but some distinct patterns were observed. Gravel tended to be dispersed within narrow bands along the shoreline. These bands were generally just above the current waterline and were created primarily during high wind and wave events of relatively short duration. During the yellow and orange drawdown test, the presence of separate bands of gravel was noticed at different elevations and in different directions along the shoreline (Figure 4.13). At many sites during the green and silver low water test (Figure 4.14), a number of bands had developed at different elevations, both above and below the waterline.

DISCUSSION

The original concern was that siltation would, in time, make the newly inundated shoreline gravel unusable (gravel between 625.1 m and 626.1 m). Our findings show that a gradual siltation of spawning gravels did not occur with higher water levels. Instead, we found a trend toward a reduction in silt and gravel and an increase in cobbles at most shoreline spawning areas at these depths. The result of having winter water levels higher for five consecutive years was an armoring of the shoreline at these depths; which turned potential spawning sites into cobble areas with substrate that was mostly too large for kokanee to build redds.

The key area of shoreline during this study was the newly inundated substrate in historic spawning areas (areas between the elevations of 625.1 m [2051 ft] and 626.1 m [2054 ft]). This area was submerged from 0.3 to 1.2 m during the first three winters by keeping the water level 1.2 m higher. Kokanee used the gravels in this area even during the first year of changed lake levels, particularly the deeper edge at elevation 625.1 m (Chapter 1). After about three years of higher water levels, these areas showed noticeable declines in the quantity of spawning gravel (Figures 4.3, 4.5, 4.7, 4.9). During the last two years of this study (2000 and 2001), the lake was held 0.6 m higher than normal (625.8 m). The deepest of the newly inundated gravel was then only 0.6 m below the surface, where wave action could scour this gravel at any but the most protected sites.

The white line study showed the effect of wave action on the shorelines. Gravel on the shorelines down to a maximum depth of 1.4 m (at the Maiden Rock site) was disturbed, and it was unlikely that eggs buried within this gravel would have survived. Depth of the wave action varied considerably between sites. Wave action at the most protected sites would not have disturbed eggs in Buttonhook Bay that were spawned at depths greater than 0.1 m. These findings suggested that holding the lake level up 1.2 m higher would provide benefits to kokanee spawning in most areas of the lake. Holding the lake, for example, 0.6 m higher would provide good gravel under 0.6 m of water on many of the lake shoreline areas, but in many locations the eggs would be dislodged by wave action.

The colored gravel was placed on the shorelines between the high and the low pool levels to see if the fall drawdowns would pull the gravel down the banks to the low water line. Gravel was found to move as much as 100 m horizontally, but generally moved less than 1 m in elevation. It was common to find the colored gravel had been pushed uphill. Wave action on the shorelines had considerable energy, and the net movement of the gravel could go either direction (Tables 4.2 and 4.3). Of the six gravel samples monitored (two at each location), five had positive (uphill) mean movement, while the sixth (Evans' Landing) had a negative (or downhill) net movement.

Colored gravels that were placed immediately above and below the waterline at low pool also showed the effects of along-shore currents. Gravel moved more than 170 m horizontally along Bernard Beach, showing that the substrates in these spawning areas are fairly dynamic (Table 4.3). These gravels can remain relatively free from silt because they are being resorted with every major storm event. We also noted a pattern of gravel to build into bars just above the waterline. This is consistent with the trend we noted in depletion of gravels in the area below the waterline at places like Ellisport Bay (Figure 4.2).

This study began by changing the lake levels to put the shoreline gravels underwater. Kokanee immediately used the newly available gravel for spawning and had good survival. Changing lake levels, however, modified the locations of those gravels after several years. Holding the lake 1.2 m higher for three winters and then 0.6 m higher for two winters allowed the gravel to be pushed up to the water line and build into bars that would be unusable by spawning kokanee. By the end of this study, lake levels needed to be lowered again to the low pool level (625.1 m) to allow gravel bars to reform at a lower elevation. Studies utilizing the painted gravel (Figure 4.14) showed that declining water levels pulled some of the gravel downward on the beaches. These deeper gravels could then be inundated again by keeping lake levels higher in subsequent years.

This study shows that gravels on the beaches are very mobile, and if given the right conditions, gravel bars build rather quickly (a few days of high winds). The challenge in the future will be to balance the benefits of lake level changes for fish with the associated formation and degradation of spawning areas. The early operation of the dam gives a strong clue as to how this could be done. Minimum lake levels from 1955 to 1966 showed a pattern of considerable variation. One year the lake would be lowered to its low pool elevation, the next year it would be higher, and the following year at an altogether different elevation. Based on the current study we would expect that during the low water years, gravel bars probably formed at the water line and then were inundated the following year when the drawdowns were reduced. The result of varying the winter lake levels in the 1950s and 1960s was that three generations of kokanee were produced that were numerically strong enough to provided a mean harvest of 1 million fish annually. Therefore, the recommendation of this study, to raise and lower winter lake levels to improve spawning areas, has been used in the past and produced good results.

The testing in this study, and the recommendation to vary winter lake levels by 1.2 m, were consistent with the operating rule curves established for Albeni Falls Dam. Other options, such as varying lake levels in a more natural pattern, were not tested. Such changes may warrant testing in the future if changes to the rule curves could be made.

CONCLUSION

We conclude that lake level management affects the amount of shoreline gravel available for kokanee spawning. It also determines where, and at what elevation, the gravel bars will form. These spawning areas, in turn, control the abundance of kokanee in the lake. Kokanee abundance determines the kokanee fishery, and to a large extent, the rainbow trout and lake trout fishery. In short, proper lake level management determines the quality of the sport fishing on the lake.

RECOMMENDATIONS

1. We recommend a minimum of 1.2 m variations in the minimum pool level of Lake Pend Oreille between years. During years with lower pool levels, gravel bars will form near the water lines. During higher water years, these gravel bars will be inundated to form high quality kokanee spawning areas in some sections of the lake.

2. To get the maximum benefit for the kokanee population, water levels should be raised for three consecutive years followed by one winter of low pool level. The kokanee population can currently be described as collapsing. For the short term (one or two generations of kokanee), the approach of three years up and one year down provides the greatest benefit. Egg-to-fry survival would be enhanced in the winters of high water level benefiting that year class of kokanee. During the winter of lower water levels, gravels would be cleaned and resorted, but egg-to-fry survival would likely return to a lower level. A pattern of one year up and one year down should be considered after the population becomes more stable as a method to maximize our understanding of the effect of lake levels on kokanee population dynamics, if questions remain. The experimental design would be more powerful with equal numbers of test and control samples.

3. In the future, the years of full drawdown to 625.1 m should be timed to coincide with weak year classes of kokanee. Less spawning gravel may be needed during those years and it may be available at deep-water sites.

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CHAPTER 5: WATERFOWL AND VEGETATION

ABSTRACT

We monitored winter waterfowl abundance and riparian vegetation as part of our studies on changing lake levels. Waterfowl were counted annually between 1997 and 2001 from a fixed-wing aircraft during the first week of January. Their numbers were highly variable with a range in the total count of ducks, geese, and swans from 10,073 during the winter of 1997 to 31,520 in 1998. No clear relationship was found between lake levels and waterfowl utilizing the lake. Ice cover on other area waters, weather conditions, and region-wide population fluctuations likely influence waterfowl abundance. Riparian vegetation was documented photographically in 1998 and 1999. Reducing the fall drawdown from 3.5 m to 2.3 m had no visually noticeable effect on shoreline riparian vegetation. It did not recolonize the drawdown zone during the time of this study. The drawdown zone is underwater during summer and exposed to drying and freezing during winter, making it an inhospitable environment for most wetland vegetation.

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INTRODUCTION

Researchers were asked to monitor shoreline vegetation and waterfowl on Lake Pend Oreille as part of the current study. One of the initial reviewers thought that changes in winter lake elevation could result in expansion of the riparian vegetation, which in turn would cause increases in the wildlife usage of the shoreline. A quick and simple approach to monitor vegetation was therefore conducted to determine if shoreline areas were being recolonized. We were also requested to monitor waterfowl to see if changing lake levels caused large-scale changes in their usage of the lake. Prior to this study, annual waterfowl surveys showed highly variable numbers. It was decided that these surveys should continue, regardless of the variability, to document possible effects.

METHODS

Waterfowl Counts

During the first week in January, from 1997 to 2001, wildlife biologists flew in a fixed-wing aircraft and counted waterfowl in the vicinity of the lake. Survey areas included the Clark Fork River (Idaho portion), Pend Oreille River (Idaho portion), and Lake Pend Oreille. The classification of waterfowl was divided into dabblers, divers, mergansers, geese, and swans.

Riparian Area Analysis

We monitored the shoreline riparian areas of the lake to determine if riparian vegetation would colonize the drawdown zone. A photographic record of shoreline vegetation was collected from nine shoreline locations around Lake Pend Oreille, including Farragut State Park, Leiberg Point, Idlewilde Bay, Bernard Beach, Sand Creek, Denton Slough, Long Bridge shoreline, Trestle Creek, and West Trestle Creek. These photographs were taken to document any obvious changes in riparian vegetation in the drawdown zone. Photographs were taken in December of 1998 and 1999 during the second and third years of lake level changes.

RESULTS

Waterfowl Counts

We observed a range in the total count of ducks, geese, and swans from 10,073 during the winter of 1997 to 31,520 during the 1998 season (Figure 5.1; Table 5.1). The count of ducks (including dabblers, divers, and mergansers) ranged from 9,690 in the winter of 1997 to 30,787 in 1998. The count of geese ranged from 201 in the winter of 1996 to 2,700 in 1999. The count of swans ranged from 73 in 1997 to 194 during the 1999 season (Table 5.1).

Riparian Areas

Higher winter lake levels did not cause a recolonization of vegetation in the drawdown zone during this study. Since the drawdown zone is underwater during the summer growing season and exposed to freezing temperatures during winter, it remains an inhospitable habitat for riparian vegetation (Figure 5.2). No visual differences were noted between 1998 and 1999.

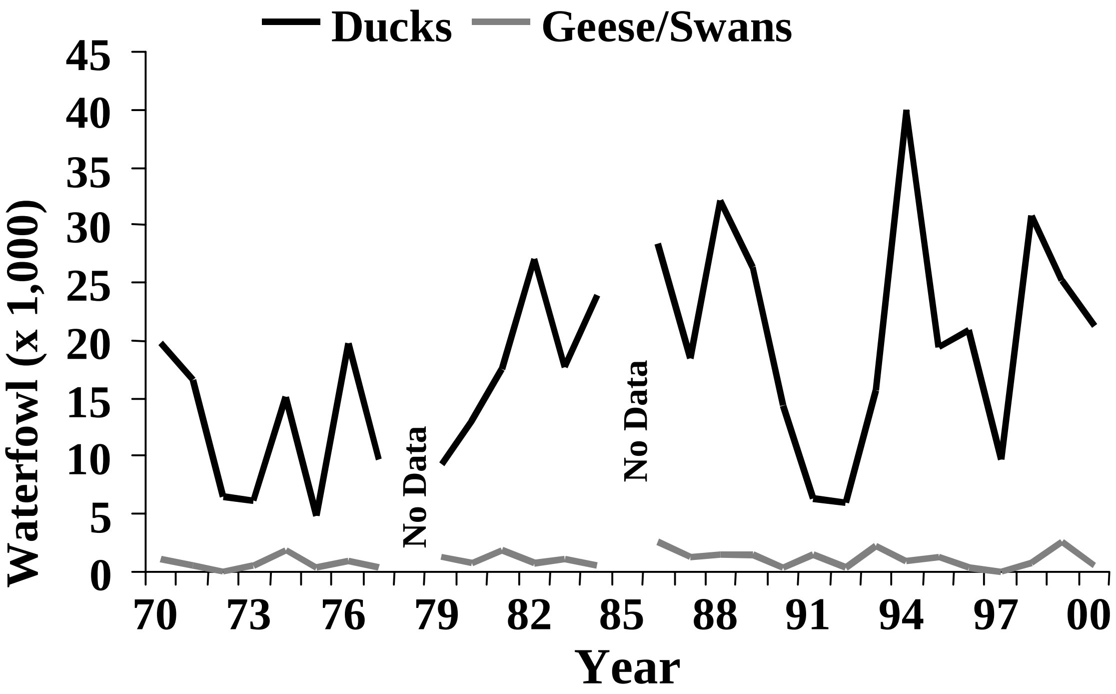
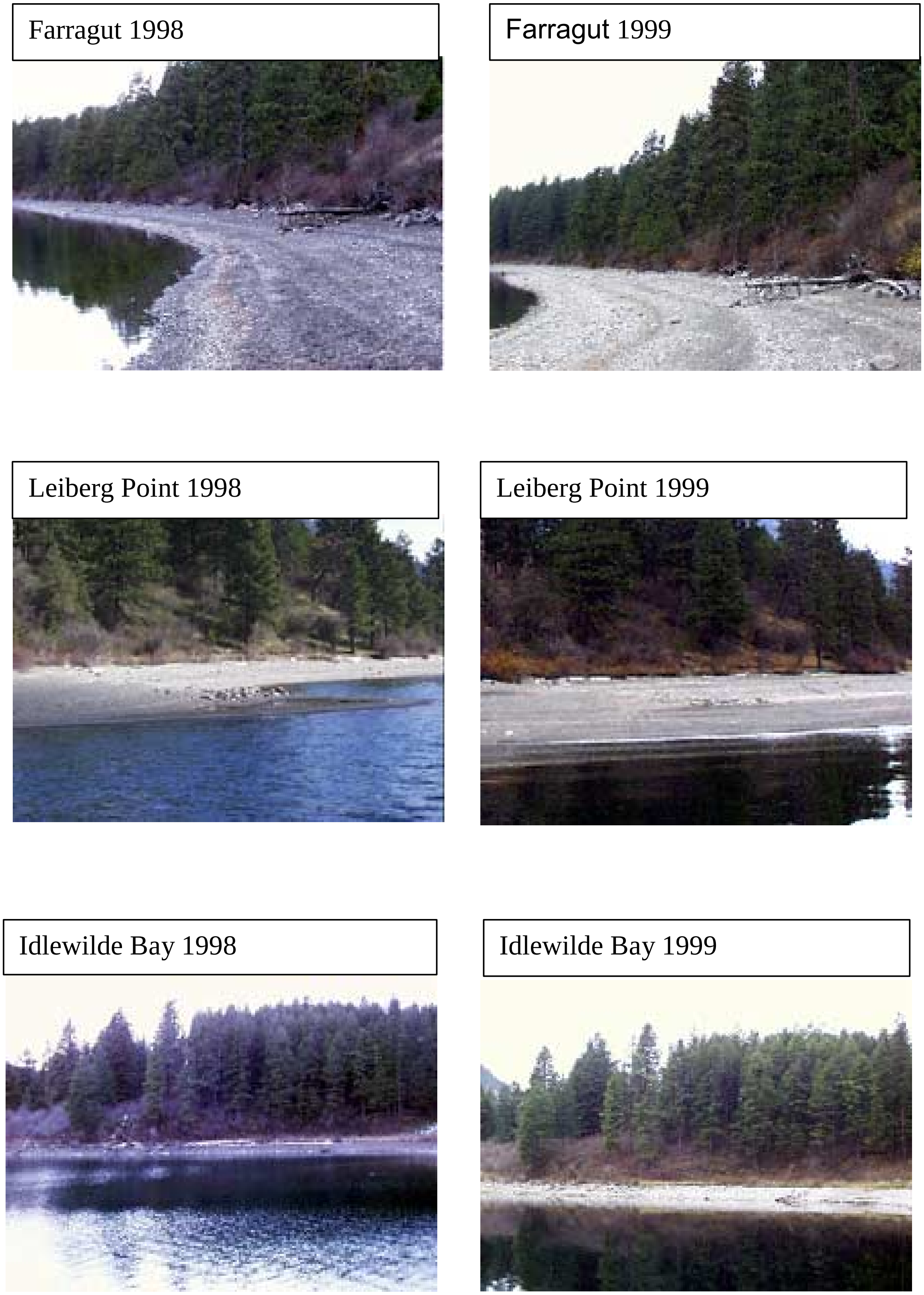


Figure 5.1. Estimated mid-winter waterfowl abundance on Lake Pend Oreille, the Pend Oreille River, and the Clark Fork River, Idaho. Points are shown for each winter season (e.g., the 2000 count was conducted in January of 2001).

Table 5.1. Midwinter waterfowl counts on Lake Pend Oreille, Idaho. Surveys were conducted from an aircraft in early January of each winter season, 1997-2001.

Year	Ducks	Geese	Swans	Total
1996-97	20,932	201	130	21,263
1997-98	9,690	310	73	10,073
1998-99	30,787	635	98	31,520
1999-00	25,161	2,700	194	28,055
2000-01	21,300	405	150	21,855



Farragut 1998

Farragut 1999

Leiberg Point 1998

Leiberg Point 1999

Idlewilde Bay 1998

Idlewilde Bay 1999

Figure 5.2. Photographs of riparian vegetation at selected sites around Lake Pend Oreille, Idaho 1998 and 1999.

Bernard 1998

Bernard 1999

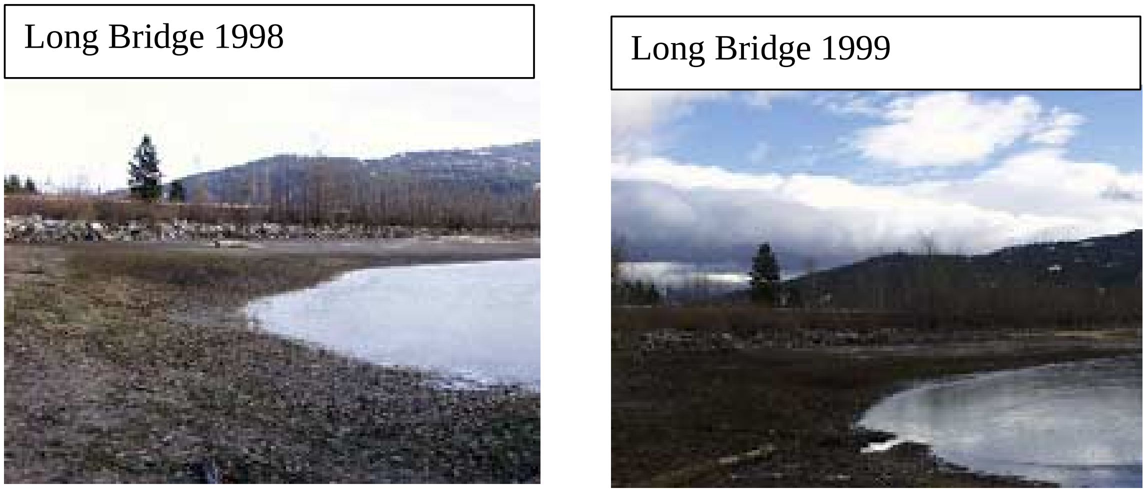
Denton Slough 1998

Denton Slough 1999

Sand Creek 1998

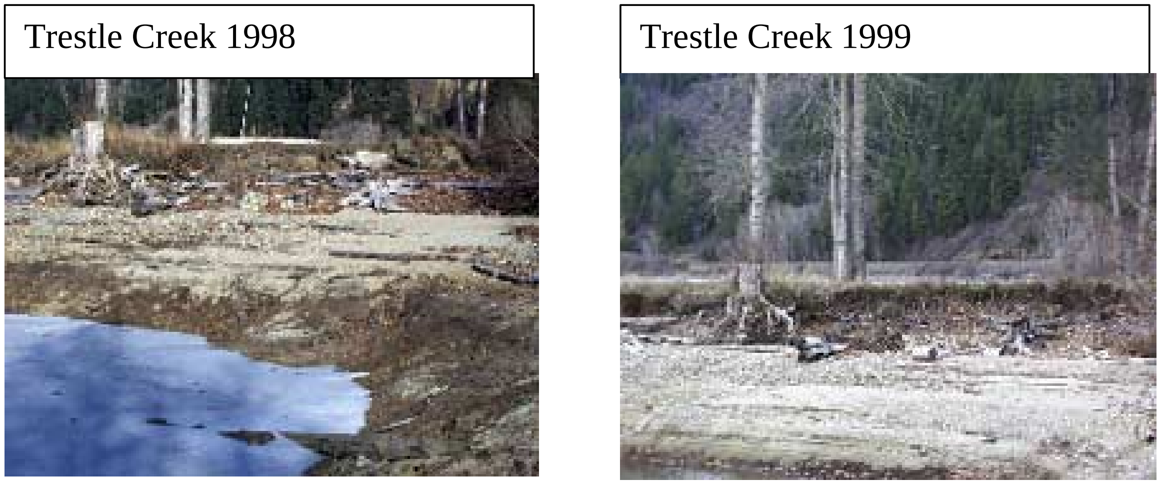
Sand Creek 1999

Figure 5.2 Photographs of riparian vegetation at selected sites around Lake Pend Oreille, Idaho 1998 and 1999 (Continued).



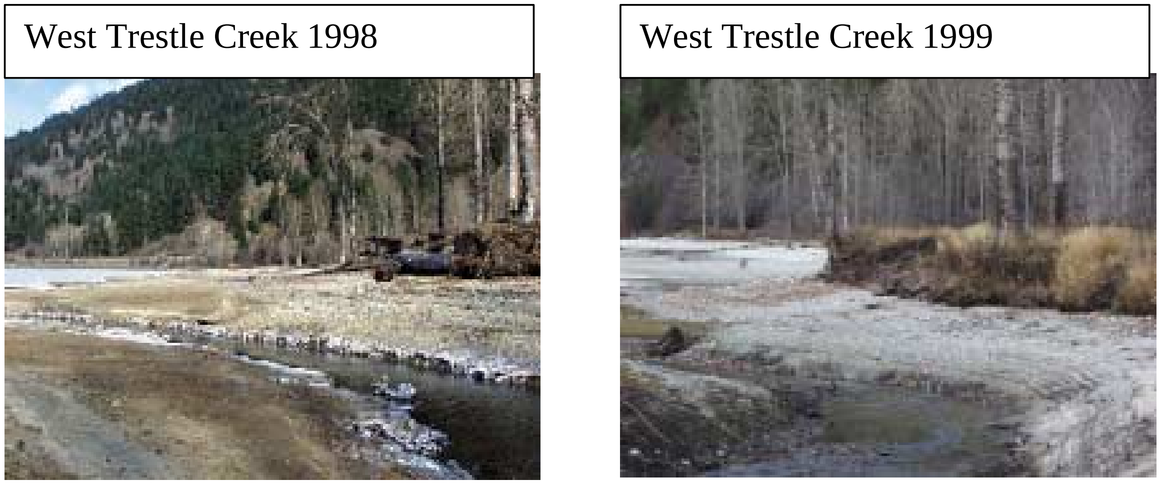
Long Bridge 1998

Long Bridge 1999



Trestle Creek 1998

Trestle Creek 1999



West Trestle Creek 1998

West Trestle Creek 1999

Figure 5.2 Photographs of riparian vegetation at selected sites around Lake Pend Oreille, Idaho 1998 and 1999 (Continued).

DISCUSSION

Waterfowl counts were highly variable before and during the lake level study. It was, therefore, difficult to relate them to lake level changes. Waterfowl counts could have varied with regional population fluctuations, ice cover on other local waters, and weather conditions. There was some concern that a higher winter pool level would make it more difficult for waterfowl to feed on aquatic vegetation. Yet, in the first and third years of the study, waterfowl abundance was relatively high.

We observed no expansion of the riparian area around Lake Pend Oreille into the drawdown zone as a response to the changes in the lake levels. The drawdown zone remained nearly barren. Prior to the construction of Albeni Falls Dam, this area of the lakeshore was well vegetated, at least in some areas. Under a pattern of natural lake levels, which would rise in the spring and decline during the summer, the banks would be exposed during the growing season and allow emergent vegetation to grow. Vegetation likely stabilized the banks and prevented erosion. Each May and June, 3.5 vertical meters, roughly 30 to 60 horizontal meters, of vegetation would be flooded by spring runoff. This likely provided a considerable boost to the productivity of near-shore species such as cutthroat trout and forage species such as redside shiners *Richardsonius balteatus.*

CONCLUSIONS

Riparian vegetation and winter waterfowl abundance have at this time no documented link to the lake level changes made during this study.

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JUVENILE KOKANEE DIET AND GROWTH, AND ZOOPLANKTON COMMUNITY DYNAMICS IN LAKE PEND OREILLE, IDAHO

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Forestry, Wildlife and Range Science

in the

College of Graduate Studies

University of Idaho

by

Lance Clark

November 1999

Major Professor: David H. Bennett, Ph. D.

ABSTRACT

The kokanee population in Lake Pend Oreille has been declining since the 1960s. Some research suggests that competition for food with Mysis shrimp may limit kokanee survival. This study was initiated to quantify food abundance for kokanee, and to understand predator prey relationships between juvenile kokanee and zooplankton. I studied zooplankton community dynamics in bays and open water sites, diet of newly emerged kokanee, and growth of age-0 kokanee in June and October in Lake Pend Oreille, Idaho from 1997-1998.

Total zooplankton density estimates for May through September, 1998 ($39.1 \cdot L^{-1}$) were higher than any comparable reported estimate since 1974, and similar estimates for 1997 ($23.5 \cdot L^{-1}$) were higher than most years. Zooplankton densities in summer 1998 were higher than normal because (i) the copepod *Cyclops bicuspidatus thomasi* was unusually abundant in June, and (ii) the cladoceran zooplankton *Daphnia* and *Bosmina longirostris* became abundant earlier in the summer and remained abundant later in autumn than in normal years. I did not find evidence that kokanee zooplanktivory was impacting August-September *Daphnia* populations in 1997 and 1998, suggesting that mid-summer food densities were sufficient to support current kokanee densities.

The most important zooplankter in the diet of newly emerged kokanee in May-June 1998, *Cyclops bicuspidatus thomasi,* was also the most abundant prey item. The copepod *Diaptomus ashlandi* and *Daphnia* were also important prey items for kokanee fry, and young-of-the-year *Mysis relicta* appeared in stomachs in late June. I found a higher incidence of empty kokanee stomachs in May and early June, but I speculate that this was due to scant feeding by recently emerged fry, rather than an indication of food limitation.

Results of *in-situ* growth experiments performed in June and October 1998, in which kokanee fry were fed a range of zooplankton food rations, showed positive kokanee growth at ambient food levels. In both experiments, kokanee fed much higher than ambient food rations did not grow significantly more than fish fed ambient food rations, but in the June experiment fish fed low food rations did grow significantly slower. Significant kokanee mortality did not occur in either experiment. My results indicate that wild kokanee in Lake Pend Oreille would not have grown significantly more in June and October 1998 if zooplankton were more abundant.

Based on the results of this study, I do not believe that zooplankton densities limited juvenile kokanee growth in 1998. Kokanee diet analysis and growth experiments were not performed in 1997, therefore I cannot conclude that zooplankton densities were sufficient to support kokanee growth in June and October 1997. However, juvenile kokanee survival was strong in 1977, a year with similar mean May-September zooplankton densities as 1997.

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In 1995, I quit a career in sales to pursue my interests in fish, and fulfill my goal of attaining a master's degree in fishery biology. Without the technical and spiritual support of many people, I could not have completed this thesis... this journey. I wish to thank Dr. David Bennett, my advisor, for guidance and encouragement, and his generally calming influence. Be well, Dr. Bennett. Thanks also to Drs. C. Michael Falter and Christopher Williams, committee members, for their contributions towards completing my project.

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CHAPTER 1. Introduction, objectives and study area.

Introduction

Kokanee *Oncorhynchus nerka* are valued by fisheries managers as both a sport-fish and forage species for piscivorous salmonids such as Kamloops rainbow trout *O. mykiss gairdneri*, lake trout *Salvelinus namaycush,* and bull trout *S. confluentas* (Wydoski and Bennett 1981). As a pelagic planktivore, kokanee fill an "empty" niche in many coldwater lakes and reservoirs (Nesler and Bergersen 1991). Successful establishment of kokanee in lakes and man-made impoundments throughout the western United States has often resulted in increased numbers and size of the piscivores.

Kokanee and the freshwater shrimp *Mysis relicta* both utilize zooplankton as a primary food source (Nesler and Bergersen 1991). As a result of widespread *Mysis* introductions in the mid 1960s, the two species now co-occur in many western U.S. lakes and reservoirs. Prior research has reported declines in kokanee fisheries that roughly correspond to the timing of *Mysis* introductions within many of those systems (Beattie and Clancy 1991; Martinez and Bergersen 1991; Northcote 1991). Declines in cladoceran macrozooplankton densities, specifically species of *Daphnia* and *Bosmina*, due to overgrazing by the predaceous *Mysis* may have caused the loss of numerous kokanee fisheries (Martinez and Bergersen 1991; Spencer et al. 1991; Morgan et al. 1978). Lake Pend Oreille, a naturally occurring lake in northern Idaho, experienced a similar decline in the kokanee fishery following the introduction of *Mysis* by the Idaho Department of Fish and Game (IDFG) from 1966 to 1970 (Rieman and Falter 1981). However, declines in the kokanee population of Lake Pend Oreille also parallel operational changes at Albeni Falls Dam, which was built in 1952 on the lake's outlet.

Operated for hydropower production, Albeni Falls Dam regulates water level fluctuations within the lake. Since 1966, minimum pool levels of 625.14 m (2051.71 ft) occur in late winter at Lake Pend Oreille. Research by IDFG indicates that kokanee year- classes were stronger in the first 13 years of dam operation, when winter lake levels were maintained at 626.67 m (2056.73 ft). At the lower winter lake levels, key shoreline spawning sites are above waterline, forcing kokanee to spawn in less suitable locations. A 5-year study was initiated in October, 1996 to assess effects of maintaining the lake's minimum pool level at 626.36 m (2055.71 ft). By keeping pool levels 1.22 m (4.0 ft) higher in winter, IDFG personnel believe that egg to fry survival of kokanee will increase. My research is one part of the study on lake level manipulations, and will evaluate interactions between the lake's macrozooplankton community and kokanee. My goal was to quantify spatial and temporal distribution of the macrozooplankton community and investigate the growth and survival of age-0 kokanee as a function of zooplankton abundance and community structure. From this study, fishery managers will be able to better predict the growth and survival of young-of-the-year kokanee in Lake Pend Oreille, determine optimum stocking levels of hatchery reared kokanee, and potentially calculate the carrying capacity of Lake Pend Oreille for kokanee.

Objectives

1. To quantify temporal and spatial variations in crustacean zooplankton density and biomass in selected bays and open water sites in Lake Pend Oreille, Idaho.
2. To evaluate the diet of newly emerged kokanee fry in Lake Pend Oreille.
3. To determine the importance of varied crustacean zooplankton composition and abundance on the survival and growth of both newly emerged kokanee fry in June, and age-0 kokanee in October in Lake Pend Oreille.

Study Area

As glacial ice retreated from Idaho into British Columbia near the end of the Pleistocene era, a trough known as the Purcell trench emerged in its wake (Merriam 1975). Lake Pend Oreille, in the northern Panhandle of Idaho, lies within this glacially carved trench, which had been subsequently over-deepened by 70-100 Missoula flood episodes (Figure 1.1). The 383 km^2 lake has a mean depth of 164 m, a maximum depth of 351 m, and a shoreline length of approximately 310 km (Rieman and Bowler 1980). Mean surface elevation before the lake level manipulations was 629 m above sea level (Rieman and Bowler 1980). The Clark Fork River and numerous smaller streams supply the lake's water, while the Pend Oreille River is the outlet.

Lake Pend Oreille is a temperate lake that cools below 4° C but rarely freezes (Rieman 1976). Warming of the epilimnion begins in April and continues into August, a thermocline is typically established in July at a maximum depth of about 20 m; and the lake remains

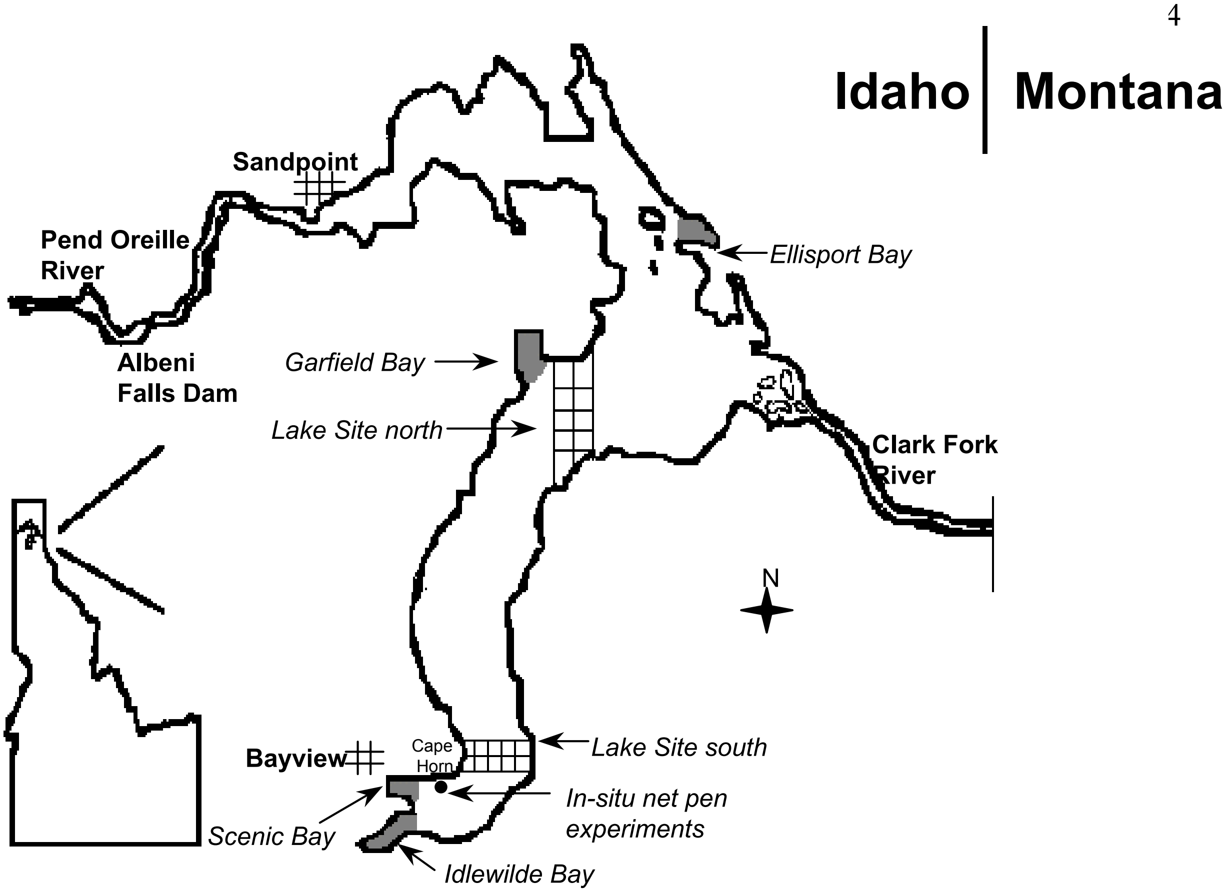


Figure 1.1. Map of Lake Pend Oreille showing zooplankton sampling sites and approximate location of *in situ* net pen experiments in italic.

stratified into September. The northern end of the lake warms more quickly in spring, perhaps due to inflows of turbid, warmer water from the Clark Fork River.

Nutrient inputs from the Clark Fork River settle into the extensive hypolimnion of Lake Pend Oreille, and become unavailable for primary productivity. As a consequence, total nitrogen, total phosphorus, secchi disk readings and chlorophyll-a concentrations verify that the lake is oligotrophic (Woods 1991). No significant water quality changes have occurred in the main channel of Lake Pend Oreille since the first limnological study was conducted at the lake in 1954, although cultural eutrophication is increasing the nutrient levels of some bays (Falter and Olson 1990).

CHAPTER 2. Temporal and spatial variations in crustacean zooplankton density and biomass in selected bays and open water sites of Lake Pend Oreille, Idaho.

Introduction

The kokanee fishery at Lake Pend Oreille, Idaho once produced annual harvests in excess of 1 million kokanee (Rieman and Bowler 1980), but declined in the late 1960s. Researchers postulated that introductions of omnivorous *Mysis relicta* reduced densities of crustacean zooplankton available as food for kokanee (Rieman 1976; Rieman and Falter 1981). Limnological studies at Lake Pend Oreille in the mid 1970s (Rieman and Bowler 1980) documented temporal shifts in the zooplankton community that coincided with increased abundance of *Mysis relicta*, providing evidence to support the theory. Stross (1954) studied the lake before *Mysis* introductions and collected an average of 3.0 *Daphnia*$\cdot L^{-1}$ from August to October and 7.1 *Bosmina*$\cdot L^{-1}$ from mid June to August. In contrast, Rieman and Falter (1981) found an average of only 2.1 cladocera$\cdot L^{-1}$ (including *Daphnia spp.*, *Bosmina longirostris*, *Diaphanasoma leuchtenbergianum*, and *Leptodora kindtii*) in comparable seasons while studying the lake from 1974 to 1978. Chipps (1997) linked fluctuations in cladoceran zooplankton densities at Lake Pend Oreille with seasonal consumption rates of *Mysis relicta*.

Spatial distribution of freshwater zooplankton is not uniform. Previous research has reported zooplankton swarms (Colebrook 1960), wind-induced zooplankton patches (McNaught and Hasler 1961), vertical and horizontal heterogeneity (Malone and McQueen 1983), and heterogeneity from mesoscale to microscale patterns (Pinel Alloul et al. 1988). Shifts in the zooplankton community structure of near-shore and offshore regions attributable to predation from *Mysis* shrimp and planktivorous fishes also have been reported (Evans and Jude 1986).

Since zooplankton distributions are not uniform, and variations in zooplankton density and composition at a sampling site can occur daily (Watson 1975), a complete description of the temporal, horizontal, and vertical changes of the zooplankton community throughout Lake Pend Oreille is not realistic. However, this study explores the zooplankton community dynamics of Lake Pend Oreille on a finer time scale than previous studies (Stross 1954; Rieman 1976; Rieman and Bowler 1980; Paragamian and Bowles 1995) and is the first known project to characterize the horizontal zooplankton distribution within selected bays in Lake Pend Oreille, Idaho.

Methods

Six sampling locations were established in Lake Pend Oreille for quantification of macrocrustacean zooplankton composition and abundance (Figure 1.1). Scenic, Idlewilde, Garfield and Ellisport bays represent current or historical kokanee spawning sites (Jeppson 1959), and thus were chosen for examining differences in horizontal distribution. The remaining two sampling locations, sampled vertically, are open water sites in the northern and southern portion of Lake Pend Oreille. In 1997, all locations were sampled weekly from June 8 to October 27, and bimonthly in November and December, except the northern open water site which was established on July 30. I sampled zooplankton monthly from January through April 1998, weekly from May 21 to July 10, 1998 and monthly from August through November, 1998. Surface water temperatures at each location were measured using a Yellow Springs Instruments Model-54 temperature probe. I collected measurements of water transparency in Lake Pend Oreille using a standard 20 cm secchi disk.

Horizontal Sampling Protocol

Horizontal sampling was conducted during daylight hours using a 10 L Schindler box (Schindler 1969). Extending out from the shoreline, one sample was collected at the following depths: (*i*) in 1 m deep water, (*ii*) at 5 m depth at 10 m total depth, and at depths of (*iii*) 5 m and (*iv*) 10 m in water deeper than 50 m, except at Ellisport Bay, which is a shallower bay, and had a total depth deeper than 25 m. All crustacean zooplankton were preserved in sugared, 4% formalin (Haney and Hall 1973). Within each bay, samples were collected at three conveniently selected sampling sites from June 1997 to April 1998, and at six randomly selected sites from May through November, 1998. The randomly selected sites were chosen using the following protocol: the shoreline of each bay was divided into 10 units of equal length, with each unit assigned a number. Six units were then randomly selected, and horizontal sampling extending out from the shoreline began at the center-points of these units.

Lake Site Sampling Protocol

I collected crustacean zooplankton by vertical sampling using a 10 L Schindler box at two main lake locations (hereafter referred to as Lake Sites; Figure 1.1) at depths of 5, 10, 15, and 20 m. One sample was collected at each depth. Within each Lake Site location, samples were collected by convenience sampling at three sampling sites from June 1997 to April 1998, and at six randomly selected sites from May through November, 1998. The randomly selected sites were chosen using the following protocol: a grid pattern overlaying a map of each Lake Site location partitioned the location into a number of boxes. Six boxes were then randomly selected, and vertical samples were collected from the center-points of those boxes. A GPS unit (Magellan model Nav 5000DX) was used to locate the box center-points, which represent the sampling sites at each Lake Site location.

Lab Analysis

In the laboratory, I identified, enumerated, and measured crustacean zooplankton. Samples were subsampled when necessary, washed into a counting chamber, and counted by species. Subsampling methods closely followed procedures detailed in Edmundson (1971). Briefly, the whole sample was washed into a beaker with a known amount of water; that varied in volume depending on the abundance of zooplankton. The diluted sample was mixed to assure a random distribution of organisms, and 2-4 5 ml aliquot subsamples were taken with a wide-mouth Henson "Stemple pipette" to achieve a target density of 200 subsampled zooplankton. Subsamples were then placed in the counting chamber, identified, enumerated and measured following identical procedures used for total counts, except that entire samples were also sorted for enumeration of the less abundant *Leptodora*. Using an occular micrometer, the first 25 individuals of the commonly occurring species (*Daphnia spp.*, *Bosmina longirostris*, *Cyclops bicuspidatus* and *Diaptomus ashlandi*) were measured according to body shape (Figure 2.1). *Cyclops bicuspidatus* is referred to as *Diacyclops bicuspidatus* in some studies (Watson 1976; Martinez and Bergersen 1991). Two ecologically and morphologically similar species of *Daphnia* (*D. thorata* and *D. galeata mendotae*) occur in Lake Pend Oreille (Rieman 1976). However, I did not identify *Daphnia* to the species level.

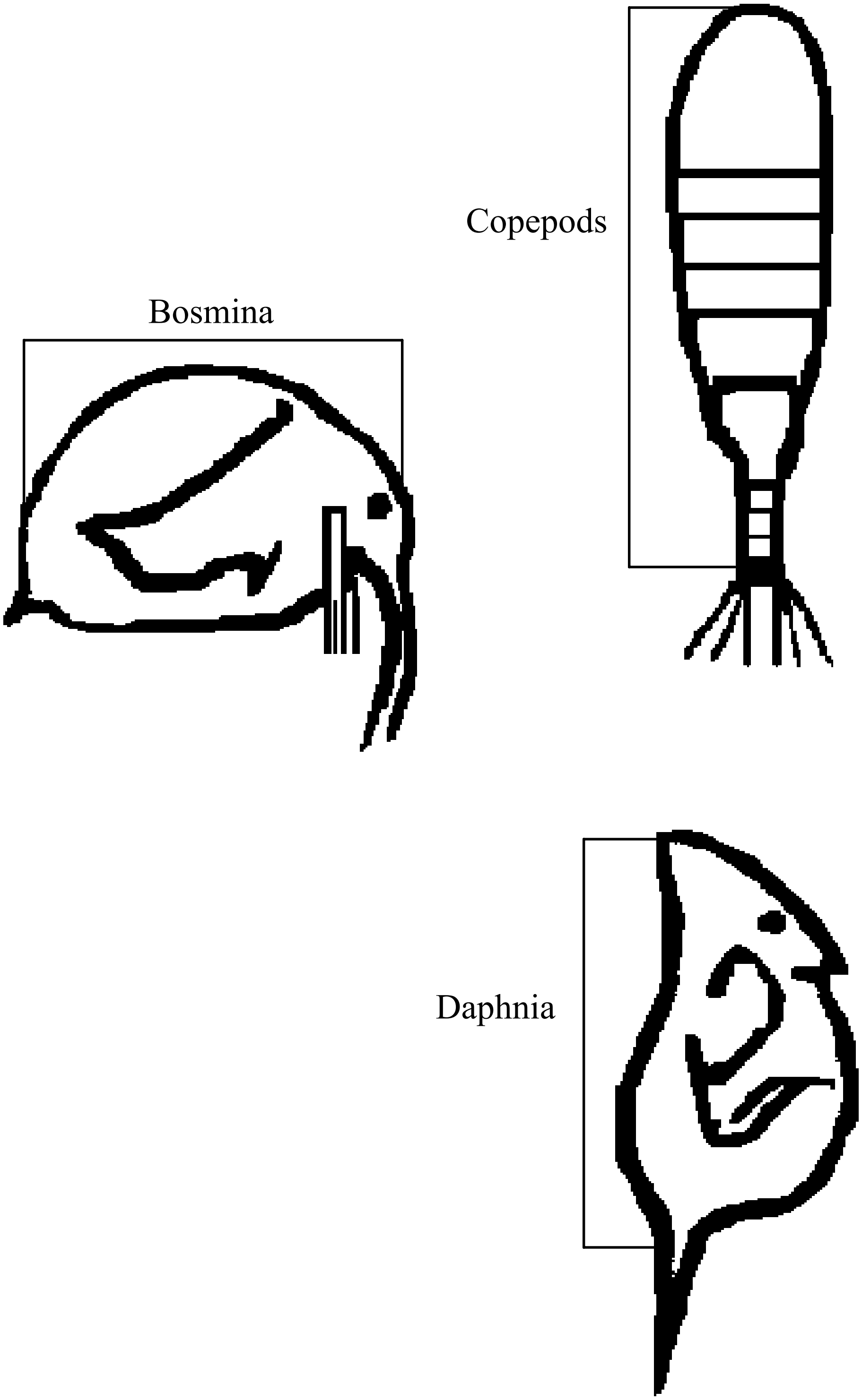


Figure 2.1. Approximate location of body length measurements for three zooplankton body shapes.

Biomass Estimates

I estimated total zooplankton biomass, in milligrams, by converting length to weight for each zooplankton species from established length-weight relationships.

Length(L)- wet-weight(W) relationships for selected zooplankton are as follows (Culver et al. 1985):

Bosmina longirostris $W=17.7369 \times L^{2.2291}$ (1)
Daphnia spp. $W=7.4997 \times L^{1.5644}$ (2)
Diaphanasoma leuchtenbergianum $W=5.0713 \times L^{1.0456}$ (3)
Leptodora kindtii $W=1.5605 \times L^{1.8730}$ (4)
Chydorus sphaericus $W=14.0793 \times L^{1.9796}$ (5)
Cyclops bicuspidatus thomasi $W=5.6713 \times L^{1.9347}$ (6)
Diaptomus ashlandi $W=7.8273 \times L^{2.6484}$ (7)

where: W = the zooplankter wet weight (μg) and,
L = the zooplankter length (mm) according to body shape (Figure 2.1).

I used estimated mean lengths for *Diaphanasoma* (1.0 mm) and *Leptodora* (4.0 mm) in Lake Pend Oreille as reported by Rieman an Bowler (1980). Mean length for *Chydorus* (0.3 mm) and mean biomass for copepod nauplii (0.25 μg) were from McCauley (1984).

Statistical Analysis

I tested for differences in mean monthly crustacean zooplankton biomass estimates among bays and between lake sites (i.e. Lakes Sites north and south) from May-November 1998 using an aligned ranks test ($\propto=0.05$). All statistical analyses in this objective were performed using SAS statistical software (SAS institute, version 6.11).

I used an ANOVA with repeated measures by depth stratum to test for mean monthly differences in estimated horizontal zooplankton densities. The model for this analysis is:

$$Y=\mu + \alpha_i + \beta_j + \gamma_k + \alpha_i\beta_j + \alpha_i\gamma_k + \beta_j\gamma_k + \varepsilon_{ijk} \qquad (8)$$

where:

α = the effect of months on zooplankton densities,

β = the effect of sampling location (e.g. bays) on zooplankton densities,

γ = the effect of depth strata on zooplankton densities,

$\alpha\beta$ = the interactive effect of months and sampling locations on zooplankton densities,

$\alpha\gamma$ = the interactive effect of months and depth strata on zooplankton densities and,

$\beta\gamma$ = the interactive effect of sampling locations and depth strata on zooplankton densities.

Two zooplankton density estimates in my study, occurring in June 1997 at the 1 m depth strata in Ellisport Bay and in June 1998 at the 10 m at 50 m depth strata in Idlewilde Bay, were unusually high. While these two outlier density estimates were accurate, and probably represented dense microscale zooplankton patches, they were excluded from statistical analysis to maintain homogeneity of variance. An initial statistical analysis using the model described above showed an interaction between months and depth strata (i.e. $\alpha\gamma$ in the above model) which influenced zooplankton densities. Therefore, the effect of individual sampling months on zooplankton densities by depth strata was tested by ANOVA (Slice Procedure; SAS institute, version 6.11).

Results

Zooplankton Density

Zooplankton densities were highest in June, 1998 and lowest in March, 1998 at all sampling locations in Lake Pend Oreille (Figures 2.2-2.4; Appendix Table 2.1). Annual peak zooplankton densities, which occurred in July 1997 and in June 1998, were between 149% (Lake Site south) and 262% (Scenic Bay) higher in 1998 than in 1997. Zooplankton densities were similar in August 1997 and 1998. Cladoceran zooplankton (e.g. *Daphnia spp. Bosmina longirostris, Diaphanasoma leuchtenbergianum, Chydorus sphaericus, and Leptodora kindtii*) densities increased earlier in the summer, and remained higher in autumn 1998, than in 1997. Mean copepod (e.g. *Cyclops bicuspidatus*, *Diaptomus ashlandi* and *Epischura nevadensis*) densities were approximately 8x higher in June 1998 than in June 1997.

Zooplankton species composition varied slightly by sampling location, but the copepod *Cyclops* was generally the most abundant zooplankter in this study. For all sampling locations, the highest observed *Cyclops* densities occurred in June, 1998 with peak *Cyclops* densities ranging from $39.64 \cdot L^{-1}$ at Lake Site north to $103.46 \cdot L^{-1}$ in Idlewilde Bay (Figures 2.2-2.4; Appendix Table 2.1). *Diaptomus* was the second most abundant zooplankter, with trends in density following those of *Cyclops.* The highest observed density of *Epischura* was $0.77 \cdot L^{-1}$, making it the least abundant copepod.

Daphnia became abundant earlier in the summer, and remained abundant later into the fall of 1998 than in 1997. Mean *Daphnia* densities for all sampling locations were $1.87 \cdot L^{-1}$ in the second week of July and $0.20 \cdot L^{-1}$ in the third week of October, 1998 versus $0.028 \cdot L^{-1}$ and $0.07 \cdot L^{-1}$ during the same weeks in 1997. However, for most sampling locations, peak summer

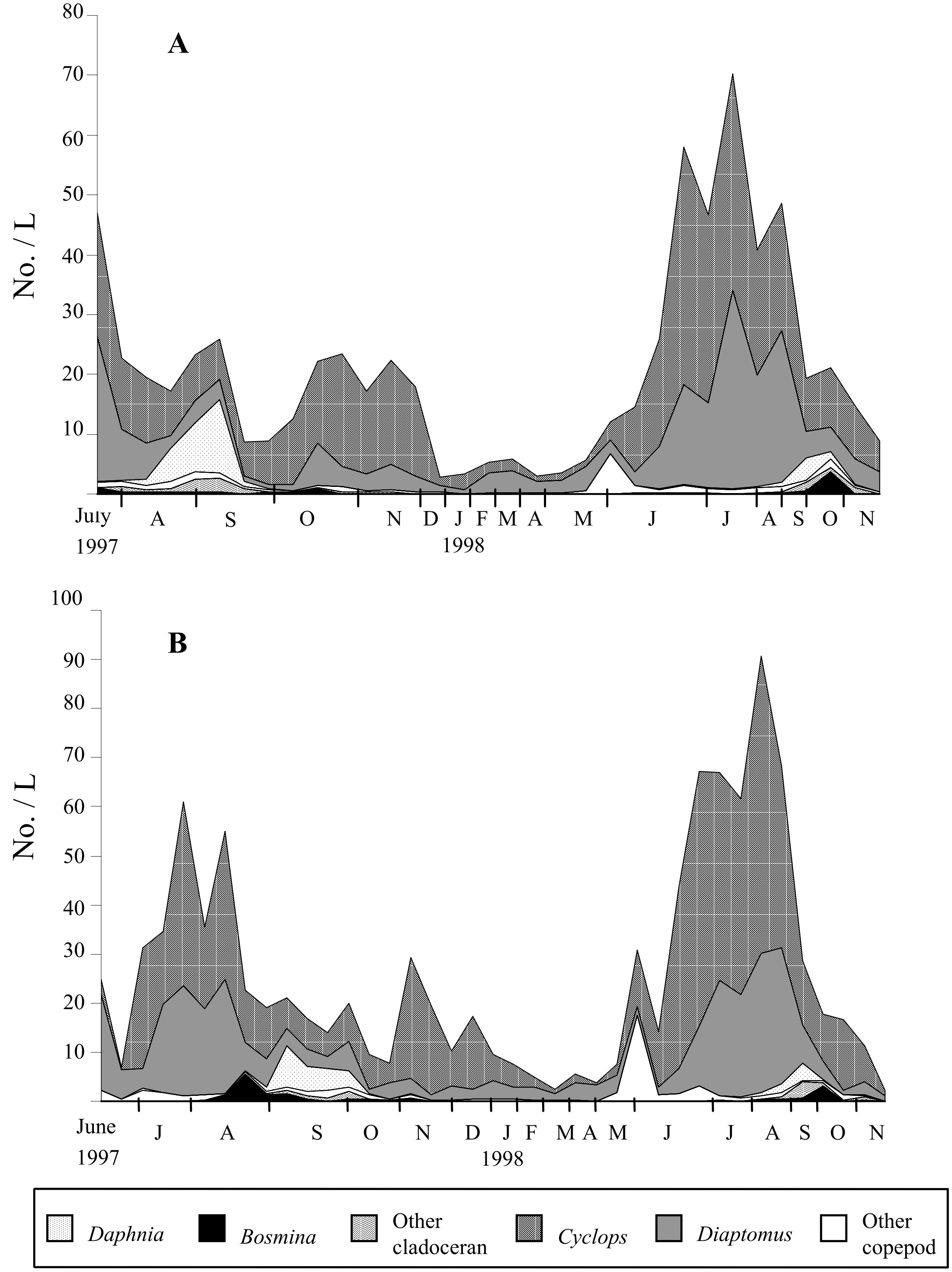


Figure 2.2. Estimated crustacean zooplankton density in Lake Site north (A) and Lake Site south (B) in Lake Pend Oreille, 1997-1998.

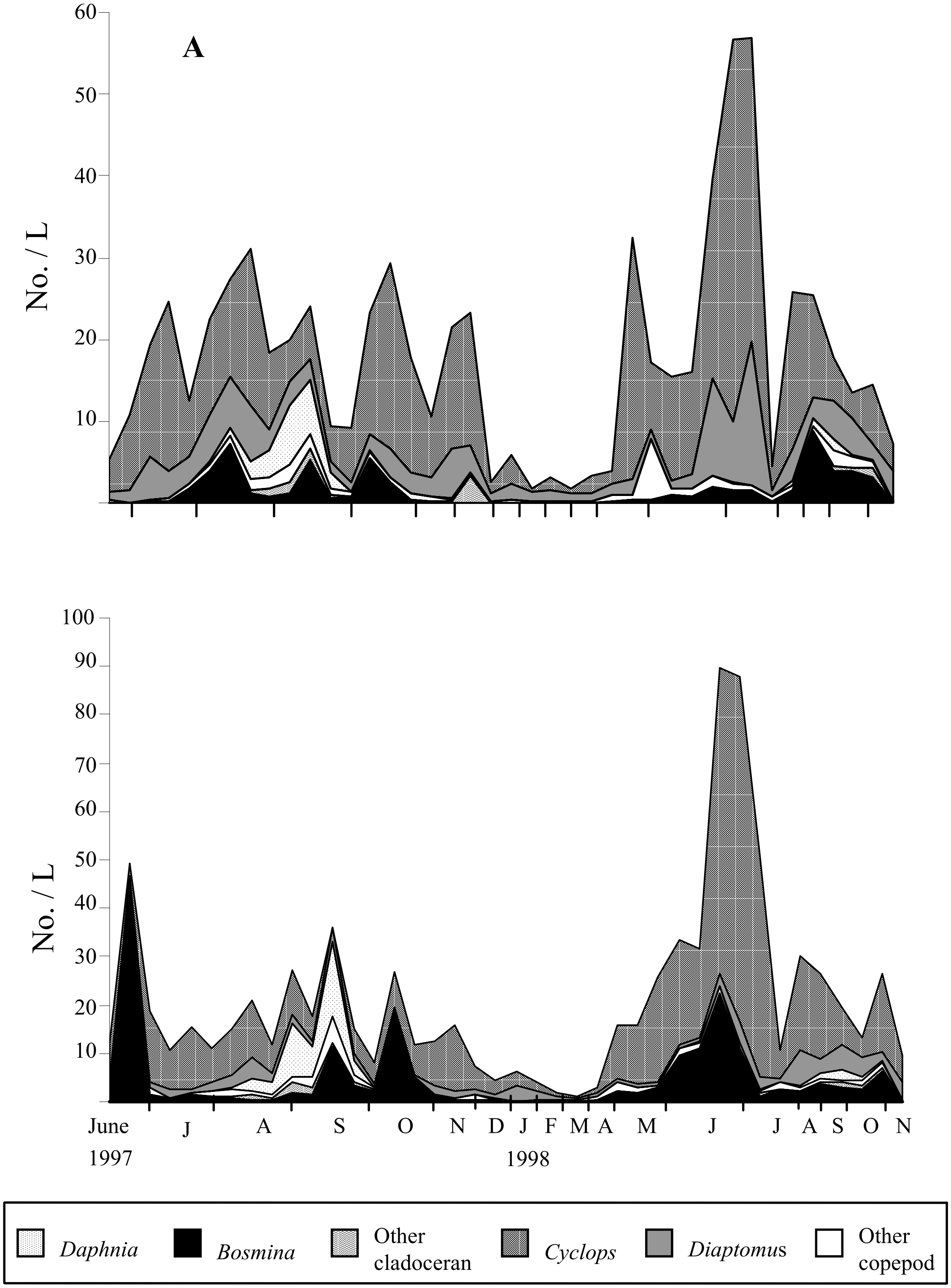


Figure 2.3. Estimated crustacean zooplankton density in Garfield Bay (A) and Ellisport Bay (B) in Lake Pend Oreille 1997-1998.

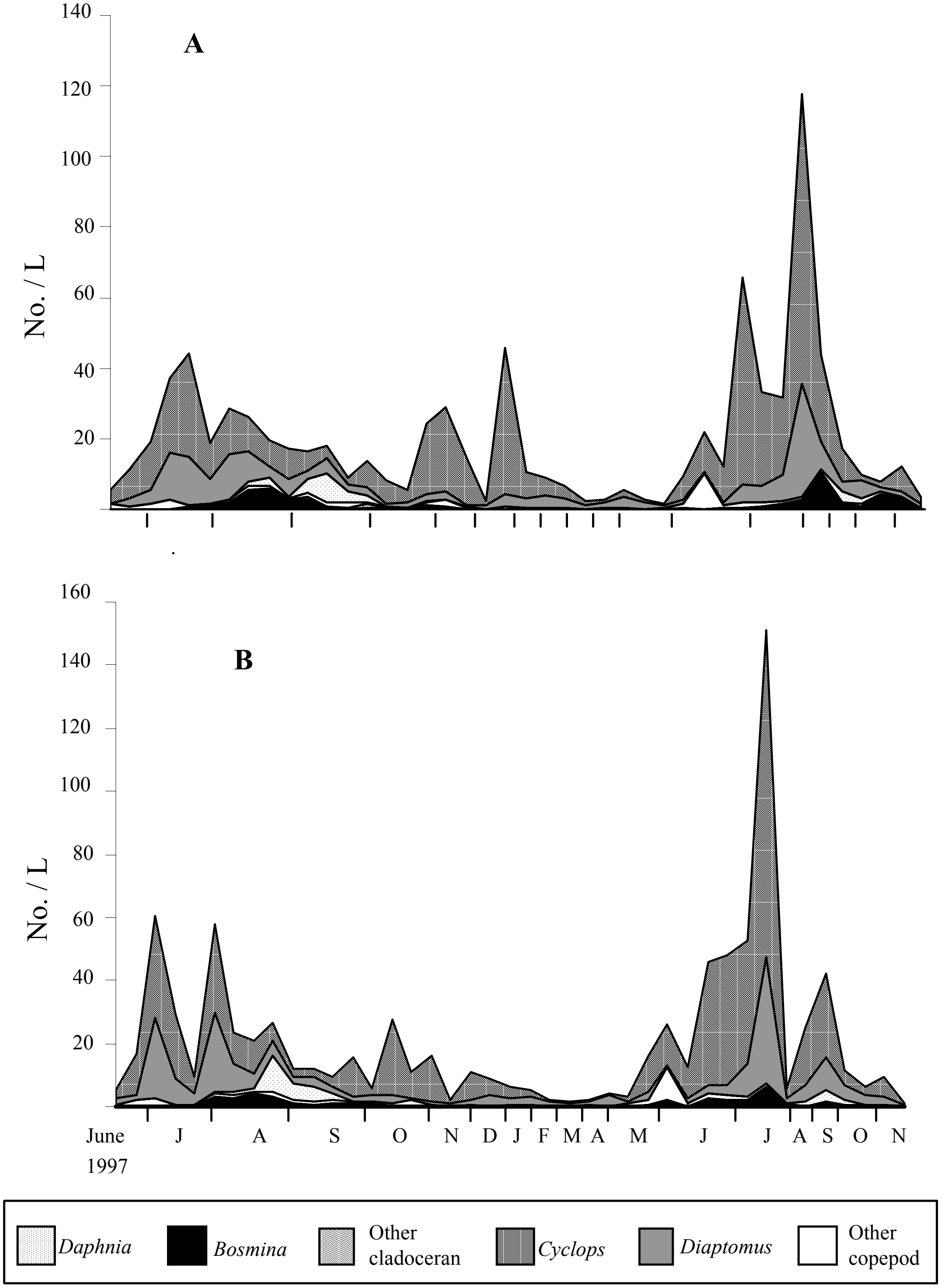


Figure 2.4. Estimated crustacean zooplankton density in Scenic Bay (A) and Idlewilde Bay (B) in Lake Pend Oreille 1997-1998.

Daphnia densities were higher in 1997 than 1998. I observed a higher abundance of *Bosmina* in Ellisport Bay than in other sampling locations, and *Bosmina* densities increased earlier in the summer in 1997 and 1998 at Ellisport Bay than at the other locations. At Ellisport Bay, peak *Bosmina* densities occurred in June 1997 and 1998, but did not occur until mid-summer at other sampling locations. Population trends for *Diaphanasoma* were similar to those of *Daphnia*, although *Diaphanasoma* was usually much less numerous. *Chydorus* and *Leptodora* were the least abundant cladocerans in this study.

Zooplankton Biomass

No statistically significant differences in mean zooplankton biomass existed either among bays ($F=0.19_{27}$; $p=0.9020$) or between lake sites ($F=0.19_{13}$; $p=0.6710$) at Lake Pend Oreille, although Garfield Bay consistently had lower standing zooplankton biomass than Scenic and Idlewilde bays on most sampling dates (Figures 2.5-2.7; Appendix Table 2.1). During this study, mean estimated zooplankton biomass was highest in late June 1998 (1923 $mg \cdot L^{-1}$) and lowest in March 1998 (57.60 $mg \cdot L^{-1}$). The most abundant zooplankters, *Cyclops* and *Diaptomus*, represented the highest overall percentages of zooplankton biomass in this study (48.80% and 33.65%, respectively). However, in mid-August to mid-September 1997, *Daphnia* represented 57.48% of the total zooplankton biomass. During the same period in 1998, *Daphnia* biomass was 19.69% of the total standing biomass. Generally, biomass of *Diaphanasoma* exceeding 10% of the total standing biomass was rare in mid-summer, although the overall August-September mean *Diaphanasoma* biomass was 3.95% of the total. Mean *Bosmina* biomass was highest in mid-summer (7.86%), with isolated measurements exceeding 20% of total standing biomass. However, among bay locations in June 1998,

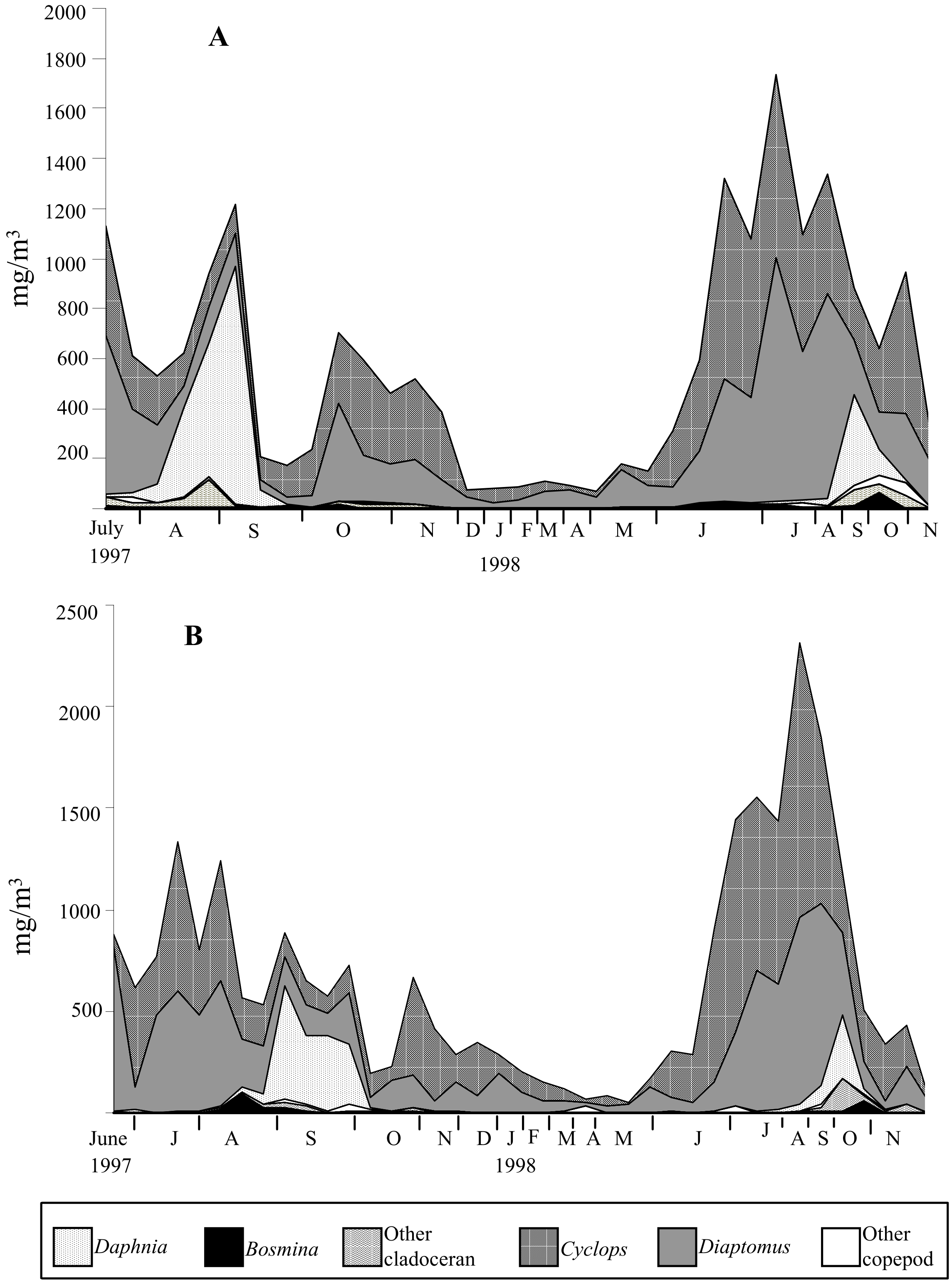


Figure 2.5. Estimated crustacean zooplankton biomass (mg wet weight) in Lake Site north (A) and Lake Site south (B) in Lake Pend Oreille, 1997-1998.

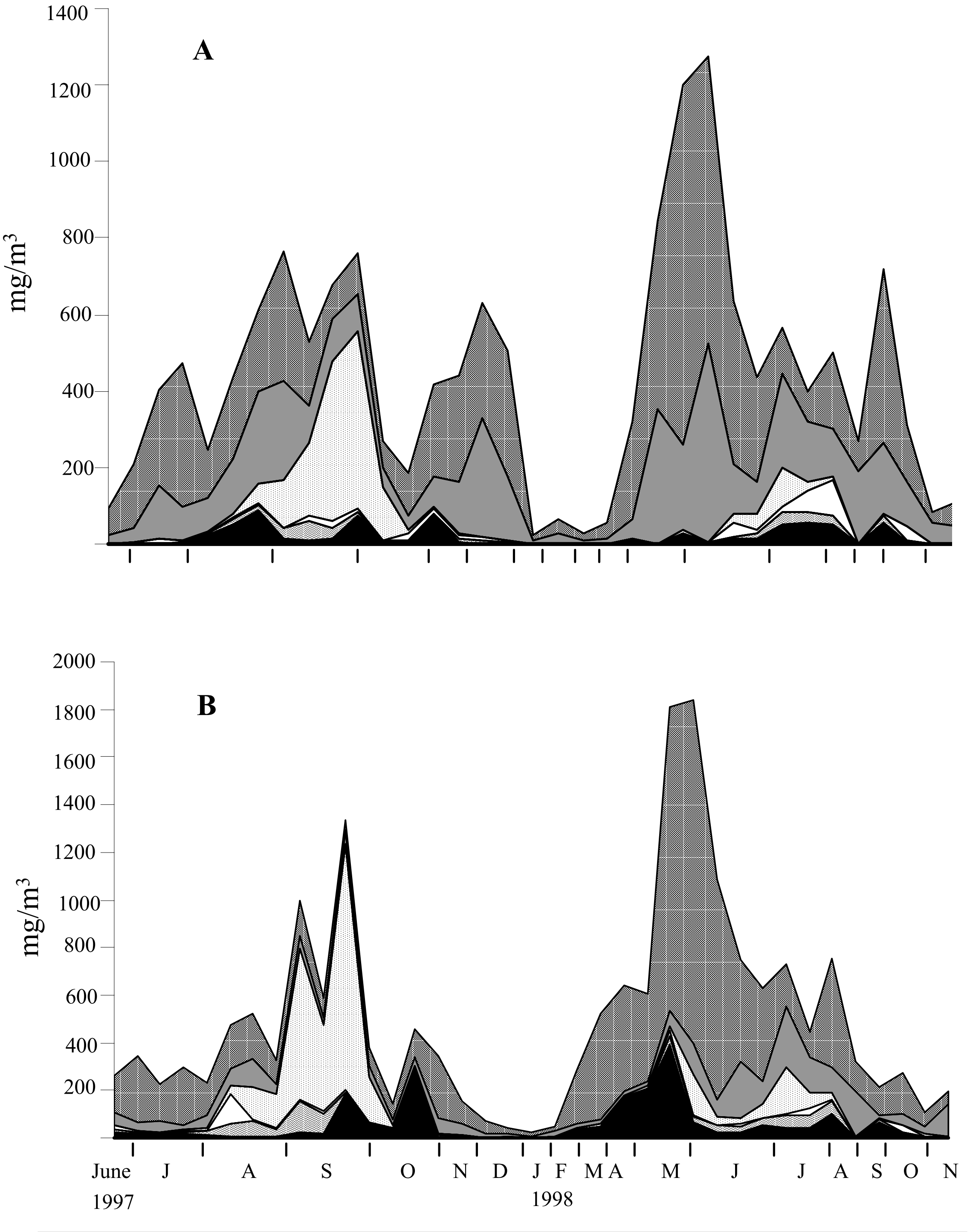


Figure 2.6. Estimated crustacean zooplankton biomass (mg wet weight) in Garfield Bay (A) and Ellisport Bay (B) in Lake Pend Oreille 1997-1998.

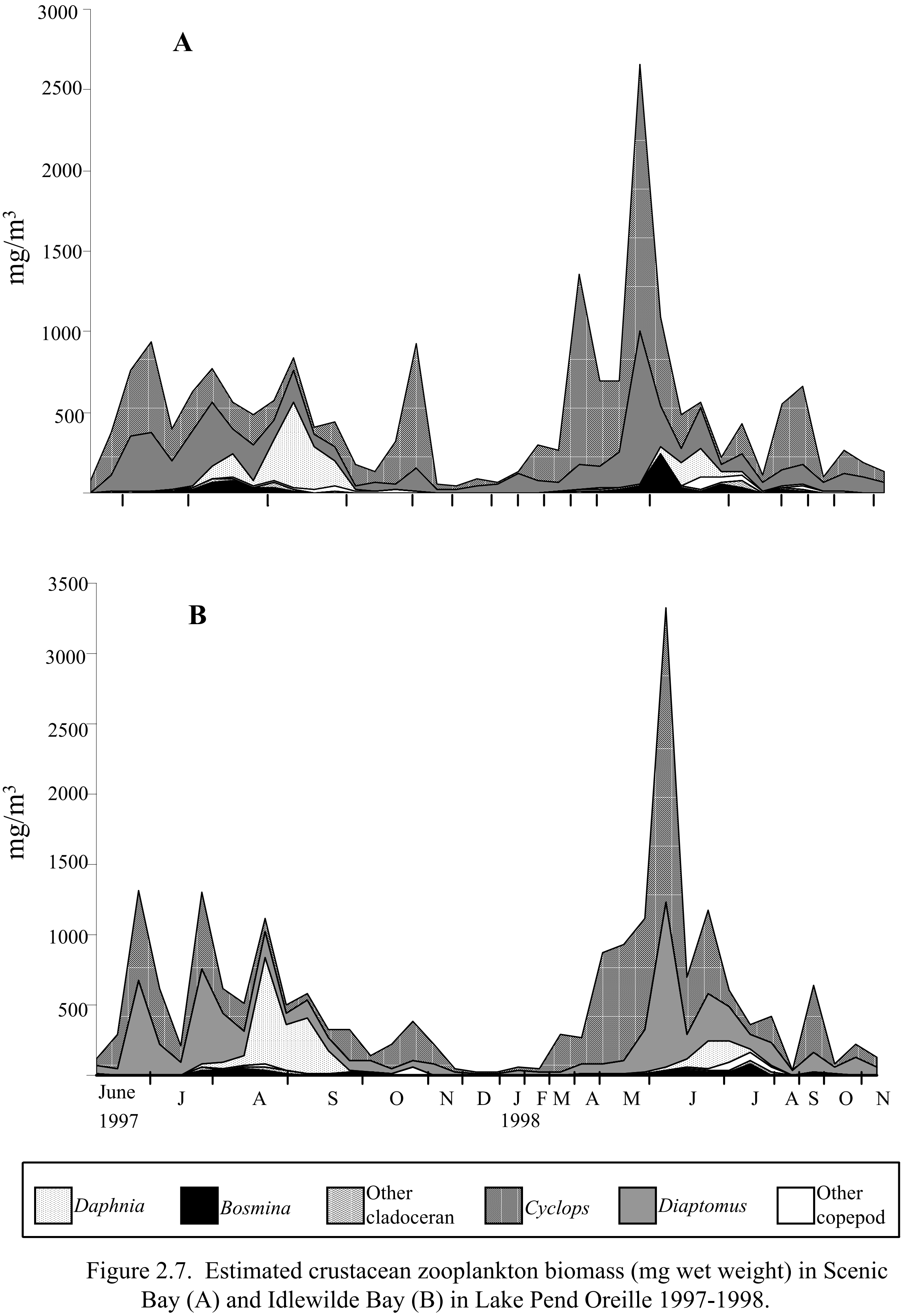


Figure 2.7. Estimated crustacean zooplankton biomass (mg wet weight) in Scenic Bay (A) and Idlewilde Bay (B) in Lake Pend Oreille 1997-1998.

Bosmina biomass represented the highest percentage of standing zooplankton biomass in Ellisport Bay (13.20%) and the lowest percentage in Idlewilde Bay (0.71%). *Epischura* and *Leptodora* represented 1.42% and 0.71% of the mean summer (e.g. June-September) biomass.

Horizontal distribution within bays

Significant differences in total zooplankton densities between depth strata existed for some summer months (e.g. June-September) in 1997 and 1998, but were not detected in the spring, autumn or winter (Appendix Table 2.2). In the summer, the lowest density measurements were consistently nearest to shore (e.g. the 1 m depth stratum), whereas the highest densities were usually at the 10 m at deeper than 50 m depth strata (Figure 2.8). In the winter, zooplankton densities were consistently low across all depth strata. Peak zooplankton densities varied by sampling location and by depth strata within locations in 1997, but in 1998 occurred in June for all depth strata and locations. During this study, mean peak zooplankton densities for each depth strata were lowest for the 1 m stratum ($65.38 \cdot L^{-1}$) and highest for the 10 m at deeper than 50 m depth stratum ($158.64 \cdot L^{-1}$).

Copepod zooplankton was more abundant than cladoceran zooplankton at each depth stratum (Figures 2.9-2.12). Across all sampling locations, cladocerans represented the highest proportion of the total zooplankton density at the 1 m depth stratum (22.06%) and the lowest proportion at the 10 m depth at deeper than 50 m total depth stratum (8.50%). Differences in the relative proportions of cladocerans to copepods between depth strata were more pronounced at Ellisport Bay than other locations, where cladocerans accounted for 40.70% of total zooplankton densities at 1 m versus 11.24% at the 10 m depth at deeper than 50 m total depth stratum.

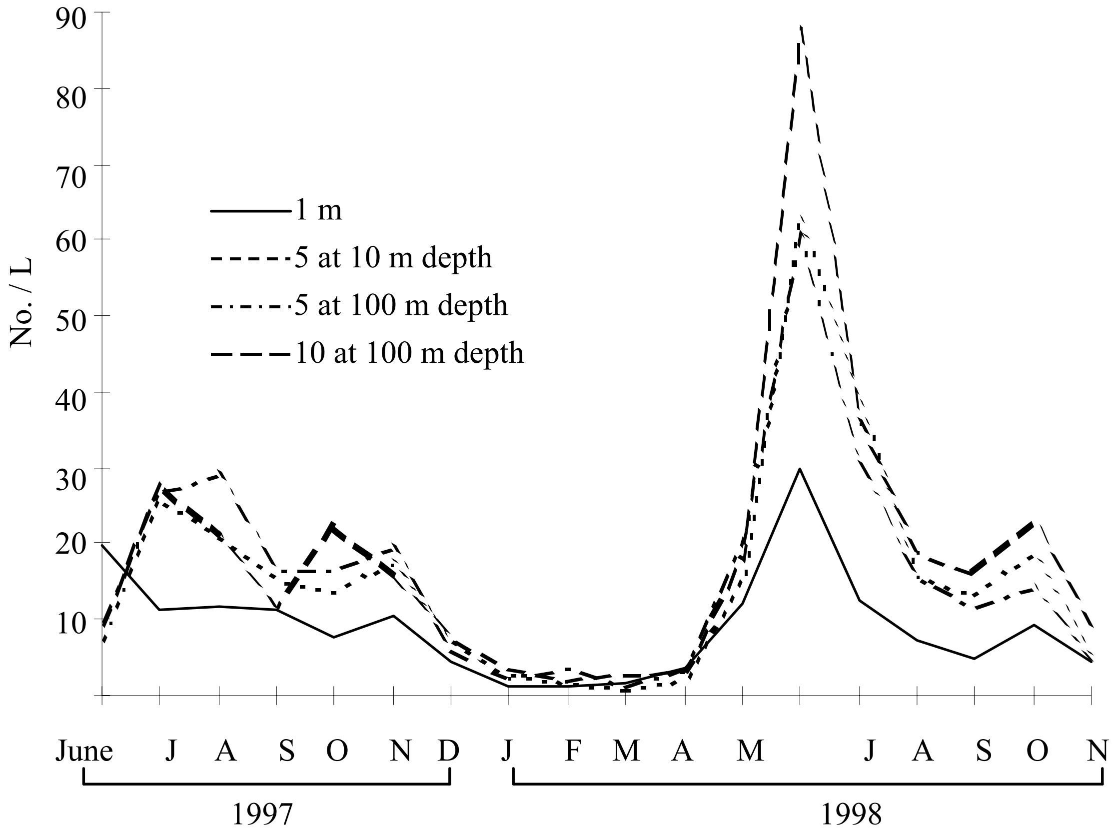


Figure 2.8. Mean zooplankton density (No./ L) by depth strata across all horizontal sampling locations in Lake Pend Oreille, 1997-1998.

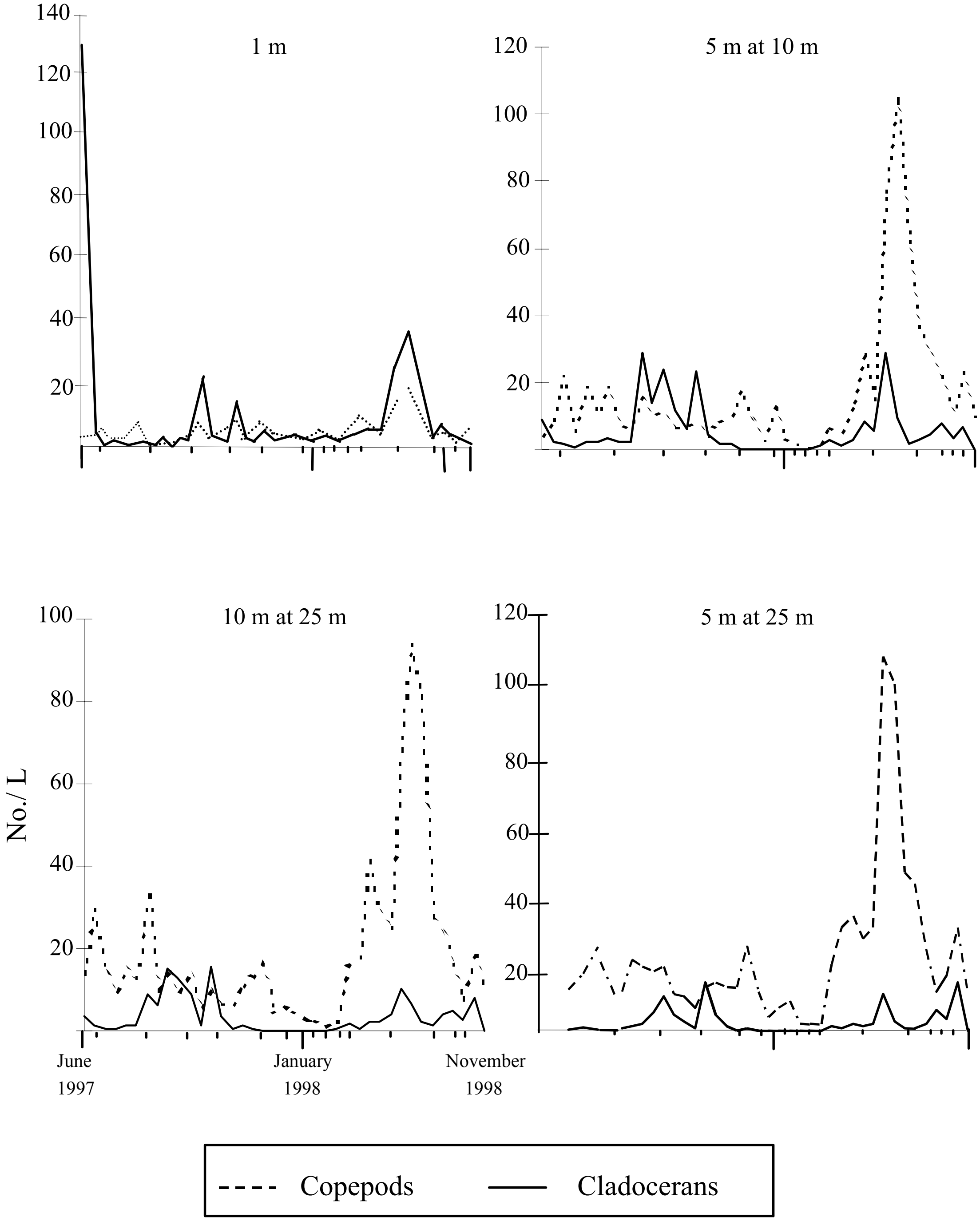


Figure 2.9. Estimated densities of copepods and cladocerans at four depth strata in Ellisport Bay, Lake Pend Oreille 1997-1998.

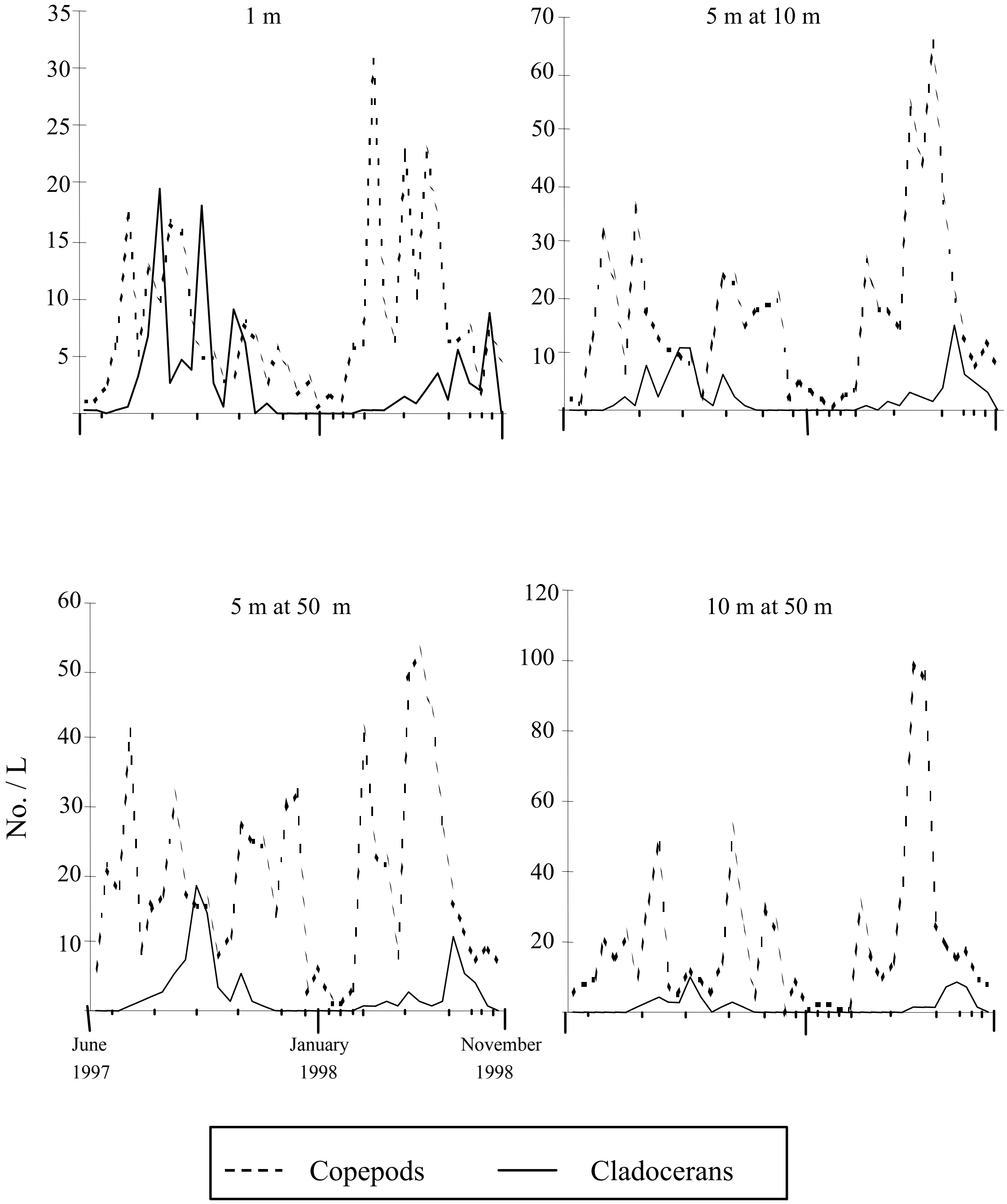


Figure 2.10. Estimated densities of copepods and cladocerans at four depth strata in Garfield Bay, Lake Pend Oreille 1997-1998.

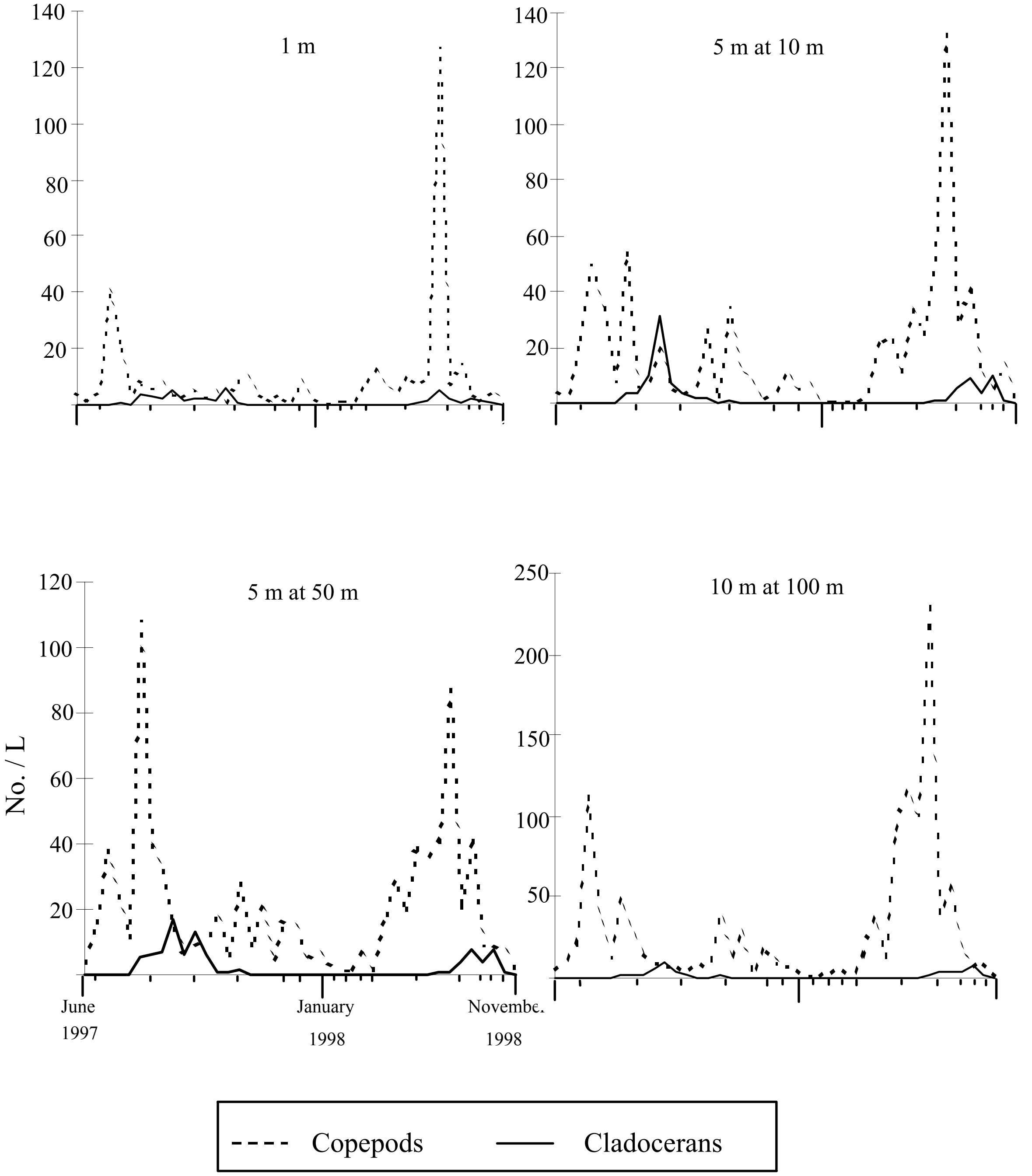


Figure 2.11. Estimated densities of copepods and cladocerans at four depth strata in Idlewilde Bay, Lake Pend Oreille 1997-1998.

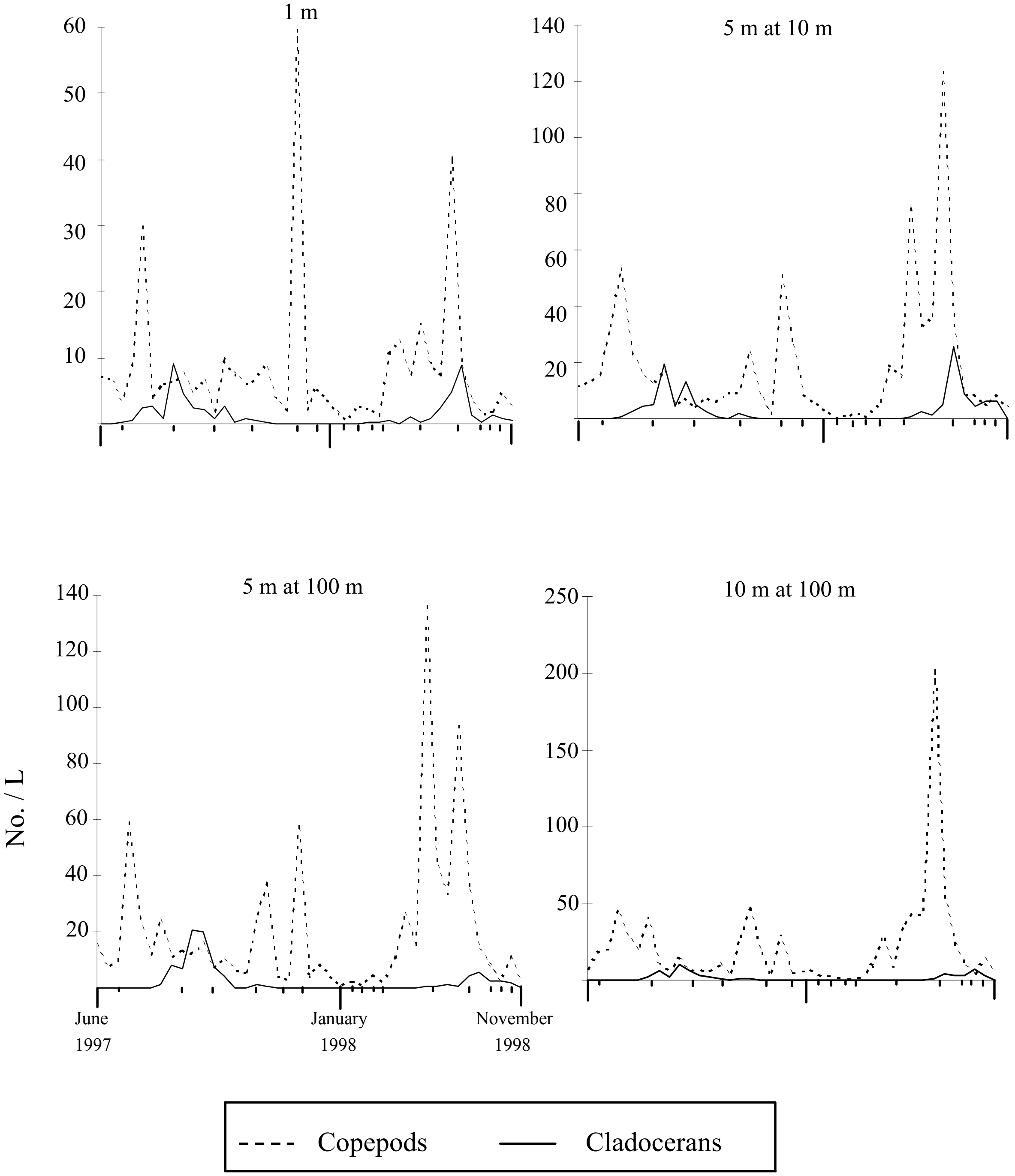


Figure 2.12. Estimated densities of copepods and cladocerans at four depth strata in Scenic Bay, Lake Pend Oreille 1997-1998.

Zooplankton Lengths

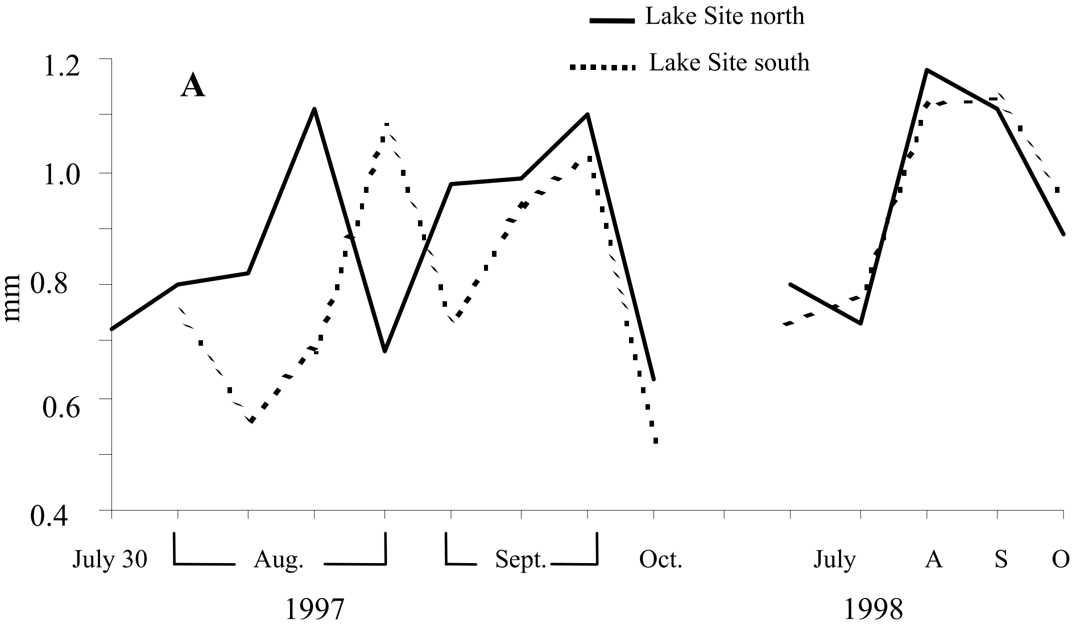
Length measurements for *Cyclops*, *Diaptomus* and *Bosmina* varied little seasonally, and among sampling locations, in Lake Pend Oreille from 1997-1998 (Appendix Table 2.2). *Daphnia* lengths fluctuated widely by sampling date and among sampling locations in the summer of 1997 (Figure 2.13), but changes in *Daphnia* length were generally consistent among sampling locations in 1998. *Daphnia* lengths peaked in September at most sampling locations, and declined quickly in October. Mean *Daphnia* lengths were similar between 1 m (0.81 mm) and 5 m at 10 m (0.83 mm) depth strata, and at the 5 m at 100 m (0.91 mm) and 10 m at 100 m (0.89 mm) depth strata.

Water Temperatures

Surface temperatures in 1998 were warmer in June, but slightly cooler in mid-summer at most sampling locations compared to 1997 (Figure 2.14). At Ellisport Bay, water temperatures warmed above 15°C earlier in the spring than at other sampling locations. By late September 1997, water temperatures had cooled below 15°C, except at Ellisport Bay, whereas in 1998 water temperatures at all locations remained above 15°C until October. Mean zooplankton densities were correlated with water temperature ($r=0.46$, $p=0.0027$).

Water Transparency

At most sampling locations, spring and early summer secchi disk measurements were comparable, but measurements were generally lower in late summer and fall 1997 compared to 1998 (Figure 2.15). Secchi depths were often lower in the northern sampling locations (e.g. Lake Site north and Ellisport Bay) than in southern locations. The highest secchi disk measurements occurred in mid winter, and were generally between 9 and 10 m. Mean zooplankton densities were inversely correlated to water transparency ($r=-0.41$, $p=0.0089$).



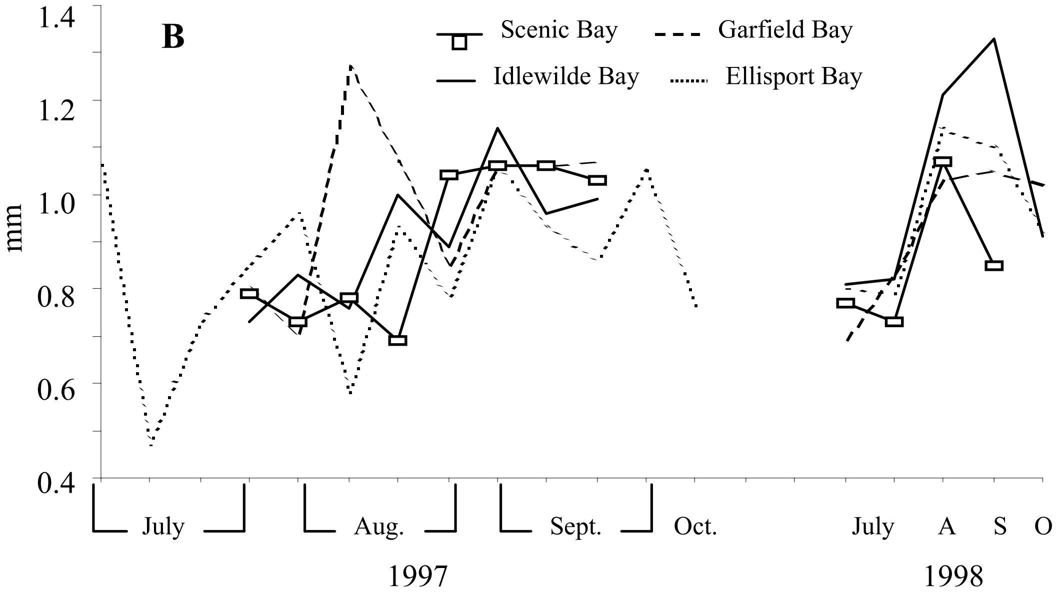


Figure 2.13. Lengths (mm) of *Daphnia spp.* for Lake Sites (A) and bays (B) in Lake Pend Oreille, 1997-1998.

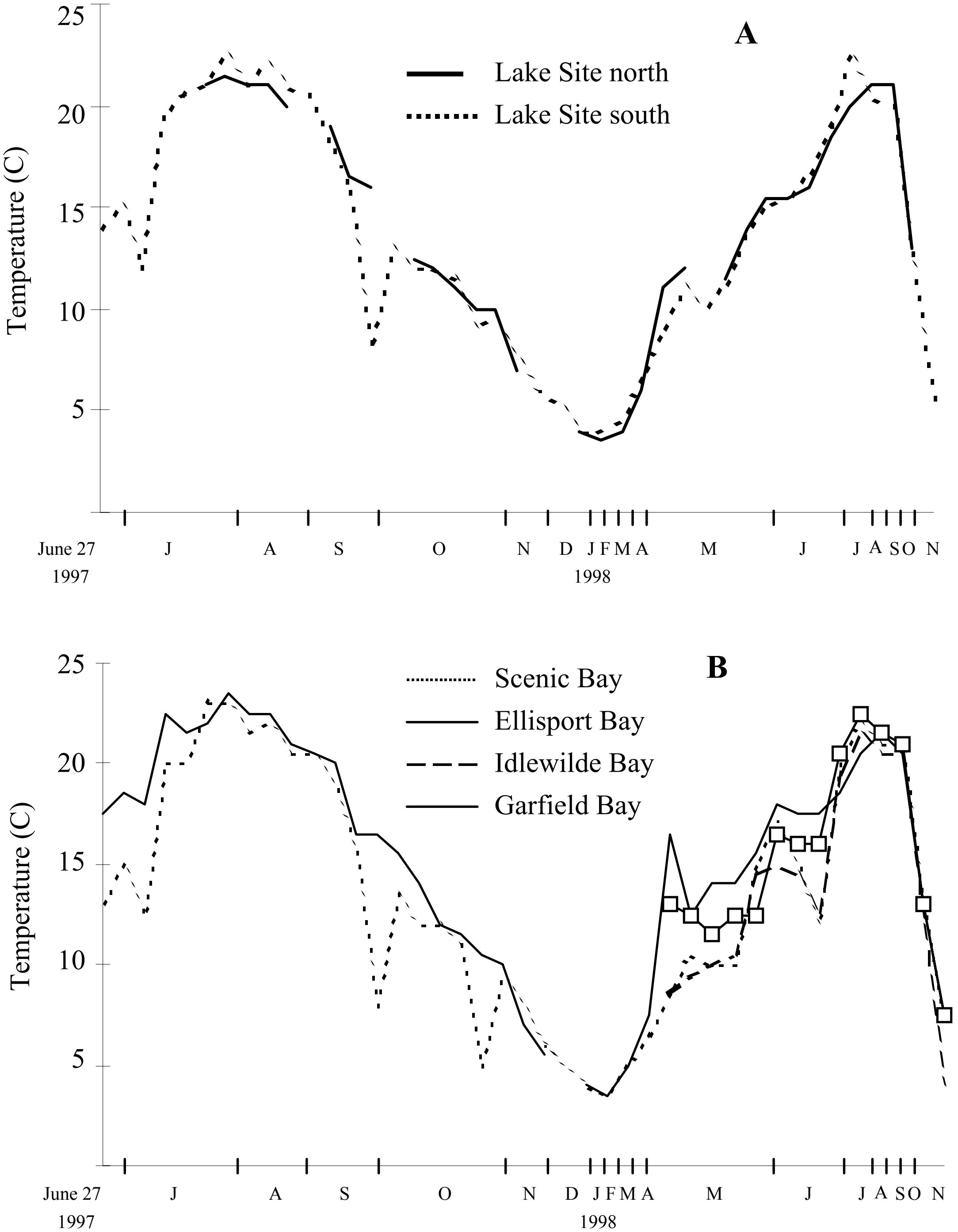


Figure 2.14. Surface temperatures (degrees C) for Lake Sites (A) and bays (B) in Lake Pend Oreille, 1997-1998.

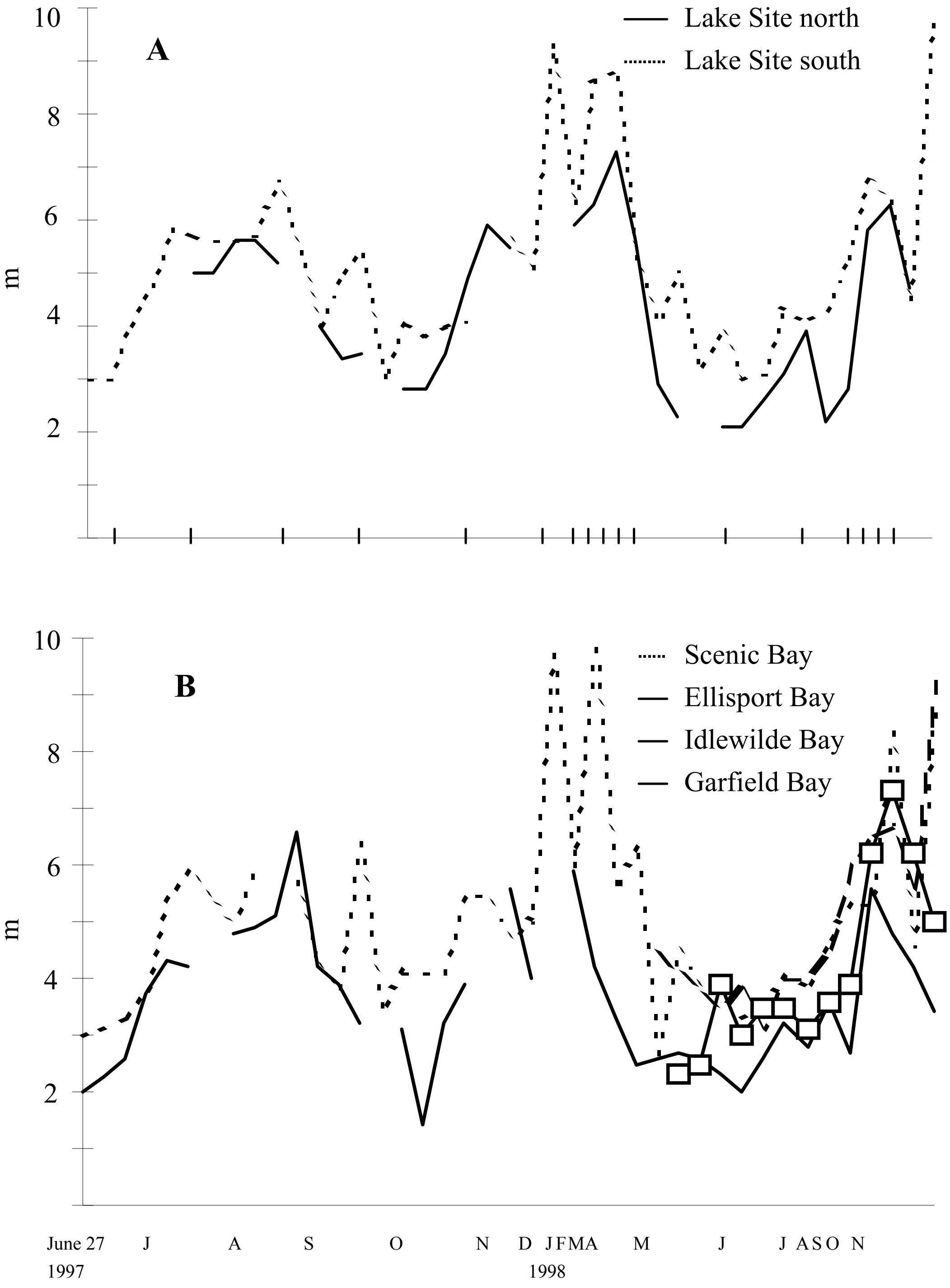


Figure 2.15. Secchi disk measurements (meters) for Lake Sites (A) and bays (B) in Lake Pend Oreille, 1997-1998.

Discussion

I examined temporal and spatial factors influencing crustacean zooplankton community dynamics in Lake Pend Oreille in 1997-1998 by collecting zooplankton samples from bays located on the northern (Ellisport Bay), middle (Garfield Bay), and southern (Scenic and Idlewilde bays) sections of the lake, and the main body of the lake in the northern (Lake Site north) and southern (Lake Site south) sections. Limnological variables such as water column transparency, nutrient dynamics and temperature gradients differ between northern and southern regions of Lake Pend Oreille (Woods 1991). My sampling locations were thus chosen to capture the breadth of limnological conditions which could influence secondary productivity, and therefore zooplanktivorous kokanee in Lake Pend Oreille. I also included a horizontal sampling component in this study because (*i*) studies have documented patchy zooplankton distributions on horizontal spatial scales (Watson 1976; Malone and McQueen 1983; Verreth 1990; Pinel-Alloul and Pont 1991), (*ii*) near-shore zooplankton abundance and species composition may be more important to newly emerging kokanee fry than zooplankton community composition in pelagic zones, (*iii*) shifts in zooplankton community structure as a result of other environmental factors (i.e. eutrophication or pollution) may affect near-shore regions before affecting off-shore regions (Evans and Jude 1986).

I observed variable zooplankton community dynamics on all temporal and spatial scales investigated. However, general trends in the zooplankton community of Lake Pend Oreille following establishment of *Mysis relicta* and described by Rieman and Falter (1981), Paragamian and Ellis (1994) and Chipps (1997) were similar to those observed here. Zooplankton species composition appears to have remained unchanged since the establishment of *Mysis relicta*, and the suite of commonly occurring cladocerans identified in this study (e.g. *Daphnia spp., Bosmina longirostris, Diaphanasoma leuchtenbergianum, Chydorus sphaericus, Leptodora kindtii*) were similar to previous Lake Pend Oreille studies. The copepods *Cyclops* and *Diaptomus* were numerically the dominant zooplankters in previous studies and in 1997-1998. In addition, I observed mid-summer increases in cladoceran zooplankton abundance following establishment of a thermocline at Lake Pend Oreille, and decreased cladoceran densities immediately after the thermocline dissipated; a trend originally described by Rieman and Falter (1981).

Zooplankton Abundance

In 1997 and 1998, peak total zooplankton densities occurred in early summer. In 1998 however, *Cyclops* was unusually abundant in June and July, causing total zooplankton density estimates also to be unusually high. This phenomenon was most evident at Scenic and Idlewilde bays, where peak zooplankton estimates were 117.85 and $146.86 \cdot L^{-1}$. Zooplankton density estimates were much higher in 1998 than in previous studies. Stross (1954) recorded a peak total zooplankton density of nearly $160 \cdot L^{-1}$ east of the mouth of Scenic Bay, and an average peak zooplankton density across all sampling locations of approximately $50 \cdot L^{-1}$ in June 1953. From 1974-1978 the highest reported peak *Cyclops* density at Lake Pend Oreille was approximately $25 \cdot L^{-1}$ in July 1977 (Rieman and Bowler 1980). By comparison, across all sampling locations the mean peak *Cyclops* density in 1998 was $67.30 \cdot L^{-1}$. From 1985-1992 Paragamian and Ellis (1994) reported that the highest mean zooplankton densities (approximately $45 \cdot L^{-1}$) occurred in July 1992. Chipps (1997) reported peak copepod densities estimates in July 1995 (approximately $50 \cdot L^{-1}$) and 1996 (approximately $85 \cdot L^{-1}$) that were lower than those I recorded in 1998 ($91.83 \cdot L^{-1}$). In 13 years of study (spanning 16 years from 1974-1989) conducted after the establishment of *Mysis* at Lake Pend Oreille, the average estimated mid-summer (May-September) total zooplankton density was $17.5 \cdot L^{-1}$, and ranged from 10.0 to $25.0 \cdot L^{-1}$ (Table 2.1). A comparable estimate in my study, spanning May-September 1998 at similar sampling locations (samples in previous studies were collected mostly from the main lake, thus I include only Lake Sites north and south in this estimate) is $39.12 \cdot L^{-1}$. From late June-September 1997 a comparable estimate is $23.54 \cdot L^{-1}$.

Researchers believe that factors influencing zooplankton abundance include physical variables such as water temperature (Patalas 1972; Johannsson and O'Gorman 1991), top-down variables such as planktivory (Johannsson and O'Gorman 1991), and bottom-up variables that include production of zooplankton food resources including bacteria, phytoplankton, rotifers, and copepod nauplii (Neill and Peacock 1980; Williamson and Gilbert 1980; Johannsson and O'Gorman 1991). Water temperatures were generally higher in the southern sampling locations and lower in the northern sampling locations of Lake Pend Oreille in June 1998 than in June 1997. Thus, the unusually abundant *Cyclops* populations in Scenic and Idlewilde bays in June 1998 may be partially explained by earlier warming of the epilimnion in spring 1998. In addition, planktivory by *Mysis relicta* probably exerts a controlling influence over early season zooplankton communities in Lake Pend Oreille (Chipps 1997). High June 1998 zooplankton abundance in the southern sections of the lake could therefore be related to low *Mysis* densities. Moreover, adult *Mysis* population estimates in the southern sections of Lake Pend Oreille in 1998 were approximately one third of 1997 estimates (M. Maiolie, Idaho Department of Fish and Game, unpublished data). Food for *Cyclops* might also have been more abundant early in the summer of 1998 than in normal years. Inflows into Lake Pend Oreille from the Clark Fork River reached record levels in 1997, resulting in

Table 2.1. Mean summer (May-September) total zooplankton densities (No./L) for most years from 1974-1998 in Lake Pend Oreille. Data in years 1974-1989 were summarized in Hoelscher (1993).

Year	Total Density
1974	13.3
1975	10.0
1976	15.0
1977	25.0
1978	15.7
1979	21.0
1980	15.9
1981	16.6
1985	19.8
1986	13.7
1987	16.6
1988	23.3
1989	22.0
1997	23.5
1998	39.1

localized flooding of low lying areas surrounding the lake. Nutrient levels at Lake Pend Oreille should have been exceptionally high in 1997 as a result of flooding. Water transparency remained low through late summer and fall 1997, providing evidence that higher nutient loads caused higher phytoplankton growth in 1997. I believe that residual effects from flooding in 1997 may have spurred increased food production for *Cyclops* early in the summer of 1998. Flooding at Lake Pend Oreille in 1974, similar to that in 1997, resulted in increased phytoplankton production in 1975 (Rieman 1976). In addition, median chloraphyll "a" values in Scenic Bay (≈10 µg/L) suggests that phytoplankton production was higher than normal in September 1998 (Anonymous 1999). Also, *Cyclops bicuspidatus thomasi* is a divoltine species, with one cohort over-wintering (i.e. diapause) in the bottom sediments as stage V copepodids and re-appearing in the spring (Rieman 1976). Perhaps the high flows and nutrient loading to Lake Pend Oreille in 1997 resulted in a stronger over-wintering *Cyclops* cohort.

Daphnia Abundance

Summer trends in *Daphnia* abundance and temporal distribution were noticeably different between 1997 and 1998. I recorded *Daphnia* in zooplankton samples earlier in the summer in 1998 than in 1997, which I attribute to lower planktivory by *Mysis relicta* in 1998. *Mysis* prefer cool water temperatures, and will not migrate into the epilimnion when water temperatures exceed 15ºC (Chipps 1997). In 1997 surface water temperatures did not warm above 15ºC until mid July, but water temperatures warmed above 15ºC in early June 1998, providing an early refuge to *Daphnia* from *Mysis* predation.

The earlier appearance of *Daphnia* in 1998 did not, however, result in a more abundant mid-summer *Daphnia* population. Peak *Daphnia* densities among sampling locations were 2.5-7 times higher in 1997 than in 1998. Density differences between 1997 and 1998 could theoretically be explained by increased planktivory from a more abundant kokanee population, although kokanee population estimates were lower in 1998 than 1997 (M. Maiolie, Idaho Department of Fish and Game, unpublished data). An alternative explanation is that abundant *Cyclops*, an omnivore whose diet includes phytoplankton and small zooplankton (Neill and Peacock 1980), suppressed *Daphnia* populations through either competition for phytoplankton or possibly predation on newly hatched *Daphnia.*

Kokanee are size selective predators and will generally select larger *Daphnia* over smaller bodied individuals (Rieman 1978). If kokanee foraging did suppress *Daphnia* populations in 1998, then shorter *Daphnia* length measurements in my study would indicate cropping of larger individuals. However, mid-summer *Daphnia* lengths at most sampling locations increased or remained stable until cooler water temperatures in October facilitated increased *Mysis* predation in the epilimnion. A possible cropping effect by kokanee was only identified in Scenic Bay, where estimated *Daphnia* lengths declined from 1.07 to 0.85 mm from August to September, 1998.

Horizontal Zooplankton Abundance

Lake Pend Oreille supports a substantial community of redside shiners *Richardsonius balteatus* and other juvenile cyprinids and centrarchids along its limited littoral zone (D. Vidergar, University of Idaho, unpublished data). Redside shiners and most juvenile fish are shallow-water planktivores (Wydoski and Whitney 1979), hence zooplanktivory could influence the zooplankton community at the 1 m sampling depth stratum. I believe that smaller mean *Daphnia* lengths at the 1 m depth stratum versus the off-shore depth strata suggests cropping of larger bodied cladocerans, and provides evidence that fishes can structure the near shore zooplankton communities of Lake Pend Oreille. Lower total zooplankton densities and lower proportions of copepods to cladocerans in near-shore areas versus pelagic zones, as I observed, have been reported by investigators elsewhere (Watson 1976; Pinel-Alloul and Pont 1991).

Temporal and Spatial Variability

On a lake-wide scale, the zooplankton abundance and species compositions described in this study show considerable variability among sampling dates and locations. Variability appears to be higher among bays in Lake Pend Oreille than in the main lake. However, previous studies at Lake Pend Oreille have mostly focused zooplankton sampling efforts on the main body of the lake (Rieman 1976; Rieman and Bowler 1980; Paragamian and Ellis 1994) and have largely ignored conditions within bays. Varying basin morphologies, levels of cultural eutrophication, and proximity to nutrient and thermal inputs from the Clark Fork River are probably factors that best explain the zooplankton variability observed among bays in my study. Scenic and Idlewilde bays are deeper, cooler and farther from the Clark Fork River than Garfield and Ellisport bays. Hence the timing and magnitude of zooplankton production was similar in Scenic and Idlewilde bays. Ellisport Bay is the shallowest bay in this study, is in close proximity to the Clark Fork River, and has the highest shoreline development of the four bays I sampled. Also, Ellisport Bay is the only bay in this study located north of the Clark Fork River. Rieman (1976) believed that most of the Clark Fork River water is channeled into the north arm of the lake, resulting in higher turbidity and dilution in the north. Although Ellisport Bay is off the main lake channel and is likely sheltered from direct river inflows, it may receive higher nutrient loads from the Clark Fork River than Garfield, Idlewilde or Scenic bays. Among the four bays I studied, secchi disk measurements were usually lowest at Ellisport Bay. I believe that turbidity from Clark Fork River inflows caused lower early summer secchi disk measurements at Ellisport Bay, but lower measurements in mid to late summer show higher rates of primary productivity than at other bay locations. Furthermore, I believe that higher primary productivity and warmer water temperatures resulted in higher cladoceran abundance and earlier increases in cladoceran populations at Ellisport Bay than at other sampling locations. Of the cladocerans, *Bosmina* was especially abundant at Ellisport Bay compared to the other sampled bays.

Peak zooplankton density estimates in my study would likely have been much lower if samples had been collected monthly or twice monthly rather than weekly. Zooplankton populations increased rapidly to peak abundance in June, 1998 and then declined quickly thereafter. For example, total zooplankton density estimates in Idlewilde Bay in the weeks immediately before and after the peak density estimate was recorded, were approximately 33% and 20% of the peak estimate. Such rapid population fluxes suggest the importance of frequent sampling to adequately characterize population level variability, especially in early summer when peak zooplankton densities at Lake Pend Oreille are known to occur.

Trophic Level Interactions

When cladoceran zooplankton are abundant, kokanee will feed preferentially upon them (Foerster 1968). Therefore, diminished spring and autumn *Daphnia* and *Bosmina* abundance from densities observed before establishment of *Mysis relicta* in Lake Pend Oreille should represent a decrease in preferred prey biomass available to kokanee. Reduced cladoceran zooplankton abundance from *Mysis* zooplanktivory has been implicated in kokanee population declines at Lake Pend Oreille (Rieman and Falter 1981) and elsewhere (Morgan et al. 1978; Beattie and Clancey 1991; Martinez and Bergersen 1991), although the mechanisms directly responsible for those declines could not be identified. Some researchers speculate that diminished cladoceran zooplankton biomass in spring and autumn from *Mysis* grazing can slow growth of planktivorous fish (Langeland et al. 1991; Chipps 1997). Rieman and Bowler (1980) report lower juvenile kokanee growth in some years following *Mysis* establishment, a result they attribute to changes in *Daphnia* and *Bosmina* availability. Decreased cladoceran zooplankton densities and slower kokanee growth were also reported in Lake Tahoe, Nevada (Morgan et al. 1978) and Lake Granby, Colorado (Martinez and Bergersen 1991) after establishment of *Mysis relicta*. However, investigations examining kokanee population declines occurring concurrent to *Mysis* introductions found no difference in mean kokanee spawner lengths despite reduced cladoceran densities (Lasenby et al. 1986; Beattie and Clancey 1991).

In 1998, however, *Cyclops* biomass was unusually high at Lake Pend Oreille, and likely provided additional forage for kokanee. Results from kokanee diet analysis (Objective 2) and growth experiments (Objective 3) in 1998 indicate that newly emerged kokanee achieved strong growth on a diet composed mostly of *Cyclops*. In addition, *Cyclops* abundance at Lake Pend Oreille was high in the spring of 1977, an occurrence that was attributed to early warming of the lake, and survival of age-0 kokanee was also strong (Rieman and Bowler 1980). Thus, I believe that the loss of early season cladoceran forage for kokanee may be compensated in some years by high *Cyclops* biomass. Conversly, kokanee growth and survival could also be affected in years when spring *Cyclops* biomass is low, and does not replace the lost cladoceran biomass.

A number of proposals have been suggested to recover kokanee in Lake Pend Oreille (Rieman and Bowler 1980; Bowles et al. 1991; Paragamian and Bowles 1995). However, I believe that spring fertilization to increase zooplankton standing biomass in areas of kokanee emergence coupled with on-going efforts to improve egg to fry survival of wild kokanee through lake level manipulations may be the most successful approach to kokanee recovery. If a relationship between growth of newly emerged kokanee and spring zooplankton biomass exists in Lake Pend Oreille, then increasing zooplankton biomass through food web alterations may prove beneficial, especially in seasons when zooplankton biomass is low. The concept of cascading trophic interactions (Carpenter et al. 1985) predicts that decreasing planktivore abundance (e.g. top-down effects) and/or increasing nutrient levels (e.g. bottom-up effects) should result in higher zooplankton abundance. By applying fertilizer to the epilimnion of nutrient poor lakes, numerous *in-situ* and whole lake experiments have demonstrated the utility of bottom-up manipulations for increasing zooplankton biomass (LeBrasseur et al. 1978; Kyle 1994; Budy et al. 1998). Studies have also demonstrated increased growth of juvenile kokanee and sockeye salmon following fertilization of oligotrophic lakes (LeBrasseur et al. 1978; Stockner and Macisaac 1996; Budy et al. 1998). Furthermore, studies have shown only small declines in water transparency resulting from increased phytoplankton abundance through fertilization (Budy et al. 1998).

Conclusions

In conclusion, the generally abundant zooplankton community among all sampling locations in June and July 1998 suggests that food should not limit kokanee fry growth during that period. Crustacean zooplankton biomass appears lower in June 1997 than in 1998, but I do not know if zooplankton availability in 1997 was sufficient for kokanee fry growth, since kokanee growth experiments (Objective 3) were performed only in 1998. In 1977, kokanee year-class survival was high, and mean May-September zooplankton density estimates were approximately equal to those I recorded from June-September in 1997 (Rieman and Bowler 1980). Total zooplankton densities, and densities of cladocerans, were higher in autumn 1998 than 1997. Based on the results of October growth experiments (Objective 3) and of zooplankton density estimates that showed above normal cladoceran zooplankton densities in October, I believe that autumn 1998 zooplankton densities were sufficient for juvenile kokanee growth. The lower *Daphnia* densities in the summer of 1998 versus 1997 could suggest food limitations for kokanee, resulting in slower growth. However, except in Scenic Bay, *Daphnia* lengths did not decline throughout the summer of 1998, leading to my conclusion that *Daphnia* abundance was probably sufficient to support mid-summer kokanee growth. In addition, I believe that the location specific variability exhibited by zooplankton populations in my study reinforces the need for location specific zooplankton sampling to describe food resources for kokanee stocks in Lake Pend Oreille. If the goal of a zooplankton sampling program were to describe food availability for newly emerging kokanee, then sampling should occur in Scenic and Idlewilde bays, where most of the kokanee egg deposition occurs (Rieman and Bowler 1980).

Summary

1. I examined zooplankton community dynamics in Lake Pend Oreille in 1997-1998 by collecting zooplankton samples in Ellisport, Garfield, Scenic and Idlewilde bays, and from northern and southern sections of the main lake. Zooplankton densities and biomass were estimated for each location. I also estimated the horizontal distribution of zooplankton in bays by collecting samples along transects extending out from the shoreline.
2. Zooplankton species composition at Lake Pend Oreille has remained unchanged from previous studies conducted after the establishment of *Mysis relicta.* As in previous studies, *Cyclops bicuspidatus thomasi* and *Diaptomus ashlandi* were the most numerous zooplankters, and cladoceran zooplankton *(*e.g. *Daphnia spp. Bosmina longirostris, Diaphanasoma leuchtenbergianum, Cydorus sphaericus, Leptodora kidtii)* became numerous following lake stratification in mid-summer.
3. Zooplankton densities and biomass were much higher at all sampling locations in the summer of 1998 compared to 1997. My mean summer (May-September) zooplankton density estimate was $23.54 \cdot L^{-1}$ in 1997 and $39.12 \cdot L^{-1}$ in 1998. My 1998 estimate is considerably higher that comparable estimates from previous Lake Pend Oreille studies conducted after the establishment of *Mysis relicta*
4. Summer trends in *Daphnia* abundance and temporal distribution were noticeably different between 1997 and 1998. *Daphnia* appeared earlier in samples in 1998 than in 1997, but peak *Daphnia* densities among sampling locations were 2.5-7 times higher in 1997 than in 1998. A possible cropping effect by kokanee on larger sized *Daphnia* was identified in Scenic Bay in September, 1998.
5. No statistically significant differences in zooplankton biomass among bays or between main lake sampling locations were identified, however zooplankton community dynamics

at Ellisport Bay appeared to be different from other bay locations. Cladoceran zooplankton became abundant earlier in summer, and remained abundant later in autumn, at Ellisport Bay than at other bay locations.

6. In bays, summer zooplankton densities were usually lowest in near-shore areas. Copepods were more abundant than cladocerans at each horizontal depth stratum sampled in this study, but cladocerans represented the highest proportion of total zooplankton densities at the near-shore depth.
7. Crustacean zooplankton were more abundant than normal in the summer of 1998. Based on the results of juvenile kokanee growth experiments in June and October, 1998 (Objective 3), and the zooplankton density estimates recorded in this study, I believe that zooplankton densities were sufficient to support juvenile kokanee survival and growth in June and October, 1998.

CHAPTER 3. The diet of newly emerged kokanee fry in Lake Pend Oreille, Idaho.

Introduction

Kokanee eggs deposited in the gravel along shorelines at the southern end of Lake Pend Oreille typically initiate emergence in May, with peak emergence occurring in June (Rieman and Bowler 1980). Emerging fry feed on zooplankton soon thereafter (Burgner 1991). Following the establishment of *Mysis relicta* in the early 1970's, researchers reported changes in the lake's springtime zooplankton community (Rieman and Falter 1981). Rieman and Falter (1981) speculated that reduced kokanee survival was due to the delay in *Daphnia* production later in the summer, and depressed springtime densities of *Bosmina longirostris*. Stross (1954) and Rieman and Bowler (1980) demonstrated that *Daphnia* are an important component in the summer diet of kokanee in Lake Pend Oreille. Similarly, dietary analyses and bioenergetic simulations of kokanee in other western region lakes illustrate the importance of *Daphnia* as a food source (Northcote and Lorz 1966; Narver 1970; Morgan et al. 1978; Martinez and Bergersen 1991; Beauchamp et al 1995). Although *Bosmina* are smaller and numerically less abundant in Lake Pend Oreille than the copepod *Cyclops bicuspidatus,* Stross (1954) found that *Bosmina* comprised 80% of the organisms in kokanee stomachs (n=25) in early June, suggesting that *Bosmina* was a preferred food source for kokanee. Also, limited stomach analysis of age-0 kokanee (n=7) sampled from Lake Pend Oreille in July, 1976, showed that *Bosmina* was numerically the most important prey item, accounting for 42% of the average prey biomass (Rieman 1980). *Bosmina* were selected by sockeye salmon *O. nerka* fry in Cultus Lake, British Columbia (Foerster 1968). Researchers at Cultus Lake hypothesized that smaller fish selected *Bosmina* over *Cyclops* because of the smaller size and higher visibility of *Bosmina*. The presence of pigmented eggs carried under the carapace may further increase *Bosminas*' visibility (Flinkman and Vuorinen 1991; see also Mellors 1975).

The purpose of this study was to quantify diets of kokanee fry shortly after emergence in Lake Pend Oreille. Specifically, two questions are answered from this project: 1) Which zooplankton species were utilized as prey by recently emerged kokanee fry? and 2) Are kokanee fry feeding selectively?

Methods

I collected larval kokanee by trawling during the 4 h period following dusk in Scenic and Idlewilde bays and in the main lake south of Cape Horn from May 15th through June, 1998 (Figure 1.1). Initially, larval kokanee were captured using a 1 m diameter larval fish net with 1 mm mesh netting. To improve capture efficiency, in early June I changed to a 750 µm mesh net with an opening measuring approximately 181 cm high and 128 cm wide. All larval kokanee were immediately preserved in 10% buffered formalin, and later length (mm total length) and weight (mg blotted wet weight) were recorded. Fulton's condition factor {K} (Anderson and Neumann 1996) was calculated for each fish using the formula:

$$K = (W/L^3) \times 10^5 \qquad (1)$$

where: K = condition factor of a kokanee,

W = weight (grams) and,

L = total length (millimeters;).

I used a Kruskal Wallis ranked ANOVA to test for differences in kokanee condition factor by week for the 5-week sampling period (SAS Institute, Version 6.11).

Prey Analysis

Prey items from each captured kokanee were identified to the lowest practical taxon under a dissecting microscope in the laboratory. Number, and when practical, lengths, of crustacean zooplankton were recorded. I estimated the relative contribution of each zooplankton species to total ingested mass by measuring lengths from a sample of each zooplankton species present, and converting length to weight from established length-weight relationships (Culver et al. 1985; Objective 2) Unidentifiable prey items were counted, but were excluded from further dietary analysis.

Diet Analysis

For each prey type I calculated the following parameters : Frequency of occurrence (FO), the percentage of fish in a sample that ate a food item, the percentage of each food type of the total number of food items eaten by all fish in the sample (%N), and the percent mass (mg of wet biomass) of the total mass of all food items eaten (% M; Carpenter and Kitchell 1993). From those parameters an index of absolute importance (IAI) was calculated for each prey type using the formula:

$$\mathrm{IAI} = \%\mathrm{N} + \%\mathrm{M} + \mathrm{FO} \qquad (2)$$

From the calculated IAI values I generated an Index of Relative Importance (IRI) using the formula:

$$\mathrm{IRI} = 100 \times \mathrm{IAI} / \Sigma\ \mathrm{IAI} \qquad (3)$$

Selectivity Index

I used a selectivity index first proposed by Strauss (1979) to compare zooplankton species ingested by kokanee with potentially available prey. The index is defined as:

$$\mathrm{L}_i = \mathrm{r}_i - \mathrm{p}_i \qquad (4)$$

where: L_i = selectivity index value ranging from -1 to +1, indicating strong avoidance or preferential prey selection,

r_i = the relative abundance by number of prey taxon in kokanee stomachs,

p_i = the relative abundance of the same taxon estimated from weekly sampling in the upper 10 m of Scenic and Idlewilde bays in Lake Pend Oreille in May and June 1998 (Objective 1).

Weekly *Mysis relicta* population estimates, specific to my kokanee capture and zooplankton sampling sites, are not available for June 1998. Therefore I excluded *Mysis* from the selectivity index.

Results

I examined the stomachs of 322 newly emergent kokanee sampled during 5 weeks from May through June, 1998. Approximately 69% (n=225) of the stomachs were from kokanee 23-25 mm in length, while 48 stomachs were from kokanee 25-36 mm in length (Figure 3.1). The condition factor of sampled fish changed significantly over the 5 week period ($F=10.49$, $p<0.0001$; Figure 3.2, Appendix Table 3.1). Eighty-two of the sampled stomachs were empty; the percentage of empty stomachs declined over the sampling period (Figure 3.2) and as kokanee lengths increased (Figure 3.3). Four stomachs from fish ranging in size from 20 to 24 mm contained only egg yolk and were excluded from diet analysis. Length, weight, condition factor, and stomach biomass for each sampled fish is summarized in Appendix Table 3.2.

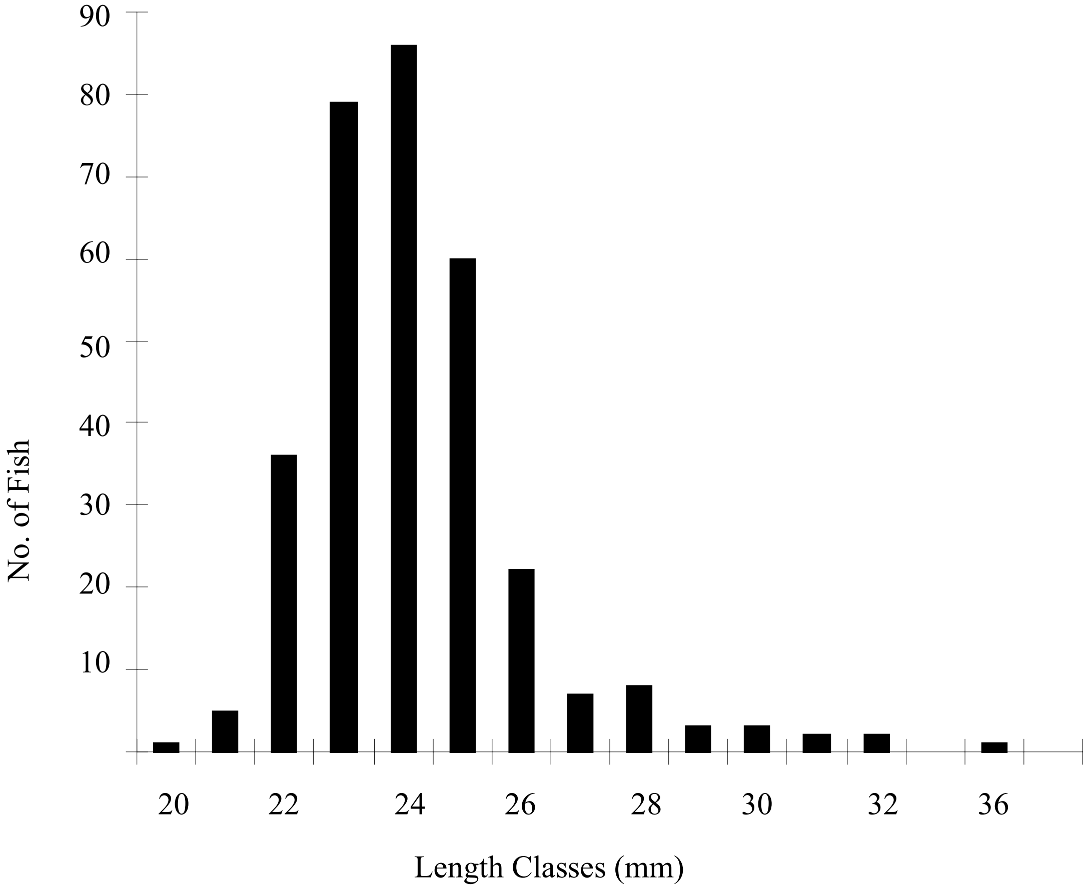


Figure 3.1. Length classes for age-0 kokanee captured for diet analysis in Lake Pend Oreille, May and June 1998.

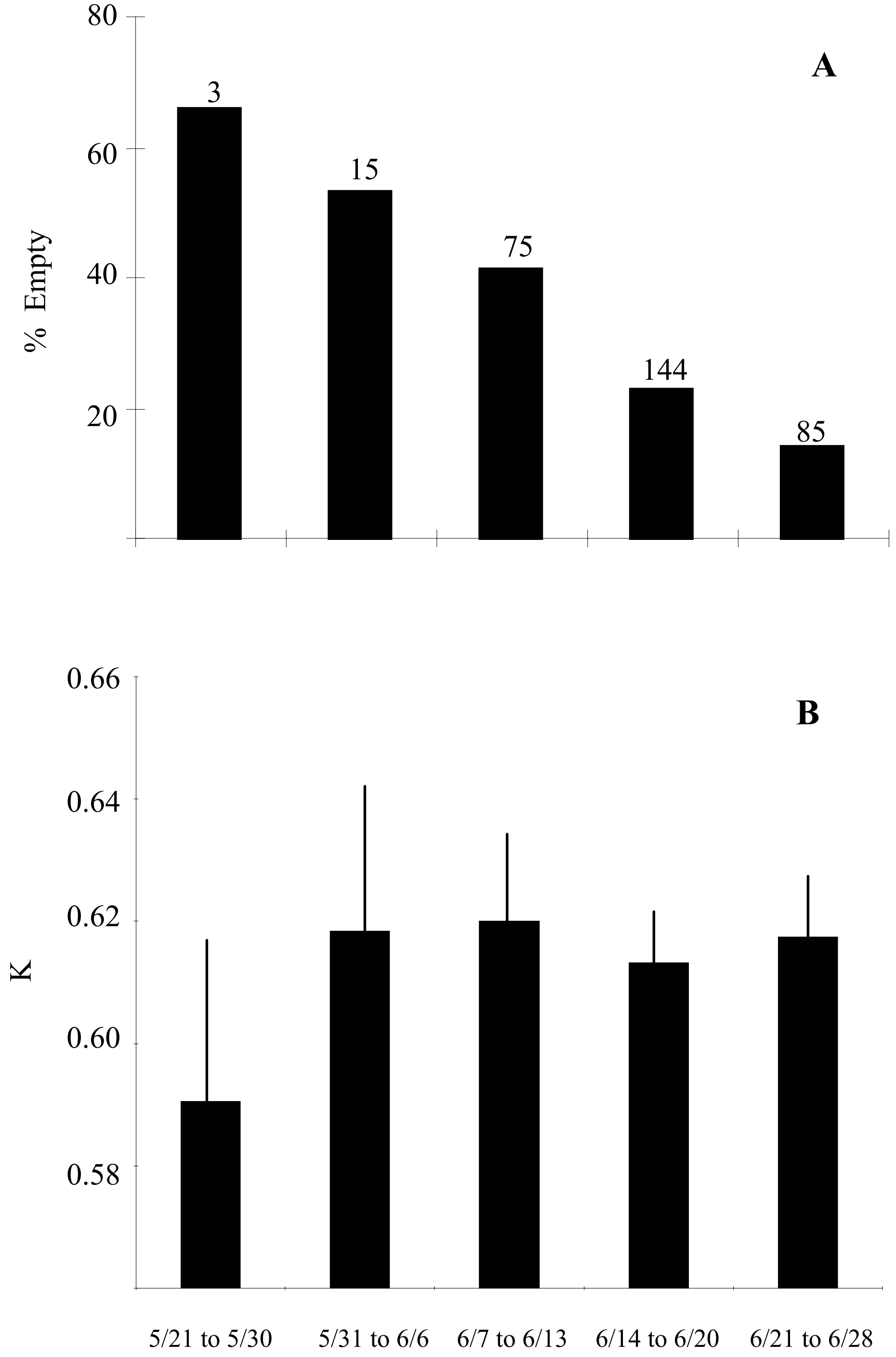


Figure 3.2. Percent empty stomachs (A) and Fulton condition factor (K, B) by week for age-0 kokanee sampled in Lake Pend Oreille in May and June 1998. Vertical bars represent 2 standard errors. Numbers above bars represents number of fish sampled.

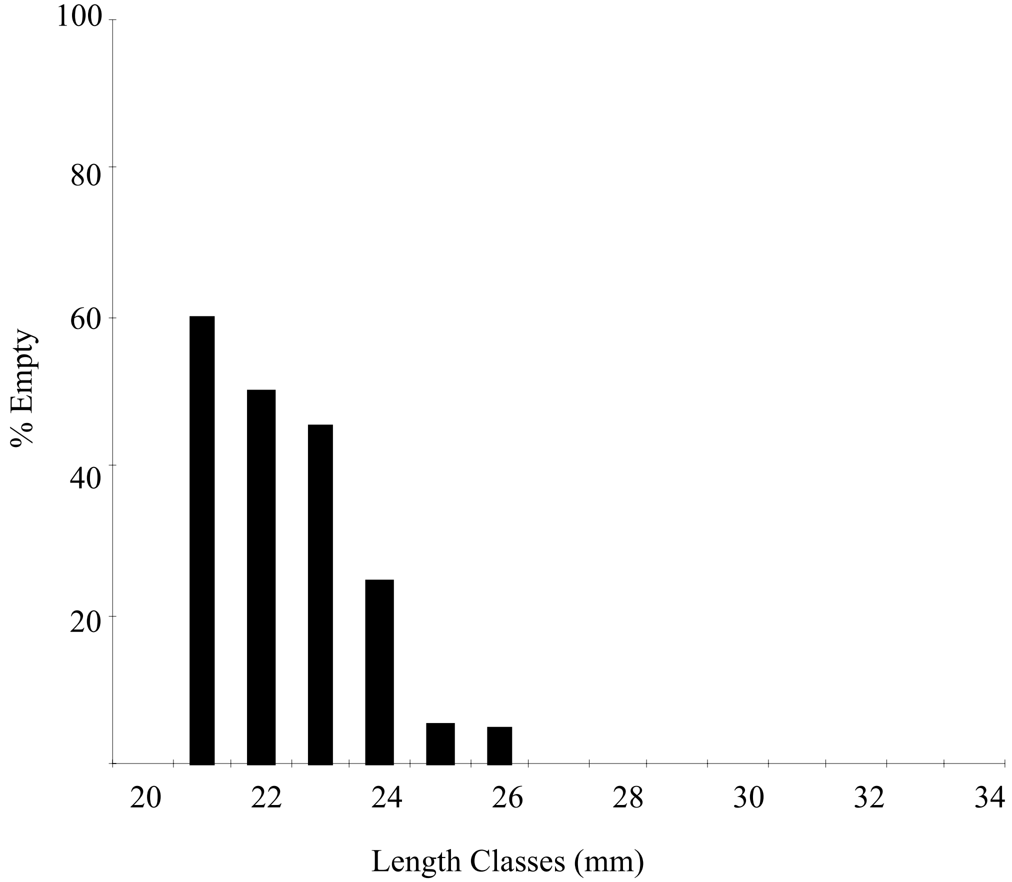


Figure 3.3. Percent empty stomachs by length class for age-0 kokanee captured for diet analysis in Lake Pend Oreille, May and June 1998.

Diet Analysis

The diet of kokanee varied slightly over the 5-week sampling period (Figure 3.4, Appendix Table 3.3). The copepod *Cyclops bicuspidatus thomasi* was the most abundant prey item in stomachs in each sampling week, and represented almost 91% (n=12,469) of the 13,705 prey items identified. The copepod *Diaptomus ashlandi* and the cladoceran *Daphnia* represented 5.65% (n=774) and 2.65% (n=363) of the identified prey items respectively, whereas all other prey types accounted for 0.7% of identifiable items. *Cyclops* also occurred most frequently in stomach samples (70.53%), with *Diaptomus* identified in 49.84% and *Daphnia* seen in 21.94% of all stomachs. *Daphnia* and *Mysis relicta* were first identified in stomach samples on June 11 (n=1), and all other occurrences of *Daphnia* were from fish collected on or after June 16th. Mean length measurements for the individual prey types are summarized in Table 3.1.

Cyclops accounted for the highest amount of prey biomass identified in kokanee stomachs (79.28%). However, *Cyclops* were generally smaller than *Diaptomus* and *Daphnia*. Consequently, *Cyclops*' contribution to overall prey biomass was lower than their contribution to the number of items consumed (90.98%). *Cyclops* and *Diaptomus* represented over 99% of the total prey biomass during the first 2 sampling weeks (Figure 3.4). Later in the sampling period, stomach biomass from *Daphnia* and *Mysis relicta* increased; together they accounted for nearly 28% of consumed biomass in week 5. *Mysis relicta* were identified from stomachs of kokanee as small as 23 mm in length. Twenty-five individuals of *Bosmina* were counted in stomach samples and *Bosmina* accounted for 0.2% of total ingested biomass.

Results of the index of relative importance (IRI) show that the copepods were most important to the diet of newly emerged kokanee in the spring of 1998. Overall, copepods represented 86.61% of the index, with C*yclops* being the largest contributor to the index (66.52%, Table 3.2). Although D*iaptomus* was consumed by nearly half the sampled fish, it represented only 18.40% of the index, while D*aphnia* accounted for 8.68%.

Selectivity Index

Cyclops and *Diaptomus* were the only zooplankton species with weekly index values larger than ± 0.10 (Figure 3.5). *Cyclops* was actively selected by kokanee in all but the second sampling week, with index values ranging from -0.056 to 0.695. *Diaptomus* was actively

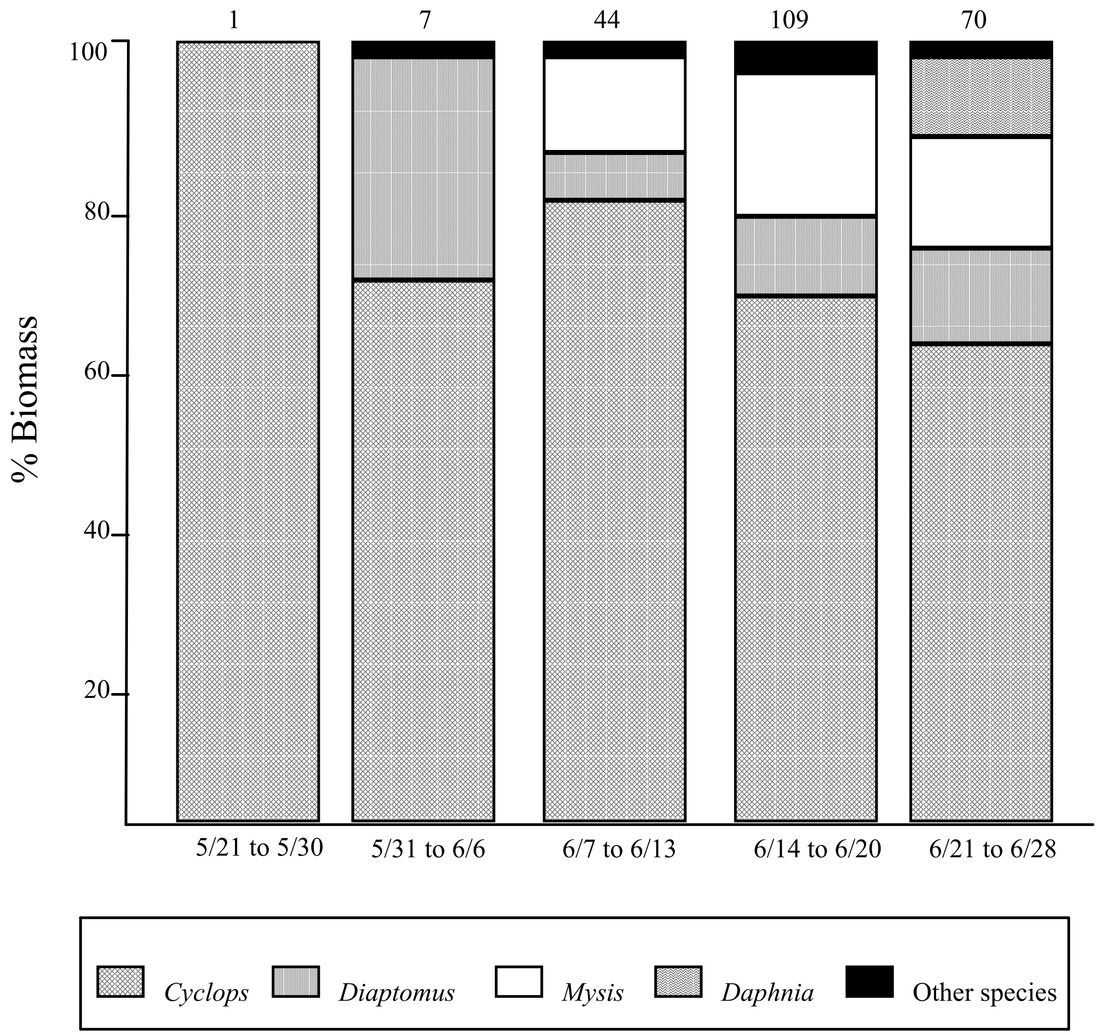


Figure 3.4. Diet composition (percent biomass) by week of newly emergent kokanee collected in Lake Pend Oreille in May and June, 1998. Numbers above bars indicate number of stomachs sampled.

Table 3.1. Mean lengths of individual prey items identified in kokanee stomachs from Lake Pend Oreille, May-June 1998.

Prey Item	Number Sampled	Mean Length (mm) ± (SE)[a]
Cyclops	385	0.71 ± (.0060)
Diaptomus	96	0.95 ± (.0123)
Epischura	2	1.74
Daphnia spp.[b]	74	1.11 ± (.0260)
Bosmina	13	0.51 ± (.0511)
Mysis	1	3.10

[a] SE represents one standard error.
[b] *Daphnia thorata* and *D. galeata mendotae*.

avoided in all but the second sampling week, with index values ranging from -0.23 to 0.08. In each week, the two cladocerans *Daphnia* and *Bosmina* were preyed upon in nearly the same proportion as their availability in the environment, and had index values no larger than ± 0.028. Age-0 kokanee did not actively select nor avoid other zooplankton species occurring in the diet. Selectivity index values for each zooplankton species are listed in Appendix Table 3.4.

Discussion

The copepod *Cyclops bicuspidatus thomasi* occurred most frequently and represented the largest biomass of prey items identified in age-0 kokanee stomachs in Lake Pend Oreille in May and June, 1998. As judged by those criteria, *Cyclops* represented the most important prey item in this diet analysis. The cladoceran *Bosmina longirostris,* which had been identified in studies as an important early-season kokanee food source before the introduction of *Mysis relicta* to Lake Pend Oreille (Stross 1954), and in some years following the establishment of *Mysis relicta* (Rieman and Bowler 1980), was an unimportant dietary item in my study. The cladoceran *Daphnia,* identified in studies as a preferred prey item of all age classes of kokanee

Table 3.2. Index of relative importance calculated for stomach contents of age-0 kokanee captured in Lake Pend Oreille in May and June, 1998.

Prey Item	%IRI
Cladocera	
Daphnia spp.[a]	8.68
Bosmina longirostris	1.66
Diaphansoma leuchtenbergianum	0.28
Leptodora kindtii	0.00
Chydorus sphaericus	0.20
Copepoda	
Cyclops bicuspidatus thomasi	66.52
Diaptomus ashlandi	18.40
Epischura nevadensis	0.89
nauplii	0.80
Mysis relicta	2.57
	TOTAL = 100.00

[a] *Daphnia thorata* and *D. galeata mendotae*.

when abundant (Rieman and Bowler 1980; Beattie and Clancy 1991; Martinez and Bergersen 1991) was only an important prey item in my study in the final sampling week. Age-0 kokanee also preyed upon *Mysis relicta* in sampling weeks three through five. The copepod *Diaptomus ashlandi* was present in the diet in sampling weeks two through five, but were not selected by emerging kokanee

The feeding behavior of *O. nerka* is plastic, their prey selection depends greatly on the availability and relative abundance of prey items (Burgner 1991). In my study, the predominance of *Cyclops* in the stomach contents of kokanee fry reflected *Cyclops'* higher abundance in Lake Pend Oreille in May and June, 1998. Prey selectivity index values showed

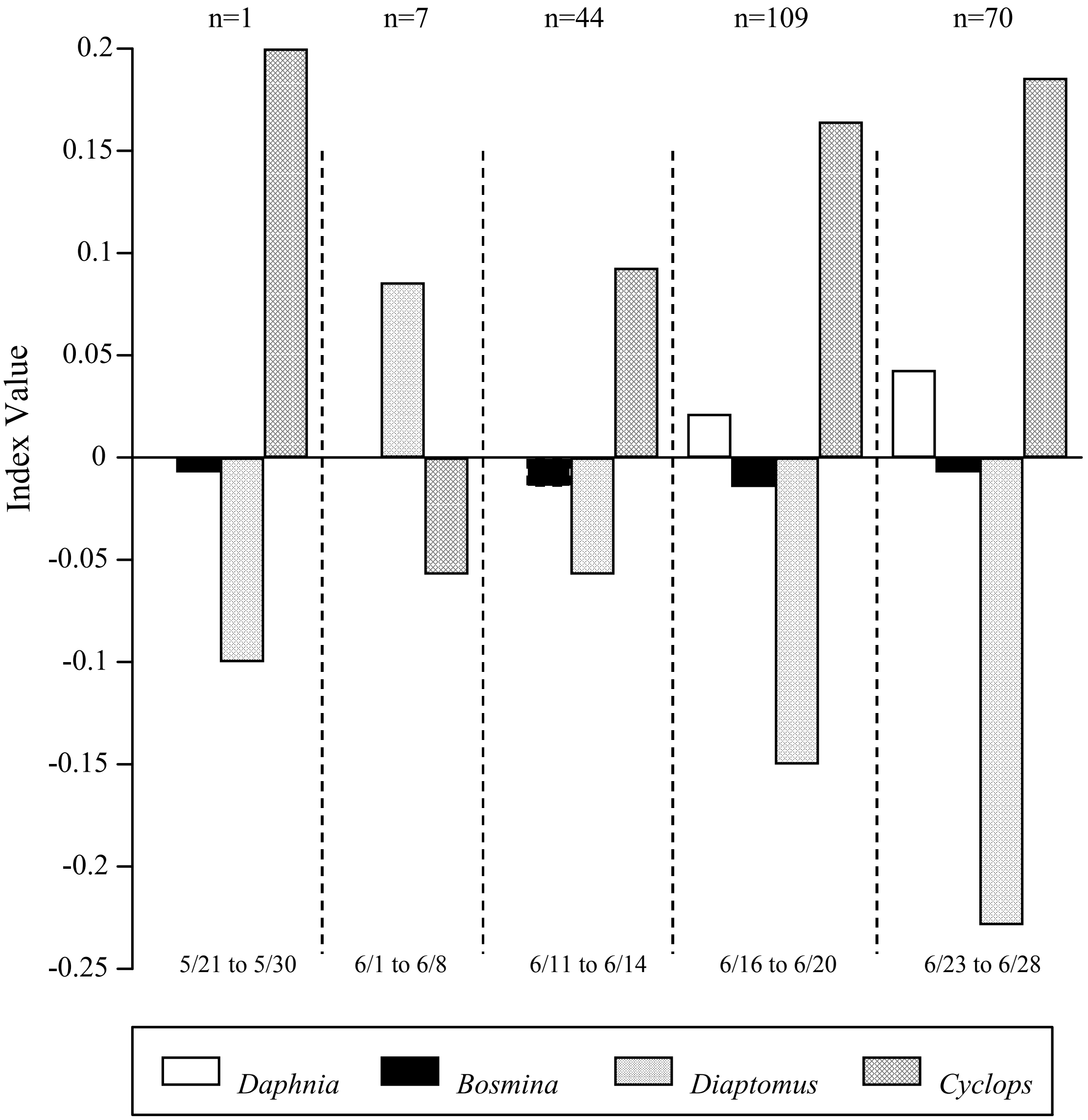


Figure 3.5. Prey selectivity by age-0 kokanee in Lake Pend Oreille, May-June 1998, for the four highest represented zooplankton species in the index of relative importance. Numbers above bars indicate number of stomachs sampled.

only slight positive or negative selection for *Cyclops* in all 5 sampling weeks, further demonstrating that kokanee prey selection generally mirrored prey abundance. However, active predatory avoidance of the copepod *Diaptomus ashlandi* by kokanee fry in four of the five sampling weeks may have reflected a preference by kokanee for the smaller *Cyclops*, or a greater ability by *Diaptomus* to avoid predation through faster movement rates (O'Brien 1979). My study did not detect a strong selection for the larger bodied *Daphnia*, although late June *Daphnia* densities were higher than 0.2 *Daphnia*· L^{-1} (Objective 1). In contrast, Beattie and Clancy (1991) found selective predation on *Daphnia* by newly emerged kokanee in Flathead Lake, Montana, despite *Daphnia* densities that were nearly undetectable by zooplankton sampling.

Prior kokanee diet analyses at Lake Pend Oreille, and at other western region lakes, have shown significant predation on *Cyclops* by newly emerged kokanee fry. In a 1986-1987 study of young of the year kokanee feeding at Flathead Lake, *Cyclops* represented 69% of the diet (Beattie and Clancey 1991). At Lake Granby, Colorado, *Cycops* was the only crustacean zooplankton identified in the stomachs of age-0 kokanee collected in mid June, 1982 (Martinez and Bergersen 1991). In 1977, *Cyclops* was unusually abundant in the spring at Lake Pend Oreille, and was the dominant diet source for newly emerged kokanee (Rieman and Bowler 1980).

The presence of *Mysis relicta* in the stomach contents of kokanee captured in this study was unexpected. I am not aware of any other study that has identified *Mysis* in the diet of newly emerged kokanee, though larger kokanee have been shown to consume *Mysis* in Lake Pend Oreille (Rieman and Bowler 1980) and elsewhere (Morgan et al. 1978; Martinez and Bergersen 1991; Northcote 1991). Although easily identifiable, the *Mysis* I observed in stomach contents were often partially digested or fractionated, making accurate length measurements difficult. However, I estimate that *Mysis* prey length was less than 5 mm, consistent with the length range of individuals from a newly released spring brood (Chipps 1997). That kokanee as small as 23 mm total length contained *Mysis* in the gut suggests that gape limitations do not preclude newly emerged kokanee from feeding upon them as suggested by other researchers (Rieman and Bowler 1980). In my study, kokanee stomachs typically contained less than three *Mysis*, though one stomach contained seven *Mysis,* and most stomachs with *Mysis* also contained crustacean zooplankton prey items. *Mysis* did not contribute substantially to the diet of newly emerged kokanee in my study, and were identified in about 7% of fish captured after June 11. By comparison, *Mysis* were identified in 19-23% of the stomachs of larger kokanee at Lake Pend Oreille in 1977-1978 (Rieman and Bowler 1980), and in 16-29% of kokanee stomachs at Lake Granby, Colorado in 1982-1983 (Martinez and Bergersen 1991). I conclude from these observations that young of the year *Mysis* were preyed upon opportunistically by age-0 kokanee in Lake Pend Oreille, but did not provide a principal food source to kokanee fry.

My observation of predation on *Mysis* by kokanee fry may represent an anomaly. Increased predatory interactions between kokanee and *Mysis relicta* resulting from an unusual set of limnological conditions (e.g. water temperatures, turbidity) may have caused changes in the vertical distributions of *Mysis* and kokanee fry. Most kokanee fry, and large quantities of *Mysis,* were captured by trawling the surface 20 m of the pelagic zone after sunset. Perhaps lake conditions unique to 1998 caused juvenile *Mysis* to ascend to the surface earlier in the evening, or descend from the surface later in the morning, reducing spatial segregation and affording greater opportunities for kokanee predation on *Mysis*.

The high incidence of empty kokanee stomachs in my study, especially in the first 2 sampling weeks, could be attributed to several factors. Empirical observations by other researchers suggest that kokanee fry may feed sparingly immediately following emergence. A diet analysis of kokanee fry at Lake Pend Oreille, before *Mysis* were introduced, showed that stomachs of fry caught in June were "empty of any recognizable material" (Allison 1958). In addition, Lebrasseur et al. (1978) report that sockeye *O nerka* fry in Great Central Lake, British Columbia, typically feed little for the first 2 weeks following their emergence in April. Also, my sample sizes in weeks 1-2 were small, and may not adequately represent the population. However, given the unusually high zooplankton densities in Lake Pend Oreille during kokanee fry sampling in 1998 (Figure 3.5), it appears unlikely that limited food availability was directly related to the high incidence of empty stomachs in this study.

I do not know whether a switch from a diet dominated by *Bosmina* before the introduction of *Mysis* to the *Cyclops*-dominated diet observed in this study has consequences for kokanee fry survival and growth. Some studies suggest that smaller prey items, such as *Bosmina*, are a better diet source for smaller fish (Mills et al. 1984; Confer and Lake 1987). Kokanee can reduce the water content of the cladoceran *Daphnia* during ingestion, thereby allowing kokanee to increase the biomass of prey packed into the stomach (Stockwell et al. 1999). Similar information is not available for *Bosmina* and copepod zooplankton. However, if kokanee fry in Lake Pend Oreille were similarly able to "squeeze" water from the cladoceran *Bosmina*, but not from the copepod *Cyclops*, then kokanee preying on *Bosmina* could benefit from a meal with a higher biomass, and potentially a higher energy content, at each feeding. It is possible that crustacean zooplankton biomass, rather than community

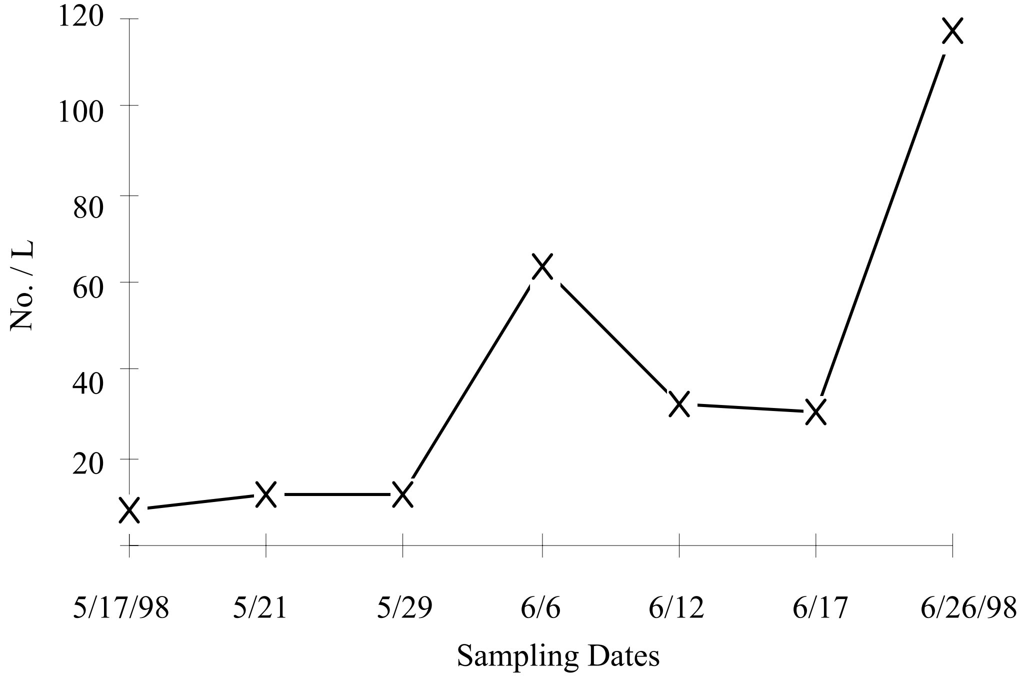


Figure 3.6. Estimate of zooplankton food densities available (No./L) to kokanee fry in Scenic Bay, Lake Pend Oreille, in May and June 1998. Estimate excludes copepod nauplii, which are not considered a food source.

composition, is more important to the growth and survival of newly emerged fry. In May-June 1977 at Lake Pend Oreille, kokanee fry preyed heavily on a dense *Cyclops* population, and age-0 kokanee survival was higher than in 1975, 1976, and 1978; three years characterized by low spring zooplankton densities, but higher incidence of feeding on *Bosmina* (Rieman and Bowler 1980). Because zooplankton densities and *Cyclops* consumption by kokanee in 1998 were similar to 1977, I believe that kokanee fry survival in 1998 should be similar to 1977, assuming other sources of mortality were also similar.

Summary

1. I investigated the diet of newly emerged kokanee in Lake Pend Oreille in May and June, 1998. Larval kokanee were collected by trawling after dusk in Scenic and Idlewilde bays, and in the main lake south of Cape Horn.
2. The copepod *Cyclops bicuspidatus thomasi* was the most important prey item for newly emerged kokanee fry in May and June, 1998, whereas the copepod *Diaptomus ashlandi* was the next most important zooplankter preyed upon. The first occurrence of both the cladoceran *Daphnia* and *Mysis relicta* in stomach samples was on 11 June. *Daphnia* and *Mysis relicta* together accounted for nearly 28% of prey biomass in the 5th sampling week. The cladoceran *Bosmina longirostris* was unimportant in the diet of larval kokanee in this study.
2. *Cyclops* was an actively selected prey item by newly emerged kokanee in this study, whereas *Diaptomus* was actively avoided. The two cladocerans *Daphnia* and *Bosmina* were preyed upon in nearly the same proportion as their availability in the environment.
3. This is the only study I am aware of to document predation on *Mysis relicta* by newly emerged kokanee, although *Mysis* did not contribute substantially to the diet of kokanee in my study.

CHAPTER 4. The importance of varied crustacean zooplankton composition and abundance on the survival and growth of both newly emerged kokanee fry in June and age-0 kokanee in October in Lake Pend Oreille.

Introduction

Water temperature, density-dependent competition for food, and zooplankton abundance and species composition influence juvenile kokanee *Onchorhynchus nerka* growth (Goodlad et al. 1974; Rieman and Myers 1992; LeBrasseur et al. 1978). Results from net pen experiments conducted in Lake Pend Oreille in 1993 to understand effects of sustained underwater sound on the feeding and growth of kokanee suggest that kokanee growth may be sensitive to small fluctuations in zooplankton abundance (Bennett et al. 1994). Bennett et al. (1994) observed lowered growth rates in September that were attributed to " a concomitant decrease in zooplankton abundance in Lake Pend Oreille in mid-September". Other work has demonstrated the relationship between zooplankton community dynamics and the growth or survival of both kokanee and sockeye *O. nerka*. In Great Central Lake, British Columbia, a nine-fold increase in zooplankton biomass following lake fertilization resulted in increased survival of age-0 and increased growth of age-2 sockeye (LeBrasseur et al. 1978). Paragamian and Bowles (1995) reported a correlation between mean zooplankton densities from May through October, and the survival of hatchery reared age-0 kokanee in Lake Pend Oreille. In Lake Granby, Colorado, kokanee survival and growth to maturation was thought to be controlled by the timing of appearance and peak biomass of *Daphnia* populations (Martinez and Wiltzius 1995). During a 20-year period, the mean length of sockeye salmon smolts in Frazer Lake, Alaska, decreased from 148 mm to 89 mm as seasonal zooplankton densities dropped from an average of 10,620/m^3 to 1,450/m^3 (Kyle et al. 1988).

Correlations between kokanee growth and zooplankton densities are not always evident. In Flathead Lake, Montana, age-0 kokanee continued to grow in the fall, after zooplankton abundance and water temperatures began to decline (Beattie and Clancey 1991). In a study of four lakes of the Fraser river system, British Columbia, Goodlad et al. (1974) concluded that relationships between growth of sockeye salmon *O. nerka* fry and zooplankton densities existed in two lakes, but found a stronger correlation between kokanee growth and water temperature in the deepest, coldest lake investigated

Temporal shifts in the zooplankton community at Lake Pend Oreille, characterized by reduced spring and autumn densities of cladoceran zooplankton (Rieman and Falter 1981), may cause starvation or slow growth for newly emergent kokanee. Using bio-energetics modeling, Chipps (1997) predicted that *Mysis* predation on cladoceran zooplankton in Lake Pend Oreille would be highest in June and October because (*i*) two omnivorous *Mysis* cohorts exist in early summer (e.g. June) and autumn (e.g. October), whereas in mid-summer one *Mysis* cohort is omnivorous, and an immature second cohort feeds predominantly on algae or detritus and (*ii*) A combination of optimum water temperatures (*Mysis* prefer water temperatures between 9-11 °C) and lower light levels (*Mysis* are light sensitive) in spring and autumn allow increased *Mysis* foraging time in the epilimnion. Although research has been conducted to understand how such shifts in the zooplankton community have impacted kokanee (Rieman and Bowler 1980; Rieman 1981; Paragamian and Ellis 1992), questions persist about the growth and survival of Age-0 kokanee (Williams et al. 1997). I conducted *in situ* experiments to test whether ambient food resources in Lake Pend Oreille were sufficient for newly emerged kokanee to survive and grow in June 1998, and for age-0 kokanee to grow in October, 1998. In both experiments I compared the growth of kokanee exposed to higher and lower zooplankton densities against kokanee fed at ambient zooplankton densities.

Methods

I conducted *in-situ* experiments in the southern basin of Lake Pend Oreille (Figure 1.1). For the June experiments, I obtained newly emerged kokanee from Cabinet Gorge Hatchery. On May 30, 1998 three fish were stocked into each of 15 cylindrical net pen enclosures measuring 78 cm in diameter and 2 m long, enclosing approximately 1,000 liters of water each. Net pens were randomly suspended approximately 1 m below the water from either side of a dock located on the north side of Scenic Bay. Eleven zooplankton-impervious treatment pens were constructed of 153 μm mesh net, while four pens were made of 1,590 μm (1/16th inch) mesh, allowing ambient drift of zooplankton from the lake into the pens. I estimated the mean beginning dry weight of individual larval kokanee at 15.48 mg (n=36; SE=0.90 mg) by drying kokanee to a constant weight in an 80° C oven, and weighing them to the nearest 0.0001 g.

I designed four treatment levels for this experiment, corresponding to "HIGH", "AMBIENT", "LOW", and "VERY LOW" zooplankton densities (Figure 4.1). The zooplankton impervious pens used for "HIGH", "LOW", and "VERY LOW" treatments were stocked with zooplankton collected with vertical tows using a 20 cm diameter Wisconsin-style plankton net. Four replicate pens of the "HIGH" treatment group contained higher than

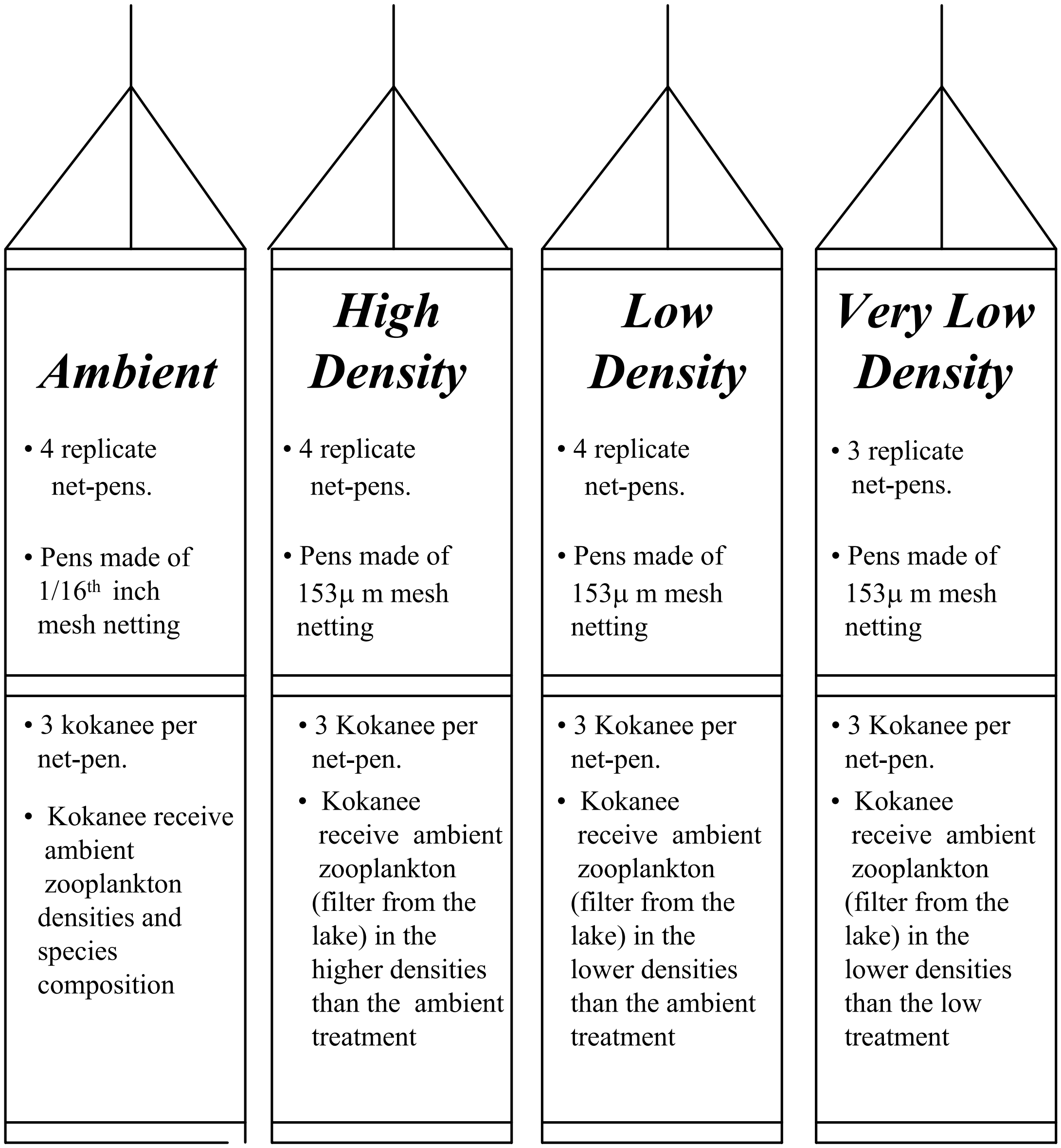


Figure 4.1. Schematic of experimental design showing four treatment groups (i.e. AMBIENT, HIGH, LOW, VERY LOW) used in kokanee growth experiments conducted in June and October, 1998 in Lake Pend Oreille, Idaho.

ambient zooplankton densities, four replicates of the “LOW” treatment group contained lower than ambient zooplankton densities, while three “VERY LOW” replicate pens contained the lowest zooplankton densities.

Target zooplankton densities within each treatment pen were maintained and confirmed approximately twice a week by zooplankton sampling. One 44 L sample was collected in each pen by first raising the top of the net pen slightly above the surface, opening the zippered access, then lowering the Wisconsin-style plankton net 140 cm to the pen bottom, and hauling the net to the surface. Samples were preserved in 70 % ethyl alcohol, and soon thereafter the contents were identified and enumerated under a dissecting microscope. Adjustments to zooplankton densities in individual net pens were made within 24 hours after sampling. To reduce algae growth on the outside of net pens, each pen was cleaned every 3-4 days with a pressure sprayer.

Larval kokanee in the ambient treatment pens could potentially graze down zooplankton densities faster than they could be replenished. I therefore compared zooplankton densities within AMBIENT treatment pens to densities outside the pens on the last three sampling dates of the June experiment and on all sampling dates of the October experiment, by taking one sample from each side of the dock, collected within 2 m of ambient pens, with a 140 cm vertical tow of the plankton net. I tested for differences in mean zooplankton densities between the ambient treatment group and samples taken from outside the net pens using a Kruskal Wallis ranked ANOVA (SAS Institute, Version 6.11).

After 21 days , all kokanee were removed and preserved in 10 % formalin. In the lab, fish were measured for total length, dried, and weighed. Instantaneous growth rate (G) and Fulton condition factor (K) were calculated for each fish using the following equations:

$$G = \ln W_1 - \ln W_0 / (t_1 - t_2) \qquad (1)$$

where: W_1 = the ending weight,

W_o = the beginning weight and,

$(t_1 - t_2)$ = the elapsed time of the experiment (Van Den Avyle 1993).

$$K = (W/L^3) \times 10^5 \qquad (2)$$

where: W = weight (grams) and,

L = total length (millimeters; Anderson and Neumann 1996).

The October experiment, initiated on October 10th, was conducted in a similar manner as the June experiment with the following exceptions. Kokanee for the October experiment were age-0 fish originally obtained from the Cabinet Gorge Hatchery in June, but not used in the spring experiment (Mean dry weight=305.02 mg, SE=13.38). Net pens suspended from a Navy barge anchored near the mouth of Scenic Bay were used to hold these fish until the initiation of the October experiment. These fish were assumed to be representative of wild age-0 kokanee in the lake. The four treatment groups employed in June were unchanged, except I used two net pens for the “VERY LOW” treatment group.

For each experiment, I used a Kruskal Wallis ranked ANOVA to test for differences in growth among treatments (SAS institute, version 6.11). When appropriate, I performed post hoc pair-wise comparisons using Fisher’s Least Significant Difference.

Results

During the June experiment, I visually confirmed two dead kokanee on June 10, one each from a HIGH and AMBIENT density treatment pen. Also on June 10, I located only two live kokanee from a high density treatment pen, although one dead fish could not be found. Thereafter, each pen was maintained with two kokanee. One kokanee perished from a HIGH density treatment pen early during the October experiment, and was replaced with a fish from a “holdover” group maintained in a net pen at the dock. Surface water temperatures in Scenic

Bay were 10.5°C when the June experiments began, and 16°C at their conclusion. Water temperatures in Scenic Bay in October were not recorded, however surface temperatures in the main lake were 15°C on October 10th and 11.5°C on October 31st.

June Experiment

The mean kokanee dry weight at the beginning of growth studies in June was 0.0154 g, and the mean ending dry weights for individual treatment pens ranged from 0.0216 g for a VERY LOW treatment to 0.0789 g for a HIGH treatment pen (Table 4.1). Mean total kokanee biomass increased with increasing zooplankton densities, with the highest growth occurring in the HIGH treatment group (Figure 4.2). Final mean kokanee dry weights were significantly different among treatment groups ($F=19.09$, $p>0.0001$), but no significant differences were identified between HIGH and AMBIENT treatments ($F=3.44$, $p>0.1130$) or between LOW and VERY LOW treatments ($F=2.50$, $p>0.1747$).

In the June experiments mean instantaneous growth rates for age-0 kokanee ranged from 1.53 to $7.72\%\cdot\text{day}^{-1}$, and condition factor varied from 0.58 to 0.92 (Table 4.1). Mean instantaneous growth and condition factor both increased with increasing zooplankton densities, although the highest observed mean condition factor was in an AMBIENT zooplankton density net pen (0.92). Instantaneous growth positively corresponded to condition factor ($r=0.84$, $p=0.0002$, Figure 4.3). The densities of food resources available to kokanee in the HIGH treatment were higher than in the AMBIENT treatment, but mean

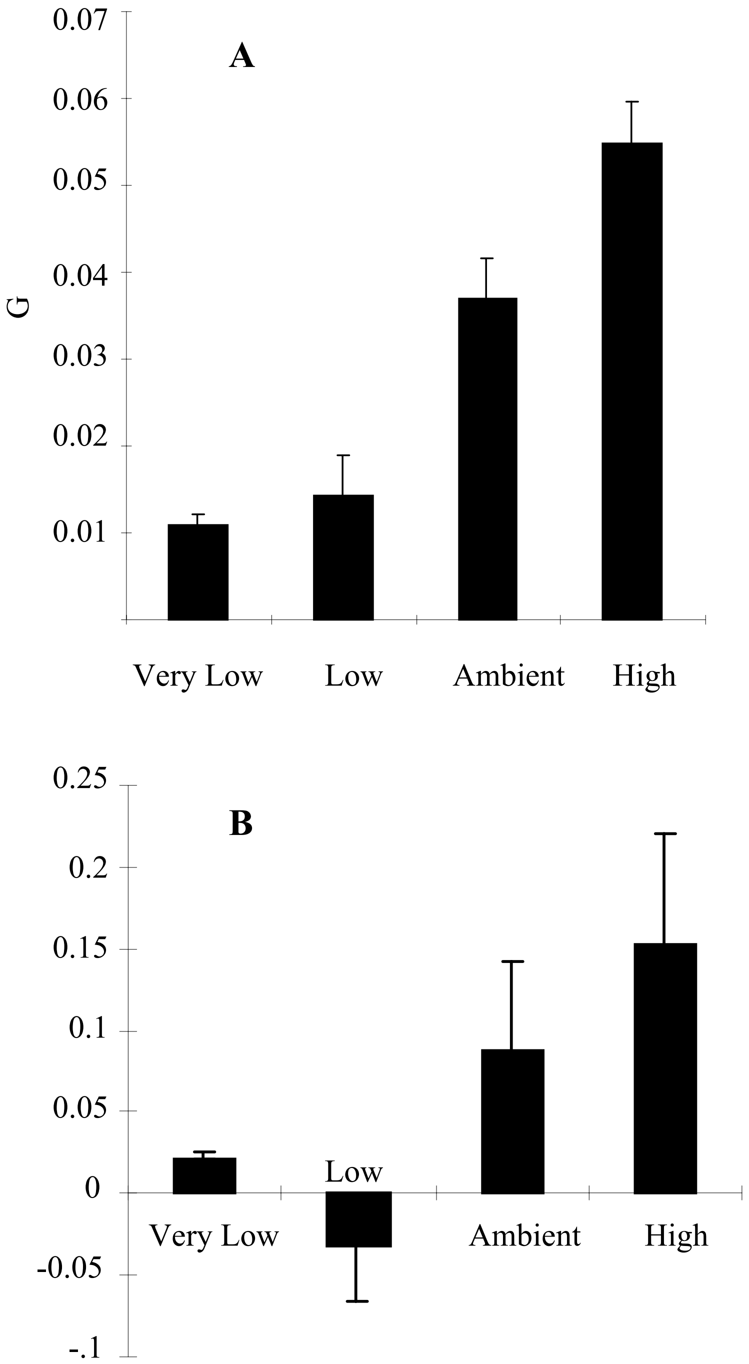


Figure 4.2. Mean increase in kokanee biomass (grams dry weight) by treatment for June (A) and October (B) net pen experiments conducted in Lake Pend Oreille, 1998. Vertical bars represent 2 SE.

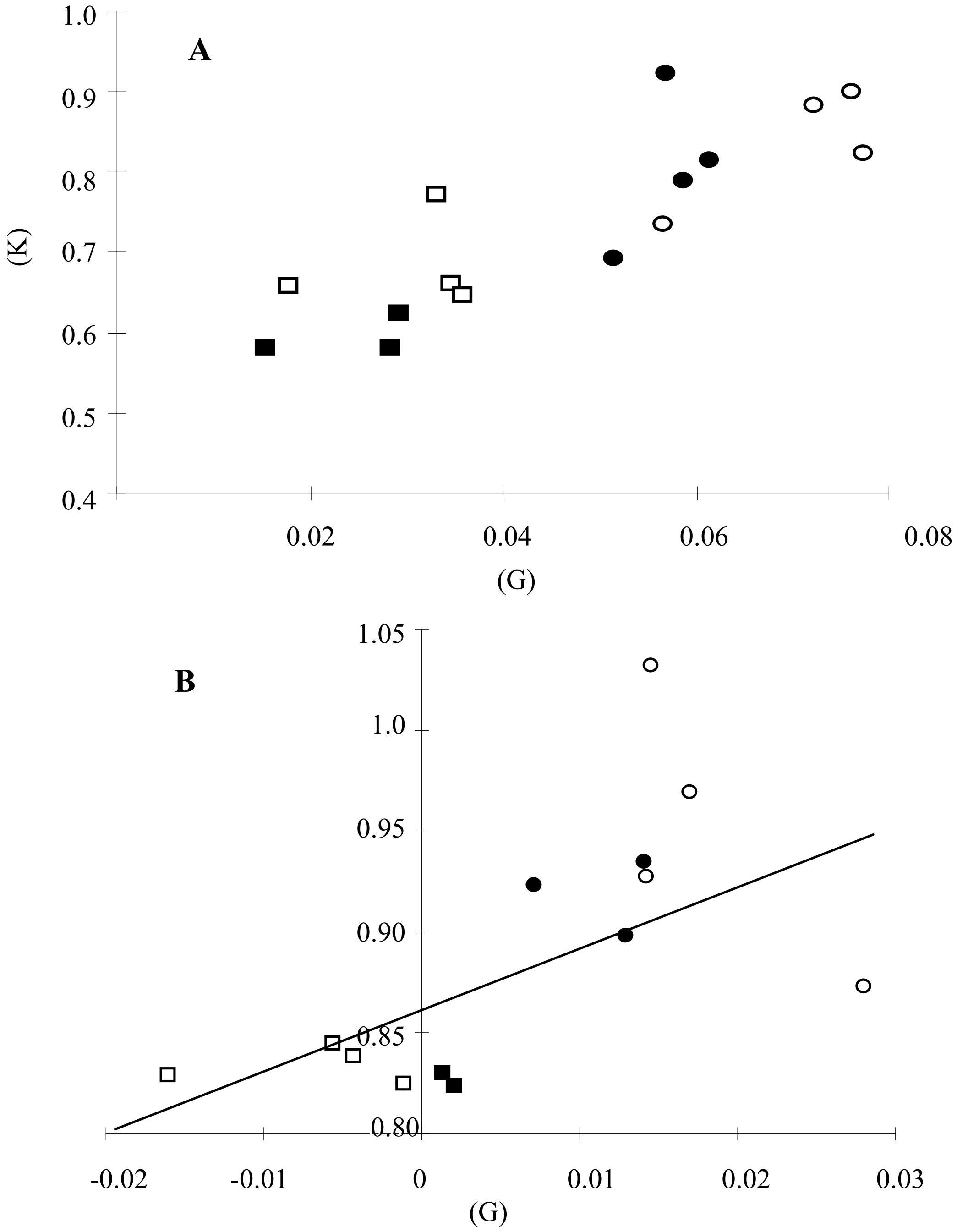


Figure 4.3. Relationship between condition factor (K) and instantaneous growth (G) from June (A) and October (B) experiments in Lake Pend Oreille, 1998. Treatment groups are represented as follows: Solid square is VERY LOW, open square is LOW, solid circle is AMBIENT, open circle is HIGH.

Table 4.1. Mean final biomass (grams dry weight) and standard error (SE), instantaneous growth rate (G), and ending condition factor (K) for age-0 kokanee used in June *in situ* growth experiments. n represents the concluding number of fish in a treatment net pen.

Treatment Pen	n	Mean Final Biomass (g) ± (SE)	G^a	K
VERY LOW 13		.0284 ± (.0102)	2.82	0.58
VERY LOW 23		.0292 ± (.0042)	2.92	0.62
VERY LOW 33		.0216 ± (.0025)	1.53	0.58
LOW 1	3	.0321 ± (.0006)	3.47	0.66
LOW 2	3	.0225 ± (.0006)	1.78	0.66
LOW 3	3	.0329 ± (.0014)	3.58	0.65
LOW 4	3	.0313 ± (.0024)	3.32	0.77
AMBIENT 1	3	.0577 ± (.0092)	6.13	0.82
AMBIENT 2	3	.0460 ± (.0040)	5.13	0.69
AMBIENT 3	3	.0531 ± (.0018)	5.86	0.79
AMBIENT 4	2	.0532 ± (.0150)	5.68	0.92
HIGH 1	2	.0706 ± (.0025)	7.22	0.88
HIGH 2	3	.0530 ± (.0108)	5.65	0.74
HIGH 3	2	.0789 ± (.0102)	7.72	0.82
HIGH 4	3	.0788 ± (.0132)	7.62	0.90

[a] Expressed as % change in body weight·day^{-1}.

instantaneous growth in the AMBIENT treatment (5.7%·day^{-1}) was nearly that of fish in the HIGH treatment (7.0%·day^{-1}; Figure 4.4). Mean instantaneous growth of kokanee in LOW and VERY LOW treatments was similar (3.0%·day^{-1} and 2.4%·day^{-1} respectively).

Mean zooplankton densities in the HIGH treatment pens were generally higher than in the AMBIENT treatment, except for the June 10th sampling date (Figure 4.5). The AMBIENT treatment had higher mean zooplankton densities than the LOW and VERY LOW treatments for each sampling date except the first date (June 4), when densities were approximately equal among the three treatments. The LOW treatment had higher zooplankton densities than the VERY LOW treatment on June 4th and 14th. No statistically significant difference in mean zooplankton densities existed between the AMBIENT treatment and samples taken from outside the net pens (F=2.10, $p>0.1665$), although zooplankton densities were consistently higher outside the net pens than within AMBIENT pens.

October Experiment

The mean beginning kokanee dry weight for the October experiment was 0.3050 g and the mean ending dry weights for individual treatment pens ranged from 0.2192 g for a LOW treatment to 0.5530 g for a HIGH treatment pen (Table 4.2). Mean total kokanee biomass increased with increasing zooplankton densities, except for the LOW treatment, which had a mean decline in overall kokanee biomass (Figure 4.2). Final mean kokanee dry weights were significantly different among all treatment groups (F=16.4, $p>0.0009$), but no significant differences were identified between HIGH and AMBIENT treatments (F=0.83, $p>0.4144$) or between AMBIENT and VERY LOW treatments (F=8.0, $p>0.1056$).

Mean Instantaneous growth rates for age-0 kokanee in October ranged from -1.61 to 2.79%$\cdot$day^{-1} and condition factor varied from 0.82 to 1.03 (Table 4.2). The highest observed mean condition factor (K=1.03) and instantaneous growth rate (2.79%$\cdot$day^{-1}) were in HIGH treatment pens. The lowest condition factors were in both the LOW and VERY LOW treatments and the lowest instantaneous growth rates were observed in LOW treatment pens, despite the LOW treatments having higher zooplankton densities than the VERY LOW treatments (Table 4.2, Figure 4.6). Increases in instantaneous growth corresponded to increases in condition factor ($r=0.65$, $p=0.0169$, Figure 4.3). Zooplankton densities within

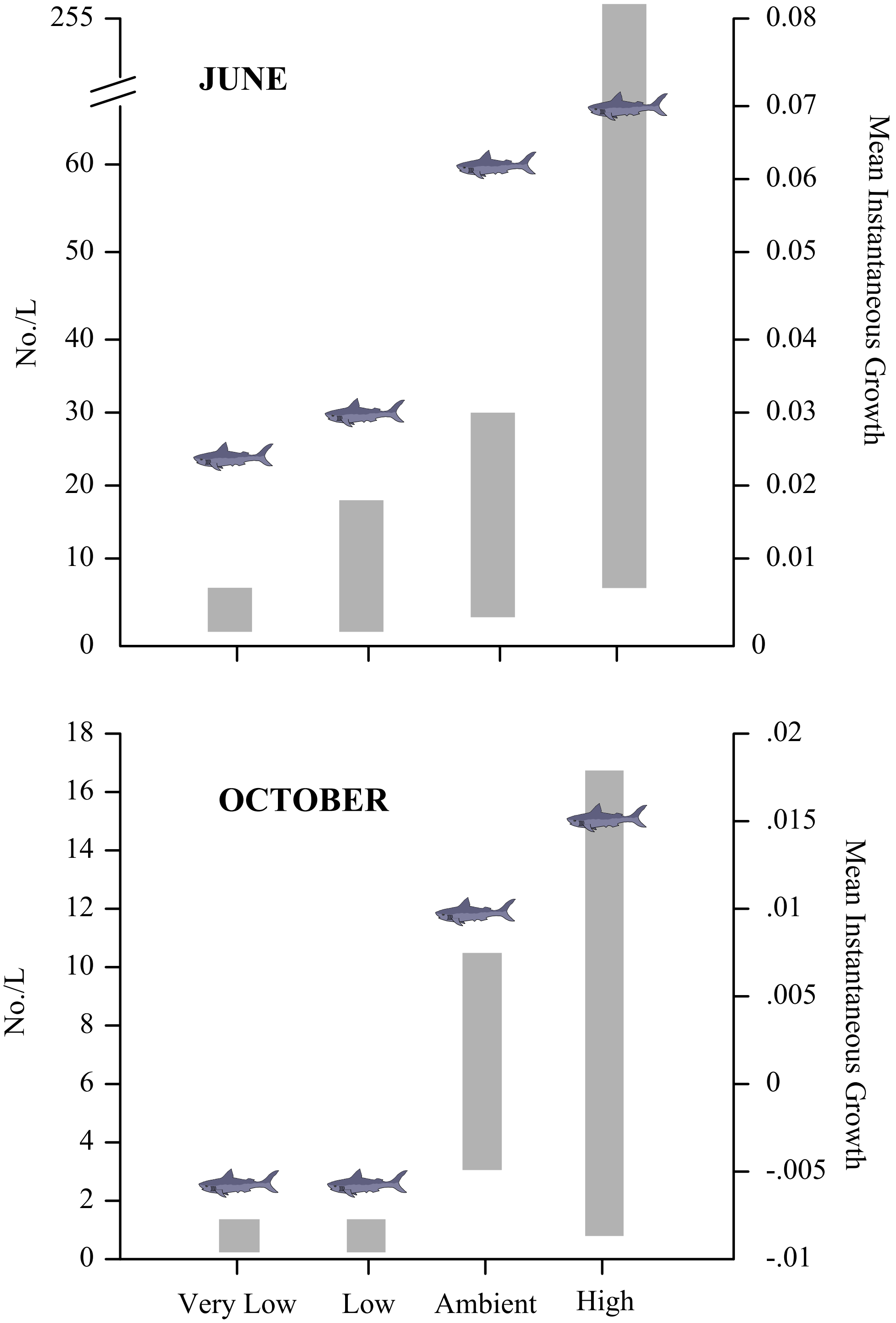


Figure 4.4. Relationship between the range of mean zooplankton densities by treatment group (indicated by solid bars) and mean instantaneous growth by treatment group (indicated by 🐟) for juvenile kokanee experiments conducted in Lake Pend Oreille in June and October, 1998.

HIGH treatment pens were sometimes lower than in AMBIENT pens. Despite a wider range of food resources (e.g. zooplankton densities), mean instantaneous growth for kokanee in the HIGH treatment pens(1.84%·day^{-1}) were higher than those in the AMBIENT treatment pens (0.83%·day^{-1}; Figure 4.4)

Age-0 kokanee in the October experiment quickly grazed down zooplankton densities within treatment pens, causing HIGH density treatments to have lower zooplankton levels than AMBIENT treatments on two sampling dates (Figure 4.6). On each sampling date, AMBIENT zooplankton densities were higher than LOW zooplankton densities, and the VERY LOW treatment had the lowest zooplankton densities. No statistically significant difference in mean zooplankton densities existed between the AMBIENT treatment and samples taken from outside the net pens (F=0.55, p>0.4760), although zooplankton densities were generally higher outside the net pens than within AMBIENT pens (Figure 4.6).

Discussion

This study demonstrated that growth of age-0 kokanee in Lake Pend Oreille can be influenced by food (e.g. zooplankton) densities. In laboratory studies Brett et al. (1969) found growth of fingerling sockeye salmon to be a function of both food rations and temperature. In each treatment group in these studies, except the LOW treatment in the October experiment, kokanee growth fluctuated directly with levels of zooplankton densities. Differences in kokanee growth rates (i.e. % change in body weight·day^{-1}) were smallest between the LOW and VERY LOW treatments and the HIGH and AMBIENT treatments, and were highest between the LOW and AMBIENT treatments for both experiments, suggesting that a

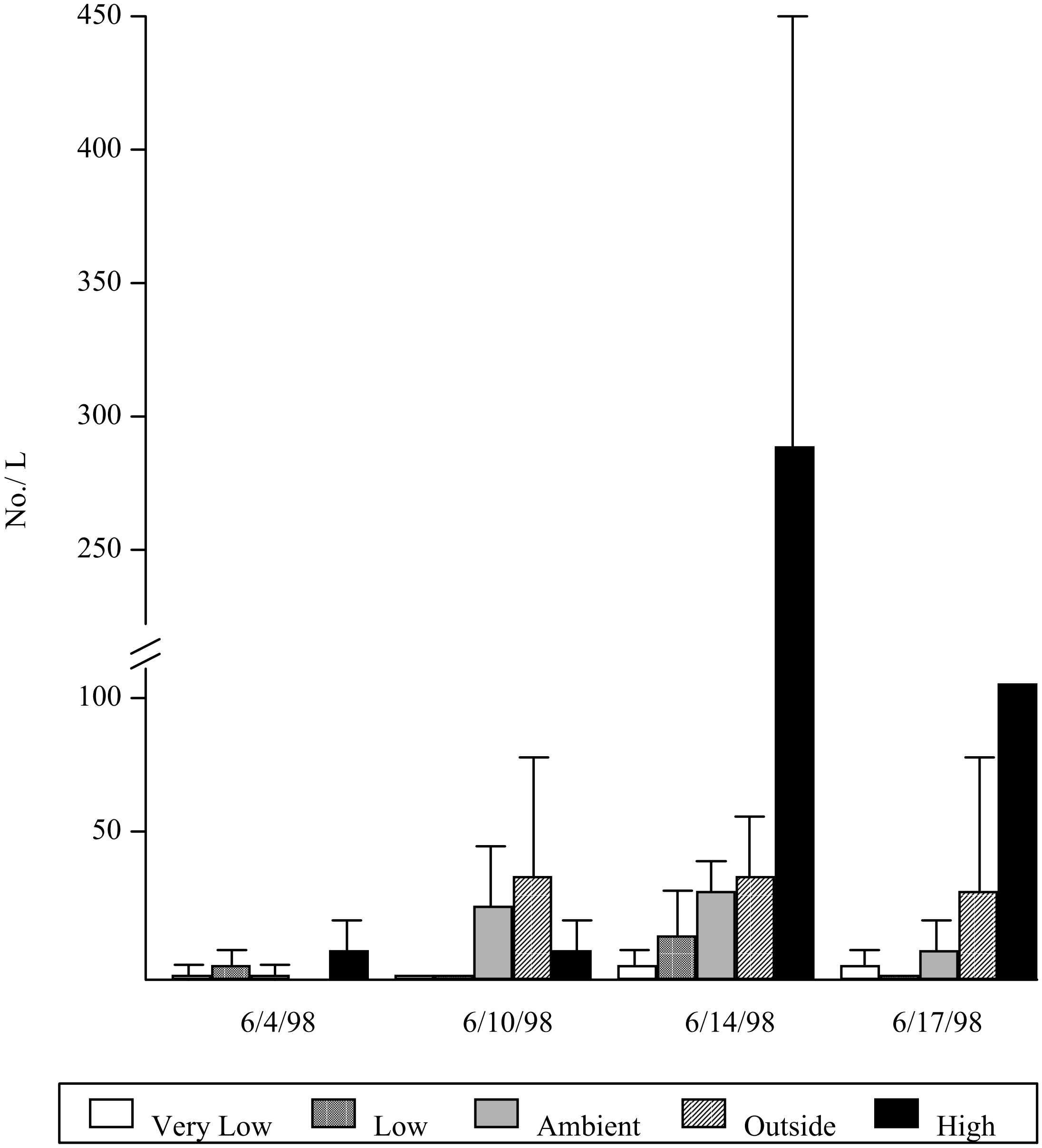


Figure 4.5. Total zooplankton per liter by treatment group for June 1998 net pen experiments conducted on age-0 kokanee in Lake Pend Oreille. Vertical bars represent 2 SE. Standard error for HIGH treatment on 6/17 is 47.4.

Table 4.2. Mean final biomass (grams dry weight) and standard error (SE), instantaneous growth rate (G), and ending condition factor (K) for age-0 kokanee used in October *in situ* growth experiments. n represents the concluding number of fish in a treatment net pen.

Treatment Pen	n	Mean Final Biomass (g) ± (SE)	G[a]	K
VERY LOW 13		0.3235 ± (.0368)	0.21	0.82
VERY LOW 23		0.3185 ± (.0383)	0.13	0.83
LOW 1	3	0.3009 ± (.0329)	-0.12	0.83
LOW 2	3	0.2784 ± (.0478)	-0.57	0.84
LOW 3	2	0.2192 ± (.0284)	-1.61	0.83
LOW 4	3	0.2803 ± (.0251)	-0.44	0.84
AMBIENT 1	3	0.3091 ± (.0548)	-0.11	0.83
AMBIENT 2	3	0.4158 ± (.0452)	1.41	0.93
AMBIENT 3	3	0.4005 ± (.0177)	1.29	0.90
AMBIENT 4	3	0.3608 ± (.0517)	0.71	0.92
HIGH 1	3	0.4365 ± (.0109)	1.70	0.97
HIGH 2	3	0.4116 ± (.0151)	1.42	0.93
HIGH 3	3	0.4139 ± (.0030)	1.45	1.03
HIGH 4	3	0.5530 ± (.0570)	2.79	0.87

[a] Expressed as % change in body weight·day^{-1}.

threshold of food densities existed for kokanee in my experiments. At food densities below the threshold, kokanee growth rates quickly declined with decreasing food, whereas increases in growth rates slowed at increasing food densities above the threshold. Although zooplankton density differences between treatment groups were generally maintained in these experiments, zooplankton densities within treatment groups did fluctuate. In addition, water temperatures either increased (June experiment) or decreased (October experiment) throughout the experiments. Betsill and Van Den Ayle (1997) suggest that the effect of temperatures can mask prey effects. Also, bio-energetics modeling on sockeye salmon *O. nerka* demonstrates the sensitivity of sockeye growth to temperature changes (Beauchamp et al. 1989). Consequently, I cannot estimate the zooplankton density that resulted in growth thresholds observed in these two experiments. However, the growth trends I describe are consistent with relationships exhibited between *Cyclops* biomass and larval kokanee growth in earlier net pen experiments at Lake Pend Oreille (Rieman 1981). In addition, research on other larval fishes suggests the existence of a growth threshold at high zooplankton densities (Betsill and Van Den Avyle 1997).

Three kokanee deaths were confirmed during the June and October experiments combined, and those deaths occurred in HIGH and AMBIENT treatment pens. I therefore conclude that starvation was likely not a cause of mortality in these experiments. If the performance of kokanee fry in these experiment were indicative of wild fry, then starvation from June-October was not a major source of mortality for the 1998 kokanee cohort in Lake Pend Oreille.

Lake levels declined several meters at Lake Pend Oreille throughout October 1998. Consequently, two AMBIENT treatment pens, positioned closest to shoreline on either side of the dock by random selection, and suspended in approximately 3 m deep water at the experiments' initiation, were lying on the lake bottom when the experiment ended. Benthic organisms that are not normally utilized as prey by the pelagic wild kokanee of Lake Pend Oreille were therefore available to kokanee in those pens. For that reason, I excluded the kokanee from these pens from analysis.

Mean instantaneous growth rates of kokanee fry fed ambient zooplankton densities in the June experiment ($5.7\%\cdot\text{day}^{-1}$) were slightly higher than the highest rates observed by

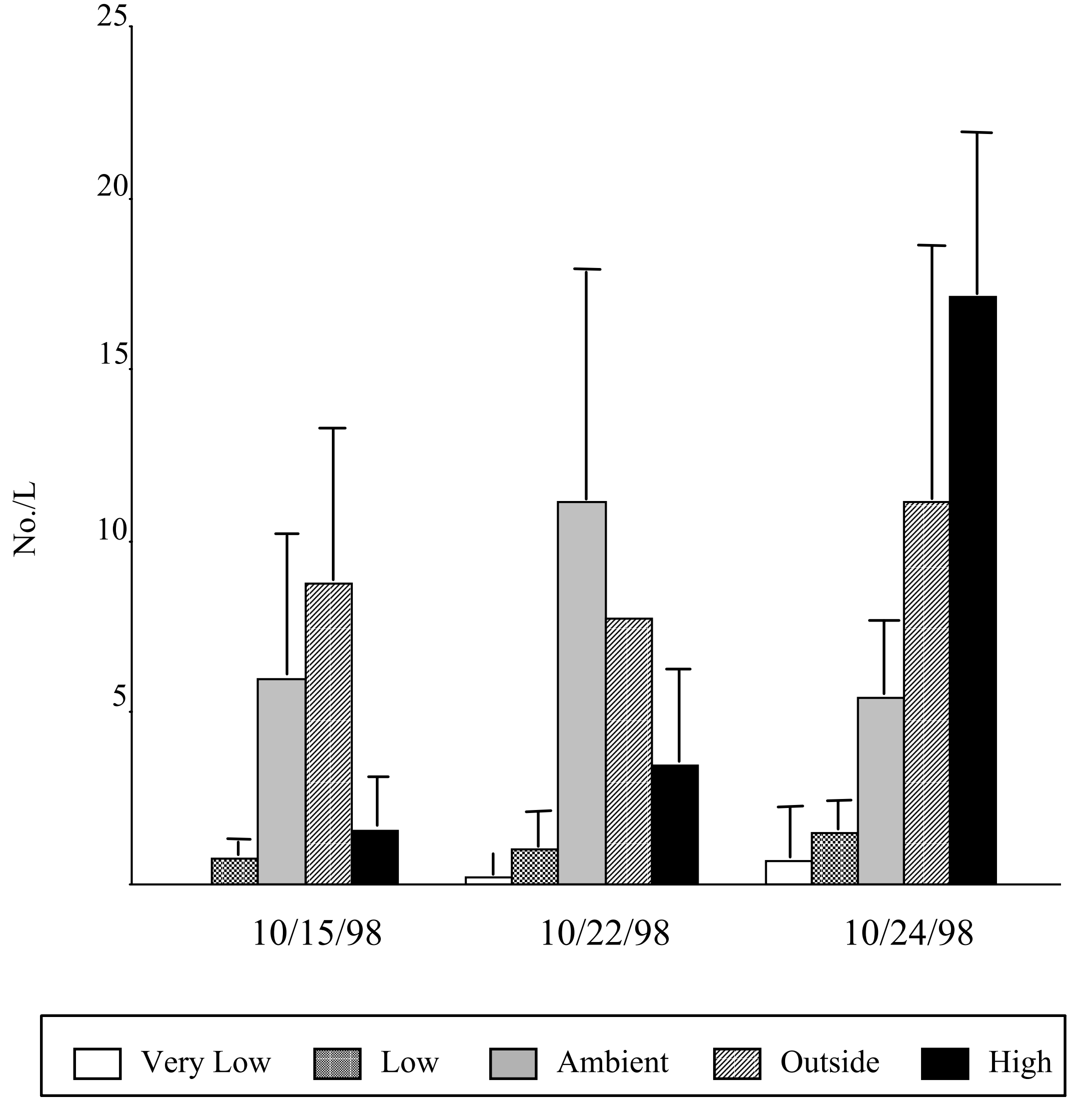


Figure 4.6. Total zooplankton per liter by treatment group for October 1998 net pen experiments conducted on age-0 kokanee in Lake Pend Oreille. Vertical bars represent 2 SE.

Rieman ($5.1\%\cdot\text{day}^{-1}$; 1981) for a similar set of experiments conducted on newly emerged kokanee fry at Lake Pend Oreille from April-July, 1980. Comparisons of temperature profiles and zooplankton density estimates in Lake Pend Oreille for both years suggest that June, 1998 was warmer and had higher zooplankton abundance than June, 1980. Thus, the higher growth rates observed in this study are not surprising. In addition, Rieman (1981) measured positive growth from kokanee fry exposed to zooplankton biomass as low as 2 mg (dry weight)$\cdot\text{m}^{-3}$. Positive kokanee growth was also measured at the lowest zooplankton biomass in the June experiment, which I estimated between about 2-8 $\text{mg}\cdot\text{m}^{-3}$ over the 21-day experiment for the VERY LOW treatment group.

Growth rates for kokanee receiving ambient food densities in these experiments may not represent growth rates of wild fish. Indeed, the consistently lower zooplankton density measurements inside AMBIENT treatment pens versus outside the pens suggests the possibility that treatment fish received less food than wild fish. Rieman (1981) also measured consistently higher zooplankton densities outside net pens than inside kokanee holding pens. However, Rieman (1981) experimented with densities of 0 $\text{kokanee}\cdot\text{net pen}^{-1}$ and 50 $\text{kokanee}\cdot\text{net pen}^{-1}$ and found the same relationship between zooplankton densities outside the pens versus inside the pens, leading him to conclude that zooplankton density differences were due to net pen clogging with algae, rather than grazing by kokanee. If kokanee in AMBIENT treatments pens in my study received the same food rations as wild fish, then growth of treatment fish should also be similar to wild fish. However, other *in situ* growth studies with juvenile salmonids have shown growth rates for confined fish equal to, or greater than, their free-roaming counterparts (Lebrasseur 1969; English 1983; Johnston 1990). In this study, net pens were not long enough to allow vertical migration by kokanee, nor did they force kokanee to expend energy searching for prey.

Restrictions of these two metabolic activities probably resulted in higher growth by kokanee in these experiments than would be observed from kokanee encountering similar prey densities in the wild.

Results from experiments conducted at Kootenay Lake, British Columbia by Johnston (1990) could aid in estimating the growth rates of wild kokanee fry in Lake Pend Oreille, using measured growth rates from AMBIENT treatment fish. At Kootenay Lake, newly emerged kokanee were confined in small net pens in the epilimnion, and instantaneous growth rates of confined fry were compared to those of wild fry. Growth rates for fry confined from May-October were approximately 20% higher than those of wild fish. By applying a 20% correction to the growth rates measured in my experiment, I estimate instantaneous growth rates of wild fry in Lake Pend Oreille in June could be 4.1-4.9%$\cdot$day^{-1} and in October could be -0.009-0.01%$\cdot$day^{-1}.

Observed kokanee growth rates in HIGH treatment pens in the June experiments probably represent the maximum possible growth by kokanee fry given excess food rations consisting mostly of *Cyclops* (the most abundant zooplankter in June zooplankton samples and in the diet of wild kokanee fry, Objectives 1 and 2) , and given the specific water temperatures present in June and October. However, growth in the HIGH treatments pens in October might be lower than the maximum. More effective grazing by the larger kokanee in the October experiments made it difficult to maintain targeted zooplankton densities in HIGH treatment pens. Therefore, kokanee growth could have been higher if a consistently higher ratio of food density to kokanee density had been achieved over the 21 day October experiment.

A paradigm exists in fisheries which states that the strength of a cohort is often directly related to survival rates of post-emergent fry (Wootton 1990; Van Den Avyle 1993).

Studies have clearly demonstrated direct relationships between fry survival and year-class strength (Le Cren 1987). Furthermore, relationships between fry survival and the timing of production of suitable prey (i.e. zooplankton) also have been demonstrated (Cushing 1995). In Lake Pend Oreille, kokanee fry emergence initiates in May, peaks in June, and diminishes in July (Rieman and Bowler 1980). Historically, the timing of increases in zooplankton abundance at Lake Pend Oreille corresponded closely with kokanee emergence (Stross 1954). However, since the introduction of omnivorous *Mysis relicta* to the lake, spring zooplankton densities have been reduced, prompting speculation that low zooplankton densities may retard growth of kokanee fry (Hassemer 1984). Based on my zooplankton abundance estimates (Objective 1) and results presented here, I believe that zooplankton densities in Lake Pend Oreille probably did not limit survival or growth of newly emerged kokanee in June 1998. Also, based on the results of my October experiment, I conclude that growth by wild kokanee did occur in October, but growth was slower than in June. If these *in-situ* studies are accurate predictors of kokanee fry survival, then survival should be strong for that portion of the 1998 kokanee cohort to emerge in June-July. Furthermore, continued application of kokanee fry *in-situ* growth studies in future years, similar to those conducted by Rieman (1981) and myself, combined with adequate wild kokanee population estimates, may show relationships between kokanee growth and year class strength that could aid fisheries managers in predicting cohort abundance as adults.

Summary

1. I investigated the growth and survival of newly emerged kokanee in June, and age-0 kokanee in October, by conducting in-situ net-pen experiments in Lake Pend Oreille in 1998. I had four treatment levels for these experiments, corresponding to “HIGH”, “AMBIENT”, “LOW”, and “VERY LOW” zooplankton densities
2. Starvation was not a source of mortality in either experiment, suggesting that the 1998 kokanee cohort in Lake Pend Oreille would not die of starvation from June-October.
3. With the exception of a treatment group in October, kokanee growth increased with increasing food resources in both experiments. Differences in kokanee growth were smallest between kokanee fed low zooplankton densities (e.g. the LOW treatment) and kokanee fed very low zooplankton densities (e.g. the VERY LOW treatment) and also between kokanee fed ambient zooplankton densities (e.g. the AMBIENT treatment) and those fed high zooplankton densities (e.g. the HIGH treatment). Growth differences were highest between the LOW and AMBIENT treatments for both experiments. My results suggest that food availability did not limit the growth of wild kokanee in June or October, 1998.
4. Continued application of *in-situ* kokanee growth studies, similar to those conducted by Rieman (1981) and myself, combined with wild kokanee population estimates, may show relationships between kokanee growth and year-class strength. Such relationships could be useful in predicting cohort strength as adults.

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Appendix Table 2.1. Estimates of zooplankton densities (No./L) and biomass (mg live weight / m3) for sampling locations in Lake Pend Oreille, Idaho, 1997-1998.

Date and		*Cyclops*		*Diaptomus*		*Epischura*		Nauplii		Total Copepods	
Location	N	No./L	%Total	No./L	%Total	No./L	%Total	No./L	%Total	No./L	Biomass/m3
June 20-22, 1997											
Scenic Bay	9	4.11	72.71	0.00	0.00	0.00	0.00	1.53	27.14	5.64	79.99
Idlewilde Bay	9	2.56	50.71	2.11	42.00	0.06	1.10	0.29	5.73	5.02	115.45
Garfield Bay	9	3.94	75.42	0.89	17.00	0.00	0.00	0.30	5.74	3.07	94.63
Ellisport Bay	9	2.74	5.55	0.39	0.80	0.00	0.00	0.18	0.36	3.32	63.49
Lake Site south	9	2.99	12.08	19.60	79.22	0.03	0.13	2.12	8.58	24.74	882.38
June 27-28, 1997											
Scenic Bay	12	8.13	72.40	2.42	21.52	0.04	0.37	0.55	4.90	11.14	620.16
Idlewilde Bay	11	3.05	63.10	1.59	32.95	0.00	0.00	0.13	2.76	4.78	102.64
Garfield Bay	12	3.06	66.97	0.76	16.59	0.03	0.55	0.53	11.67	4.38	84.87
Ellisport Bay	12	5.91	54.58	0.82	7.54	0.02	0.15	1.36	12.55	2.73	1 82.61
Lake Site south	9	0.43	6.24	6.06	87.17	0.09	1.32	0.33	4.68	14.35	278.96
July 2-3, 1997											
Scenic Bay	12	13.49	70.99	3.92	20.63	0.00	0.00	1.48	7.77	18.89	364.64
Idlewilde Bay	12	12.81	77.30	1.60	9.66	0.01	0.05	2.10	12.67	16.51	294.89
Garfield Bay	12	9.19	78.90	1.46	12.52	0.00	0.00	0.92	0.87	11.57	204.77
Ellisport Bay	11	14.89	78.92	1.14	6.03	0.03	0.15	1.29	6.83	17.34	321.17
Lake Site south	11	24.76	78.92	3.99	12.72	0.00	0.00	2.27	7.23	31.02	601.98
July 11-12, 1997											
Scenic Bay	12	21.08	56.98	13.17	35.62	0.00	0.00	2.62	7.08	36.87	754.25
Idlewilde Bay	12	32.40	53.74	25.36	42.06	0.00	0.00	2.30	3.81	60.06	1308.08
Garfield Bay	12	13.82	71.26	5.19	26.77	0.08	0.43	0.18	0.95	19.28	400.54
Ellisport Bay	12	8.26	76.61	1.68	15.62	0.04	0.39	0.13	1.16	10.11	211.47
Lake Site south	12	14.82	42.87	17.97	51.98	0.02	0.05	1.74	5.04	34.54	770.28
July 16-17, 1997											
Scenic Bay	12	29.11	66.02	13.90	31.54	0.02	0.05	0.42	0.96	43.46	932.05

Appendix Table 2.1. Cont.

Date and	*Daphnia*		*Bosmina*		*Diaphanasoma*		*Leptodora*		*Chydorus*		Total Cladoceran		Overall Total	
Location	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	Biomass[a]/m3	No./L	Biomass[a]/m3
June 20-22, 1997														
Scenic Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.15	0.01	0.11	5.65	80.10
Idlewilde Bay	0.00	0.00	0.01	0.22	0.00	0.00	0.00	0.00	0.01	0.22	0.02	0.26	5.04	115.45
Garfield Bay	0.00	0.00	0.08	1.49	0.00	0.00	0.00	0.00	0.02	0.42	0.10	1.22	5.23	94.63
Ellisport Bay	0.01	0.02	45.61	92.21	0.06	0.11	0.00	0.00	0.47	0.94	46.14	663.27	49.46	726.77
Lake Site south	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	24.74	882.38
June 27-28, 1997														
Scenic Bay	0.00	0.00	0.08	0.74	0.00	0.00	0.00	0.00	0.01	0.07	0.09	1.80	11.23	620.16
Idlewilde Bay	0.00	0.00	0.05	1.04	0.00	0.00	0.00	0.00	0.01	0.17	0.06	0.66	4.83	102.64
Garfield Bay	0.02	0.36	0.13	2.92	0.02	0.36	0.02	0.36	0.01	0.18	0.19	6.65	4.57	84.87
Ellisport Bay	0.05	0.46	2.57	23.71	0.03	0.23	0.01	0.08	0.08	0.69	2.73	43.93	10.83	182.61
Lake Site south	0.01	0.12	0.02	0.24	0.01	0.12	0.01	0.12	0.00	0.00	0.04	2.82	6.95	278.78
July 2-3, 1997														
Scenic Bay	0.00	0.00	0.04	0.20	0.00	0.00	0.03	0.18	0.04	0.23	0.07	8.13	19.01	372.78
Idlewilde Bay	0.00	0.00	0.04	0.25	0.00	0.00	0.00	0.00	0.02	0.10	0.06	0.81	16.57	295.70
Garfield Bay	0.00	0.00	0.07	0.57	0.00	0.00	0.01	0.07	0.01	0.07	0.08	2.78	11.65	207.55
Ellisport Bay	0.02	0.11	1.23	6.49	0.02	0.11	0.01	0.07	0.24	1.28	1.52	25.69	18.86	346.85
Lake Site south	0.33	1.06	0.00	0.00	0.00	0.00	0.01	0.03	0.01	0.03	0.34	16.62	31.37	618.61
July 11-12, 1997														
Scenic Bay	0.03	0.08	0.04	0.12	0.02	0.06	0.00	0.00	0.03	0.08	0.12	3.56	36.99	757.81
Idlewilde Bay	0.04	0.07	0.19	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.23	4.87	60.29	312.95
Garfield Bay	0.02	0.09	0.08	0.43	0.00	0.00	0.00	0.00	0.02	0.09	0.12	1.96	19.39	402.51
Ellisport Bay	0.04	0.39	0.60	5.57	0.00	0.00	0.03	0.23	0.01	0.08	0.68	16.58	10.78	228.05
Lake Site south	0.01	0.02	0.01	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.61	34.56	770.89
July 16-17, 1997														
Scenic Bay	0.02	0.04	0.52	1.20	0.04	0.09	0.00	0.00	0.05	0.11	0.63	10.97	44.09	943.02
Idlewilde Bay	0.00	0.00	0.25	0.86	0.02	0.06	0.00	0.00	0.03	0.09	0.29	4.73	29.05	617.20

Appendix Table 2.1. Cont.

Date and Location	N	*Cyclops* #/L	%Total	*Diaptomus* #/L	%Total	*Epischura* #/L	%Total	Nauplii #/L	%Total	Total Copepods #/L	Biomass/m3
July 16-17, 1997 Cont.											
Idlewilde Bay	12	20.23	69.62	8.11	27.91	0.01	0.03	0.42	1.43	28.76	612.47
Garfield Bay	12	20.78	84.11	3.29	13.32	0.03	0.10	0.32	1.28	24.42	466.43
Ellisport Bay	12	12.66	82.90	0.81	5.29	0.03	0.16	0.28	1.80	13.77	268.47
Lake Site south	12	37.29	61.25	22.53	37.00	0.01	0.01	0.98	1.60	60.80	1329.49
July 23, 1997											
Scenic Bay	12	10.04	53.48	6.99	37.21	0.02	0.09	0.70	3.73	17.75	380.61
Idlewilde Bay	11	5.50	57.51	3.54	36.96	0.00	0.00	0.37	3.83	9.41	201.74
Garfield Bay	12	6.80	53.86	3.43	27.19	0.00	0.00	0.50	3.96	10.73	214.00
Ellisport Bay	12	7.11	63.61	1.78	15.96	0.01	0.07	0.92	8.20	9.82	187.15
Lake Site south	12	16.68	46.87	17.63	49.54	0.01	0.02	0.94	2.65	35.25	796.02
July 30-31, 1997											
Scenic Bay	12	12.83	44.79	12.99	45.35	0.01	0.04	0.78	2.74	26.61	590.88
Idlewilde Bay	12	27.94	48.42	25.15	43.58	0.03	0.06	1.08	1.88	54.21	1220.37
Garfield Bay	12	11.77	52.18	5.79	25.68	0.03	0.15	0.81	3.58	18.40	362.64
Ellisport Bay	12	9.63	63.25	2.50	16.41	0.77	5.03	0.64	4.21	13.54	376.67
Lake Site north	12	20.85	44.29	24.03	51.05	0.01	0.02	0.87	1.84	45.76	1076.08
Lake Site south	12	30.13	54.73	23.27	42.26	0.02	0.03	0.22	0.39	53.63	1210.32
August 6-7, 1997											
Scenic Bay	12	9.81	37.54	8.52	32.59	0.01	0.04	1.21	4.61	19.54	612.15
Idlewilde Bay	12	10.10	42.78	9.06	38.37	0.01	0.04	0.87	3.67	20.03	531.06
Garfield Bay	12	12.02	43.78	6.23	22.71	0.02	0.09	1.03	3.76	19.31	456.23
Ellisport Bay	12	11.57	55.40	4.66	22.31	0.03	0.16	0.88	4.23	17.14	313.09
Lake Site north	12	11.80	53.47	8.53	38.63	0.14	0.64	0.78	3.51	21.24	568.65
Lake Site south	12	10.71	47.17	5.68	25.00	0.03	0.11	0.49	2.17	16.90	444.71
August 14-15, 1997											
Scenic Bay	12	8.70	50.53	4.82	27.98	0.02	0.10	0.53	3.10	14.07	416.52
Idlewilde Bay	12	10.79	51.27	4.46	21.18	0.04	0.20	0.48	2.26	15.77	373.09

Appendix Table 2.1. Cont.

Date and	*Daphnia*		*Bosmina*		*Diaphanasoma*		*Leptodora*		*Chydorus*		Total Cladoceran		Overall Total	
Location	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	Biomass^a/m3	No./L	Biomass^a/m3
July 16-17, 1997 Cont.														
Garfield Bay	0.02	0.07	0.22	0.88	0.04	0.17	0.00	0.00	0.02	0.07	0.29	5.92	24.71	472.34
Ellisport Bay	0.06	0.38	1.39	9.11	0.01	0.05	0.03	0.16	0.02	0.11	1.50	29.51	15.27	297.98
Lake Site south	0.04	0.07	0.01	0.01	0.00	0.00	0.00	0.00	0.03	0.05	0.08	2.70	60.88	1332.19
July 23, 1997														
Scenic Bay	0.02	0.12	0.71	3.76	0.03	0.18	0.00	0.00	0.27	1.42	1.03	16.31	18.78	396.92
Idlewilde Bay	0.00	0.00	0.15	1.57	0.01	0.09	0.00	0.00	0.00	0.00	0.16	2.56	9.57	204.30
Garfield Bay	0.03	0.26	1.66	13.14	0.16	1.25	0.03	0.26	0.01	0.07	1.89	39.20	12.63	253.21
Ellisport Bay	0.19	1.72	0.74	6.64	0.06	0.52	0.06	0.52	0.31	2.76	1.36	41.91	11.18	229.07
Lake Site south	0.03	0.07	0.22	0.61	0.07	0.19	0.01	0.02	0.01	0.02	0.33	9.61	35.58	805.63
July 30-31, 1997														
Scenic Bay	0.14	0.48	1.80	6.28	0.07	0.23	0.01	0.04	0.02	0.06	2.03	38.38	28.64	629.26
Idlewilde Bay	0.44	0.77	2.71	4.69	0.34	0.59	0.00	0.00	0.01	0.01	3.50	78.74	57.71	1299.11
Garfield Bay	0.27	1.18	3.73	16.52	0.09	0.41	0.03	0.15	0.03	0.15	4.15	186.58	22.55	548.92
Ellisport Bay	0.58	3.83	0.59	3.88	0.33	2.13	0.16	1.04	0.03	0.22	1.69	95.40	15.23	472.07
Lake Site north	0.18	0.37	1.02	2.16	0.09	0.19	0.03	0.07	0.00	0.00	1.13	33.02	47.08	1109.11
Lake Site south	0.03	0.06	1.22	2.21	0.16	0.29	0.00	0.00	0.02	0.03	1.43	27.27	55.06	1237.60
August 6-7, 1997														
Scenic Bay	1.23	4.70	4.98	19.05	0.36	1.38	0.00	0.00	0.02	0.09	6.59	162.58	26.13	774.73
Idlewilde Bay	0.77	3.25	2.71	11.47	0.08	0.35	0.00	0.00	0.02	0.07	3.58	88.43	23.61	619.49
Garfield Bay	0.91	3.31	6.99	25.47	0.23	0.82	0.02	0.06	0.00	0.00	8.14	153.51	27.45	609.75
Ellisport Bay	2.37	11.33	0.39	1.88	0.88	4.19	0.10	0.48	0.01	0.04	3.74	207.60	20.88	520.69
Lake Site north	0.26	1.17	0.35	1.59	0.17	0.76	0.04	0.19	0.01	0.04	0.83	39.03	22.07	608.68
Lake Site south	0.32	1.40	5.43	23.90	0.04	0.18	0.01	0.04	0.01	0.04	5.80	118.97	22.70	563.68
August 14-15, 1997														
Scenic Bay	0.53	3.10	2.55	14.81	0.07	0.39	0.00	0.00	0.00	0.00	3.15	79.00	17.22	487.53
Idlewilde Bay	1.13	5.34	3.95	18.76	0.20	0.95	0.00	0.00	0.01	0.04	5.28	133.18	21.05	506.27
Garfield Bay	2.18	7.00	1.10	3.54	0.46	1.48	0.02	0.05	0.03	0.11	3.78	164.80	31.07	766.30
Ellisport Bay	2.50	20.75	0.34	2.84	0.54	4.50	0.03	0.21	0.01	0.07	3.42	182.04	12.06	326.59

Appendix Table 2.1. Cont.

Date and		*Cyclops*		*Diaptomus*		*Epischura*		Nauplii		Total Copepods	
Location	N	#/L	%Total	#/L	%Total	#/L	%Total	#/L	%Total	#/L	Biomass/m3
August 14-15, 1997 Cont.											
Garfield Bay	12	19.25	61.96	6.73	21.67	0.02	0.05	1.28	4.13	27.29	601.49
Ellisport Bay	12	6.11	50.69	1.71	14.18	0.01	0.07	0.82	6.78	8.64	144.56
Lake Site north	12	10.94	56.30	6.08	31.26	0.00	0.00	0.67	3.43	17.68	434.85
Lake Site south	12	10.53	15.15	5.72	29.93	0.02	0.09	0.48	2.49	16.74	441.77
August 22-23, 1997											
Scenic Bay	12	5.50	33.32	2.58	15.62	0.06	0.34	1.16	7.00	9.29	248.99
Idlewilde Bay	12	5.29	20.05	4.78	18.09	0.08	0.28	1.34	5.08	11.48	290.87
Garfield Bay	12	9.54	51.67	2.50	13.54	0.10	0.54	1.13	6.14	13.28	280.62
Ellisport Bay	12	9.17	33.70	1.98	7.26	0.03	0.12	1.08	3.95	12.25	205.05
Lake Site north	12	7.48	43.42	2.16	12.52	0.03	0.19	1.15	6.67	10.83	223.98
Lake Site south	12	6.02	28.68	3.62	17.24	0.08	0.36	0.64	3.06	10.35	277.56
August 30, 1997											
Scenic Bay	12	3.40	18.95	4.33	24.12	0.09	0.50	1.04	5.79	1.13	289.93
Idlewilde Bay	12	2.66	22.11	2.18	18.09	0.05	0.42	1.10	9.15	5.98	139.65
Garfield Bay	12	5.01	26.37	2.93	15.45	0.10	0.53	1.98	10.40	10.02	217.81
Ellisport Bay	12	5.13	28.92	1.24	7.00	0.09	0.52	2.29	12.91	8.76	130.42
Lake Site north	12	7.53	32.48	3.72	16.04	0.05	0.22	1.29	5.58	12.58	289.03
Lake Site south	12	6.23	36.80	3.61	21.33	0.04	0.25	0.89	5.27	10.77	275.91
September 6, 1997											
Scenic Bay	12	2.14	23.53	1.90	20.90	0.16	1.71	1.28	14.06	5.47	142.38
Idlewilde Bay	12	2.62	22.00	3.06	25.72	0.04	0.35	0.68	5.75	6.40	181.39
Garfield Bay	12	6.35	26.47	2.57	10.70	0.05	0.21	1.63	6.77	10.59	209.70
Ellisport Bay	6	2.86	7.61	1.76	4.67	0.08	13.33	5.53	14.69	10.25	119.94
Lake Site north	12	6.66	25.78	3.38	13.07	0.04	0.16	0.80	3.10	10.88	255.31
Lake Site south	12	4.72	34.00	2.49	17.92	0.02	0.16	1.46	10.48	8.68	194.44
September 13, 1997											
Scenic Bay	12	7.26	53.37	2.33	17.16	0.27	1.96	0.40	2.94	10.26	278.82

Appendix Table 2.1. Cont.

Date and	*Daphnia*		*Bosmina*		*Diaphanasoma*		*Leptodora*		*Chydorus*		Total Cladoceran		Overall Total	
Location	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	Biomass[a]/m3	No./L	Biomass[a]/m3
August 14-15, 1997 Cont.														
Lake Site north	1.08	5.57	0.28	1.46	0.36	1.84	0.02	0.09	0.01	0.04	1.75	96.66	19.43	531.50
Lake Site south	0.78	4.06	1.33	6.94	0.25	1.31	0.02	0.09	0.00	0.00	2.37	89.96	19.11	531.74
August 22-23, 1997														
Scenic Bay	3.89	23.56	2.69	16.32	0.61	3.67	0.02	0.10	0.01	0.07	7.22	319.31	16.51	568.30
Idlewilde Bay	11.88	45.03	2.46	9.32	0.39	1.48	0.05	0.19	0.13	0.47	14.91	824.51	26.39	1115.38
Garfield Bay	3.36	18.19	0.87	4.69	0.89	4.78	0.01	0.05	0.08	0.41	5.19	249.70	18.47	530.32
Ellisport Bay	11.03	40.53	1.73	6.37	2.03	7.44	0.13	0.46	0.04	0.15	14.95	790.52	27.20	995.57
Lake Site north	5.48	31.77	0.33	1.93	0.58	3.38	0.02	0.10	0.00	0.00	6.41	396.36	17.23	620.34
Lake Site south	8.52	50.66	1.66	7.91	0.45	2.15	0.00	0.00	0.00	0.00	0.00	609.56	20.975	887.12
August 30, 1997														
Scenic Bay	8.13	45.33	0.69	3.84	0.26	1.42	0.00	0.00	0.01	0.06	9.09	544.36	17.94	834.29
Idlewilde Bay	5.08	42.20	0.58	4.78	0.38	3.12	0.02	0.14	0.00	0.00	6.04	354.86	12.03	494.51
Garfield Bay	7.30	38.44	1.09	5.75	0.58	3.07	0.00	0.00	0.00	0.00	8.98	429.66	18.99	677.05
Ellisport Bay	6.18	34.84	1.41	7.93	1.34	7.56	0.06	0.33	0.00	0.00	8.97	376.62	17.75	587.30
Lake Site north	8.15	35.18	0.43	1.87	1.93	8.35	0.07	0.29	0.00	0.00	10.58	651.92	23.17	940.95
Lake Site south	5.15	30.44	0.54	3.20	0.44	2.61	0.02	0.10	0.00	0.00	6.15	372.68	16.92	648.58
September 6, 1997														
Scenic Bay	3.23	35.57	0.11	1.22	0.27	3.00	0.00	0.00	0.00	0.00	3.62	261.01	9.09	403.39
Idlewilde Bay	4.77	40.08	0.41	3.43	0.32	2.66	0.00	0.00	0.00	0.00	5.49	401.60	11.89	582.99
Garfield Bay	6.73	28.07	5.23	21.78	1.40	5.84	0.04	0.17	0.00	0.00	13.40	548.81	23.99	758.51
Ellisport Bay	15.38	33.35	11.28	24.46	0.68	1.48	0.02	0.04	0.03	0.07	27.40	1216.78	37.65	1336.73
Lake Site north	12.29	47.60	0.33	1.26	2.30	8.91	0.03	0.13	0.00	0.00	14.95	958.76	25.83	1214.07
Lake Site south	4.46	32.08	0.02	0.16	0.72	5.20	0.00	0.00	0.00	0.00	5.20	377.65	13.89	572.10
September 13, 1997														
Scenic Bay	1.88	13.85	0.33	2.41	1.12	8.26	0.01	0.04	0.00	0.00	3.34	157.08	13.59	435.91
Idlewilde Bay	2.00	21.49	0.48	5.19	0.78	8.42	0.00	0.00	0.00	0.00	3.27	172.98	9.31	325.48
Garfield Bay	1.98	20.93	0.49	5.19	0.57	5.98	0.00	0.00	0.00	0.00	3.04	143.93	9.48	270.67
Ellisport Bay	2.89	19.36	3.45	23.16	0.75	5.03	0.01	0.06	0.01	0.06	7.11	251.42	14.92	379.30

Appendix Table 2.1 Cont.

Date and Location	N	*Cyclops* #/L	%Total	*Diaptomus* #/L	%Total	*Epischura* #/L	%Total	Nauplii #/L	%Total	Total Copepods #/L	Biomass/m3
September 13, 1997 Cont.											
Idlewilde Bay	12	3.17	34.02	2.23	23.90	0.02	0.18	0.63	6.80	6.04	152.50
Garfield Bay	12	4.45	46.97	1.32	13.90	0.03	0.26	0.64	6.77	6.43	126.74
Ellisport Bay	11	4.99	33.44	1.35	9.02	0.03	0.17	1.45	9.72	7.81	127.88
Lake Site north	12	5.58	64.45	1.01	11.66	0.04	0.48	0.31	3.56	6.93	141.14
Lake Site south	12	7.72	38.68	5.98	29.99	0.21	1.04	0.60	3.01	14.51	426.19
September 20, 1997											
Scenic Bay	12	6.50	80.70	0.73	9.10	0.06	0.76	0.42	5.17	7.71	168.09
Idlewilde Bay	10	12.58	79.36	1.62	10.23	0.06	0.37	0.54	3.42	14.80	302.92
Garfield Bay	12	6.71	72.85	1.06	11.49	0.09	1.00	0.43	4.62	8.28	164.03
Ellisport Bay	12	4.24	53.41	0.68	8.50	0.02	0.21	0.43	5.46	5.37	91.63
Lake Site north	12	7.39	82.59	0.70	7.82	0.17	0.19	0.37	4.10	8.48	155.14
Lake Site south	12	7.00	73.55	1.06	11.12	0.05	0.53	0.80	8.41	8.91	178.92
September 27, 1997											
Scenic Bay	12	3.24	61.22	1.65	31.13	0.01	0.10	0.06	1.15	4.98	130.28
Idlewilde Bay	12	2.08	36.18	1.93	33.58	0.00	0.00	0.01	0.14	4.03	118.06
Garfield Bay	12	14.81	63.83	2.02	8.69	0.09	0.40	0.71	3.05	17.63	332.07
Ellisport Bay	12	7.45	27.68	1.15	4.27	0.05	0.19	0.47	1.73	9.12	162.95
Lake Site north	12	10.98	87.17	1.11	8.80	0.02	0.13	0.12	0.93	12.23	231.89
Lake Site south	11	3.94	50.35	3.40	43.52	0.05	0.59	0.13	1.60	7.50	222.41
October 4, 1997											
Scenic Bay	12	20.23	83.09	1.82	7.48	0.03	0.14	0.68	2.81	22.77	512.98
Idlewilde Bay	12	23.88	84.36	2.68	9.45	0.03	0.09	0.69	2.44	27.27	609.10
Garfield Bay	12	22.62	76.28	3.48	11.72	0.01	0.03	0.53	1.80	26.63	637.61
Ellisport Bay	12	6.36	53.93	0.39	3.32	0.00	0.00	0.51	4.31	7.26	129.80
Lake Site north	12	13.76	61.97	6.95	31.31	0.01	0.04	0.36	1.61	21.08	673.04
Lake Site south	12	24.57	83.73	3.17	10.79	0.03	0.11	0.71	2.41	28.48	642.21

Appendix Table 2.1. Cont.

Date and	*Daphnia*		*Bosmina*		*Diaphanasoma*		*Leptodora*		*Chydorus*		Total Cladoceran		Overall Total	
Location	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	Biomass[a]/m3	No./L	Biomass[a]/m3
September 13, 1997 Cont.														
Lake Site north	0.84	9.73	0.03	0.39	0.84	9.73	0.00	0.00	0.00	0.00	1.72	65.40	8.65	206.54
Lake Site south	3.46	17.34	0.47	2.34	1.51	7.56	0.01	0.04	0.00	0.00	5.44	302.89	19.95	729.08
September 20, 1997														
Scenic Bay	0.08	1.03	0.21	2.62	0.05	0.62	0.00	0.00	0.00	0.00	0.34	9.75	8.06	177.84
Idlewilde Bay	0.13	0.79	0.90	5.65	0.03	0.18	0.00	0.00	0.00	0.00	1.05	23.11	15.85	326.03
Garfield Bay	0.13	1.45	0.73	7.96	0.04	0.45	0.00	0.00	0.02	0.18	0.93	20.03	9.21	184.07
Ellisport Bay	0.16	1.99	2.35	29.59	0.07	0.84	0.00	0.00	0.00	0.00	2.58	49.03	7.94	140.66
Lake Site north	0.12	1.30	0.28	3.17	0.07	0.74	0.01	0.09	0.00	0.00	0.48	15.33	8.95	170.48
Lake Site south	0.15	1.58	0.35	3.68	0.11	1.14	0.00	0.00	0.00	0.00	0.61	18.90	9.52	197.81
September 27, 1997														
Scenic Bay	0.01	0.21	0.32	6.08	0.00	0.00	0.00	0.00	0.01	0.10	0.34	5.64	5.30	135.92
Idlewilde Bay	0.00	0.00	1.72	29.81	0.02	0.29	0.00	0.00	0.00	0.00	1.73	24.39	5.76	142.45
Garfield Bay	0.07	0.29	5.38	23.20	0.10	0.43	0.00	0.00	0.03	0.11	5.58	82.88	23.20	414.95
Ellisport Bay	0.10	0.37	17.43	64.77	0.27	0.99	0.00	0.00	0.00	0.00	17.8	291.91	26.92	454.87
Lake Site north	0.03	0.26	0.17	1.32	0.18	1.39	0.00	0.00	0.00	0.00	0.38	5.29	12.60	237.18
Lake Site south	0.00	0.00	0.27	3.41	0.03	0.43	0.00	0.00	0.01	0.11	0.31	4.83	7.81	227.23
October 4, 1997														
Scenic Bay	0.22	0.89	1.14	4.68	0.21	0.84	0.00	0.00	0.02	0.07	1.58	43.75	24.35	556.74
Idlewilde Bay	0.00	0.00	0.76	2.68	0.28	0.97	0.00	0.00	0.00	0.00	1.03	24.75	28.30	633.85
Garfield Bay	0.07	0.22	2.58	8.71	0.38	1.26	0.00	0.00	0.00	0.00	3.03	79.09	29.66	716.71
Ellisport Bay	0.14	1.20	4.16	35.27	0.17	1.41	0.00	0.00	0.07	0.57	4.53	83.65	11.79	213.45
Lake Site north	0.03	0.11	0.95	4.28	0.16	0.71	0.00	0.00	0.00	0.00	1.13	27.99	22.21	701.04
Lake Site south	0.11	0.37	0.38	1.31	0.37	1.25	0.00	0.00	0.01	0.03	0.87	21.70	29.34	670.36
October 17, 1997														
Scenic Bay	0.22	0.77	0.46	1.57	0.24	0.81	0.00	0.00	0.02	0.06	0.93	35.21	28.99	666.63
Idlewilde Bay	0.00	0.00	0.12	1.05	0.04	0.38	0.00	0.00	0.00	0.00	0.16	3.77	11.11	215.81
Garfield Bay	0.08	0.47	0.22	1.22	0.17	0.94	0.00	0.00	0.00	0.00	0.47	18.21	17.69	441.29
Ellisport Bay	0.05	0.41	1.34	11.00	0.23	1.91	0.00	0.00	0.01	0.07	1.64	36.12	12.20	259.57

Appendix Table 2.1. Cont.

Date and Location	N	*Cyclops* #/L	%Total	*Diaptomus* #/L	%Total	*Epischura* #/L	%Total	Nauplii #/L	%Total	Total Copepods #/L	Biomass/m3
October 17, 1997											
Scenic Bay	12	23.77	81.97	2.42	8.34	0.13	0.44	1.75	6.04	28.06	631.42
Idlewilde Bay	12	8.35	75.17	0.78	6.98	0.05	0.45	1.78	15.99	10.95	212.04
Garfield Bay	12	13.91	78.61	2.56	14.46	0.06	0.33	0.70	3.96	17.23	423.08
Ellisport Bay	12	8.25	67.65	1.67	13.67	0.13	1.02	0.52	4.27	10.56	223.45
Lake Site north	12	14.41	86.67	0.90	5.41	0.01	0.05	1.11	6.66	16.43	326.86
Lake Site south	12	18.87	80.37	3.30	14.06	0.06	0.25	0.89	3.80	23.12	578.95
October 24, 1997											
Scenic Bay	12	13.32	92.06	0.56	3.84	0.09	0.65	0.37	2.57	14.34	316.00
Idlewilde Bay	12	14.40	90.24	0.87	5.43	0.34	2.14	0.29	1.83	15.90	382.56
Garfield Bay	12	7.38	70.52	2.25	21.51	0.23	2.23	0.31	2.95	10.17	304.14
Ellisport Bay	12	9.30	74.10	1.62	12.88	0.17	1.33	0.32	2.52	11.40	248.01
Lake Site north	12	13.93	80.74	2.73	15.84	0.04	0.24	0.20	1.16	16.91	443.94
Lake Site south	12	18.30	93.49	1.05	5.36	0.00	0.00	0.13	0.68	19.48	408.45
October 31 - November 1, 1997											
Scenic Bay	12	1.27	50.13	1.22	48.16	0.04	1.53	0.01	0.22	2.54	95.46
Idlewilde Bay	12	1.10	50.57	0.97	44.44	0.06	2.68	0.03	1.53	2.16	79.05
Garfield Bay	12	14.86	69.01	6.18	28.72	0.07	0.31	0.23	1.05	21.25	622.01
Ellisport Bay	12	13.46	85.59	1.53	9.75	0.03	0.21	0.43	2.70	15.45	333.05
Lake Site north	12	17.49	78.12	4.20	18.76	0.03	0.11	0.38	1.67	22.09	504.62
Lake Site south	12	7.11	69.13	2.93	28.45	0.03	0.24	0.13	1.30	10.19	289.36
November 7-8, 1997											
Scenic Bay	11	41.39	90.90	3.57	7.83	0.01	0.02	0.52	1.14	45.49	922.09
Idlewilde Bay	12	8.41	78.10	2.03	18.81	0.01	0.08	0.29	2.71	10.73	224.61
Garfield Bay	12	16.13	69.63	3.32	14.31	0.04	0.18	0.37	1.58	19.86	500.77
Ellisport Bay	12	4.76	72.53	1.17	17.78	0.01	0.15	0.35	5.28	6.28	143.71
Lake Site north	12	14.85	83.24	2.59	14.53	0.01	0.05	0.32	1.78	17.77	385.48
Lake Site south	11	14.76	85.48	2.16	12.50	0.02	0.10	0.28	1.64	17.21	343.48

Appendix Table 2.1. Cont.

Date and	*Daphnia*		*Bosmina*		*Diaphanasoma*		*Leptodora*		*Chydorus*		Total Cladoceran		Overall Total	
Location	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	Biomass^a/m3	No./L	Biomass^a/m3
October 17, 1997 Cont.														
Lake Site north	0.03	0.14	0.05	0.21	0.28	1.17	0.00	0.00	0.00	0.00	0.36	16.39	23.48	595.35
Lake Site south	0.01	0.05	0.03	0.15	0.17	1.00	0.00	0.00	0.00	0.00	0.20	9.10	16.63	335.96
October 25, 1997														
Scenic Bay	0.03	0.23	0.01	0.08	0.08	0.58	0.00	0.00	0.00	0.00	0.13	6.80	14.47	322.80
Idlewilde Bay	0.00	0.00	0.03	0.21	0.03	0.16	0.00	0.00	0.00	0.00	0.06	1.74	15.96	384.30
Garfield Bay	0.00	0.00	0.27	2.55	0.03	0.24	0.00	0.00	0.00	0.00	0.29	7.05	10.46	311.19
Ellisport Bay	0.03	0.27	0.98	7.77	0.13	1.06	0.01	0.07	0.00	0.00	1.15	25.94	12.55	273.95
Lake Site north	0.00	0.00	0.01	0.05	0.34	1.98	0.00	0.00	0.00	0.00	0.35	17.49	17.26	461.44
Lake Site south	0.00	0.00	0.03	0.13	0.07	0.34	0.00	0.00	0.00	0.00	0.09	3.80	19.58	412.25
October 31 – November 1, 1997														
Scenic Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.54	95.46
Idlewilde Bay	0.00	0.00	0.02	0.77	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.24	2.18	79.28
Garfield Bay	0.02	0.08	0.00	0.00	0.17	0.77	0.00	0.00	0.02	0.08	0.20	9.68	21.53	631.69
Ellisport Bay	0.00	0.00	0.08	0.53	0.14	0.90	0.01	0.05	0.04	0.26	0.28	11.60	15.73	344.65
Lake Site north	0.00	0.00	0.03	0.11	0.28	1.23	0.00	0.00	0.00	0.00	0.30	14.51	22.39	519.13
Lake Site south	0.00	0.00	0.00	0.00	0.09	0.89	0.00	0.00	0.00	0.00	0.09	4.65	10.28	294.01
November 7-8, 1997														
Scenic Bay	0.00	0.00	0.01	0.02	0.04	0.08	0.01	0.02	0.00	0.00	0.08	4.45	45.55	926.53
Idlewilde Bay	0.00	0.00	0.00	0.00	0.03	0.31	0.00	0.00	0.00	0.00	0.03	1.69	10.77	226.30
Garfield Bay	0.00	0.00	0.00	0.00	3.32	14.31	0.00	0.00	0.00	0.00	3.32	168.19	23.18	668.97
Ellisport Bay	0.00	0.00	0.24	3.66	0.04	0.61	0.00	0.00	0.00	0.00	0.28	8.16	6.56	151.87
Lake Site north	0.00	0.00	0.01	0.05	0.07	0.37	0.00	0.00	0.00	0.00	0.08	3.57	17.84	389.04
Lake Site south	0.01	0.05	0.01	0.05	0.03	0.19	0.00	0.00	0.00	0.00	0.05	2.11	17.27	345.58
November 22, 1997														
Scenic Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.61	266.36
Idlewilde Bay	0.02	0.19	0.00	0.00	0.01	0.09	0.01	0.09	0.00	0.00	0.03	3.37	8.88	224.84
Garfield Bay	0.01	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.51	2.61	83.40
Ellisport Bay	0.20	4.49	0.04	0.94	0.00	0.00	0.00	0.00	0.29	6.55	0.53	13.92	4.45	104.38

Appendix Table 2.1. Cont.

Date and		*Cyclops*		*Diaptomus*		*Epischura*		Nauplii		Total Copepods	
Location	N	#/L	%Total	#/L	%Total	#/L	%Total	#/L	%Total	#/L	Biomass/m3
November 22, 1997											
Scenic Bay	12	7.52	70.90	2.82	26.60	0.06	0.58	0.21	1.94	10.61	266.36
Idlewilde Bay	12	5.44	61.28	3.22	36.22	0.01	0.09	0.18	2.06	8.85	221.47
Garfield Bay	12	1.41	54.00	1.06	40.58	0.01	0.32	0.13	4.79	2.60	82.89
Ellisport Bay	12	3.00	67.42	0.73	16.29	0.01	0.19	0.18	4.12	3.92	90.45
Lake Site north	12	5.42	52.29	4.74	45.78	0.02	0.16	0.18	1.69	10.35	343.48
Lake Site south	12	1.49	52.75	1.08	37.85	0.01	0.30	0.25	8.87	2.81	73.77
December 6, 1997											
Scenic Bay	12	5.11	56.35	3.54	39.12	0.00	0.00	0.41	4.48	9.06	191.26
Idlewilde Bay	12	3.55	57.19	2.40	38.74	0.00	0.00	0.26	4.20	6.21	128.36
Garfield Bay	12	3.55	60.37	1.95	33.16	0.00	0.00	0.38	6.52	5.88	109.82
Ellisport Bay	10	2.78	44.68	3.17	50.98	0.05	0.80	0.22	3.55	6.22	197.17
Lake Site north	11	2.54	77.49	0.69	21.09	0.00	0.00	0.05	1.52	3.28	79.85
Lake Site south	12	5.40	56.25	3.83	39.84	0.01	0.09	0.37	3.82	9.60	205.32
December 19, 1997											
Scenic Bay	12	3.38	51.26	2.67	40.40	0.00	0.00	0.55	8.33	6.60	135.23
Idlewilde Bay	12	2.18	39.98	2.71	49.79	0.00	0.00	0.55	10.11	5.43	110.55
Lake Site south	12	4.78	62.94	2.31	30.37	0.00	0.00	0.52	6.80	7.61	152.26
January 17-18, 1998											
Scenic Bay	12	1.25	50.91	1.11	45.25	0.00	0.00	0.09	3.62	2.45	58.64
Idlewilde Bay	12	0.78	37.61	1.23	58.81	0.00	0.00	0.05	2.40	2.06	47.35
Garfield Bay	12	0.50	27.65	1.18	65.98	0.00	0.00	0.13	7.37	1.81	25.44
Ellisport Bay	12	1.94	46.23	1.75	41.67	0.00	0.00	0.49	11.71	4.18	72.75
Lake Site north	11	1.71	32.11	3.40	63.75	0.00	0.00	0.20	3.75	5.31	85.85
Lake Site south	12	1.94	39.90	2.71	55.83	0.00	0.00	0.21	4.28	4.87	110.97
February 20-22, 1998											
Scenic Bay	12	0.72	26.81	1.67	62.07	0.00	0.00	0.29	10.93	2.69	41.17
Idlewilde Bay	12	0.61	39.68	0.77	50.01	0.00	0.00	0.15	9.78	1.53	24.29

Appendix Table 2.1. Cont.

Date and	*Daphnia*		*Bosmina*		*Diaphanasoma*		*Leptodora*		*Chydorus*		Total Cladoceran		Overall Total	
Location	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	Biomass^a/m3	#/L	Biomass^a/m3
November 22, 1997 Cont.														
Lake Site north	0.00	0.00	0.00	0.00	0.01	0.30	0.00	0.00	0.00	0.00	0.01	0.42	2.82	74.19
Lake Site south	0.00	0.00	0.00	0.00	0.01	0.08	0.00	0.00	0.00	0.00	0.01	0.42	10.35	283.99
December 06, 1997														
Scenic Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.06	0.01	0.07	9.06	191.34
Idlewilde Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.21	128.36
Garfield Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.88	109.82
Ellisport Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.22	197.17
Lake Site north	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.28	79.85
Lake Site south	0.00	0.00	0.01	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.14	9.61	205.46
December 19, 1997														
Scenic Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.60	135.23
Idlewilde Bay	0.00	0.00	0.01	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.14	5.44	110.69
Lake Site south	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.61	152.26
January 17, 1998														
Scenic Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.23	0.01	0.07	2.46	58.71
Idlewilde Bay	0.00	0.00	0.03	1.20	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	2.08	47.35
Garfield Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.81	25.44
Ellisport Bay	0.00	0.00	0.02	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.22	4.20	72.97
Lake Site north	0.01	0.23	0.01	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.70	5.33	86.55
Lake Site south	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.87	110.97
February 22, 1998														
Scenic Bay	0.00	0.00	0.01	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.11	2.69	41.28
Idlewilde Bay	0.00	0.00	0.01	0.54	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.14	1.53	24.44
Garfield Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.14	63.91
Ellisport Bay	0.03	1.72	0.07	3.44	0.00	0.00	0.00	0.00	0.10	5.15	0.20	3.95	1.94	39.65
Lake Site north	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.14	0.01	0.11	5.86	112.34
Lake Site south	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.38	38.11

Appendix Table 2.1. Cont.

Date and		*Cyclops*		*Diaptomus*		*Epischura*		Nauplii		Total Copepods	
Location	N	#/L	%Total	#/L	%Total	#/L	%Total	#/L	%Total	#/L	Biomass/m3
February 20-22, 1998 Cont.											
Garfield Bay	12	1.58	50.14	1.43	45.37	0.00	0.00	0.14	4.51	3.14	63.91
Ellisport Bay	12	0.73	37.37	0.82	42.10	0.00	0.00	0.20	10.31	1.74	35.70
Lake Site north	12	1.89	32.29	3.83	65.30	0.00	0.00	0.13	2.28	5.85	112.24
Lake Site south	12	0.94	39.52	1.30	54.55	0.00	0.00	0.14	5.94	2.38	38.11
March 20, 1998											
Scenic Bay	12	1.63	30.52	3.41	64.01	0.00	0.00	0.28	5.16	5.31	87.04
Idlewilde Bay	12	0.35	20.40	1.21	70.42	0.00	0.00	0.14	8.26	1.70	24.10
Garfield Bay	12	0.62	36.10	0.96	56.11	0.00	0.00	0.12	6.83	1.69	28.32
Ellisport Bay	12	0.58	46.67	0.42	33.33	0.00	0.00	0.15	12.00	1.15	20.94
Lake Site north	12	0.80	26.82	2.08	69.84	0.00	0.00	0.10	3.35	2.98	94.58
Lake Site south	12	1.76	31.97	3.52	63.94	0.00	0.00	0.23	4.09	5.50	86.55
April 18, 1998											
Scenic Bay	11	0.47	18.46	1.95	76.34	0.00	0.00	0.07	2.61	2.50	66.29
Idlewilde Bay	11	0.58	13.82	3.38	81.09	0.00	0.00	0.17	4.00	4.12	51.79
Garfield Bay	12	2.09	64.70	0.98	30.42	0.00	0.00	0.13	4.12	3.21	57.07
Ellisport Bay	11	1.02	36.05	0.70	24.67	0.00	0.00	0.65	23.05	2.36	39.92
Lake Site north	12	1.23	34.12	2.18	60.82	0.00	0.00	0.18	4.87	3.58	71.87
Lake Site south	12	0.45	12.03	3.21	85.78	0.00	0.00	0.07	1.78	3.73	51.58
May 9-10, 1998											
Scenic Bay	12	0.40	24.10	0.91	54.77	0.00	0.00	0.27	16.06	1.58	40.98
Idlewilde Bay	11	1.51	50.28	0.54	18.06	0.00	0.00	0.95	31.67	3.00	50.35
Garfield Bay	12	1.61	41.13	1.29	33.03	0.00	0.00	0.91	23.23	3.81	79.46
Ellisport Bay	12	10.96	69.89	0.53	3.40	0.01	0.05	1.98	12.60	13.48	242.99
Lake Site north	12	1.14	19.68	4.16	72.05	0.00	0.00	0.39	6.74	5.69	173.70
Lake Site south	12	2.36	30.99	3.38	44.46	0.01	0.11	1.82	23.87	7.57	171.77
May 16-17, 1998											
Scenic Bay	11	6.33	68.42	1.46	15.79	0.00	0.00	1.19	12.88	8.98	181.22

Appendix Table 2.1. Cont.

Date and	*Daphnia*		*Bosmina*		*Diaphanasoma*		*Leptodora*		*Chydorus*		Total Cladoceran		Overall Total	
Location	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No,/L	Biomass^a/m3	No./L	Biomass^a/m3
March 20, 1998														
Scenic Bay	0.00	0.00	0.02	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.32	5.31	87.36
Idlewilde Bay	0.00	0.00	0.01	0.49	0.00	0.00	0.00	0.00	0.01	0.49	0.02	0.25	1.72	24.46
Garfield Bay	0.01	0.49	0.00	0.00	0.00	0.00	0.01	0.49	0.00	0.00	0.02	1.67	1.71	29.99
Ellisport Bay	0.01	0.67	0.03	2.67	0.00	0.00	0.00	0.00	0.06	4.67	0.10	1.73	1.25	22.67
Lake Site north	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.98	94.58
Lake Site south	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.50	86.55
April 18, 1998														
Scenic Bay	0.04	1.52	0.02	0.87	0.00	0.00	0.00	0.00	0.01	0.22	0.07	2.36	2.56	68.65
Idlewilde Bay	0.01	0.30	0.03	0.60	0.00	0.00	0.00	0.00	0.01	0.20	0.05	1.13	4.16	52.92
Garfield Bay	0.00	0.00	0.03	0.77	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.48	3.23	57.55
Ellisport Bay	0.00	0.00	0.01	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.17	3.59	72.04
Lake Site south	0.00	0.00	0.01	0.22	0.01	0.22	0.00	0.00	0.00	0.00	0.02	0.57	3.74	52.15
May 9-10, 1998														
Scenic Bay	0.03	2.01	0.02	1.01	0.00	0.00	0.00	0.00	0.03	2.01	0.08	2.28	1.66	43.27
Idlewilde Bay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	50.35
Garfield Bay	0.00	0.00	0.07	1.71	0.00	0.00	0.00	0.00	0.03	0.85	0.10	1.71	3.91	81.17
Ellisport Bay	0.05	0.32	2.07	13.18	0.01	0.05	0.00	0.00	0.08	0.53	2.21	40.12	15.68	283.11
Lake Site north	0.01	0.22	0.04	0.72	0.00	0.00	0.03	0.43	0.01	0.22	0.07	6.69	5.78	180.29
Lake Site south	0.00	0.00	0.02	0.22	0.00	0.00	0.00	0.00	0.03	0.33	0.04	0.32	7.61	172.10
May 16-17, 1998														
Scenic Bay	0.01	0.09	0.17	1.85	0.00	0.00	0.05	0.54	0.04	0.41	0.27	14.59	9.25	195.83
Idlewilde Bay	0.00	0.00	0.13	0.84	0.00	0.00	0.00	0.00	0.03	0.21	0.17	2.69	15.78	325.31
Garfield Bay	0.00	0.00	0.44	1.36	0.00	0.00	0.00	0.00	0.02	0.05	0.46	8.71	32.40	690.56
Ellisport Bay	0.00	0.00	1.58	10.12	0.00	0.00	0.02	0.11	0.08	0.53	1.68	31.77	15.64	304.91
May 21-22, 1998														
Scenic Bay	0.00	0.00	0.08	0.34	0.00	0.00	0.00	0.00	0.01	0.06	0.09	1.59	21.95	248.83
Idlewilde Bay	0.01	0.04	0.05	0.22	0.00	0.00	0.00	0.00	0.01	0.03	0.07	1.47	24.12	288.20

Appendix Table 2.1. Cont.

Date and Location	N	*Cyclops* #/L	*Cyclops* %Total	*Diaptomus* #/L	*Diaptomus* %Total	*Epischura* #/L	*Epischura* %Total	Nauplii #/L	Nauplii %Total	Total Copepods #/L	Biomass/m3
May 16-17, 1998 Cont.											
Idlewilde Bay	12	11.33	71.77	2.53	16.05	0.01	0.05	1.74	11.04	15.61	322.62
Garfield Bay	12	29.43	90.84	1.97	6.07	0.09	0.28	0.45	1.39	31.94	681.86
Ellisport Bay	12	12.12	77.47	0.65	4.16	0.03	0.16	1.17	7.46	13.96	273.13
May 21-22, 1998											
Scenic Bay	24	11.26	51.31	0.43	1.94	0.01	0.04	10.17	46.34	21.86	247.25
Idlewilde Bay	23	13.04	54.05	0.54	2.24	0.00	0.02	10.47	43.39	24.05	286.74
Garfield Bay	24	8.18	47.72	1.18	6.88	0.00	0.00	7.37	42.95	16.73	210.12
Ellisport Bay	24	21.84	84.65	0.54	2.10	0.05	0.19	0.49	1.92	22.93	469.69
Lake Site north	22	2.87	23.89	2.44	20.35	0.01	0.08	6.65	55.38	11.96	149.36
Lake Site south	24	11.52	37.36	1.87	6.07	0.00	0.00	17.41	56.49	30.80	305.07
May 28-30, 1998											
Scenic Bay	24	10.11	82.91	0.82	6.73	0.00	0.03	0.82	6.75	11.75	235.02
Idlewilde Bay	24	9.70	78.19	1.63	13.14	0.10	0.77	0.85	6.89	12.28	270.75
Garfield Bay	24	12.63	82.19	0.95	6.21	0.00	0.00	0.79	5.15	14.37	290.32
Ellisport Bay	23	21.77	65.15	0.53	1.59	0.05	0.13	1.51	4.51	23.85	467.63
Lake Site north	24	10.89	74.55	2.27	15.54	0.01	0.06	1.22	8.41	14.40	304.24
Lake Site south	24	11.35	80.17	1.42	10.00	0.00	0.03	1.32	9.30	14.09	282.10
June 3-6, 1998											
Scenic Bay	24	58.45	89.05	5.10	7.77	0.09	0.14	1.61	2.46	65.27	1345.21
Idlewilde Bay	23	39.18	89.90	2.56	5.87	0.03	0.06	1.71	3.93	43.49	871.19
Garfield Bay	24	12.60	78.34	1.80	11.19	0.01	0.03	0.85	5.28	15.26	308.33
Ellisport Bay	24	18.42	58.47	0.55	1.76	0.02	0.05	1.19	3.78	20.18	390.96
Lake Site north	24	17.90	69.07	7.18	27.69	0.00	0.00	0.63	2.44	25.70	572.97
Lake Site south	24	27.06	84.96	4.93	11.30	0.04	0.09	1.55	3.55	43.58	899.64
June 11-13, 1998											
Scenic Bay	24	26.59	80.22	4.52	13.64	0.05	0.14	0.97	2.92	32.12	677.40
Idlewilde Bay	23	40.89	88.64	3.25	7.05	0.03	0.05	1.66	3.59	45.82	925.37

Appendix Table 2.1. Cont.

Date and	*Daphnia*		*Bosmina*		*Diaphanasoma*		*Leptodora*		*Chydorus*		Total Cladoceran		Overall Total	
Location	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	Biomass^{a}/m3	No./L	Biomass^{a}/m3
May 21-22, 1998 Cont.														
Garfield Bay	0.07	0.41	0.28	1.65	0.06	0.36	0.00	0.00	0.01	0.05	0.43	11.68	17.15	221.80
Ellisport Bay	0.04	0.16	2.76	10.70	0.03	0.12	0.00	0.00	0.04	0.16	2.87	52.03	25.80	521.72
Lake Site north	0.00	0.00	0.02	0.19	0.00	0.00	0.00	0.00	0.01	0.11	0.04	0.66	12.00	150.02
Lake Site south	0.00	0.00	0.03	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.44	30.83	305.51
May 28-30, 1998														
Scenic Bay	0.03	0.27	0.37	3.02	0.00	0.03	0.00	0.00	0.03	0.27	0.44	9.12	12.19	244.14
Idlewilde Bay	0.00	0.00	0.06	0.50	0.00	0.00	0.00	0.00	0.06	0.50	0.13	1.87	12.40	272.61
Garfield Bay	0.01	0.05	0.94	6.13	0.00	0.00	0.00	0.00	0.04	0.24	0.99	18.93	15.36	309.26
Ellisport Bay	0.14	0.43	9.31	27.87	0.00	0.01	0.02	0.05	0.09	0.26	9.56	173.69	33.42	641.32
Lake Site north	0.02	0.11	0.20	1.34	0.00	0.00	0.00	0.00	0.00	0.00	0.21	4.62	14.61	308.87
Lake Site south	0.00	0.00	0.03	0.18	0.00	0.00	0.00	0.00	0.05	0.32	0.07	1.04	14.16	282.69
June 3-6, 1998														
Scenic Bay	0.01	0.01	0.28	0.42	0.03	0.04	0.00	0.00	0.07	0.11	0.38	7.62	65.64	1352.83
Idlewilde Bay	0.03	0.06	0.07	0.16	0.01	0.01	0.00	0.00	0.00	0.00	0.11	2.88	43.59	874.07
Garfield Bay	0.01	0.03	0.78	4.87	0.00	0.00	0.00	0.00	0.05	0.31	0.84	11.36	16.10	319.69
Ellisport Bay	0.24	0.75	11.04	35.04	0.01	0.03	0.03	0.08	0.02	0.05	11.32	217.13	31.50	608.08
Lake Site north	0.07	0.27	0.14	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.21	20.03	25.91	593.00
Lake Site south	0.01	0.02	0.04	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.05	1.16	43.62	900.80
June 11-13, 1998														
Scenic Bay	0.14	0.41	0.85	2.55	0.01	0.01	0.00	0.00	0.04	0.12	1.03	22.16	33.14	699.57
Idlewilde Bay	0.06	0.12	0.24	0.52	0.01	0.01	0.00	0.00	0.01	0.02	0.31	7.08	46.13	932.45
Garfield Bay	0.02	0.04	1.96	4.93	0.01	0.01	0.01	0.01	0.02	0.04	2.00	28.10	39.65	871.52
Ellisport Bay	0.27	0.30	22.06	24.61	0.05	0.05	0.16	0.18	0.07	0.07	22.60	445.58	89.64	1812.08
Lake Site north	0.08	0.13	0.16	0.28	0.01	0.01	0.01	0.01	0.01	0.01	0.26	21.74	57.93	1320.95
Lake Site south	0.06	0.09	0.04	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.10	4.87	67.26	1444.38
June 17-20, 1998														
Scenic Bay	0.07	0.21	1.30	4.14	0.01	0.03	0.01	0.01	0.06	0.19	1.44	28.85	31.51	690.03
Idlewilde Bay	0.12	0.24	0.50	0.97	0.01	0.02	0.00	0.00	0.05	0.09	0.68	15.50	51.33	1118.80

Appendix Table 2.1. Cont.

Date and Location	N	*Cyclops* #/L	*Cyclops* %Total	*Diaptomus* #/L	*Diaptomus* %Total	*Epischura* #/L	*Epischura* %Total	Nauplii #/L	Nauplii %Total	Total Copepods #/L	Total Copepods Biomass/m3
June 11-13, 1998 Cont.											
Garfield Bay	24	24.45	61.66	11.85	29.88	0.00	0.00	1.36	3.43	37.65	843.22
Ellisport Bay	24	63.29	70.61	2.34	2.61	0.13	0.14	1.29	1.44	67.04	1366.50
Lake Site north	25	39.64	68.43	16.71	28.85	0.04	0.06	1.29	2.22	57.68	1299.20
Lake Site south	24	52.02	77.35	12.13	18.03	0.20	0.29	2.82	4.19	67.16	1439.52
June 17-20, 1998											
Scenic Bay	22	21.83	69.26	7.43	23.57	0.01	0.03	0.81	2.57	30.07	661.19
Idlewilde Bay	22	39.13	76.24	10.51	20.47	0.02	0.04	0.99	1.93	50.65	1103.30
Garfield Bay	23	46.65	82.36	7.49	13.22	0.01	0.02	0.66	1.17	54.82	1164.54
Ellisport Bay	23	71.45	81.35	4.31	4.91	0.01	0.02	0.82	0.93	76.59	1571.25
Lake Site north	24	31.51	67.50	14.18	30.36	0.01	0.01	0.77	1.65	46.46	1054.97
Lake Site south	24	42.47	63.35	23.42	34.93	0.00	0.00	0.96	1.43	66.85	1548.25
June 24-26, 1998											
Scenic Bay	24	82.10	69.67	32.04	27.19	0.01	0.01	0.88	0.74	115.03	2603.76
Idlewilde Bay	24	103.46	70.45	40.00	27.24	0.03	0.02	1.02	0.70	144.52	3273.10
Garfield Bay	24	37.09	65.25	17.60	30.96	0.01	0.02	0.47	0.82	55.18	1270.01
Ellisport Bay	23	45.71	89.97	2.52	4.95	0.01	0.01	0.39	0.76	48.61	997.29
Lake Site north	23	36.18	51.49	33.15	47.18	0.01	0.01	0.70	0.99	70.04	1709.73
Lake Site south	24	39.82	64.64	20.85	33.85	0.01	0.01	0.60	0.98	61.28	1420.22
July 2-3, 1998											
Scenic Bay	24	24.56	56.18	7.84	17.73	0.03	0.08	0.50	1.13	32.93	804.93
Idlewilde Bay	23	17.89	65.42	5.57	20.37	0.08	0.28	0.14	0.52	23.68	590.14
Garfield Bay	23	19.13	74.11	4.03	15.60	0.24	0.93	0.40	1.55	23.80	594.16
Ellisport Bay	24	19.23	64.15	7.35	24.54	0.07	0.22	0.72	2.41	27.37	676.08
Lake Site north	24	20.97	51.41	18.49	45.34	0.10	0.26	0.86	2.10	40.42	1081.33
Lake Site south	23	60.52	66.70	28.51	31.41	0.13	0.15	0.50	0.55	89.66	2288.95
July 9-10, 1998											
Scenic Bay	24	9.37	54.56	2.75	16.00	0.03	0.15	0.33	1.89	12.46	301.09

Appendix Table 21. Cont.

Date and	*Daphnia*		*Bosmina*		*Diaphanasoma*		*Leptodora*		*Chydorus*		Total Cladoceran		Overall Total	
Location	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	Biomass^a/m3	No./L	Biomass^a/m3
June 17-20, 1998 Cont.														
Garfield Bay	0.25	0.43	1.45	2.56	0.02	0.04	0.01	0.02	0.10	0.18	1.83	34.79	56.65	1199.33
Ellisport Bay	1.03	1.17	9.89	11.27	0.11	0.12	0.10	0.11	0.12	0.13	11.24	27.76	87.83	1598.99
Lake Site north	0.12	0.25	0.08	0.17	0.02	0.04	0.00	0.00	0.01	0.02	0.23	23.63	46.69	1078.60
Lake Site south	0.05	0.07	0.14	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.19	5.67	67.04	1553.93
June 24-25, 1998														
Scenic Bay	0.21	0.18	2.52	2.14	0.05	0.04	0.00	0.00	0.04	0.03	2.82	58.15	117.85	2661.91
Idlewilde Bay	0.32	0.22	1.91	1.30	0.02	0.01	0.00	0.00	0.09	0.06	2.33	49.63	146.86	3322.73
Garfield Bay	0.07	0.13	1.43	2.51	0.02	0.03	0.01	0.01	0.15	0.27	1.67	25.91	56.85	1295.91
Ellisport Bay	0.52	1.03	1.22	2.39	0.27	0.53	0.08	0.16	0.10	0.20	2.19	86.36	50.80	1083.65
Lake Site north	0.19	0.26	0.04	0.06	0.00	0.00	0.00	0.00	0.01	0.01	0.23	26.14	70.27	1735.87
Lake Site south	0.25	0.40	0.02	0.03	0.01	0.01	0.00	0.00	0.05	0.08	0.33	18.22	61.61	1438.45
July 2-3, 1998														
Scenic Bay	0.93	2.13	9.68	22.14	0.07	0.15	0.01	0.01	0.11	0.26	10.79	285.95	43.72	1090.89
Idlewilde Bay	1.12	4.08	2.39	8.73	0.14	0.51	0.00	0.00	0.02	0.09	3.66	103.48	27.35	693.63
Garfield Bay	0.42	1.64	1.47	5.70	0.06	0.23	0.01	0.02	0.06	0.22	2.02	39.26	25.82	633.41
Ellisport Bay	0.42	1.39	1.93	6.45	0.10	0.33	0.08	0.26	0.08	0.25	2.60	69.96	29.97	746.04
Lake Site north	0.21	0.51	0.08	0.18	0.07	0.17	0.00	0.00	0.01	0.03	0.37	15.62	40.79	1096.95
Lake Site south	0.67	0.73	0.33	0.37	0.07	0.08	0.00	0.00	0.01	0.01	1.08	41.92	90.74	2330.88
July 9-10, 1998														
Scenic Bay	3.06	17.84	1.57	9.15	0.05	0.29	0.01	0.02	0.02	0.10	4.70	186.89	17.17	487.98
Idlewilde Bay	3.62	8.41	1.69	3.92	0.21	0.48	0.00	0.00	0.01	0.01	5.53	230.63	43.11	1172.36
Garfield Bay	0.86	3.36	8.70	34.10	0.26	1.03	0.00	0.00	0.06	0.23	9.88	69.78	25.53	437.18
Ellisport Bay	1.18	4.44	3.81	14.31	0.11	0.41	0.13	0.47	0.02	0.06	5.25	143.59	26.64	631.66
Lake Site north	0.57	1.16	0.20	0.41	0.07	0.14	0.00	0.00	0.01	0.01	0.84	35.61	48.66	1336.34
Lake Site south	1.93	2.82	0.50	0.73	0.32	0.46	0.01	0.02	0.00	0.00	2.75	119.61	68.37	1855.23
August 23-24, 1998														
Scenic Bay	1.74	17.73	0.67	6.85	0.29	2.93	0.00	0.00	0.01	0.05	2.70	206.94	9.80	566.27
Idlewilde Bay	1.50	11.01	1.61	11.80	0.33	2.42	0.01	0.03	0.04	0.31	3.48	192.38	13.63	600.80

Appendix Table 2.1. Cont.

Date and		*Cyclops*		*Diaptomus*		*Epischura*		Nauplii		Total Copepods	
Location	N	#/L	%Total	#/L	%Total	#/L	%Total	#/L	%Total	#/L	Biomass^a/m3
July 9-10, 1998 Cont.											
Idlewilde Bay	25	26.75	62.07	10.43	24.20	0.06	0.14	0.34	0.79	37.58	941.73
Garfield Bay	24	12.40	48.59	2.63	10.28	0.04	0.16	0.58	2.25	15.65	367.40
Ellisport Bay	24	17.70	66.43	2.90	10.90	0.01	0.02	0.79	2.96	21.39	488.07
Lake Site north	24	21.43	44.04	25.36	52.12	0.02	0.04	1.01	2.07	47.82	1300.72
Lake Site south	24	37.18	54.38	27.58	40.34	0.10	0.15	0.75	1.10	65.61	1735.62
August 23-24, 1998											
Scenic Bay	22	1.73	17.66	4.82	49.21	0.45	4.58	0.10	0.99	7.10	359.32
Idlewilde Bay	24	4.82	35.37	4.86	35.67	0.30	2.20	0.17	1.22	10.15	408.42
Garfield Bay	22	5.29	29.69	4.75	26.68	0.09	0.51	2.01	11.30	12.15	380.96
Ellisport Bay	14	7.72	39.99	4.94	25.60	0.03	0.16	0.53	2.76	13.23	436.38
Lake Site north	24	8.97	46.26	4.32	22.30	0.10	0.53	0.33	1.69	13.72	444.40
Lake Site south	19	12.98	45.47	7.90	27.69	0.11	0.39	0.20	0.69	21.19	721.48
September 12-13, 1998											
Scenic Bay	22	1.64	20.72	1.36	17.17	0.19	2.38	0.23	2.90	3.42	123.99
Idlewilde Bay	24	2.57	20.57	3.03	24.23	0.35	2.80	0.15	1.20	6.10	232.62
Garfield Bay	24	3.10	22.95	4.48	33.17	0.27	1.98	1.06	7.88	8.90	296.39
Ellisport Bay	24	4.18	31.30	4.10	30.70	0.13	0.94	0.87	6.50	9.26	285.48
Lake Site north	24	9.88	46.91	4.07	19.34	0.09	0.44	1.30	6.20	15.34	432.05
Lake Site south	24	9.71	54.45	3.71	20.82	0.18	0.98	0.25	1.40	13.85	414.58
October 17-18, 1998											
Scenic Bay	24	6.91	56.97	1.72	14.18	0.26	2.16	0.28	2.27	9.17	345.77
Idlewilde Bay	24	6.45	63.28	2.60	25.53	0.20	1.96	0.13	1.23	9.38	378.57
Garfield Bay	24	7.16	52.24	1.96	14.30	0.59	4.29	0.33	2.40	10.04	419.97
Ellisport Bay	24	16.28	61.37	1.63	6.13	0.06	0.22	1.00	3.77	18.96	571.44
Lake Site north	24	8.95	60.54	4.24	28.66	0.09	0.62	0.32	2.14	13.60	885.76
Lake Site south	24	7.15	63.57	2.88	25.55	0.10	0.85	0.17	1.52	10.30	398.76

Appendix Table 2.1. Cont.

Date and	*Daphnia*		*Bosmina*		*Diaphanasoma*		*Leptodora*		*Chydorus*		Total Cladoceran		Overall Total	
Location	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	% total	No./L	Biomass[a]/m3	No./L	Biomass[a]/m3
August 23-24, 1998 Cont.														
Garfield Bay	1.27	7.12	3.82	21.46	0.53	2.95	0.04	0.24	0.01	0.06	5.67	186.72	17.82	567.19
Ellisport Bay	2.16	11.19	2.88	14.92	1.00	5.16	0.03	0.13	0.02	0.11	6.16	292.99	19.31	729.25
Lake Site north	3.80	19.58	0.59	3.05	1.28	6.60	0.00	0.00	0.01	0.05	5.60	438.50	19.40	882.90
Lake Site south	3.45	12.08	0.71	2.49	2.84	9.94	0.05	0.19	0.31	1.09	7.36	479.37	28.55	1200.86
September 12-13, 1998														
Scenic Bay	0.42	5.34	4.00	50.53	0.08	1.00	0.00	0.00	0.00	0.00	4.50	97.09	7.91	221.09
Idlewilde Bay	0.24	1.90	5.58	44.63	0.34	2.70	0.00	0.00	0.25	1.97	6.40	130.00	12.50	362.62
Garfield Bay	0.27	1.98	3.85	28.54	0.45	3.30	0.02	0.15	0.01	0.06	4.59	104.35	13.49	400.74
Ellisport Bay	0.75	5.62	2.53	18.96	0.71	5.31	0.08	0.56	0.02	0.12	4.08	158.89	13.34	444.36
Lake Site north	1.21	5.74	3.75	17.81	0.75	3.56	0.01	0.04	0.00	0.00	5.72	207.32	21.06	639.37
Lake Site south	0.27	1.50	3.11	17.43	0.60	3.34	0.00	0.00	0.01	0.07	3.98	114.15	17.83	528.74
October 17-18, 1998														
Scenic Bay	0.25	2.06	1.85	15.21	0.87	7.14	0.00	0.00	0.00	0.00	2.96	87.69	12.13	433.46
Idlewilde Bay	0.10	0.94	0.22	2.17	0.50	4.86	0.00	0.00	0.01	0.04	0.82	35.93	10.20	414.50
Garfield Bay	0.13	0.96	3.11	22.66	0.44	3.18	0.00	0.00	0.00	0.00	3.67	81.60	13.71	501.57
Ellisport Bay	0.50	1.89	6.07	22.88	0.93	3.49	0.01	0.03	0.06	0.24	7.56	181.79	26.52	753.22
Lake Site north	0.16	1.13	0.06	0.39	0.96	6.51	0.00	0.00	0.00	0.00	1.19	61.69	14.78	683.28
Lake Site south	0.05	0.41	0.15	1.41	0.75	6.70	0.00	0.00	0.00	0.00	0.96	43.19	11.25	441.95
November 22, 1998														
Scenic Bay	0.00	0.00	0.15	3.41	0.01	0.42	0.00	0.00	0.00	0.00	0.16	3.83	3.41	113.96
Idlewilde Bay	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.39	0.85	35.95
Garfield Bay	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.02	1.06	7.25	268.71
Ellisport Bay	0.03	0.00	0.05	0.01	0.01	0.00	0.00	0.00	0.05	0.01	0.13	4.00	9.63	322.48
Lake Site north	0.00	0.00	0.00	0.00	.05	0.01	0.00	0.00	0.00	0.00	0.05	2.34	8.87	302.57
Lake Site south	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.48	2.27	83.64

Appendix Table 2.1. Cont.

Date and Location	N	*Cyclops* #/L	*Cyclops* %Total	*Diaptomus* #/L	*Diaptomus* %Total	*Epischura* #/L	*Epischura* %Total	Nauplii #/L	Nauplii %Total	Total Copepods #/L	Total Copepods Biomass^a/m3
November 22, 1998											
Scenic Bay	24	1.95	57.10	1.14	33.38	0.04	1.10	0.13	3.91	3.25	110.13
Idlewilde Bay	23	0.26	31.16	0.55	64.79	0.00	0.00	0.02	2.47	0.84	35.56
Garfield Bay	24	3.44	47.44	3.58	49.34	0.00	0.00	0.21	2.87	7.23	267.66
Ellisport Bay	24	5.50	57.16	3.67	38.12	0.00	0.00	0.32	3.33	9.50	318.48
Lake Site north	24	5.11	57.63	3.48	39.22	0.01	0.06	0.23	2.57	8.82	300.24
Lake Site south	24	1.12	49.27	1.10	48.35	0.00	0.00	0.04	1.84	2.25	83.16

Appendix Table 2.2. Results (F value and probability>F) from statistical analysis of mean monthly zooplankton density differences among depth strata.

Year	Month	F Value	Pr>F
1997	June	2.94	0.0350
	July	5.76	0.0009
	August	4.61	0.0041
	September	0.62	0.6013
	October	3.46	0.0179
	November	1.44	0.2327
	December	0.18	0.9081
1998	January	0.09	0.9663
	February	0.11	0.9570
	March	0.06	0.9801
	April	0.06	0.9815
	May	1.23	0.3014
	June	53.14	0.0001
	July	13.05	0.0001
	August	2.39	0.0709
	September	2.29	0.0803
	October	3.27	0.0228
	November	0.50	0.6808

Appendix Table 2.3. Estimated lengths of the four most abundant zooplankters in Lake Pend Oreille, 1997-1998.

Month and		*Cyclops*		*Diaptomus*		*Daphnia*		*Bosmina*
Location	N	Length ± (CI)	N	Length ± (CI)	N	Length ± (CI)	N	Length ± (CI)
June, 1997								
Scenic Bay							10	0.35 ± (0.059)
Idlewilde Bay							8	0.29 ± (0.061)
Garfield Bay					1	1.30	18	0.35 ± (0.043)
Ellisport Bay					1	0.90	360	0.28 ± (0.010)
Lake Site north								
Lake Site south							1	0.35
July, 1997								
Scenic Bay	1333	0.57 ± (0.012)	1227	0.66 ± (0.016)	23	0.75 ± (0.213)	402	0.32 ± (0.010)
Idlewilde Bay	791	0.58 ± (0.016)	731	0.66 ± (0.020)	24	0.78 ± (0.200)	243	0.32 ± (0.013)
Garfield Bay	740	0.55 ± (0.019)	605	0.65 ± (0.024)	39	0.80 ± (0.081)	385	0.32 ± (0.011)
Ellisport Bay	544	0.56 ± (0.021)	444	0.68 ± (0.042)	242	0.89 ± (0.060)	532	0.32 ± (0.013)
Lake Site north	399	0.60 ± (0.025)	400	0.72 ± (0.023)	13	0.72 ± (0.255)	68	0.31 ± (0.026)
Lake Site south	994	0.58 ± (0.007)	965	0.79 ± (0.103)	5	0.70 ± (1.058)	101	0.32 ± (0.021)
August, 1997								
Scenic Bay	1692	0.61 ± (0.028)	1528	0.82 ± (0.064)	1068	0.90 ± (0.027)	1172	0.31 ± (0.012)
Idlewilde Bay	1040	0.55 ± (0.013)	900	0.76 ± (0.021)	640	0.90 ± (0.034)	610	0.31 ± (0.009)
Garfield Bay	740	0.55 ± (0.019)	912	0.76 ± (0.024)	685	0.84 ± (0.036)	508	0.30 ± (0.009)
Ellisport Bay	1127	0.52 ± (0.013)	615	0.65 ± (0.029)	857	0.85 ± (0.030)	308	0.31 ± (0.019)
Lake Site north	399	0.60 ± (0.014)	975	0.77 ± (0.019)	633	0.88 ± (0.035)	173	0.32 ± (0.018)
Lake Site south	1128	0.57 ± (0.014)	965	0.79 ± (0.017)	584	0.92 ± (0.039)	132	0.35 ± (0.020)
September, 1997								
Scenic Bay	1240	0.58 ± (0.031)	895	0.77 ± (0.020)	669	1.04 ± (0.039)	103	0.33 ± (0.022)
Idlewilde Bay	720	0.55 ± (0.015)	572	0.79 ± (0.024)	445	1.06 ± (0.045)	187	0.32 ± (0.021)
Garfield Bay	780	0.52 ± (0.014)	459	0.76 ± (0.031)	410	0.95 ± (0.043)	292	0.32 ± (0.013)
Ellisport Bay	645	0.51 ± (0.021)	312	0.73 ± (0.040)	346	0.92 ± (0.053)	491	0.34 ± (0.014)

Appendix Table 2.3. Cont.

Month and	*Cyclops*		*Diaptomus*		*Daphnia*		*Bosmina*	
Location	N	Length ± (CI)	N	Length ± (CI)	N	Length ± (CI)	N	Length ± (CI)
September, 1997 Cont.								
Lake Site north	993	0.53 ± (0.013)	500	0.78 ± (0.024)	409	1.02 ± (0.049)	47	0.34 ± (0.036)
Lake Site south	986	0.55 ± (0.017)	785	0.79 ± (0.022)	436	1.08 ± (0.045)	60	0.36 ± (0.030)
October, 1997								
Scenic Bay	1572	0.59 ± (0.011)	893	0.85 ± (0.018)	2	0.98 ± (4.139)	247	0.33 ± (0.014)
Idlewilde Bay	948	0.58 ± (0.015)	450	0.84 ± (0.023)			65	0.32 ± (0.026)
Garfield Bay	867	0.58 ± (0.016)	567	0.86 ± (0.023)	5	0.87 ± (0.409)	230	0.39 ± (0.023)
Ellisport Bay	866	0.56 ± (0.017)	262	0.91 ± (0.025)	15	0.72 ± (0.593)	339	0.34 ± (0.013)
Lake Site north	900	0.59 ± (0.016)	756	0.88 ± (0.017)	6	0.71 ± (0.940)	128	0.37 ± (0.027)
Lake Site south	1312	0.57 ± (0.012)	695	0.84 ± (0.018)	14	0.52 ± (0.188)	37	0.35 ± (0.013)
November, 1997								
Scenic Bay	831	0.56 ± (0.016)	620	0.78 ± (0.020)			1	0.48
Idlewilde Bay	532	0.54 ± (0.017)	428	0.77 ± (0.027)				
Garfield Bay	665	0.59 ± (0.019)	500	0.84 ± (0.025)	1	0.75		
Ellisport Bay	830	0.58 ± (0.016)	346	0.79 ± (0.038)			30	0.41 ± (0.045)
Lake Site north	864	0.56 ± (0.014)	630	0.79 ± (0.020)			5	0.39 ± (0.159)
Lake Site south	522	0.54 ± (0.017)	385	0.77 ± (0.025)			1	0.26
December, 1997								
Scenic Bay	724	0.57 ± (0.012)	724	0.66 ± (0.023)				
Idlewilde Bay	490	0.56 ± (0.017)	444	0.66 ± (0.028)				
Garfield Bay	220	0.55 ± (0.028)	173	0.63 ± (0.047)	1	0.75		
Ellisport Bay	204	0.58 ± (0.028)	190	0.79 ± (0.039)				
Lake Site north	194	0.61 ± (0.025)	45	0.75 ± (0.105)				
Lake Site south	516	0.57 ± (0.017)	473	0.66 ± (0.028)			1	0.52

Appendix Table 2.3. Cont.

Month and	*Cyclops*		*Diaptomus*		*Daphnia*		*Bosmina*	
Location	N	Length ± (CI)	N	Length ± (CI)	N	Length ± (CI)	N	Length ± (CI)
January, 1998 Cont.								
Scenic Bay	221	0.87 ± (0.028)	153	0.60 ± (0.058)				
Idlewilde Bay								
Garfield Bay								
Ellisport Bay								
Lake Site north								
Lake Site south								
February, 1998								
Scenic Bay	168	0.67 ± (0.028)	259	0.51 ± (0.033)				
Idlewilde Bay	68	0.63 ± (0.041)	81	0.51 ± (0.064)				
Garfield Bay	126	0.64 ± (0.034)	130	0.57 ± (0.049)				
Ellisport Bay	75	0.71 ± (0.027)	85	0.60 ± (0.070)				
Lake Site north	171	0.63 ± (0.028)	291	0.57 ± (0.033)				
Lake Site south	93	0.63 ± (0.029)	139	0.50 ± (0.031)				
March, 1998								
Scenic Bay	136	0.71 ± (0.080)	179	0.49 ± (0.090)			2	0.40 ± (0.444)
Idlewilde Bay								
Garfield Bay								
Ellisport Bay								
Lake Site north								
Lake Site south								
April, 1998								
Scenic Bay								
Idlewilde Bay								
Garfield Bay								
Ellisport Bay								

Appendix Table 2.3. Cont.

Month and	*Cyclops*		*Diaptomus*		*Daphnia*		*Bosmina*	
Location	N	Length ± (CI)	N	Length ± (CI)	N	Length ± (CI)	N	Length ± (CI)
April, 1998 Cont.								
Lake Site north								
Lake Site south								
May, 1998								
Scenic Bay	1145	0.56 ± (0.015)	337	0.74 ± (0.037)	6	0.73 ± (0.450)	75	0.37 ± (0.040)
Idlewilde Bay							29	0.35 ± (0.045)
Garfield Bay					3	0.89 ± (2.869)	1364	0.37 ± (0.016)
Ellisport Bay					10	0.74 ± (0.227)	381	0.36 ± (0.011)
Lake Site north					3	0.60 ± (0.187)	92	0.38 ± (0.049)
Lake Site south							9	0.36 ± (0.355)
June, 1998								
Scenic Bay	2241	0.58 ± (0.013)	1376	0.69 ± (0.020)	27	0.70 ± (0.136)	427	0.36 ± (0.013)
Idlewilde Bay					66	0.78 ± (0.105)	295	0.34 ± (0.105)
Garfield Bay					76	0.68 ± (0.073)	887	0.31 ± (0.012)
Ellisport Bay					324	0.88 ± (0.068)	1144	0.36 ± (0.014)
Lake Site north					54	0.80 ± (0.081)	84	0.34 ± (0.027)
Lake Site south					30	0.94 ± (0.200)	81	0.34 ± (0.028)
July, 1998								
Scenic Bay	573	0.61 ± (0.017)	348	0.71 ± (0.034)	204	0.74 ± (0.045)	271	0.41 ± (0.032)
Idlewilde Bay					386	0.81 ± (0.063)	473	0.33 ± (0.010)
Garfield Bay					123	0.76 ± (0.065)	485	0.32 ± (0.015)
Ellisport Bay					111	0.78 ± (0.107)	1144	0.36 ± (0.014)
Lake Site north					128	0.76 ± (0.076)	42	0.40 ± (0.093)
Lake Site south					304	0.76 ± (0.043)	134	0.33 ± (0.019)

Appendix Table 2.3. Cont.

Month and	*Cyclops*		*Diaptomus*		*Daphnia*		*Bosmina*	
Location	N	Length ± (CI)	N	Length ± (CI)	N	Length ± (CI)	N	Length ± (CI)
August, 1998								
Scenic Bay	143	0.64 ± (0.028)	163	0.64 ± (0.042)	94	1.24 ± (0.074)	78	0.32 ± (0.017)
Idlewilde Bay					132	1.21 ± (0.059)	62	0.32 ± (0.021)
Garfield Bay					178	1.05 ± (0.071)	338	0.31 ± (0.021)
Ellisport Bay					97	1.13 ± (0.066)	87	0.32 ± (0.013)
Lake Site north					150	1.17 ± (0.087)	49	0.33 ± (0.037)
Lake Site south					108	1.12 ± (0.067)	36	0.32 ± (0.022)
September, 1998								
Scenic Bay	157	0.59 ± (0.044)	145	0.74 ± (0.133)	5	1.07 ± (0.439)	333	0.35 ± (0.011)
Idlewilde Bay					56	1.41 ± (0.179)	352	0.33 ± (0.012)
Garfield Bay					39	1.05 ± (0.157)	280	0.31 ± (0.010)
Ellisport Bay					171	1.10 ± (0.050)	367	0.30 ± (0.013)
Lake Site north					266	1.11 ± (0.098)	510	0.32 ± (0.012)
Lake Site south					93	1.26 ± (0.112)	539	0.33 ± (0.012)
October, 1998								
Scenic Bay	529	0.70 ± (0.032)	359	0.92 ± (0.038)	56	0.87 ± (0.159)	287	0.34 ± (0.017)
Idlewilde Bay					29	0.99 ± (0.210)	65	0.34 ± (0.021)
Garfield Bay					34	0.91 ± (0.052)	211	0.34 ± (0.015)
Ellisport Bay					100	0.86 ± (0.118)	172	0.35 ± (0.012)
Lake Site north					36	0.97 ± (2.426)	3	0.30 ± (0.152)
Lake Site south					13	0.95 ± (0.449)	36	0.39 ± (0.013)
November, 1998								
Scenic Bay	321	0.62 ± (0.025)	205	0.86 ± (0.036)			32	0.40 ± (0.022)
Idlewilde Bay								
Garfield Bay								
Ellisport Bay					5	1.33 ± (0.212)	9	0.38 ± (0.048)

Appendix Table 2.3. Cont.

Month and Location	*Cyclops* N	*Cyclops* Length ± (CI)	*Diaptomus* N	*Diaptomus* Length ± (CI)	*Daphnia* N	*Daphnia* Length ± (CI)	*Bosmina* N	*Bosmina* Length ± (CI)
November, 1998 Cont.								
Lake Site north								
Lake Site south								

Appendix Table 3.1. Weekly variation in percent of empty stomachs and condition factor for age-0 kokanee captured in Lake Pend Oreille in May and June, 1998.

Week	Number Sampled	%Empty Stomachs	Condition Factor ± (SE)[a]
5/21 to 5/30	3	66.70	.590 ± (.0138)
5/31 to 6/6	15	53.3	.618 ± (.0157)
6/7 to 6/13	74	40.5	.620 ± (.0066)
6/14 to 6/20	142	23.2	.613 ± (.0061)
6/21 to 6/28	82	14.6	.617 ± (.0890)

[a] SE indicates one standard error.

Appendix Table 3.2. Capture date, total length (mm), blotted wet weight (g), Fulton condition factor (K), and prey biomass (µg) in the stomachs of individual age-0 kokanee sampled from Lake Pend Oreille in May and June, 1998.

Capture Date	Total Length	Weight	Condition Factor	Prey Biomass
5/21/98	23	0.0692	0.5688	590.86
5/30/98	24	0.0811	0.5867	0.00
5/30/98	24	0.0852	0.6163	0.00
6/1/98	23	0.0762	0.6263	29.93
6/1/98	26	0.1153	0.6560	38.64
6/1/98	25	0.1197	0.7660	1175.89
6/2/98	24	0.0873	0.6315	0.00
6/2/98	22	0.0599	0.5625	464.37
6/2/98	23	0.0745	0.6123	0.00
6/2/98	24	0.0822	0.5946	0.00
6/2/98	25	0.0937	0.5997	0.00
6/2/98	24	0.0782	0.5657	29.93
6/2/98	24	0.0719	0.5201	486.59
6/4/98	22	0.0660	0.6198	0.00
6/4/98	24	0.0944	0.6829	0.00
6/4/98	22	0.0687	0.6451	0.00
6/4/98	23	0.0815	0.6698	0.00
6/4/98	25	0.0893	0.5715	2764.91
6/8/98	21	0.0598	0.6457	329.23
6/11/98	20	0.0546	0.6825	0.00
6/11/98	21	0.0575	0.6209	0.00
6/11/98	23	0.0644	0.5293	149.65
6/11/98	22	0.0689	0.6471	89.79
6/11/98	23	0.0697	0.5729	0.00
6/11/98	21	0.0701	0.7570	0.00
6/11/98	23	0.0706	0.5803	0.00
6/11/98	23	0.0728	0.5983	589.37
6/11/98	23	0.0738	0.6066	149.65
6/11/98	24	0.0753	0.5447	389.09
6/11/98	24	0.0802	0.5802	0.00
6/11/98	23	0.0809	0.6649	0.00
6/11/98	24	0.0814	0.5888	0.00
6/11/98	23	0.0827	0.6797	0.00
6/11/98	24	0.0827	0.5982	0.00
6/11/98	25	0.1090	0.6976	2148.16
6/11/98	25	0.1127	0.7213	2505.82
6/11/98	23	0.0617	0.5071	666.17
6/11/98	22	0.0796	0.7476	0.00
6/11/98	23	0.0798	0.6559	2149.65
6/11/98	23	0.0817	0.6715	2785.31
6/11/98	23	0.0832	0.6838	0.00
6/11/98	24	0.0852	0.6163	0.00
6/11/98	25	0.0872	0.5581	0.00
6/11/98	23	0.0872	0.7167	0.00
6/11/98	24	0.0954	0.6901	0.00
6/11/98				0.00
6/13/98	23	0.0829	0.6814	0.00

Appendix Table 3.2. Cont.

Capture Datete	Total Length	Weight	Condition Factor	Prey Biomass
6/13/98	25	0.0887	0.5677	2641.55
6/13/98	22	0.0494	0.4640	0.00
6/13/98	21	0.0574	0.6198	0.00
6/13/98	22	0.0641	0.6020	478.88
6/13/98	22	0.0675	0.6339	1709.56
6/13/98	24	0.0690	0.4991	1795.8
6/13/98	22	0.0695	0.6527	389.09
6/13/98	22	0.0704	0.6612	0.00
6/13/98	23	0.0717	0.5893	0.00
6/13/98	23	0.0722	0.5934	0.00
6/13/98	23	0.0731	0.6008	0.00
6/13/98	23	0.0752	0.6181	0.00
6/13/98	24	0.0796	0.5758	3479.59
6/13/98	24	0.0831	0.6011	1354.56
6/13/98	24	0.0851	0.6156	2567.18
6/13/98	24	0.0877	0.6344	0.00
6/13/98	25	0.0947	0.6061	1826.64
6/13/98	24	0.0989	0.7154	0.00
6/13/98	25	0.0992	0.6349	2102.81
6/13/98	22	0.0640	0.6011	0.00
6/13/98	23	0.0644	0.5293	1436.64
6/13/98	22	0.0658	0.6180	1286.99
6/13/98	22	0.0669	0.6283	2934.05
6/13/98	25	0.0798	0.6559	3053.77
6/13/98	23	0.0815	0.6698	779.09
6/13/98	24	0.0854	0.6178	29.93
6/13/98	25	0.0864	0.5530	4190.20
6/13/98	25	0.0918	0.5875	3272.72
6/13/98	24	0.0927	0.6706	2828.84
6/13/98	24	0.0934	0.6756	5111.23
6/13/98	25	0.0936	0.5990	2687.81
6/13/98	23	0.0687	0.5646	0.00
6/13/98	23	0.0708	0.5819	239.44
6/13/98	23	0.0710	0.5835	119.72
6/13/98	23	0.0722	0.5934	0.00
6/13/98	23	0.0783	0.6435	2448.95
6/13/98	24	0.0795	0.5751	1773.58
6/13/98	23	0.0809	0.6649	0.00
6/13/98	24	0.0817	0.5910	0.00
6/13/98	24	0.0829	0.5997	0.00
6/13/98	24	0.0872	0.7167	867.97
6/13/98	23	0.0872	0.7167	29.93
6/13/98	25	0.0921	0.5894	3907.23
6/13/98	25	0.0929	0.5946	4029.93
6/13/98	25	0.0963	0.6163	2581.69
6/13/98	25	0.1009	0.6976	0.00
6/13/98	25	0.1095	0.7008	2029.93
6/13/98	30	0.1896	0.7022	2311.82
6/14/98	24	0.0640	0.4630	404.51
6/14/98	22	0.0672	0.6311	755.96
6/14/98	22	0.0695	0.6527	0.00
6/14/98	22	0.0732	0.6875	0.00
6/14/98	23	0.0761	0.6254	1242.55
6/14/98	24	0.0788	0.5700	1969.49

Appendix Table 3.2. Cont.

Capture Datete	Total Length	Weight	Condition Factor	Prey Biomass
6/14/98h	25	0.1000	0.6400	3310.69
6/14/98	26	0.1101	0.6264	2763.09
6/14/98	22	0.0611	0.5738	127.43
6/14/98	23	0.0776	0.6378	2627.95
6/14/98	23	0.0797	0.6551	160.00
6/14/98	24	0.0798	0.5773	935.54
6/14/98	24	0.0813	0.5881	1505.12
6/14/98	25	0.0817	0.5229	748.25
6/14/98	24	0.0851	0.6156	1706.92
6/14/98	24	0.0859	0.6214	187.29
6/14/98	24	0.0950	0.6872	2133.65
6/14/98	25	0.0967	0.6189	2364.47
6/16/98	22	0.0624	0.5860	0.00
6/16/98	22	0.0649	0.6295	0.00
6/16/98	23	0.0674	0.5540	0.00
6/16/98	24	0.0674	0.4876	508.81
6/16/98	22	0.0683	0.6414	97.50
6/16/98	24	0.0733	0.5302	966.38
6/16/98	23	0.0777	0.6386	0.00
6/16/98	24	0.0792	0.5729	1257.06
6/16/98	24	0.0819	0.5924	0.00
6/16/98	24	0.0841	0.6084	1692.50
6/16/98	25	0.0854	0.5466	2821.13
6/16/98	25	0.0856	0.5478	2610.53
6/16/98	25	0.0943	0.6035	1308.62
6/16/98	24	0.0947	0.6850	0.00
6/16/98	26	0.1062	0.6042	3311.27
6/16/98	28	0.1338	0.6095	1183.6
6/16/98	31	0.2363	0.7931	7295.61
6/16/98	23	0.0773	0.6353	0.00
6/16/98	24	0.0774	0.5598	778.18
6/16/98	24	0.0881	0.6372	1974.79
6/16/98	25	0.0987	0.6317	1203.41
6/16/98	26	0.1229	0.6992	3043.06
6/16/98	26	0.1253	0.7129	3451.57
6/16/98	23	0.0523	0.4298	89.79
6/16/98	24	0.0650	0.4702	1061.47
6/16/98	24	0.0697	0.5042	1354.56
6/16/98	23	0.0697	0.5729	1092.9
6/16/98	23	0.0701	0.5761	0.00
6/16/98	26	0.0750	0.4267	420.83
6/16/98	24	0.0795	0.5751	2424.33
6/16/98	25	0.0873	0.5587	1549.56
6/16/98	28	0.1685	0.7676	1765.87
	29	0.1784	0.7315	8171.7
6/16/98				883.39
6/16/98	22	0.0589	0.5532	0.00
6/18/98	23	0.0678	0.5572	973.18
6/18/98	22	0.0704	0.6611	0.00
6/18/98	24	0.0740	0.5353	149.65
6/18/98	27	0.1427	0.7250	6000.00
6/18/98	27	0.1526	0.7753	6742.87
6/18/98	23	0.0720	0.5918	0.00
6/18/98	24	0.0805	0.5823	1489.70
6/18/98	24	0.0914	0.6612	1280.19
6/18/98	23	0.0924	0.7594	1986.64
6/18/98	26	0.0992	0.5644	2858.77
6/18/98	23	0.0717	0.5893	0.00
6/18/98	23	0.0823	0.6764	0.00

Appendix Table 3.2. Cont.

Capture Datete	Total Length	Weight	Condition Factor	Prey Biomass
6/18/98a	23	0.0866	0.7118	29.93
6/18/98	23	0.0690	0.5671	0.00
6/18/98	24	0.0727	0.5259	2454.26
6/18/98	23	0.0701	0.5761	0.00
6/19/98	23	0.0716	0.5885	2895.82
6/19/98	23	0.0768	0.6312	0.00
6/19/98	22	0.0617	0.5794	0.00
6/19/98	24	0.0756	0.5469	718.32
6/19/98	23	0.0820	0.6740	0.00
6/19/98	25	0.1030	0.6592	3452.39
6/19/98	24	0.0790	0.5715	0.00
6/19/98	25	0.0886	0.5670	1160.47
6/19/98	25	0.1201	0.7686	2890.52
6/19/98	30	0.1928	0.7141	6067.57
6/19/98	24	0.0874	0.6322	3158.98
6/19/98	24	0.0920	0.6655	1573.78
6/19/98	25	0.0984	0.6298	5558.75
6/19/98	29	0.1732	0.7102	10312.65
6/19/98	31	0.2346	0.7875	9492.61
6/19/98	22	0.0568	0.5334	598.60
6/19/98	22	0.0658	0.6180	29.93
6/19/98	23	0.0695	0.5712	0.00
6/19/98	22	0.0696	0.6536	0.00
6/19/98	23	0.0697	0.5729	0.00
6/19/98	23	0.0728	0.5983	0.00
6/19/98	23	0.0759	0.6238	0.00
6/19/98	25	0.0945	0.6048	1423.04
6/19/98	22	0.0598	0.5616	2003.81
6/19/98	24	0.0676	0.4890	2711.74
6/19/98	23	0.0748	0.6148	4601.17
6/19/98	24	0.0769	0.5563	89.79
6/19/98	25	0.0797	0.5101	4458.60
6/19/98	25	0.0818	0.5235	1893.30
6/19/98	25	0.0867	0.5549	2617.83
6/19/98	25	0.0938	0.6003	4369.23
6/19/98	26	0.0952	0.5416	0.00
6/19/98	26	0.0971	0.5525	3176.32
6/19/98	27	0.1240	0.6300	4683.84
6/19/98	31	0.2318	0.7781	3115.18
6/19/98	23	0.0665	0.5466	269.37
6/19/98	23	0.0718	0.5901	29.93
6/19/98	23	0.0773	0.6353	2478.19
6/19/98	25	0.0889	0.5690	2677.69
6/19/98	25	0.1101	0.7046	4245.56
6/19/98	24	0.0725	0.5244	29.93
6/19/98	23	0.0767	0.6304	0.00
6/19/98	24	0.0869	0.6286	2073.20
6/19/98	26	0.1155	0.6571	2502.01
6/19/98	23	0.0773	0.6353	2478.19
6/20/98	24	0.0924	0.6684	88.29
6/20/98	25	0.0943	0.6035	4020.15
6/20/98	25	0.1002	0.6413	3560.17
6/20/98	26	0.1036	0.5894	2449.86
6/20/98	25	0.1192	0.7629	6435.86
6/20/98	22	0.0687	0.6452	0.00
6/20/98	23	0.0758	0.6230	0.00
6/20/98	24	0.0764	0.5527	718.32
6/20/98	23	0.0789	0.6485	0.00
6/20/98	24	0.0828	0.5990	2950.37

Appendix Table 3.2. Cont.

Capture Datete	Total Length	Weight	Condition Factor	Prey Biomass
6/20/98b	26	0.1124	0.6395	2628.18
6/20/98	24	0.0700	0.5264	0.00
6/20/98	25	0.0888	0.5683	862.08
6/20/98	25	0.0898	0.5747	2110.52
6/20/98	23	0.0705	0.5794	2818.13
6/20/98	23	0.0753	0.6189	1691.50
6/20/98	23	0.0775	0.6370	2664.68
6/20/98	24	0.0817	0.5910	2933.03
6/20/98	24	0.0865	0.6257	584.09
6/20/98	27	0.1598	0.8119	5317.83
6/20/98				966.38
6/20/98	25	0.1131	0.7238	3210.63
6/20/98	24	0.0984	0.7118	3175.20
6/20/98	29	0.1898	0.7782	9135.25
6/20/98	22	0.0573	0.5381	0.00
6/23/98	23	0.0626	0.5145	0.00
6/23/98	24	0.0778	0.5629	0.00
6/23/98	25	0.0818	0.5235	666.17
6/23/98	28	0.1539	0.7011	2662.48
6/23/98				3087.12
6/23/98	26	0.1090	0.6202	353.16
6/23/98	28	0.1635	0.7448	3123.85
6/23/98	24	0.0822	0.5946	2638.07
6/23/98	32	0.2422	0.7391	8706.61
6/23/98	25	0.0773	0.4947	2614.83
6/23/98	24	0.0741	0.5360	3235.35
6/23/98	24	0.0694	0.5020	2446.76
6/23/98	22	0.0571	0.5363	0.00
6/23/98	22	0.0609	0.5719	823.53
6/23/98	22	0.0661	0.6208	0.00
6/23/98	23	0.0815	0.6682	2000.00
6/23/98	24	0.0816	0.5903	0.00
6/23/98	24	0.0858	0.6207	875.68
6/23/98				696.27
6/23/98	23	0.0873	0.7175	1703.01
6/23/98	22	0.0544	0.5109	0.00
6/23/98	22	0.0584	0.5485	389.09
6/23/98	24	0.0655	0.4738	1269.69
6/23/98	23	0.0759	0.6238	0.00
6/23/98	23	0.0765	0.6288	29.93
6/23/98	23	0.0829	0.6814	1229.85
6/23/98	23	0.0835	0.6863	59.86
6/23/98	24	0.0860	0.6221	763.67
6/23/98	25	0.0861	0.5510	29.93
6/23/98	25	0.0923	0.5907	2374.86
6/23/98	24	0.0930	0.6727	1719.93
6/23/98	26	0.1209	0.6879	1865.19
6/23/98	26	0.1216	0.6918	2281.80
6/23/98	26	0.1271	0.7231	2096.92
6/23/98	27	0.1542	0.7834	4457.97
6/23/98	22	0.0633	0.5945	29.93
6/23/98	24	0.0970	0.7017	3158.98
6/23/98	25	0.0902	0.5773	4407.58
6/23/98	23	0.0750	0.6164	0.00
6/23/98	26	0.1433	0.8153	3745.37
6/23/98	34	0.3276	0.8335	4089.79
6/23/98	24	0.0806	0.5830	2089.62
6/23/98	24	0.0746	0.5396	209.51
6/24/98	26	0.0750	0.4267	269.37

Appendix Table 3.2. Cont.

Capture Datete	Total Length	Weight	Condition Factor	Prey Biomass
6/24/98	25	0.0790	0.5056	2473.41
6/24/98	25	0.0800	0.5120	2433.86
6/24/98	24	0.0849	0.6141	2505.82
6/24/98	25	0.0979	0.6266	4338.67
6/24/98	26	0.1060	0.6031	16611.15
	0.0887			
6/24/98	25	0.093	0.5952	2733.05
6/24/98	26	0.1204	0.6850	4967.83
6/24/98	28	0.1249	0.5690	6000.00
6/24/98	28	0.1373	0.6255	8030.37
6/24/98	27	0.1416	0.7194	4205.24
6/24/98	30	0.1693	0.6270	2521.45
6/24/98	24	0.0892	0.653	0.00
6/24/98	26	0.1109	0.6310	5362.39
6/24/98	25	0.0865	0.5536	2966.2
	0.0892			
6/24/98	26	0.1088	0.6190	6416.57
6/24/98	28	0.1555	0.7084	14029.93
6/24/98	24	0.0913	0.6604	0.00
6/24/98	25	0.0762	0.4877	3186.01
6/24/98	25	0.0961	0.6150	3232.38
6/24/98	23	0.0662	0.5441	2544.18
6/24/98	24	0.0869	0.6286	0.00
6/24/98	25	0.0901	0.5766	97.50
6/24/98	24	0.0873	0.6315	1903.13
6/24/98	26	0.1046	0.5951	3889.23
6/24/98	23	0.0897	0.7372	5099.05
6/24/98	24	0.0779	0.5635	1001.02
6/24/98	27	0.1191	0.6051	4661.20
6/24/98	25	0.0731	0.4678	119.72
6/27/98	23	0.0813	0.6682	4083.32
6/27/98	24	0.0859	0.6214	1385.40
6/27/98	24	0.0910	0.6583	3046.06
6/27/98	25	0.1037	0.6637	2155.87
6/27/98	28	0.1535	0.6993	2179.00
6/27/98				1436.64
6/27/98	24	0.0824	0.5961	5263.54
6/27/98	32	0.2240	0.6836	8338.42
6/28/98	25	0.1046	0.6694	5537.05
6/28/98	24	0.0852	0.6163	2619.64

Appendix Table 3.3. Percent of each food type to the total food items eaten (%N), percent wet biomass to the total mass of food items eaten (%M), and frequency of occurrence (FO) for age-0 kokanee captured in Lake Pend Oreille in May and June, 1998.

	5/21 to 5/30 (n=3)			5/31 to 6/6 (n=15)			6/7 to 6/13 (n=75)			6/14 to 6/20 (n=144)			6/21 to 6/28 (n=85)		
Prey Item	(%N)	(%M)	(FO)	(%N)	(%M)	(FO)	(%N)	(%M)	(FO)	(%N)	(%M)	(FO)	(%N)	(%M)	(FO)
Daphnia spp.[a]							0.09	0.23	2.67	1.54	3.37	19.31	5.32	11.14	48.24
Bosmina				0.64	0.68	6.67	0.05	0.05	1.33	0.12	0.12	4.83	0.28	0.26	10.59
Diaphanasoma													0.06	0.13	3.53
Leptodora															
Chydorus													0.02	0.02	1.18
Cyclops	100.00	100.00	33.33	82.80	68.42	26.67	95.79	80.86	57.33	91.24	66.81	73.79	88.43	62.06	83.53
Diaptomus				16.56	30.90	20.00	2.76	5.27	26.67	6.01	9.88	56.55	6.00	9.74	64.71
Epischura							0.18	0.82	4.00	0.08	0.30	3.45	0.02	0.08	1.18
nauplii										0.06	0.001	2.76	0.12	0.003	5.88
Mysis							0.23	12.78	5.33	0.39	19.45	8.28	0.34	16.56	7.06

[a] *Daphnia thorata* and *D. galeata mendotae*.

Appendix Table 3.4. Prey selectivity index values for individual zooplankton species. Zooplankton sampling and age-0 kokanee capture were conducted in Scenic and Idlewilde bays, Lake Pend Oreille.

		Selectivity Index[a]								
Zooplankton Sampling Dates	Kokanee Capture Dates	*Daphnia spp.*[b]	*Bosmina*	*Diaphanasoma*	*Leptodora*	*Chydorus*	*Diaptomus*	*Cyclops*	*Epischura*	nauplii
5/30/98	5/21 to 5/30/98	-0.001	-0.006	0	0	-0.003	-0.116	0.199	-0.004	-0.067
6/6/98	6/1 to 6/8/98	0.000	0.003	0.000	0	0.000	0.083	-0.056	-0.001	-0.029
6/12/98	6/11 to 6/14/98	-0.002	-0.017	0.000	0	0.000	-0.059	0.108	0.000	-0.033
6/17[c] & 6/20[d]	6/16 to 6/20/98	0.016	-0.011	0.000	0	0.000	-0.166	0.174	0.000	-0.018
6/26/98	6/23 to 6/28/98	0.002	0.028	0.000	0	0.000	0.264	0.695	0.000	0.007

[a] Selectivity Index values range from -1 to 1 (Strauss 1979). Table values of 0.000 indicate results < 0.001.
[b] *Daphnia thorata* and *D. galeata mendotae*..
[c] Samples collected in Scenic Bay.
[d] Samples collected in Idlewilde Bay.

POPULATION ESTIMATES, FOOD HABITS AND ESTIMATES OF CONSUMPTION OF SELECTED PREDATORY FISHES IN LAKE PEND OREILLE, IDAHO

A Thesis
Presented in Partial Fulfillment of the Requirements for the
Degree of Master of Science
with a
Major in Fisheries Resources
in the
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University of Idaho

by
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Major Professor: David H. Bennett, Ph.D.

ABSTRACT

In Lake Pend Oreille, Idaho from April 1997 through April 1999, 449 kamloops (rainbow trout) *Oncorhynchus mykiss*, 348 bull trout *Salvelinus confluentus*, and 165 lake trout *Salvelinus namaycush* ≥ 406 mm fork length were tagged by volunteer anglers and 39 kamloops, 42 bull trout, and 19 lake trout were recaptured. Movement of recaptured fish varied from less than 1 km to approximately 30 km, and time between tagging and recapture varied from 3 days to 667 days. A Chapman's mark-recapture model estimated 14,607 kamloops, 12,134 bull trout, and 1,792 lake trout ≥ 406 mm fork length. Kamloops ≥ 406 mm averaged 597 mm and ranged from age 4 to 9. Bull trout ≥ 406 mm averaged 524 mm and ranged from age 6 to 12, and lake trout ≥ 406 mm averaged 605 mm and ranged from age 6 to 11.

Stomach samples were collected from kamloops (n = 180), bull trout (n = 11), lake trout (n = 242), northern pikeminnow *Ptychocheilus oregonensis* (n = 3,322), and other predatory fishes (n = 782) sampled by electrofishing and angling. Stomach samples were taken from harvested fish and non-lethally from non-harvested fishes using lavage techniques. Dietary analysis indicated that kamloops (77%), bull trout (66%), and lake trout (87%) fed primarily on kokanee *O. nerka*, whereas northern pikeminnow and other predatory fishes sampled fed primarily on insects, other fishes, and miscellaneous prey items.

Bioenergetic modeling indicated that in Lake Pend Oreille kamloops, bull trout, and lake trout collectively consumed more than 153.5 metric tons-mt (65%) of the 235.2 mt of kokanee produced (e.g. biomass gained/yr) 95% CI: [105.4 mt, 286.3 mt] in 1998 explaining 73% of the kokanee biomass lost. Kamloops constitute 82% of the pelagic predator biomass and consumed 53% of the annual kokanee production, whereas bull trout (14% of the biomass) consumed 10%, and lake trout (4% of the

biomass) consumed 2%. Kamloops, bull trout, and lake trout constituted a major source of mortality to subadult/adult kokanee in Lake Pend Oreille in 1997-1998.

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INTRODUCTION

Lake Pend Oreille, Idaho, has produced the world record rainbow trout (kamloops) *Oncorhynchus mykiss* (16.8 kg) and bull trout *Salvelinus confluentus* (14.5 kg), supported commercial harvests of kokanee *O. nerka* and opossum shrimp *Mysis relicta*, and provided a variety of fishing opportunities for a wide spectrum of angler interests. However, in the last 40 years, fisheries for kokanee, rainbow trout, and bull trout have declined and presently provide limited angler opportunities. The sport fishery for lake trout *S. namaycush,* however, has increased.

Presently, Lake Pend Oreille provides fisheries for trophy kamloops and bull trout and a consumptive fishery for kokanee (Maiolie and Elam 1992). The Gerrard strain of rainbow trout (kamloops) *O. m. gairdneri* was introduced into Lake Pend Oreille in 1941. Kokanee were first observed in the early 1930's after presumably migrating downstream from Flathead Lake, Montana (Stross 1954). In addition, sport fisheries exist for brown trout *Salmo trutta*, lake whitefish *Coregonus clupeaformis*, cutthroat trout *O. clarki*, and in recent years lake trout, which were introduced in the early 1920's. Creel surveys conducted by Idaho Department of Fish and Game (IDFG) in 1990 showed approximately 38% of anglers fished for kokanee while 60% fished for trout and char species (Paragamian et al. 1991).

The kokanee harvest is presently at 20% of its historic level because of population declines, supporting a recreational fishery of less than 200,000 fish annually (Maiolie and Elam 1993; Paragamian et al. 1991). In Lake Pend Oreille, kokanee, an important component of the food web, have provided both a prey base, enhancing the growth of predatory fishes, and a fishery for over 60 years (Wydoski and Bennett 1981). One of the lake recovery goals established by IDFG is to sustain an annual harvest of 750,000 kokanee.

Understanding the flow of energy between trophic levels is imperative to effectively manage fisheries in a lentic ecosystem (Ney 1981). The bioenergetic demands of fish predators and the effect of these demands on the Lake Pend Oreille ecosystem are not fully understood. However, recently initiated research projects are examining many factors thought to be contributing to the decline of kokanee, including: kokanee/opossum shrimp interactions (Chipps and Bennett 2000), zooplankton abundance and availability (Chipps 1997; Clarke 1999), quality and quantity of spawning habitat (Idaho Department of Fish and Game, unpublished), and the influence of predation on kokanee abundance.

Predatory salmonids (kamloops, bull trout, and lake trout) in Lake Pend Oreille reportedly rely heavily on kokanee as a prey item (Anderson 1978; Pratt 1985; Rieman and Falter 1981). Finding a balance between forage fish and predators requires a detailed look at both the environment and species relationships (Wydoski and Bennett 1981). This project was conducted because no known research has quantified predation by these salmonid fishes or assessed effects of predation upon the kokanee population by these fishes in Lake Pend Oreille.

The overall objectives of the project were:

OBJECTIVES

1. Estimate the population abundance of kamloops, bull trout, and lake trout $\geq$ 406 mm in Lake Pend Oreille, Idaho;
2. Identify food items in the stomachs of kamloops, bull trout, lake trout $\geq$ 406 mm and northern pikeminnow $\geq$ 100 mm from Lake Pend Oreille, Idaho; and
3. Estimate kokanee consumed by kamloops, bull trout, lake trout $\geq$ 406 mm and relative consumption by kamloops, bull trout, lake trout and northern pikeminnow in Lake Pend Oreille, Idaho.This thesis will treat each objective as a separate chapter.

STUDY AREA

Lake Pend Oreille is a meso-oligotrophic body of water located in the Panhandle region of northern Idaho (Rieman and Falter 1981; Figure 1.1). Lake Pend Oreille is fed by streams originating in the Selkirk Mountains to the Northwest, the Cabinet Mountains to the Northeast and the Coeur d'Alene Mountains to the East. The lake is contained in the glacially formed Purcell Trench. It is the largest natural lake in Idaho and the fifth deepest lake in the nation with a mean depth of 164 m and a maximum depth of 351 m. The lake's major inlet, the Clark Fork River, is regulated by Cabinet Gorge Hydroelectric Development (circa 1952) and the outlet, the Pend Oreille River, is regulated by Albeni Falls Hydroelectric Development (circa 1952). Lake Pend Oreille has a surface area of about 38,300 ha, 59% of which is considered to be deep water habitat (>15m) suitable throughout the year for kokanee (Paragamian et al. 1991).

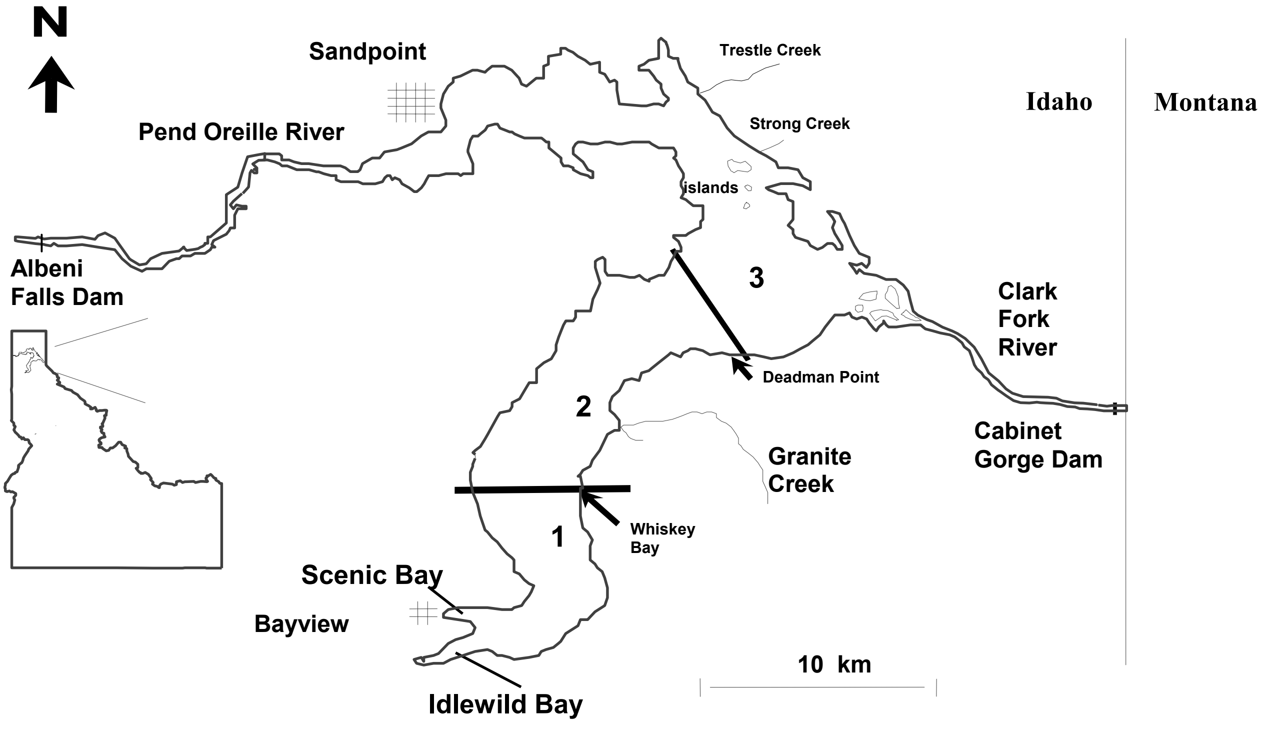


Figure 1.1. The Lake Pend Oreille study area in northern Idaho, showing samplng sections (1-3)

Objective One

POPULATION DYNAMICS

INTRODUCTION

Understanding the influence of a particular fish species upon its ecosystem involves examining each of the component parts. Multiple species must be addressed in ecosystem approaches to fisheries management; otherwise assessing individual populations can be unrealistic and misleading. Growth characteristics of each species, including length at age, weight at age, and mortality, in addition to population estimates are essential components to a thorough understanding of population dynamics. Based on sampling concerns expressed by Everhart and Youngs (1981) four major constraints are apparent in pelagic waters: 1) sampling fishes using traditional methods (electrofishing, gillnetting, trap nets, or set lines) is not always effective. Angling, in some cases, may be the only feasible sampling technique within the constraints of the project. However, without proper planning, angling may not be efficient. 2) Standardizing a mark-recapture study that can be used on multiple species is only possible if the same tag (methods) can be safely applied and retained by each species through the recapture effort. 3) Special considerations must be made when dealing directly or indirectly with threatened or endangered species. 4) Often, research involves or requires the cooperation of anglers, the media, and a variety of other constituents which demands special social, political, and economic organization. All of these constraints were factored into my assessment of the population abundance of large salmonid predators in Lake Pend Oreille.

Objective 1. Estimate population abundance of kamloops, bull trout, and lake trout $\geq$ *406 mm in Lake Pend Oreille, Idaho.*

METHODS

To tag sufficient numbers of fish, I relied on an extensive recruitment and training program of volunteer anglers. I trained anglers and charter boat captains to apply spaghetti tags to kamloops, bull trout, and lake trout $\geq$ 406 mm fork length between April 1997 and April 1999. Spaghetti tags were used because of their potential ease of application, high retention, and high detectability by anglers who may recapture them. Anglers were instructed to tag only kamloops, bull trout, and lake trout $\geq$ 406 mm fork length because this is believed the minimum size above which all three species regularly consume kokanee (Anderson 1978; Pratt 1984; Rieman and Falter 1981). Training sessions and fishery technicians accompanying fishing boats have been effectively used to tag large predatory fishes and assure minimal tag loss in other Idaho lakes using similar methods (P. Janssen and J. Fredericks, Idaho Department of Fish and Game, pers. comm.). Once netted, fish were placed in an aerated live well, examined for previous tags, and tagged through the muscle under the dorsal surface of the back posterior to the dorsal fin. Fatigue from capture proved sufficient to immobilize fish without the need for anesthetic. One person was able to safely and accurately follow the tagging protocol, following a detailed training session. Tag number, fork length, species, approximate location of catch, depth of catch, date of catch, and name of angler were recorded. Fish were allowed to recover and then gently released. Fish that appeared injured or in poor condition were not tagged.

Anglers fished all portions of Lake Pend Oreille (Figure 1.1) throughout the study and used a variety of angling techniques depending on weather conditions and time of the year. To assure quality data collection and to keep participants motivated, regular contact was made with each of the volunteers including: frequent phone calls, visits to marinas, and accompanying volunteers on tagging trips.

In addition to relying on anglers to mark and recapture lake trout, a gillnetting effort was conducted during daylight hours November 1-4, 1998. Nets were fished for 30 minute durations on the lake bottom in 10 to 30 m of water. Monofilament nets were approximately 16 m long by 3 m deep, and mesh sizes started at 50 mm and increased by 12 mm increments every 3 m of net length to a maximum of 100 mm diameter. Locations were chosen in areas of traditionally high lake trout catch rates: the islands along the northern side of the lake, the mouth of the Clark Fork River west to Deadman Point, and Whiskey Bay (Figure 1.1).

Population abundance was not estimated for northern pikeminnow *Ptychocheilus oregonensis* because of a lack of willingness among anglers to release fish, however other data were collected to assess population structure. Length at age, weight at age, catch rates, and stomach samples (Objective 2) were collected from northern pikeminnow $\geq$ 100 mm using electrofishing in areas of known kokanee spawning along the lake shore (Maiolie and Elam 1993), and with angling through the 'Summa Fun' Squawfish Derby hosted by the Lake Pend Oreille Idaho Club (LPOIC) from May 23 to August 23, 1998. Electrofishing surveys were performed weekly in June shortly after the peak kokanee emergence in Lake Pend Oreille (Mallet 1968), at monthly intervals until October prior to adult kokanee spawning, then weekly through November. One site was located along the northern portion of the lake (Trestle Creek to Strong Creek) and two in the southern portion (Scenic Bay and Idlewilde Bay; Figure 1.1). Electrofishing surveys began after dark and lasted until approximately 8 km of the shoreline were sampled (4-5 hours). All fish captured were identified, measured, and stomach samples collected. Incidental kamloops and bull trout captured were tagged and/or stomach samples collected (Objective 2).

A recapture effort for kamloops was performed during November 1998 because of traditionally high catch rates during this time and included several techniques. Catch information was collected by angler surveys and voluntarily returned survey cards. Angler surveys were performed by trained technicians at main marinas, boat launches, and the IDFG Chilco check station on U.S. Highway 95. Additional catch information was acquired from the annual LPOIC Thanksgiving Challenge Derby November 21 through 29, 1998. Survey cards were distributed with each derby entry ticket and cash drawings after the derby encouraged survey card returns. Catch information included number of hours fished, number of kamloops, bull trout, and lake trout caught and length of each fish, location of catch, date of catch, and tag number from marked fish that were caught. Angler surveys were conducted throughout the derby by trained technicians at marinas and boat launches along the north, middle, and south portions of the lake. Fish collected in November were pooled and treated as a single recapture effort.

A Chapman's estimator was used to estimate population abundance (Ricker 1975):

$$\hat{N} = \frac{(m + 1)(c + 1)}{r + 1} - 1$$

where: $\hat{N}$ = Estimated population abundance

m = Marked fish in the population at time of population estimate

c = Captured fish during recapture effort

r = Recaptured fish during the recapture effort

Approximate 95% confidence intervals:

$$\left[\frac{\hat{N}}{1+\hat{N}\ (1.96SE)}, \frac{\hat{N}}{1-\hat{N}\ (1.96SE)} \right]$$

where: $\hat{N}$ = Estimated population abundance

SE = Standard Error

$$SE = \sqrt{\text{Variance } 1/\hat{N}}$$

$$\text{Variance } 1/\hat{N} = (\hat{N} - c / \hat{N} - 1) * c*p*q/(c*m)^2$$

where: $\hat{N}$ = Estimated population abundance
c = Captured fish during recapture effort
p = r/c
q = 1-p
m = Marked fish in the population at time of population estimate

Main assumptions of this model are:

1. No mark is lost
2. Homogeneity of capture probability for all animals
3. Homogeneity of survival for all animals in the population
4. Random distribution or sampling
5. All marks are recognized and reported
6. Negligible amount of recruitment during the time the recoveries are being made

A recapture effort for bull trout was performed from August 20 – November 4, 1998 using weirs, operated on bull trout spawning tributaries, and gillnet sampling. Weirs located on Trestle Creek and East Fork of Lighting Creek (8-20-98 to 10-29-98) were monitored by U.S. Forest Service personnel. Only fish passing the weirs on their downstream migration were used for the recapture effort. Data from a gill net effort (11-1-98 to 11-4-98) provided additional recapture information for bull trout. Methods used for this effort were identical to those previously described for lake trout.

Results from weirs and gillnetting efforts in the fall of 1998 were pooled and treated as a single recapture effort, and abundance estimates were calculated similar to kamloops.

A recapture effort for lake trout was performed during the annual LPOIC Annual Spring Challenge Derby April 25 – May 1, 1999, because of traditionally high catch rates during this time. Catch information was collected by voluntarily returned survey cards and angler surveys, and included number of hours fished, number of kamloops, bull trout, and lake trout caught and length of each fish, location of catch, date of catch, and tag number from recaptured fish. Survey cards were distributed with each derby entry ticket and cash drawings after the derby encouraged survey card returns. Angler surveys were conducted throughout the derby by trained technicians at marinas and boat launches along the north, middle, and south portions of the lake. Fish collected during the derby were pooled and treated as a single recapture effort and abundance estimates were calculated similar to kamloops.

Mortality was estimated for kamloops, bull trout, lake trout, and northern pikeminnow using numbers of fish in each age cohort. Numbers of fish per age class were converted to natural log and plotted against age (determined from scale and/or otolith readings). Instantaneous mortality (Z) was estimated from the slope of the descending limb (Appendix Table 1.9; Ricker 1975). Instantaneous mortality incorporates the effects of both natural mortality and harvest, although separate measurements of each could not be calculated. All kamloops, bull trout, lake trout, and northern pikeminnow sampled in Lake Pend Oreille were used to estimate mortality per species. To account for the potential differences in mortality due to the ‘meta-population’ structure of bull trout found in Lake Pend Oreille (B. Rieman, U.S. Forest Service, pers. comm.) a weighted mortality estimate was calculated for bull trout. Mortality was weighted (by tributary) for bull trout sampled in Granite Creek, Trestle Creek, East Fork of Lighting Creek, and the Clark Fork River (Appendix Table 1.9). Numbers of marked fish alive at the time of the recapture effort were calculated using daily survival rates

(Appendix Table 1.9). Survival was summed between the day each fish was tagged to the start of the recapture effort to provide a more accurate estimate of total marked fish alive at the start of the recapture effort.

Estimates of population abundance, length at age, and mortality for kamloops, bull trout, lake trout, and northern pikeminnow were used to determine the population structure of each species. Incremental growth (length and weight) by age cohort was calculated for kamloops, bull trout, lake trout, and northern pikeminnow by subtracting the growth (length or weight) between subsequent years (Appendix Table 1.9). Population abundance of each age cohort $\geq$ 406 mm of kamloops, bull trout, and lake trout was calculated using the instantaneous mortality to adjust $\hat{N}$ (Appendix Table 1.9). Standing crop for each age class of kamloops, bull trout, and lake trout $\geq$ 406 mm was calculated by multiplying the estimated number of individuals in each age class by the mean weight of an individual fish in that age class (Appendix Table 1.9). Total biomass of each predator $\geq$ 406 mm was calculated by summing the standing crop from each age cohort $\geq$ 406 mm (Appendix Table 1.9). Density estimates were calculated by dividing the area of kokanee habitat (22,564 ha) by $\hat{N}$ for kamloops, bull trout, and lake trout.

Scales were primarily used to age kamloops, bull trout, and northern pikeminnow, whereas otoliths were primarily used to age lake trout. Scales were collected from kamloops, bull trout, lake trout, and northern pikeminnow dorsally to the lateral line and posterior to the dorsal fin using techniques described by Nielsen and Johnson (1985). Using a blunt knife, scales were loosened by quickly and firmly scraping toward the head. Six to 12 scales were collected from each fish and sealed in a coin envelope labeled with the date, species, fork length, capture location, and general information about the visual condition of the fish: post spawn, hooking scars, healthy appearance, etc. Otoliths were collected from mortalities accrued during the sampling procedures by first removing the lower jaw from the fish, then cutting longitudinally into the skull across the insertion of the second gill arch, which aided in breaking the skull to expose the otoliths where they could be removed with forceps.

Scales were prepared by pressing 6 to 12 individual scales between two glass microscope slides then taping the sides together. Kamloops and bull trout otoliths were viewed without special preparations, whereas lake trout otoliths required additional preparation. Lake trout otoliths were stored for approximately 4 weeks in a 95% ethol alcohol and 5% glycerin solution. Immediately before viewing, otoliths were coated with a thin layer of clove oil, which lightly stained the surface of the otolith accentuating the annuli. Sandpaper (# 400) was used to lightly remove excessive calcium deposits from the surface of some otoliths. A representative sample of lake trout otoliths was sent to the Pacific Biological Station in Nanaimo British Columbia, Canada to confirm my aging.

Scales were viewed using a microfiche reader, whereas otoliths were viewed using a dissecting microscope equipped with an ocular micrometer. Areas of relatively slower growth signifying each winter season or the end of one year's growth (annuli) were counted to determine age. Aging techniques and backcalculating length at age measurements for scales are described by Nielsen and Johnson (1985) and for otoliths by Hu and Todd (1981). Distances were measured from the center of the focus of scales and otoliths along a consistent line to each annuli and to the anterior margin.

To confirm accurate aging of scales, otoliths were also aged from harvested fishes and angling mortalities. Scales and otoliths were read a minimum of twice, then a subsample of 10% was read again and compared to previous readings for precision.

I quantified annual growth increments (length at age) for all species (Appendix Table 1.9). I assumed a proportional relationship between total length of the fish and radius of the scale or otolith and used the following model to backcalculate length at age (Weisberg and Frie 1987):

$$L_i = L_c * A_d/S_c$$

where: L_i = length of fish at age 'i'

L_c = length of fish at capture

A_d = distance from focus to annuli at age 'i'

S_c = length from scale focus to scale margin.

Weight at length estimates were collected from random kamloops, bull trout, lake trout, and northern pikeminnow collected throughout the study. Fish were weighed by trained technicians at marinas around the lake on scales certified to read accurately to the nearest 30 g.

I determined catch per unit effort (CPUE) using angling effort throughout the project. Angling effort was pooled from anglers of various skills, and included efforts by anglers to target each species individually.

RESULTS

Kamloops

A total of 449 kamloops was tagged in Lake Pend Oreille, and 39 were recaptured between April, 1997 and October, 1998. The majority of fish tagged and recaptured were collected by angling (Appendix Table 1.2). At the beginning of the recapture effort (November 1 –31, 1998) an estimated 331 marked kamloops were alive. There were 16 recaptures among the total 747 fish caught. The estimated abundance of kamloops on November 1, 1998 was 14,607 with a 95% confidence interval of [10,100**,** 26,381]. Estimated density per area, of kamloops was 0.64 kamloops/ ha, while estimated biomass per unit area was 2.2 kg/ha. Marked and recaptured fish were distributed throughout the lake (Table 1.1). Movement of tagged fish varied from less than 1 km to over 30 km. The median number of days between initial tagging and recapture of kamloops was 186 days and ranged from 8 to 551 days. I found no relationship between distance moved and time between tagging and recapture. The catch rate for anglers pursuing kamloops was 34 hrs/ fish $\geq$ 406 mm (1997-1998; Appendix Table 1.2).

The average fork length of kamloops sampled in Lake Pend Oreille was 597 mm (Figure 1.2). Kamloops longer than 406 mm FL (431 mm total length) ranged from age 4.5 to 9 (n = 164; Appendix Table 1.6). The oldest fish sampled was 11 years, and the largest incremental growth was at age 4 (111 mm/year), whereas individual years (ages 1 to 11) averaged 87 mm growth/year and ranged from 49 to 111 mm. Kamloops exhibited the lowest annual mortality of all predator fishes examined. Total estimated instantaneous mortality was 0.289 or an annual survival rate of 74.9%. Based on this survival and age-length data, I estimate that age 4 kamloops were the most abundant age class $\geq$ 406 mm in Lake Pend Oreille (4,452;Table 1.2). I estimated fewer than 1,050 kamloops in Lake Pend Oreille were older than 8 years.

Table 1.1. Numbers of marked and recaptured kamloops, bull trout, and lake trout from Lake Pend Oreille, Idaho, 1997-1998. See Figure 1.1 for section locations.

Kamloops

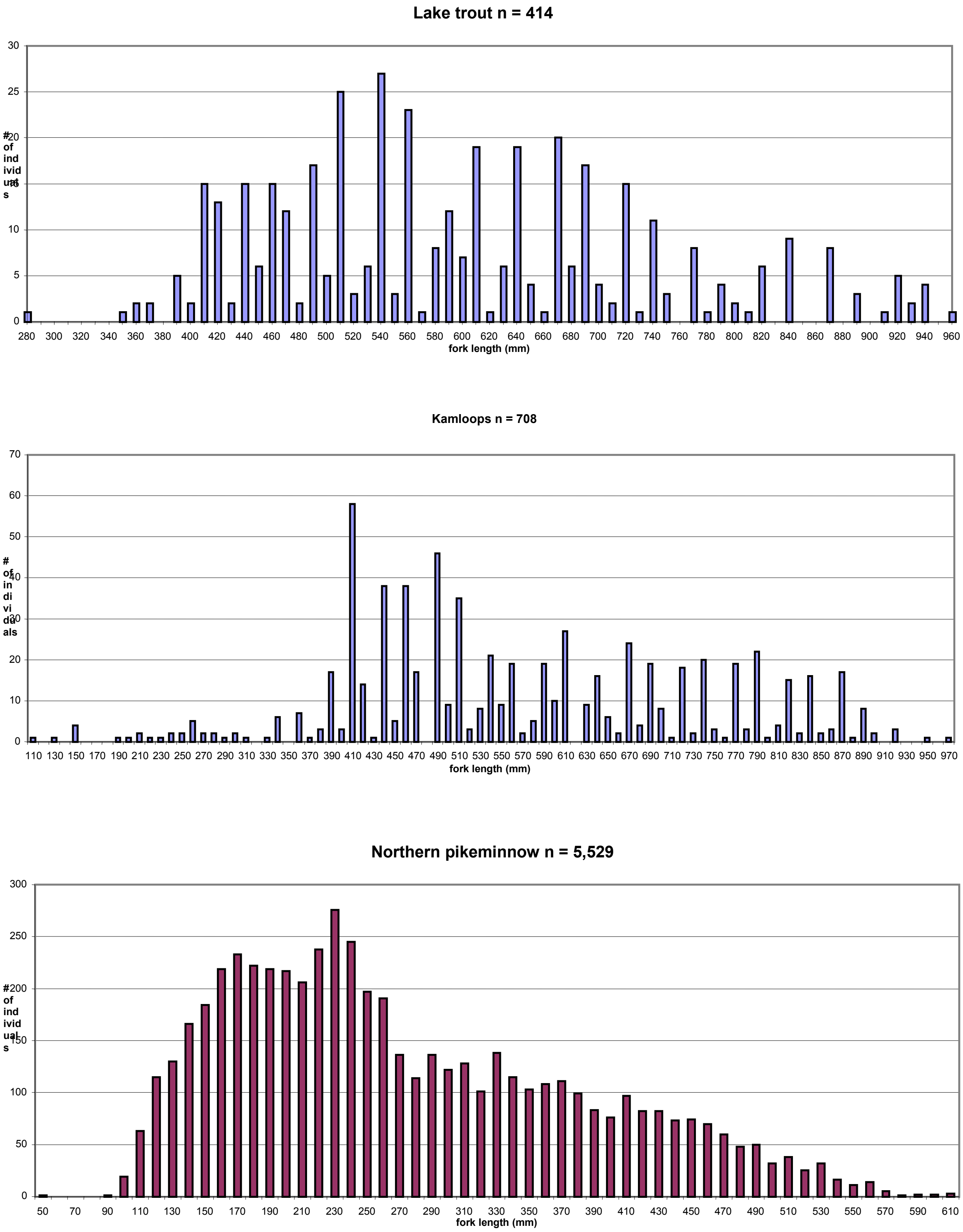
	Section 1	Section 2	Section 3	unknown locations
Marked	55	110	242	42
Recaptured	0	5	8	26
Total	55	115	250	55

Bull Trout

	Section 1	Section 2	Section 3	unknown locations
Marked	33	32	191	93
Recaptured	3	4	7	29
Total	36	36	198	122

Lake trout

	Section 1	Section 2	Section 3	unknown locations
Marked	52	13	75	25
Recaptured	2	0	2	15
Total	54	13	77	184



Lake trout n = 414

Kamloops n = 708

Northern pikeminnow n = 5,529

Figure 1.2. Length frequencies for lake trout, kamloops, and northern pikeminnow sampled in Lake Pend Oreille using all gears, 1997-1998.

Table 1.2. Estimated population abundance ($\hat{N}$) and mean length and weight for cohorts of kamloops, bull trout, and lake trout ($\geq$ 406 mm), and northern pikeminnow ($\geq$ 315 mm) including length and weight for each age cohort, Lake Pend Oreille, Idaho, 1997 - 1998. Population abundance was not estimated for northerm pikeminnow.

Kamloops

Age	Length (mm)	Mean weight (g)	$\hat{N}$
4.5*	406	2000	4452
5	495	2832	3335
6	593	3036	2498
7	676	3954	1871
8	735	6586	1401
9	816	8804	1050

Lake trout

Age	Length (mm)	Mean weight (g)	$\hat{N}$
6.75 *	406	934	849
7	427	1180	456
8	493	2235	246
9	564	2917	132
10	627	3808	71
11	700	4527	38

Bull trout

Age	Length (mm)	Mean weight (g)	$\hat{N}$
6	406	150	4347
7	475	540	2876
8	550	1050	1903
9	618	1583	1259
10	686	2222	833
11	754	2861	551
12	822	3500	365

Northern pikeminnow

Age	Length (mm)	Mean weight (g)
6	315	114
7	356	284
8	392	397
9	427	624
10	450	851
11	501	1078

* Adjusted based on predatory size.

Bull trout

A total of 349 bull trout was tagged in Lake Pend Oreille, and 43 were recaptured between April, 1997 and September, 1998. The majority of fish tagged and recaptured were collected by angling (Appendix Table 1.2). At the beginning of the recapture effort (September 4 – November 4, 1998) an estimated 224 marked bull trout were alive. There were 14 recaptures among the total 808 fish caught. The estimated abundance of bull trout on September 4, 1998 was 12,134 with a 95% confidence interval of [8,252**,** 22,915]. Estimated density per area, of bull trout was 0.54 bull trout/ ha, while estimated biomass per unit area was 0.38 kg/ha. Marked and recaptured fish were distributed throughout the lake (Table 1.1). Movement of tagged fish varied from less than 1 km to over 30 km. The median number of days between initial tagging and recapture of bull trout was 118 days and ranged from 3 to 387 days. I found no relationship between distance moved and time between tagging and recapture. Anglers pursuing kamloops caught bull trout $\geq$ 406 mm every 102 hrs; anglers pursuing lake trout caught bull trout $\geq$ 406 mm every 23 hours (1997-1998; Appendix Table 1.2).

The average fork length of bull trout sampled in Lake Pend Oreille was 524 mm (Figure 1.3). Bull trout longer than 406 mm FL (431 mm total length) ranged from ages 6 to age 11 (n = 14; Appendix Table 1.7). The oldest fish sampled was 13 years, and the largest incremental growth was at age 4 (85 mm/year); individual years (ages 1 to 12) averaged 68 mm growth/year and ranged from 49 to 85 mm.

Bull trout exhibited an annual mortality rate higher than kamloops and northern pikeminnow but lower than lake trout. Total estimated instantaneous mortality was 0.413 or an annual survival rate of 66.2%. Based on this survival and age-length data, I estimate that age 6 bull trout were the most abundant age class ≥ 406 mm in Lake Pend Oreille (4,347;Table 1.2). I estimated fewer than 3,008 bull trout in Lake Pend Oreille were older than 8 years.

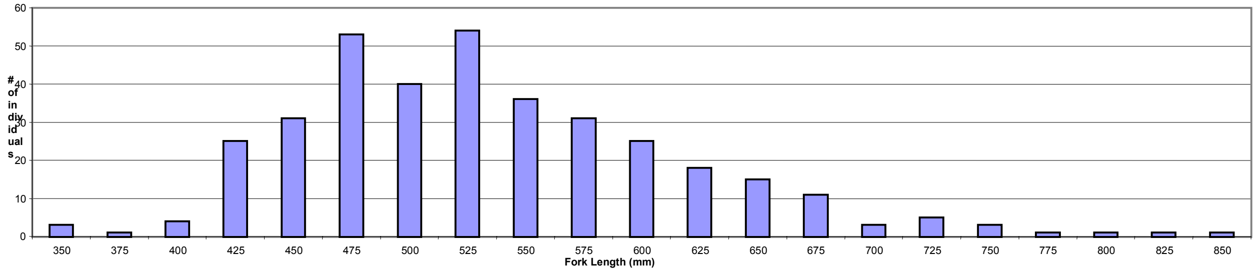
Lake trout

A total of 165 lake trout was tagged in Lake Pend Oreille, and 19 were recaptured between April 1997 and April 1999. The majority of fish tagged and recaptured were collected by angling (Appendix Table 1.2). At the beginning of the recapture effort (April 24 – May 2, 1999) an estimated 65 marked lake trout were alive. There were 5 recaptures among the total 162 fish caught. The estimated abundance of lake trout on April 24, 1999 was 1,792 with a 95% confidence interval of [1,054**,** 5,982]. Estimated density per area of lake trout was 0.08 lake trout/ ha, while estimated biomass per unit area was 0.1 kg/ha. Marked and recaptured fish were distributed widely in the lake (Table 1.1). Movement of tagged fish varied from less than 1 km to over 30 km. The median number of days between initial tagging and recapture of lake trout was 297 days and ranged from 15 to 667 days. I found no relationship between distance moved and time between tagging and recapture. The catch rate for anglers pursuing lake trout was 14 hrs/ fish ≥ 406 mm (1997-1998; Appendix Table 1.2).

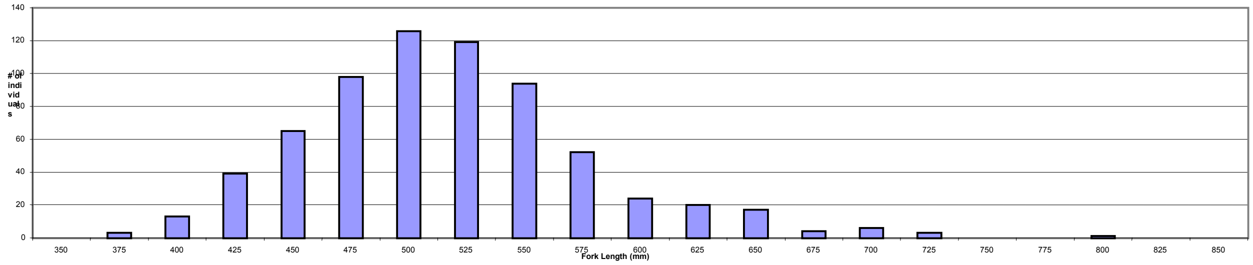
The average fork length of lake trout sampled in Lake Pend Oreille was 605 mm (Figure 1.2). Lake trout longer than 406 mm FL (442 mm total length) ranged from ages 6.75 to 11 (n = 110). The oldest fish sampled was 13 years, and the largest incremental growth was at age 10 (73 mm), whereas individual years (ages 1 to 10) averaged 64 mm growth/year and ranged from 47 to 73 mm.

Lake trout exhibited the highest annual mortality of all predator fishes examined. Total instantaneous mortality was 0.620 or an annual survival rate of 53.8%. Based on this survival and age-length data, I estimate that age 6 lake trout were the most abundant age class ≥ 406 mm in Lake Pend Oreille (849; Table 1.2). I estimated fewer than 110 lake trout in Lake Pend Oreille were older than 8 years.

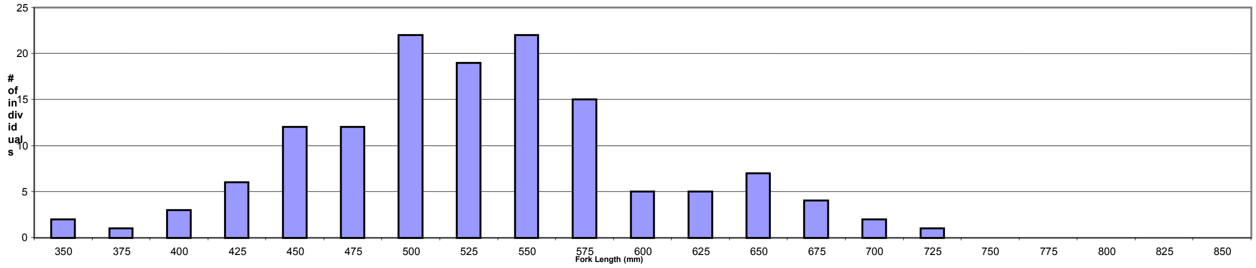
Bull trout Lake Pend Oreille n = 362



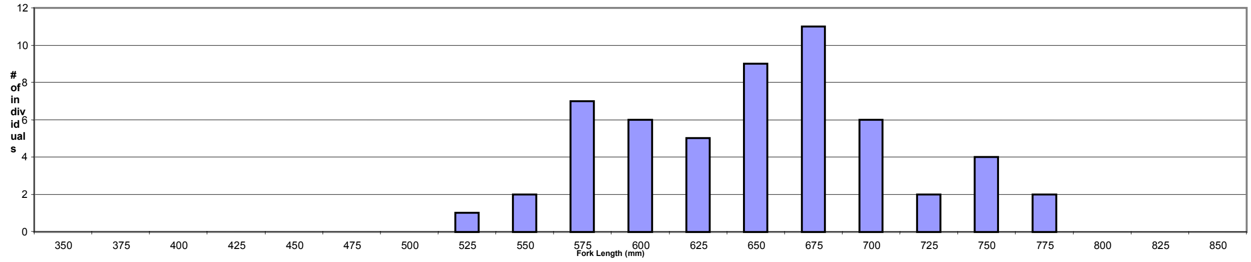
Bull trout Trestle Creek n = 684



Bull trout Granite Creek n = 138



Bull trout Clark Fork River n = 55



Bull trout East Fork Lightning Cr. n = 114

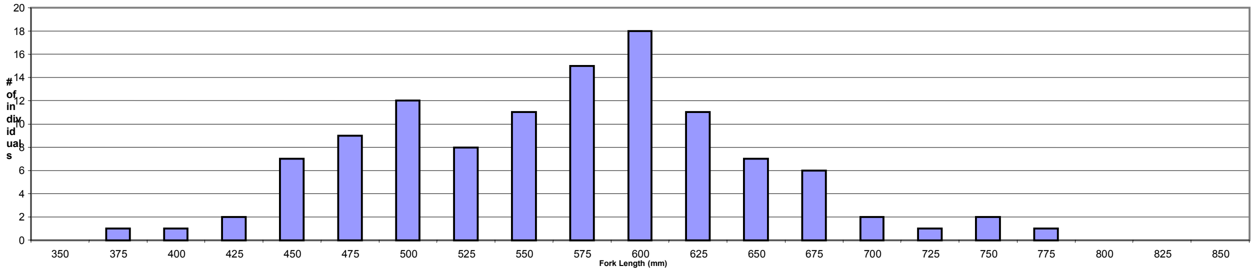


Figure 1.3. Length frequency of bull trout sampled in Lake Pend Oreille, Granite Creek, Trestle Creek, East Fork Lighting Creek, and Clark Fork River, Idaho using all gears, 1997-1998.

Northern pikeminnow

A total of 5,529 northern pikeminnow was sampled in Lake Pend Oreille between April 1997 and December 1998. The majority of fish were collected by angling. Population abundance was not estimated for northern pikeminnow because of a lack of willingness among anglers to release fish; however, relative to the abundance of other pelagic predator fishes caught by anglers for this project (kamloops, bull trout, and lake trout) northern pikeminnow were the least abundant (Appendix Table 1.2). Relative to the abundance of other littoral predator fishes collected by electrofishing (smallmouth bass *Micropterus dolomieu*, yellow perch *Perca flavescens*, pumpkinseed *Lepomis gibbosus*, bullhead *Ameiurus* spp., and sculpin *Cottus* spp.) northern pikeminnow were the most abundant (Appendix Table 1.3). The catch rate for anglers pursuing northern pikeminnow was 0.8 hrs/ fish (1997-1998; Appendix Table 1.2).

The average fork length of northern pikeminnow sampled in Lake Pend Oreille was 268 mm (Figure 1.2). Northern pikeminnow longer than 305 mm ranged from ages 6 to 12 ($n = 227$; Appendix Table 1.8). The oldest fish sampled was 13 years, and the largest incremental growth was observed at age 1 (66 mm). From ages 1 to 12, growth averaged 42 mm/year and ranged from 14 to 66 mm.

Northern pikeminnow exhibited an annual mortality similar to that of kamloops ($Z = 0.31$ and $S = 0.73$). Based on this survival and age-length data, I observed that fish < 305 were more abundant than fish ≥ 305 mm (Figure 1.2).

Other fishes

A total of 1,319 other fishes were sampled between April 1997 and December 1998 in Lake Pend Oreille. The majority of these were collected by electrofishing and gillnetting (Appendix Tables 1.3 and 1.4). Length frequencies for yellow perch, smallmouth bass, pumpkinseed, sculpin, bullhead, redside shiner *Richardsonius balteatus*, cutthroat trout *O. clarki*, and lake whitefish appear to be within expected ranges (Carlander 1969; Appendix Figures 1.1 to 1.2).

DISCUSSION

Low recapture rates demonstrate a difficulty with performing a mark-recapture study on a large system. Public education, weather conditions, and angler compliance proved to be the most important and challenging variables during this project. Return rates of marked fish throughout the project suggest the willingness of some anglers to participate and their potential to assist in making population estimates for trophy-sized sport fishes. Angler returns of tagged predatory fishes have been effectively used in Payette Lake (P. Janssen, Idaho Department of Fish and Game, pers. comm.) and Upper Priest Lake (J. Fredericks, Idaho Department of Fish and Game, pers. comm.) to estimate population abundance of lake trout.

Highly variable catch rates for lake trout throughout the year and negative angler attitudes toward releasing lake trout made tagging large numbers of lake trout difficult. Since 1995, IDFG personnel have encouraged lake trout harvest to reduce predation pressure on kokanee. My intention was to recapture 5% of the marked population (Ricker 1975). During the recapture effort used to estimate population abundance, I recaptured 5% of the marked kamloops (n = 16), 6% of the marked bull trout (n = 14), and 8% of the marked lake trout (n = 5). However, throughout the entire sampling period 39 kamloops, 42 bull trout, and 19 lake trout were recaptured. Mortality estimates used to calculate population estimates incorporated both natural mortality and mortality due to angling; estimates of annual mortality incorporate seasonal fluctuations due to angling.

In Lake Pend Oreille, anglers showed some preferences toward particular locations. However, I found no consistent trends in movements of pelagic predators. Distances traveled by marked fish between original capture and recapture showed that movements > 30 km are common.

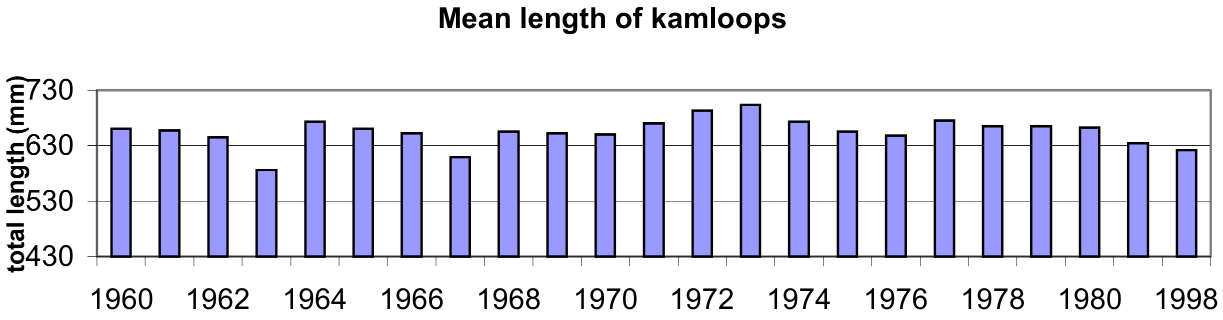
The condition of tagged fish after recapture, including tagging scars, appeared good. Tagging wounds on kamloops healed the soonest but took longer to heal on lake trout and bull trout. I found no evidence that tagging reduced survival, no fish were found dead attributable to tagging. Angling mortalities were occasionally observed floating, volunteers were instructed to net and examine these fish for tags. To minimize potential tagging mortality, anglers were instructed not to tag fish which appeared injured or unhealthy, and were extensively trained to correctly handle fish. I assume that tagged fish behaved similarly and were recaptured proportionally to untagged fish.

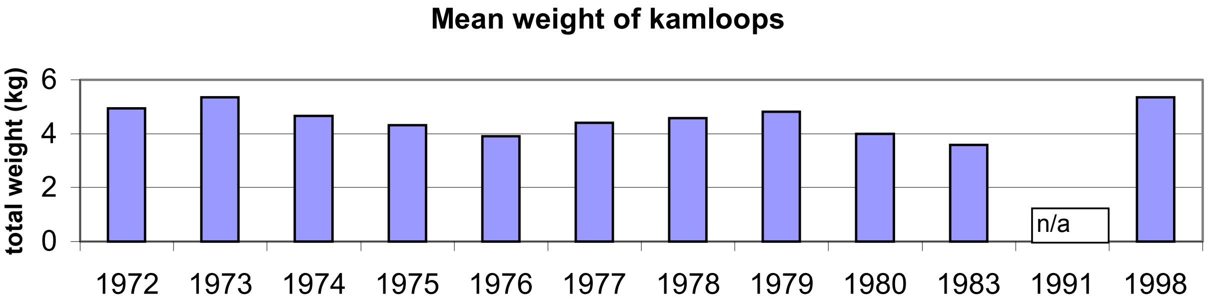
Kamloops

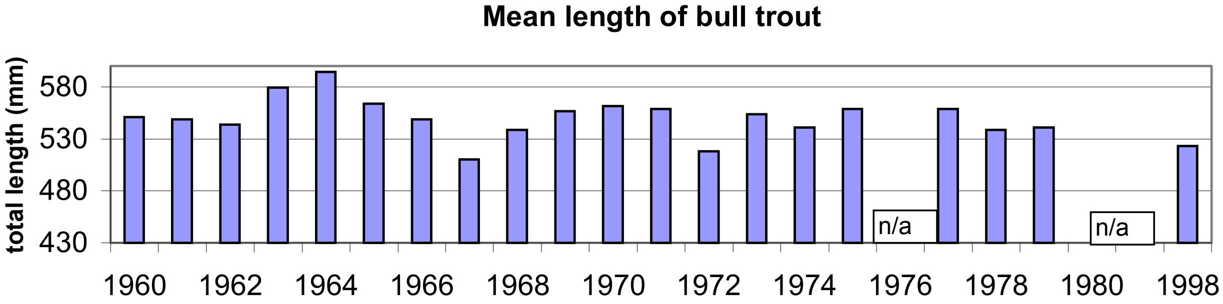
Previous studies have recorded growth characteristics of kamloops > 431 mm total length, although mark and recapture techniques have never been used to estimate the abundance of kamloops > 431 mm total length in Lake Pend Oreille. Ellis and Bowler (1981) used total catch, survival and escapement estimates to model an approximate population of 8,252 kamloops > 431 mm total length in Lake Pend Oreille. No other known estimates exist for kamloops in Lake Pend Oreille.

I compared previous growth characteristics to my estimates of growth increments, age at first spawn, mortality, average weight and length, and CPUE for kamloops > 431 mm total length. Growth characteristics of kamloops collected in Lake Pend Oreille 1997-1998 indicated similar but slower growth than fish collected in 1972-1976 (Anderson 1978) and 1983-1984 (Pratt 1985). Kamloops in 1997-1998 had a slower growth and spawned at an earlier age than fish in 1972-1976 and 1983-1984 (Appendix Tables 1.5 and 1.6). Declining growth rates can result in changes to other life history traits, such as maturation and reproductive patterns (Sogard 1994). Other researchers used catch curves to estimate annual survival for kamloops > 431 mm similar to my techniques. Ellis and Bowler (1981) estimated annual survival for kamloops in Lake Pend Oreille at 40%, Pratt (1984) estimated annual survival between 52 and 69%, and my research (1997-1998) estimated survival at 75%. Creel surveys 1960 – 1983 estimated an average length of kamloops $\geq$ 406 mm for most years ranged from 587 to 693 mm (Hoelscher 1992; Figure 1.4), compared to an average 622 mm total length in my study. Average weight of kamloops in Lake Pend Oreille from 1960 - 1983 ranged from 3.6 to 5.4 kg/fish, whereas in my study average weight was 5.4 kg/fish (Figure 1.4). Catch rates from 1960 - 1983 for anglers targeting trophy kamloops (> 431 mm total length) ranged from 59 to 165 hours/fish, as compared to catch rate which averaged 34 hours/fish in my study (Figure 1.5).

Furthermore, an analysis of catch rates during fishing derbies 1997 - 1999 reported catch rates that ranged from 21 to 56 hours/fish (Idaho Department of Fish and Game, unpublished data). Despite these differences, catch rates of kamloops in 1997 - 1998 seemed to resemble those since the early 1960’s. Successful local angling techniques coupled with strong catch and release ethics among most anglers are likely contributing to higher catch rates, lower mortality rates, and higher abundance in 1997-1998.







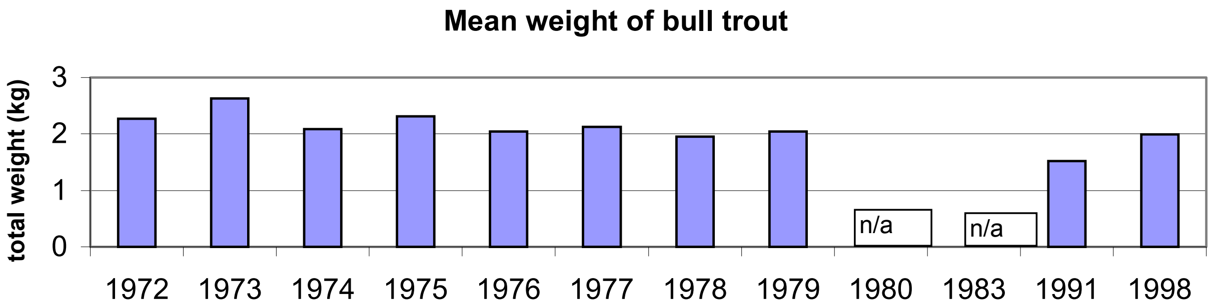


Figure 1.4. Mean length and weight of kamloops and bull trout (> 430 mm TL) in Lake Pend Oreille, Idaho. Data summarized from Hoelscher (1992). Data were not collected every year.

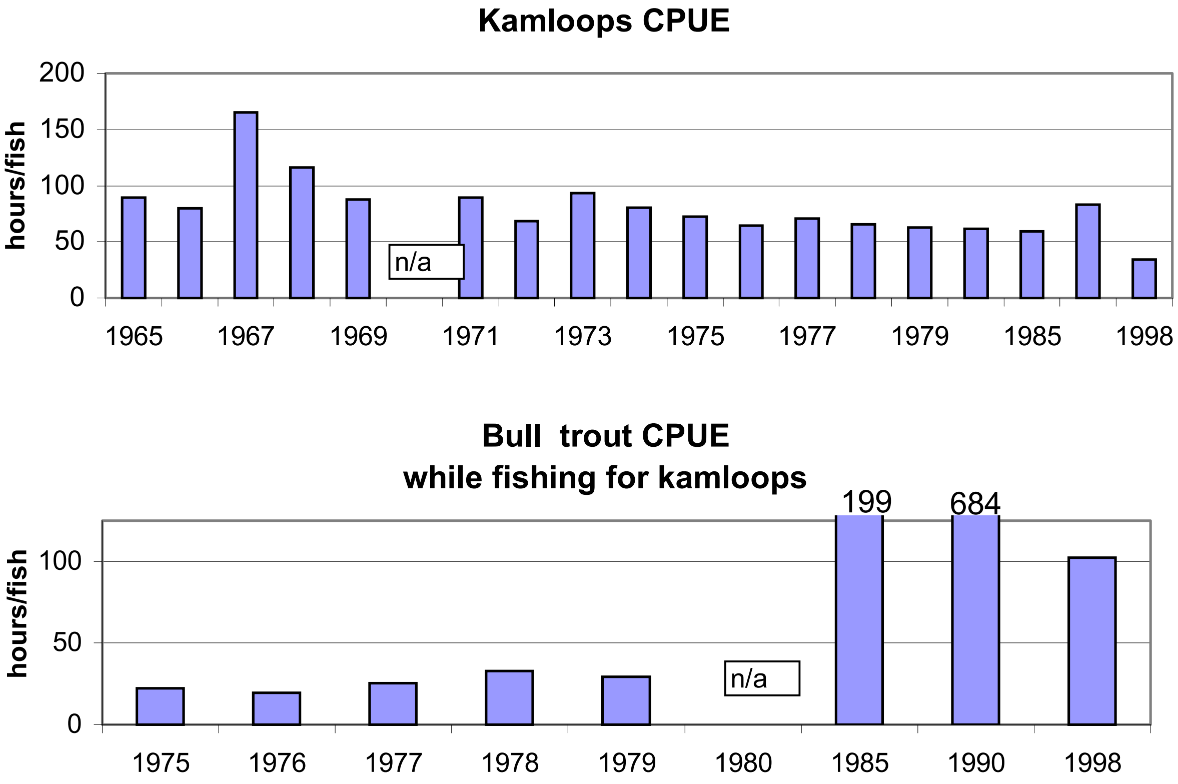


Figure 1.5. Catch Per Unit Effort (CPUE) for kamloops and bull trout (> 430 mm TL) while fishing for kamloops in Lake Pend Oreille 1965 to 1998. Data summarized from Hoelscher (1992).

I expected to see a smaller average length and weight of kamloops compared to earlier studies based on growth, age at spawn, and potential dilution of pure kamloops gene pool due to hybridization and lack of supplementation. Relying on anglers to record much of the data may have biased some of the results, reducing my ability to detect differences in the age and growth of kamloops from earlier studies. My annual mortality and length at age may have been variable due to inaccurate length records. Similar to Pratt's (1984) observations, anglers tended to release fish quickly to avoid stress, potentially resulting in inaccurate length records. Furthermore, continual changes in fishing techniques and technology may aid anglers in locating fish, thus introducing a bias in making comparisons with past years (Rand and Stewart 1998).

Bull trout

Previous studies have recorded growth characteristics of bull trout ≥ 406 mm fork length although mark and recapture techniques have never been used to estimate the abundance of bull trout ≥ 406 mm fork length in Lake Pend Oreille. Hoelscher (1992) used redd counts and average fish/redd to model an approximate escapement of 1,607 to 3,654 adult bull trout in Lake Pend Oreille, 1983 -1987. During this time, the age of first spawning for bull trout was between 4 and 6 years of age (Pratt 1984) similar to my results in 1997-1998.

I compared previous growth characteristics of bull trout to my estimates of growth increments, age at first spawn, mortality, average weight and length, and CPUE for bull trout ≥ 406 mm fork length. I found that bull trout (1997-1998) had slower growth than bull trout in 1983-1984 (Appendix Table 1.7), but spawned at similar ages. Pratt (1984) estimated annual mortality between 47 and 82%; my estimated annual mortality was lower (34%). Creel surveys 1960 – 1983 estimated an average length and weight of bull trout ≥ 406 mm FL for most years, total length for fish ≥ 406 mm ranged from 510 to 594 mm, compared to my average of 523 mm (Figure 1.4). Mean weight (1960 - 1983) ranged from 1.5 to 2.6 kg/fish, similar to my calculation of mean weight (2.0 kg/fish; Figure 1.4). Catch rates (1960-1983) for anglers catching bull trout while targeting trophy kamloops ($\geq$ 406 mm FL) ranged from 19.4 to 684 hours/fish, compared to an average of 102.3 hours/fish in my study (Figure 1.5).

Pratt (1984) observed that anglers tended to release fish quickly to avoid stress, potentially resulting in inaccurate length records. Consequently, if this occurred during my study, my estimates of length at age and annual mortality could have been variable. However, my results indicated slightly higher survival, higher population abundance, and the presence of older fish in the population than those of Pratt (1984). Some of these changes are attributable to the no-harvest regulation in the lake and all tributaries since 1996 and a strong catch and release ethic among most anglers.

Lake trout

Previously recorded growth characteristics for lake trout on Lake Pend Oreille are limited because of a small percentage of lake trout in angler catches until recent years. Successful local angling techniques for lake trout in the last 9 years have drawn attention to this fishery, particularly for anglers seeking to harvest fish for consumption. Lake trout were first documented in creel surveys in 1991 when anglers caught 25. The percent of lake trout that were caught and harvested in 1991 was 68% compared to 73% in 1997-1998. Harvest rates on Lake Michigan, where lake trout are highly exploited and rely on supplementation to maintain a fishery, are as high as 71% (Stewart et al. 1983). Average length of lake trout caught in Lake Pend Oreille in 1991 was 654 mm, and the average weight was 3.21 kg. Average length of fish caught in 1997-1998 was 605 mm, and the average weight was 3.30 kg. Weight at age of lake trout (1997-1998) in Lake Pend Oreille is less than that in other systems in the northerwestern United States and southwestern Canada (Appendix Figure 1.3). Similar research was performed on lake trout in Flaming Gorge Reservoir, WY, where annual survival of lake trout averaged 65% (Yule and Luecke 1993) compared to my estimates of 38%. Time between recaptures also varied; Yule and Luecke (1993) reported an average of 42 months between original marking and recapture for lake trout 601 to 800 mm and 51 months for lake trout > 800 mm. My data indicated an average of 10 months between original marking and recapture for lake trout ≥ 406 mm, which likely contributed to the nearly double annual mortality rates in Lake Pend Oreille.

Although catch rates for lake trout (14 hours/fish) are higher than those for kamloops (34 hours/fish), the population estimate for lake trout is considerably lower (14,007 kamloops vs 1,792 lake trout). The reason for this I believe is that angling for lake trout is labor intensive and when fishing is slow most anglers will not continue fishing for lake trout, whereas kamloops fishing is relatively easy and anglers will often continue fishing for kamloops when catch rates are low. Another explanation is that areas which are easy for lake trout anglers to fish (gradual sloping bottoms with smaller substrate in less than 40 m of water) seem to hold more lake trout. These areas are uncommon in Lake Pend Oreille; therefore, they may concentrate fish making them more susceptible to anglers.

I suggest that angler attitude encouraging the harvest of lake trout is holding the population at a low level. The lack of older fish in the age distribution suggests that harvest may be reducing the population abundance of lake trout in Lake Pend Oreille.

Northern Pikeminnow

Growth characteristics of northern pikeminnow collected in 1997-1998 indicated similar but smaller growth increments to fish collected in Lake Pend Oreille and Cocolalla Lake, Idaho 1953, 1957, and 1958. Northern pikeminnow in 1997-1998 had a slower growth than fish in 1953, 1957, and 1958 (Jeppson and Platts 1959; Appendix Table 1.8).

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Appendix Table 1.1. Fish species cited by common name and abbreviation in text.

Kokanee	ONE	*Oncorhynchus nerka*
Kamloops	OMY	*Oncorhynchus mykiss*
Cutthroat trout	OCL	*Oncorhynchus clarki*
Bull trout	SCO	*Salvelinus confluentus*
Lake trout	SNA	*Salvelinus namaycush*
Mountain whitefish	PWI	*Prosopium williamsoni*
Lake whitefish	CCL	*Coregonus clupeaformis*
Peamouth	MCA	*Mylocheilus caurinus*
Largescale sucker	CMA	*Catastomus macrocheilus*
Redside shiner	RBA	*Richardsonius balteatus*
Bullhead	AME	*Ameiurus spp.*
Sculpin	COT	*Cottus spp*.
Pumpkinseed	LGI	*Lepomis gibbosus*
Yellow perch	PFL	*Perca flavescens*
Brown trout	STR	*Salmo trutta*
Black crappie	PNI	*Pomoxis nigromaculatus*
Tench	TTI	*Tinca tinca*
Smallmouth bass	MDO	*Micropterus dolemieu*
Northern pikeminnow	POR	*Ptychocheilus oregonensis*

Appendix Table 1.2. Hook and line sampling effort and incidental catch, 1997-1998, while pursuing kamloops,lake trout, and northern pikeminnow, and total effort. Species abbreviations listed in Appendix Table 1.1.

Hook and line effort total

Year	Effort (hrs)	OMY	SCO	SNA	POR
1998	978.5	35	5	8	25
1997	1725	41	28	20	32
Total	2703.5	76	33	28	57
cpue hrs/fish		35.6	81.9	96.6	47.4

Hook and line effort while pursuing kamloops

Year	Effort (hrs)	OMY	SCO	SNA	POR
1998	911.5	34	4	4	0
1997	1543	38	20	9	2
Total	2454.5	72	24	13	2
cpue hrs/fish		34.1	102.3	188.8	1227.3

Hook and line effort while pursuing lake trout

Year	Effort (hrs)	OMY	SCO	SNA	POR
1998	45	0	1	4	0
1997	160	2	8	11	1
Total	205	2	9	15	1
cpue hrs/fish		102.5	22.8	13.7	205.0

Hook and line effort while pursuing n. pikeminnow

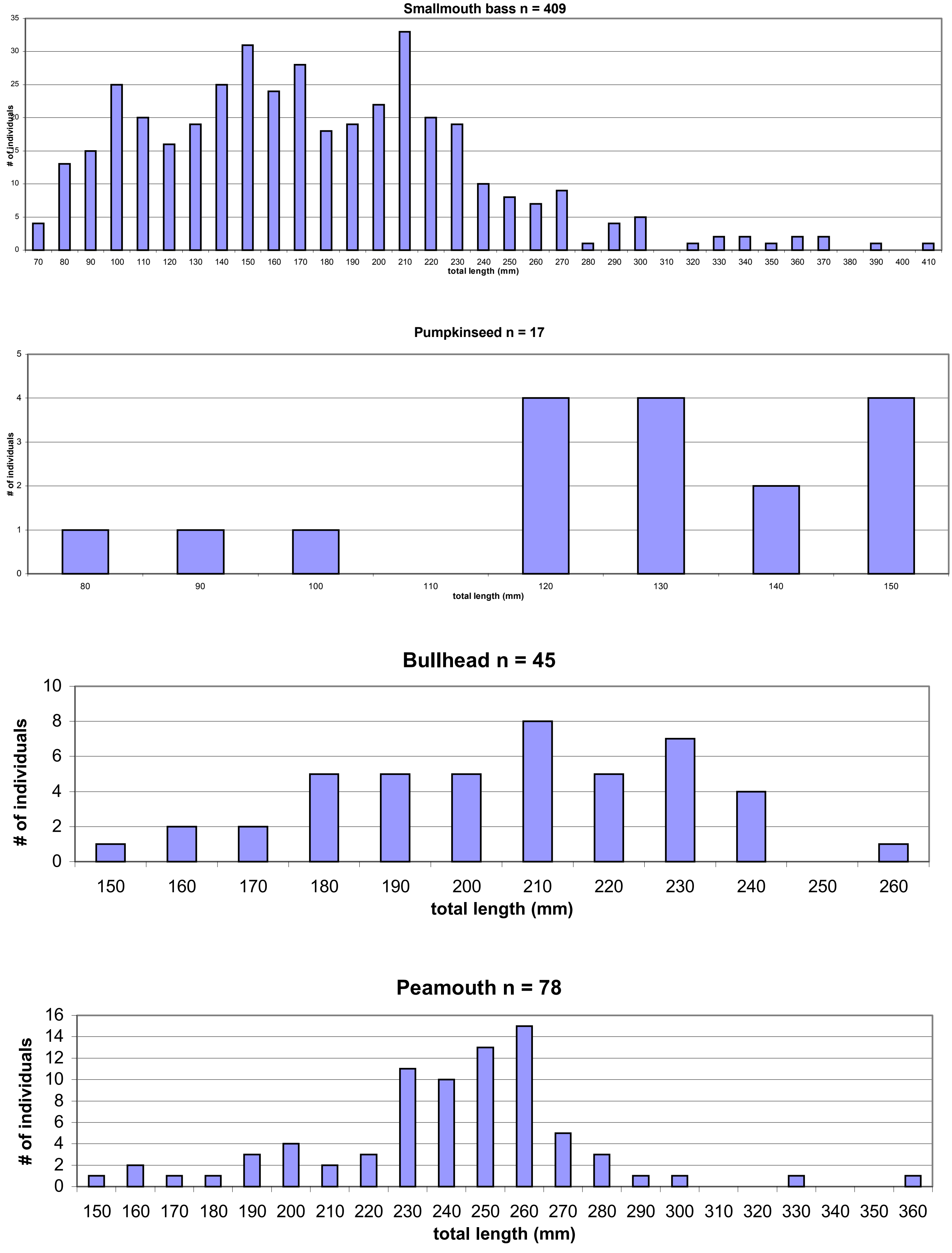
Year	Effort (hrs)	OMY	SCO	SNA	POR
1998	22	1	0	0	25
1997	22	1	0	0	29
Total	44	2	0	0	54
cpue hrs/fish		22	n/a	n/a	0.8

Appendix Table 1.3. Electrofishing catch and catch per unit effort (cpue) for 1997, 1998, and total, Lake Pend Oreille. Species abbreviations listed in Appendix Table 1.1.

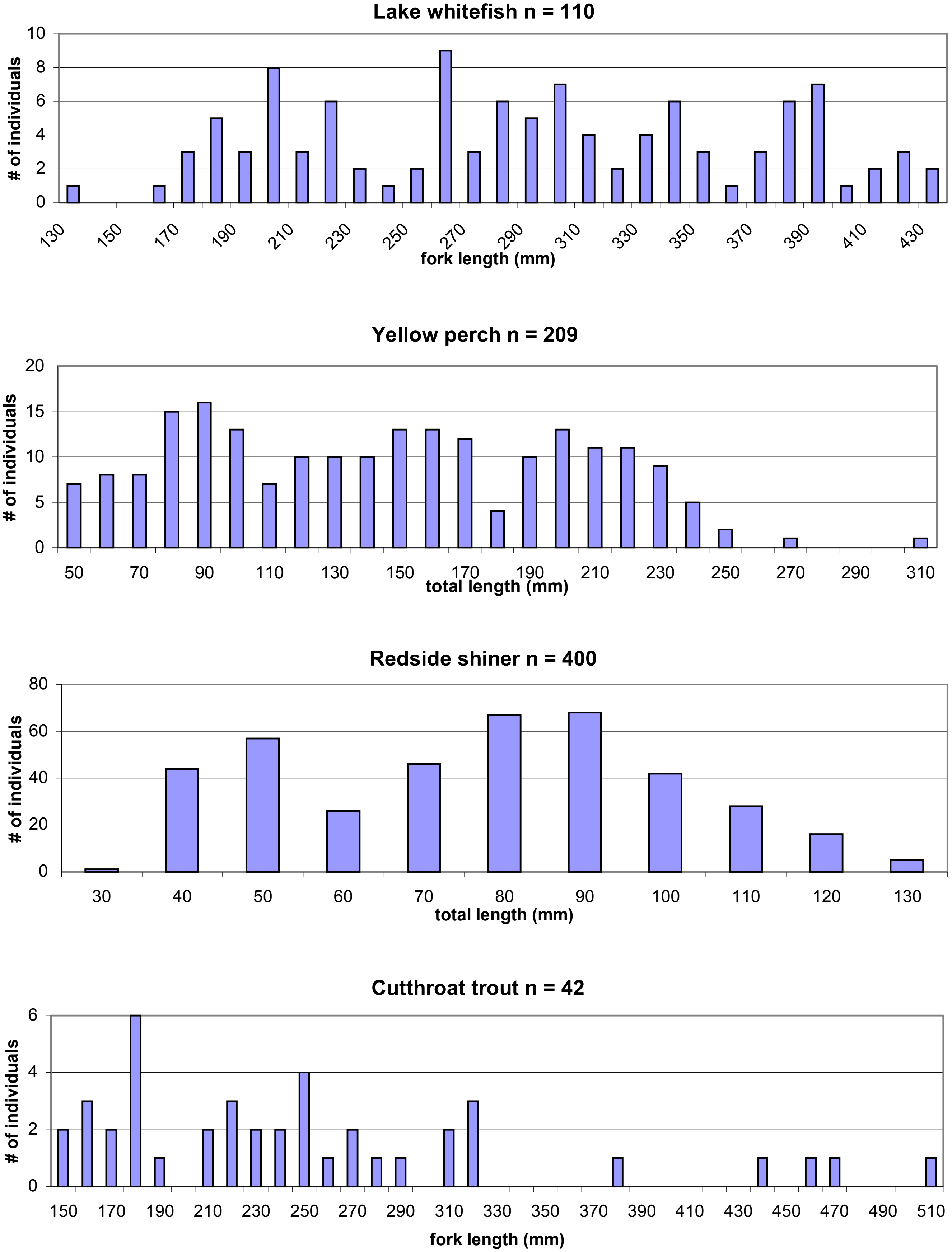
	1997		1998		Total	
Species	catch	cpue (hrs)	catch	cpue (hrs)	catch	cpue (hrs)
POR	671	0.01	2576	0.01	3247	0.01
MDO	28	0.24	410	0.07	438	0.08
PFL	8	0.84	209	0.15	217	0.17
CCL	25	0.27	38	0.80	63	0.59
OCL	11	0.61	49	0.62	60	0.62
AME	1	6.70	45	0.68	46	0.81
MSA	0	0.00	34	0.90	34	1.09
OMY	3	2.23	27	1.13	30	1.24
PWI	1	6.70	25	3.13	26	2.36
LGI	3	2.23	17	1.79	20	1.86
TTI	0	-	13	2.35	13	2.86
COT	0	-	8	3.81	8	4.65
STR	3	2.23	-	-	3	12.40
SCO	0	-	3	10.17	3	12.40
PNI	0	-	2	15.25	2	18.60
Total catch	754		3456		4210	
Total effort (hrs	6.7		30.5		37.2	

Appendix Table 1.4. Gillnet catch and catch per unit effort (cpue) for November 1-4,1998, Lake Pend Oreille, Idaho. Species abbreviations listed in Appendix Table 1.1.

		Species						
	Effort (hours)	SCO	SNA	ONE	CCL	POR	MCA	CMA
Total	2239	4	2	4	57	12	30	1
cpue (hrs/fish)	-	559.8	1119.5	559.8	39.3	186.6	74.6	2239.0



Appendix Figure 1.1. Length frequencies for all smallmouth bass, pumpkinseed, bullhead, and peamouth sampled in Lake Pend Oreille using all gears, 1997-1998.



Lake whitefish n = 110

Yellow perch n = 209

Redside shiner n = 400

Cutthroat trout n = 42

Appendix Figure 1.2. Length frequencies for all lake whitefish, yellow perch, redside shiner, and cutthroat trout sampled in Lake Pend Oreille using all gears, 1997-1998.

Appendix Table 1.5. Age at first spawn for kamloops collected in Lake Pend Oreille from 1972-1976, 1983-1984 and 1997,1998. Sample sizes are in parentheses.

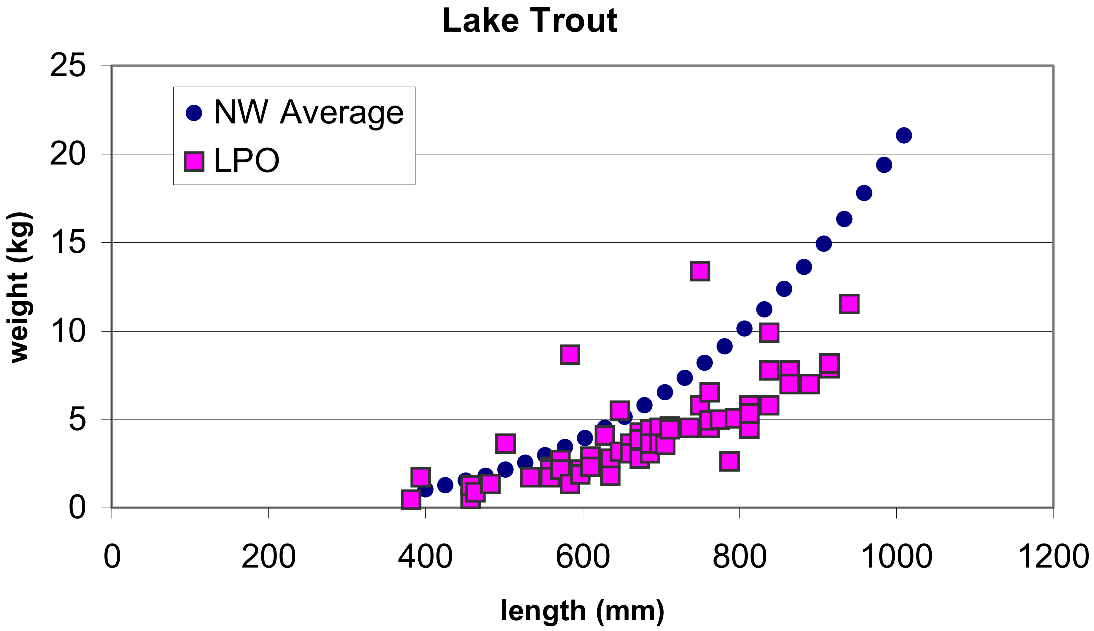
	Age					
Time period	3	4	5	6	7	8
1972-1976	-	1	18	61	20	-
(Anderson 1978)	-	(2)	(24)	(80)	(26)	-
1983-1984	5	19	22	37	17	-
(Pratt 1985)	(3)	(11)	(13)	(22)	(10)	-
1997-1998	-	4	32	26	33	5
	-	(2)	(18)	(15)	(19)	(3)

Appendix Table 1.6. Backcalculated mean length (mm) at age and increments of growth (△) for kamloops in Lake Pend Oreille, Idaho; 1972-1976 (Anderson 1976), 1983-1984, (Pratt 1985) and 1997,1998.

Time	Age										
Length at annulus	1	(△)	2	(△)	3	(△)	4	(△)	5	(△)	6
1972-1976 (Anderson 1978)	80	(63)	143	(146)	289	(145)	434	(191)	625	(154)	779
1983-1984 (Pratt 1985)	78	(83)	161	(128)	290	(156)	446	(116)	562	(101)	662
1997-1998	82	(103)	185	(104)	289	(95)	384	(111)	495	(98)	593

Appendix Table 1.7. Back calculated mean total length (mm) and increments of growth△) at age of bull trout from Lake Pend Oreille, Idaho, 1983 Pratt (1985) and 1997,1998.

		Age																
		1	(△)	2	(△)	3	(△)	4	(△)	5	(△)	6	(△)	7	(△)	8	(△)	9	(△)
Pratt (1985)	1983	91	(75)	166	(110)	276	(117)	393	(105)	498	(60)	558	(n/a)	n/a	(n/a)	n/a	(n/a)	n/a	(n/a)
	1997-1998	72	(49)	121	(54)	175	(71)	246	(85)	332	(70)	401	(74)	475	(74)	550	(n/a)	461	(n/a)



Appendix Figure 1.3. Comparison of weight at length between lake trout in Lake Pend Oreille, Idaho (squares), and the northwestern United States and Canada (circles; Carlander 1969).

Appendix Table 1.8. Estimated mean length (mm) at annulus formation of northern pikeminnow in Lake Pend Oreille, Idaho, for 1997 and 1998, and Lake Pend Oreille and Cocolalla lakes in 1953,1957, and 1958 (Jeppson and Platts1959).

	Age											
Years collected	1	2	3	4	5	6	7	8	9	10	11	12
1997-1998	56	122	178	230	277	315	356	392	427	450	501	515
1953, 1957-1958	89	152	203	267	305	356	381	406	432	483	-	-

Appendix Table 1.9. Equations used in Objective 1.

Estimator; context used	Equation
Instantaneous Mortality (Z); calculated from plot of age frequency	$\ln(n_a) = b + Za$ where: ln = natural log n_a = number of age a fish b = constant Z = instantaneous mortality a = age of cohort
Weighted Mortality (WM); calculated using mortality estimates from multiple locations	$WM = \Sigma n_l m_l / \Sigma n_l$ where: n_l = number of fish at location l m_l= mortality of fish at location l
Annual Survival (S); calculated from Z	$S = e^{-Z}$ where: e = base of the natural log (2.71828)
Daily survival (DS)	$DS = e^{-Z/365}$
Marked fish alive at start of recapture effort (M); using DS applied to days between initial tagging and recapture effort	$M = \sum_{j=1}^{\text{last day}} n_j d_{tr(j)} * DS$ where: n_j = number of fish tagged on day j $d_{tr(j)}$ = days between tagging and recapture of a fish tagged on day j
Population abundance estimate $\hat{N}_a$; for all age cohorts $\geq$ 406 mm	$\hat{N}_{age} = \hat{N}_{Initial} * e^{-Z(a\text{-initial})}$; $\hat{N}_{Initial} = \hat{N}_{Total} / \sum_{i=0}^{\#\text{ of age classes - 1}} e^{-iZ}$ where: $\hat{N}_{Initial}$ = estimated abundance of the youngest age class
Standing Crop (SC_a); standing crop for each cohorts $\geq$ 406 mm	$SC = n_a * w_a$ where: w = mean weight of individual fish in age class i
Biomass (B);	$B_i = \Sigma_a SC_a$
Incremental growth (IG_a); annual growth of average fish in each cohort	$IG_a = L_a - L_{a-1}$ where: L_a = mean length of individual fish in age class i

Objective Two

FOOD HABITS

INTRODUCTION

The kokanee harvest is presently at 20% of its historic level because of population declines, supporting a recreational fishery of less than 200,000 fish annually (Maiolie and Elam 1993; Paragamian et al. 1991). Kokanee, an important component of the Lake Pend Oreille food web, have provided both a prey base, enhancing the growth of predatory fishes, and a fishery for over 60 years (Wydoski and Bennett 1981).

The type, quantity, and choices of prey are important components in understanding the trophic dynamics of predator/prey relationships (Popova 1978). Predatory salmonids in Lake Pend Oreille (kamloops, bull trout, and lake trout) rely heavily on kokanee (Anderson 1978; Pratt 1985; Rieman and Falter 1981). However, no one has assessed the impacts of each of these predators on the kokanee populations in Lake Pend Oreille. Understanding the dynamics of predation on kokanee is especially critical at this time because of the reduced population abundance of kokanee.

Objective 2. Identify food items in the stomachs of kamloops, bull trout, lake trout $\geq$ 406 mm and northern pikeminnow $\geq$ 100 mm from Lake Pend Oreille, Idaho.

METHODS

To quantify the importance of kokanee to selected predatory fishes in Lake Pend Oreille, stomach samples were collected from kamloops, bull trout, lake trout $\geq$ 406 mm, and northern pikeminnow $\geq$ 100 mm that were sampled mostly by angling throughout 1997 and 1998. Additionally, northern pikeminnow $\geq$ 100 mm were sampled by electrofishing along the lake shore in areas of known kokanee spawning and through the 'Summa Fun' Squawfish Derby May 23 through August 23, 1998 (Objective 1). The intensity of predation changes with seasonal and ecological conditions (Popova 1978; Garvey et al. 1998); therefore, I collected stomach samples throughout 1997 and 1998 to assess seasonal variability in the diets of selected predatory fishes. Samples were collected from both harvested fish and live fish. Stomach samples were collected from harvested fishes by extracting the entire stomach from the body and stripping the stomach's contents into a sampling bottle, whereas stomach samples were collected from live fishes using lavage techniques. Stomach samples also were taken from all incidental catches of kamloops, bull trout, and lake trout < 406 mm to describe the diets of smaller fishes not thought to be kokanee predators. Lavage techniques (Light et al. 1983; Yule and Luecke 1993) involved inserting a protected tube into a fish's mouth and down the esophagus, then pumping distilled water into the stomach causing the contents to be flushed back up through the mouth, where the contents were collected in a mesh screen to remove excess water and placed in a sampling bottle. All northern pikeminnow were sacrificed for stomach analysis, after determining that lavage techniques were not effective due to the elongated gut in these fish. All stomach samples were preserved in 10% formalin and labeled with species, location of catch, length of predator, and date.

I grouped northern pikeminnow into one of four categories because of the large number of samples. Stomach samples were placed in the following groups depending on the fish's total length: 100 to 149 mm, 150 to 304 mm, 305 to 459 mm, and $\geq$ 460 mm total length.

In the laboratory, trained technicians identified prey items from stomachs to the lowest practical taxonomic level, enumerated, and weighed them (blotted dry weight, mg). Prey of the same taxon were pooled together and weighed as a group. Diagnostic bones, including the opercle, dentary, cleithrum, and/or vertebrae, in addition to external morphological characteristics were used to identify fish. Representative samples of diagnostic bones were collected from common prey species. Fork, total, nape, and/or standard length of prey fish identified in stomach samples were recorded.

Numbers of kokanee consumed/individual kamloops, bull trout, lake trout, and northern pikeminnow were recorded and the average computed. Average length and range of sizes of kokanee consumed by predator fishes were compared to length at age estimates for kokanee (Idaho Department of Fish and Game, unpublished data) to identify age classes of kokanee consumed. Total length (TL) was measured on intact kokanee; however, if kokanee were not intact, I estimated their total length from standard (SL) or nape length (NL) measurements by a model similar to methods used by Madenjian et al. (1998) and Yule and Luecke (1993). I used the relationship TL = SL + 26.5 mm and TL = NL + 51.0 mm, derived from my own corresponding measurements of kokanee 63 to 226 mm, to convert from standard (SL) or nape length (NL) to total length.

RESULTS

Kamloops

I collected 180 stomachs from kamloops that ranged from 275 to 966 mm fork length between May 1997 and November 1998. Approximately 15% (n= 27) were empty. Kokanee were the principal food item of kamloops ≥ 406 mm throughout the year, comprising 76.81% by weight, while other fishes (20.87%), insects (1.66%) and opossum shrimp (0.66%) were of lesser importance. Kamloops < 406 mm fed primarily on insects (61.09%), opossum shrimp (35.4%), northern pikeminnow (3.35%), and redside shiners (0.16%; Table 2.1). An average of 0.63 kokanee (n = 136) were observed /stomach. Kokanee consumed by kamloops ranged from 63 to 226 mm total length and averaged 176 mm (n = 48; Figure 2.1). This size range of kokanee corresponded with length at age estimates for kokanee of ages 1 to 4.

Bull trout

I collected 11 stomachs from bull trout that ranged from 406 to 583 mm fork length between July 1997 and December 1998. Approximately 27% (n = 3) were empty. Kokanee were the principal food item of bull trout ≥ 406 mm throughout the year, comprising 65.6% by weight, while unidentified salmonid prey (15.75%), non-salmonid prey (5.96%), insects (< 0.01%), and unidentified fish and other material (12.68%) were of lesser importance. An average of 0.5 kokanee (n = 8) was observed/ stomach. The small number of stomachs analyzed precluded further analysis of prey consumed.

Table 2.1. Monthly prey consumption (%) by kamloops ≥ 406 mm fork length and total consumption by kamloops < 406 mm in Lake Pend Oreille, Idaho, 1997-1998. Fish were collected by electrofishing and angling.

Identifiable prey	January	February	March	April (n=7)	May (n=11)	June (n=9)	July (n=11)	August (n=11)	September (n=8)	October (n=17)	November (n=69)	December	Total Fish ≥ 406 mm (n = 142)	Total Fish < 406 mm (n=10)
Insecta	n/a	n/a	n/a	0.42	5.45	5.54	6.01	0.02	0.05	0.39	1.15	n/a	1.66	61.09
Opossum shrimp				0.32					0.03	0.13	2.13		0.66	35.40
Larval fish							0.40						0.01	
Kokanee				99.26	94.55	34.20	39.26	39.68	62.77	99.48	71.20		76.81	
Rainbow trout							41.43	26.20	36.69		14.41		11.41	
Lake trout											3.57		1.35	
Bull trout								29.65			7.54		5.27	
Whitefish spp.								4.45					0.36	
Peamouth							12.90						0.34	
Redside shiner						60.26			0.02				2.09	0.16
Northern pikeminnow									0.44				0.03	3.35

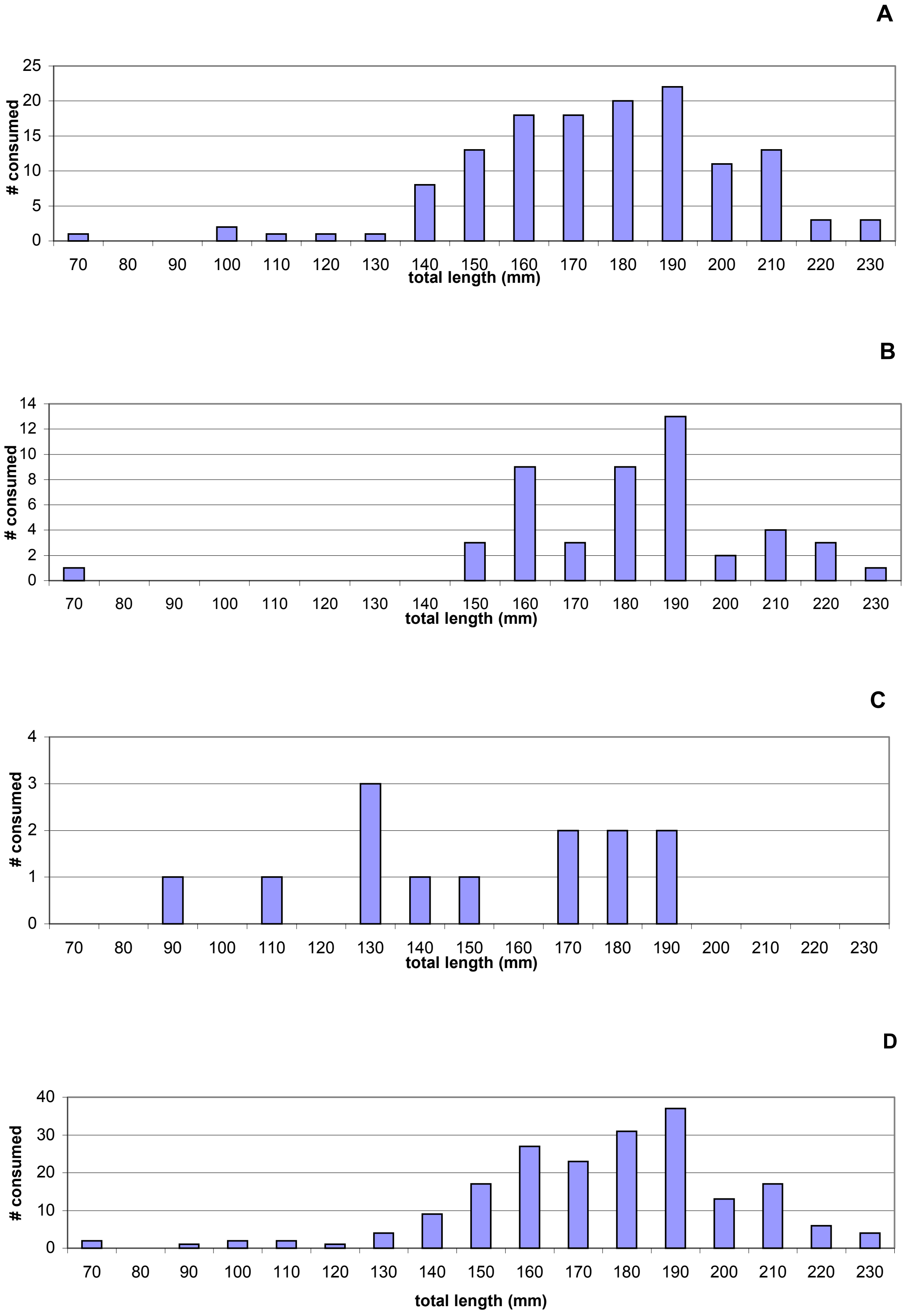


Figure 2.1. Number of kokanee consumed by various length classes of lake trout (A; n=135), kamloops (B; n=48), northern pikeminnow (C; n=13), and all predators (D; n=196) in Lake Pend Oreille, Idaho,1997-1998. Scale on axis are not equal.

Lake trout

I collected 242 stomachs from lake trout that ranged from 307 to 940 mm fork length between April 1997 and December 1998. Approximately 18% (n=42) were empty. Kokanee were the principal food item of lake trout $\geq$ 406 mm throughout the year, comprising 87.40% by weight, while other fish (12.35%), insects (0.21%), and opossum shrimp (0.04%) were of lesser importance. Lake trout < 406 mm (n = 5) fed exclusively on sculpin 68.4% and opossum shrimp 31.6%; (Table 2.2). An average of 0.88 kokanee (n =204) was observed/ stomach. Kokanee consumed by lake trout ranged from 70 to 225 mm total length and averaged 171 mm (n = 135; Figure 2.1). This size range of kokanee corresponded with length at age estimates for kokanee of ages 1 to 4.

Northern Pikeminnow

I collected 3,322 northern pikeminnow stomachs from fish that ranged from 100 to 610 mm fork length between June 1997 and December 1998. Approximately 21% (n=695) were empty. Northern pikeminnow consumed a variety of prey items. Insects were the principal food item of northern pikeminnow 100 to 150 mm (87.89%) and 150 to 305 mm (25.56%), while kokanee were the principal food item of northern pikeminnow larger than 305 mm (Tables 2.3 and 2.4). An average of 0.24 kokanee (n =250) was observed/ stomach of northern pikeminnow > 305 mm. Kokanee consumed by northern pikeminnow ranged from 84 mm to 185 mm total length and averaged 145 mm (n = 13; Figure 2.1). This size range of kokanee corresponded with length at age estimates for kokanee of ages 1 to 3.

Table 2.2. Monthly prey consumption (%) by lake trout ≥ 406 mm fork length and total consumption by lake trout < 406 mm fork length in Lake Pend Oreille, Idaho 1997-1998. Fish were collected by electrofishing and angling.

Identifiable prey	January (n=9)	February (n=8)	March	April (n=16)	May (n=20)	June (n=18)	July (n=34)
Insects		0.33	n/a	0.47	1.17		
Opossum shrimp				0.05			
Kokanee	58.71	75.16		79.90	91.46	86.86	91.16
Rainbow trout	17.27			3.63	7.37	8.42	8.84
Lake trout				14.46			
Bull trout							
Whitefish spp.	23.48						
Catostomidae				1.17		4.72	
Centrarchidae				0.32			
Cottidae							
Peamouth	0.53	24.51					
Northern pikeminnow							

Identifiable prey	August (n=20)	September (n=16)	October (n=5)	November (n=28)	December (n=21)	Total Fish ≥ 406 mm (n=195)	Total Fish < 406 mm (n=5)
Insects		0.01	0.04			0.21	
Opossum shrimp		0.13	0.44	0.14		0.04	31.60
Kokanee	85.90	99.85	99.52	82.51	87.54	87.40	
Rainbow trout				1.86	5.48	5.46	
Lake trout	0.09			0.30		0.62	
Bull trout				6.20	3.30	1.50	
Whitefish spp.	14.01				3.15	2.31	
Catostomidae						0.44	
Centrarchidae						0.01	
Cottidae							68.40
Peamouth				8.99		1.95	
Northern pikeminnow						0.05	

Table 2.3. Monthly prey consumption (%) by northern pikeminnow 100 to 150 mm and 150 to 305 mm in Lake Pend Oreille, Idaho. Fish were collected by electrofishing and angling. Sample sizes are in parentheses.

Northern pikeminnow 100-150mm

Identified prey	March (n=11)	June (n=150)	July (n=130)	August (n=110)	September (n=30)	October (n=82)	November (n=46)	Total (n=559)
Insecta	84.90	96.37	99.07	85.11	32.67	7.90	11.40	87.89
Decapoda		0.16				0.30		0.08
Opossum shrimp	14.67						19.39	0.95
Other crustacea		1.08		0.01	58.52	20.66		2.78
Mollusca		1.68	0.46	4.17	8.49	11.88	68.98	4.96
Unidentified salmonids						0.24		0.01
Cottidae						0.07		
Percidae				0.06				
Peamouth						50.12		2.27
Redside shiner				0.28	0.18	0.08		0.01
Northern pikeminnow					0.15	0.02		
Plant items	0.43	0.71	0.47	10.37		8.72	0.23	1.04

Northern pikeminnow 150-305 mm

Identifiable prey	May (n=220)	June (n=1,069)	August (n=250)	September (n=82)	October (n=71)	November (n=24)	Total (n=1,716)
Insecta	81.82	54.71	9.09	2.13	1.35	4.23	25.56
Decapoda	0.07	9.74	24.33	3.09	2.20		6.57
Opossum shrimp		0.08	0.04	25.77		1.14	4.50
Other crustacea	0.54	0.98	0.04		4.36		0.99
Mollusca	1.89	1.96	9.21	40.68	27.62	1.75	13.85
Larval fish				5.70			0.95
Kokanee		8.69	26.69		53.12		14.75
Rainbow trout							
Whitefish spp.		1.65	3.24	0.93		0.31	1.02
Cottidae	9.09	3.55	1.44				2.35
Percidae			4.01				0.67
Peamouth		1.45	2.71		8.59		2.12
Redside shiner	6.39	10.33	4.15	21.27	0.07	86.62	21.47
Northern pikeminnow		2.44	5.89				1.39
Plant items	0.20	4.42	9.18	0.42	2.69	5.95	3.81

Table 2.4. Monthly prey consumption (%) by northern pikeminnow 305 to 460 mm, and > 460 mm in Lake Pend Oreille, Idaho. Fish were collected by electrofishing and angling. Sample sizes are in parentheses.

Northern pikeminnow 305-460 mm

Identifiable prey	June (n=160)	July (n=47)	August (n=91)	September (n=8)	October (n=2)	November (n=4)	Total (n=312)
Insecta	24.78	8.73	1.21	0.03			8.73
Decapoda	11.13	2.59	32.07	20.67	100.00	77.86	23.36
Other crustacea	0.61					0.21	0.18
Mollusca	0.61		10.15	1.58			4.82
Kokanee	51.36	88.22	37.51	77.61			50.88
Rainbow trout		0.01	15.81				6.93
Bull trout	0.01						
Whitefish spp.							
Cottidae							
Peamouth	0.47			0.11			0.15
Redside shiner	0.03					21.70	0.27
Northern pikeminnow	10.18						2.97
Plant items	0.80	0.46	3.26			0.22	1.71

Northern pikeminnow > 460

Identifiable prey	April (n=1)	June (n=37)	July (n=2)	Total (n=40)
Insecta	100.00	99.00	12.00	12.00
Decapoda			3.00	3.00
Other crustacea		1.00		
Kokanee			41.00	41.00
Whitefish spp.				0.00
Plant items			44.00	44.00

Other fishes

I collected 782 stomachs from sculpin, bullhead, pumpkinseed, smallmouth bass, yellow perch, and cutthroat trout between June 1997 and December 1998. These fishes ranged in length from 50 to 508 mm. Approximately 30% (n= 237) were empty. No kokanee were identified in the stomachs of sculpin, bullhead, pumpkinseed, smallmouth bass, yellow perch, or cutthroat trout (Table 2.5). Insects were the principal food item for sculpin (72%), pumpkinseed (63%), and yellow perch (37%). Crustaceans were the principal food item for bullhead (34%). Opossum shrimp (62%) were the principal food item for cutthroat trout and redside shiners (40%) were the principal food item of smallmouth bass.

Table 2.5. Percent of prey items in the diet of selected predator fishes in Lake Pend Oreille, Idaho, 1997-1998. Sample sizes are in parentheses. Fish were sampled by electrofishing March through November 1997 and 1998.

Prey item	Sculpin spp. (n=5)	Bullhead spp. (n = 53)	Pumpkinseed (n = 12)	Smallmouth bass (n = 337)	Cutthroat trout (n= 14)	Yellow perch (n= 124)
Insecta	72.03	23.61	62.69	5.13	30.54	36.97
Decapoda		0.26				0.54
Opossum shrimp		8.60	0.59	0.01	62.17	10.18
Other crustacea	26.48	33.73	1.59	1.50	0.22	3.72
Mollusca		10.24	21.50	1.70		0.42
Larval fish			0.49	17.65		7.27
Unidentified fish			0.03		0.01	1.99
Unidentified salmonid						0.23
Kokanee						
Rainbow trout						
Lake trout						
Bull trout						
Whitefish spp.						
Unidentified non-salmonidae				17.07		3.82
Catostomida						
Centrarchidae						
Cottidae				0.92		
Ameiurus spp.						
Percidae						3.91
Unidentified cyprinidae						0.20
Peamouth				5.07		1.87
Redside shiner				39.81		
Northern pikeminnow				10.04		0.11
Plant items		0.39	0.12	0.14	0.28	0.96
Other food	1.48	17.97	1.57	0.95	0.01	5.43
Unidentified material		5.19	11.42	0.02	6.76	22.38

DISCUSSION

Predation is determined in part by spatial and temporal links to the food web influencing the predator's preference toward a particular food type and size of food and the availability of food (Popova 1978; Garvey et al. 1998). Food web interactions are difficult to assess because of multiple roles of individual fish species within an ecosystem and the potential for environmental conditions to change their ontogeny (Garvey et al. 1998). Kokanee are the preferred prey species for pelagic predator fishes throughout the year in Lake Pend Oreille although predator fishes could potentially prey on any of the 30 fishes found in Lake Pend Oreille (B. Harryman, Idaho Department of Fish and Game, pers. comm.). Kokanee numbers are presently at record low numbers; however, they are still the most commonly sampled pelagic prey fish in Lake Pend Oreille during IDFG's annual open water trawling surveys.

Some piscivorous salmonid fishes will not switch to alternative prey when their preferred prey declines and becomes more difficult to locate (Stewart and Ibarra 1991; Madenjian et al. 1998; Rand and Stewart 1998a; and Rand and Stewart 1998b). Although prey preference may not change, the size preference of a particular prey item may change depending on availability. This phenomenon could lead to a predator bottleneck resulting in a crash of the prey species, as observed with alewifes *Alosa pseudoharengus* in Lake Michigan (Rand and Stewart 1998a). Rand and Stewart (1998b) hypothesized that as the abundance of prey declined, the condition of predators may also decline. Although current data suggest that predatory fishes will consume prey relative to their own size (Garvey et al. 1998; Madenjian et al. 1998; Yule and Luecke 1993), I did not observe a preference of larger fish to consume larger prey in Lake Pend Oreille. I did observe all sizes of predatory fishes to consume a range of kokanee lengths focusing on smaller individuals, similar to the findings of Rieman and Myers (1991).

A number of characteristics may make kokanee, despite their current low numbers, highly susceptible to consumption by large predatory fishes. Kokanee exhibit schooling behavior while kamloops, bull trout, and lake trout in Lake Pend Oreille are pelagic feeders covering large areas in search of prey. Therefore, a decrease in prey abundance may not result in decreasing predation rates until prey densities are severely reduced (Eby et al. 1995; Rieman and Myers 1991). Prey distribution plays a significant role in the distribution of predators in some systems (Goyke and Brandt 1993). In recent years, anglers targeting kamloops between 30 m and the surface commonly catch lake trout and bull trout, possibly indicating that predatory fishes which prefer kokanee need to cover more area to find kokanee because of their low abundance (Idaho Department of Fish and Game, unpublished data).

Kamloops

Previous studies in Lake Pend Oreille have recorded similar diet composition of kamloops to what I found. In 1976, kamloops > 431 mm total length (n = 250) preferentially foraged on ages 2 and 3 kokanee (180 to 230 mm; Bowler et al. 1978). In 1976, the mean length of kokanee consumed by kamloops (n = 70) was 180 mm; in 1980, mean length was 100 mm, and in 1990, 58% of the kamloops (n = 12) contained kokanee that averaged 161 mm (age 2; Paragamian et al. 1991). In 1990, an average of 2.4 kokanee/stomach was found for those kamloops having consumed kokanee. In 1997-1998, 30% of the kamloops sampled (n = 180) contained kokanee with an average length of 176 mm (age 1 to 4 kokanee) with 3.2 kokanee/kamloops stomach for fish that consumed kokanee. Similar to my results, in 1976 the diets of kamloops < 431mm total length (406 mm FL) contained mostly terrestrial and aquatic invertebrates and opossum shrimp while only two of the stomachs contained fish remains (Bowler et al. 1978). The length at age for kokanee in Lake Pend Oreille has changed little since they became established in the late 1930’s (M. Maiolie, Idaho Department of Fish and Game, pers. comm.)

The percent of empty kamloops stomachs collected throughout the year was relatively low compared to those from other systems. In Lake Pend Oreille during 1997-1998, 15% of the kamloops stomachs were empty (n = 172; Table 2.6), in Lake Ontario 34% of the adfluvial steelhead stomachs were empty (n =644; Rand and Stewart 1998b), and in Lake Superior, 17% of the steelhead stomachs were empty (n=126; Conner et al. 1993).

Bull trout

Bull trout were listed under the U.S, Endangered Species Act as a threatened species in June 1998, resulting in a complete closure of the fishery making it illegal to harvest bull trout. Therefore, the capture of bull trout for this research was limited to those fish captured in the bycatch of anglers targeting other species.

Previous studies have recorded diet composition of bull trout in Lake Pend Oreille. In 1990, 37% of the bull trout sampled (n = 16) had consumed kokanee (Paragamian et al. 1991); bull trout with kokanee contained an average of 1.8 kokanee/stomach. In 1997-1998, 38% of the bull trout contained kokanee with 0.5 kokanee/stomach for those having consumed kokanee. Although both sample sizes are small, the similarity of diet composition adds credence to my proportional diet breakdown.

I compared the diets of bull trout in Lake Pend Oreille to the diets of bull trout in ‘similar systems’. Similar systems were those with stocks of adfluvial bull trout and where kokanee were the dominant available food base: Flathead Lake, MT, USA, 1979-1981 (Leathe and Graham 1982), Lake Billy Chinook, OR, USA, 1983-1984 (Ratcliff et al. 1996), Arrow Reservoir, BC, Canada, 1989-1997 (D. Sebastian, British Columbia Fisheries, pers. comm.), Libby Reservoir, MT, USA, 1983-1987 (Chisholm et al. 1989), and Priest Lake, ID, USA, 1975 (Rieman et al. 1979). Kokanee comprised the majority of the diet of bull trout in all five systems except Flathead Lake (Figure 2.2).

Lake trout

The dietary items of lake trout in Lake Pend Oreille were similar to those of lake trout in 'similar systems'. Kokanee were the single most dominant food item found in lake trout from Flathead Lake, MT (20%) and Flaming Gorge Reservoir, WY (52%). Similar research on Flaming Gorge Reservoir, WY (Yule and Luecke 1993) found that lake trout > 600 mm (n = 303) consumed kokanee that ranged in length from 50 to 425 mm. In Lake Pend Oreille, lake trout $\geq$ 406 mm (n = 195) consumed 87.4% kokanee which ranged in length from 70 to 225 mm. Rieman and Myers (1991) also observed that lake trout selected kokanee 150 to 200 mm in other kokanee lakes in Idaho. I speculate that differences in the length of kokanee consumed in Flaming Gorge Reservoir and Lake Pend Oreille is explained by different length frequencies of lake trout and kokanee in the two systems.

The percent of empty lake trout stomachs collected throughout the year from Lake Pend Oreille in 1997-1998 was less than those in Lake Ontario. In Lake Pend Oreille, 18% of the lake trout stomachs were empty (n =206; Table 2.6), compared to Lake Ontario where 40% were empty (n= 1,059; Rand and Stewart 1998b).

Northern pikeminnow

Anglers have speculated that northern pikeminnow consume large quantities of salmonids (mostly kokanee) in Lake Pend Oreille. Research on Cascade Reservoir (Casey 1962), Priest Lake (Bjornn 1961), and Lower Granite Reservoir (Naughton 1998) found that northern pikeminnow consume mostly crustaceans and insects and to a lesser extent salmonid fishes. Northern pikeminnow are, in general, opportunistic feeders (Scott and Crossman 1973) and feed on a wide range of dietary items in Lake Pend Oreille. My results indicated that diet varied between length groups; however, in general, insects were the most commonly consumed prey item, and only those fish > 305 mm regularly consumed kokanee.

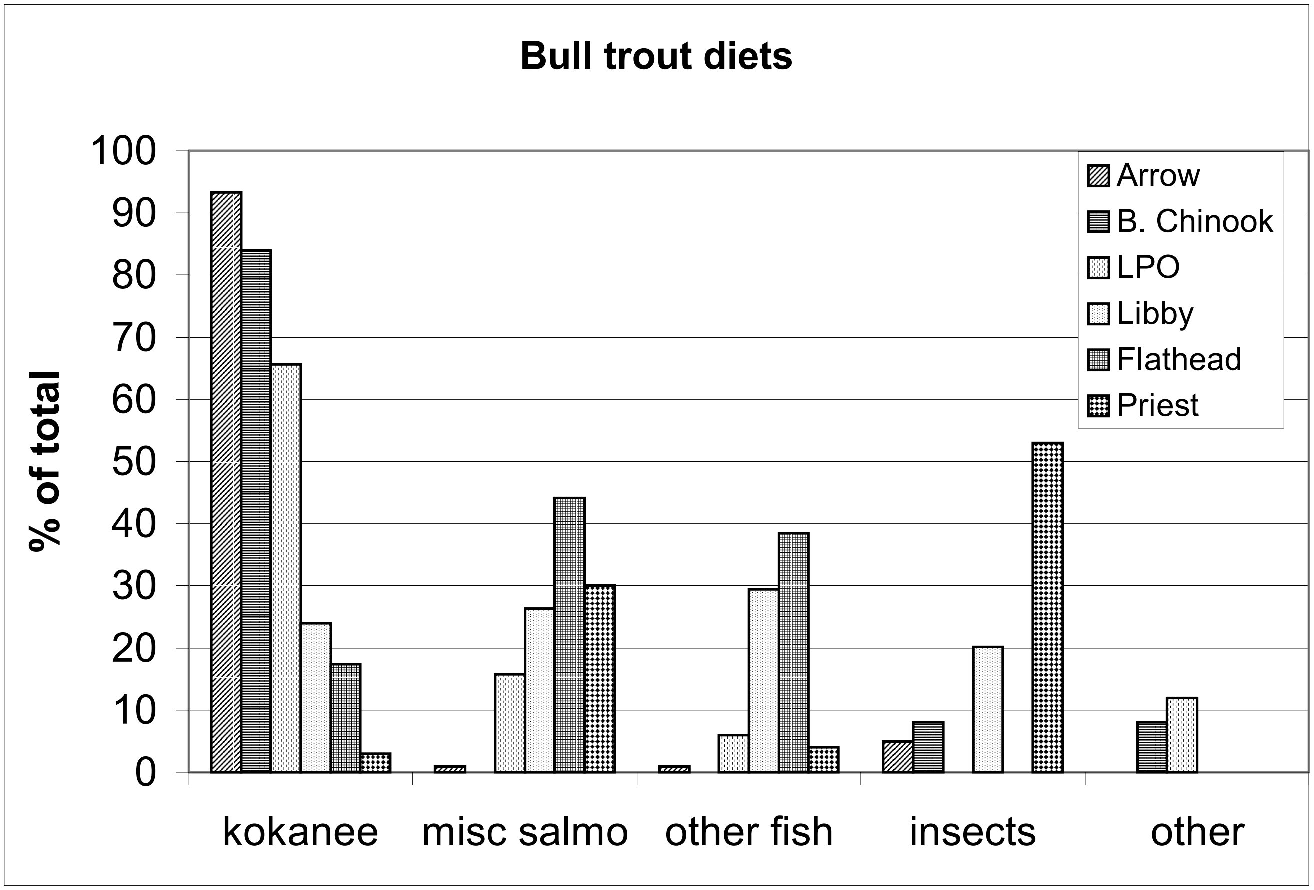


Figure 2.2. Diets of adfluvial bull trout in similar systems displaying percent kokanee, miscellaneous salmonids, other fish, insects, and other food items in diet. Flathead Lake, MT, USA ,1979-1981 (Leathe and Graham 1982), Lake Billy Chinook, OR, USA, 1983-1984 (Ratcliff et al. 1996), Arrow Reservoir, BC, Canada, 1989-1997 (D. Sebastian, British Columbia Fisheries, pers. comm.), Libby Reservoir, MT, USA 1983-1987 (Chisholm et al. 1989), and Priest Lake ID, USA, 1975 (Rieman et al. 1979)

Table 2.6. Number of full, empty and percent empty stomachs from sampled kamloops, lake trout and northern pikeminnow Lake Pend Oreille, Idaho 1997-1998. Blank spaces indicate no available data.

Kamloops

Month	Full	Empty	% empty	Total
Jan				
Feb				
Mar				
Apr	11	2	15.4	13
May	7	1	12.5	8
Jun	6	5	45.5	11
Jul	4	1	20.0	5
Aug	16	1	5.9	17
Sep	6	0	0.0	6
Oct	23	8	25.8	31
Nov	65	16	19.8	81
Dec				

Lake trout

Month	Full	Empty	% empty	Total
Jan	2	0	0.0	2
Feb				
Mar	3	0	0.0	3
Apr	18	0	0.0	18
May	20	3	13.4	23
Jun	34	0	0.0	34
Jul	24	1	4.0	25
Aug	25	1	3.8	26
Sep	12	2	14.3	14
Oct	4	1	20.0	5
Nov	28	10	26.3	38
Dec	18	0	0.0	18

Northern pikeminnow

Month	Full	Empty	% empty	Total
Jan				
Feb				
Mar				
Apr				
May				
Jun	993	579	36.8	1572
Jul	332	220	39.9	552
Aug	259	130	33.4	389
Sep	137	79	36.6	216
Oct	213	96	31.1	309
Nov	111	192	63.4	303
Dec				

The percent of empty northern pikeminnow stomachs collected throughout the year in Lake Pend Oreille was lower than in other systems. In Lake Pend Oreille, I found 21% of the stomachs were empty (n=3,341), whereas in Cascade Reservoir (n=132; Casey 1962) and the lower Columbia River (Thompson 1958) 60% and 63% were empty, respectively.

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Objective Three

PREDATORY IMPACT

INTRODUCTION

Kokanee populations in Lake Pend Oreille have declined over the last 30 years. The kokanee harvest is presently at 20% of its historic level because of population declines, supporting a recreational fishery of less than 200,000 fish annually (Maiolie and Elam 1993; Paragamian et al. 1991). Record low numbers of kokanee in the last 5 years have concerned managers, prompting research to quantify effects of predatory fishes on kokanee. In Lake Pend Oreille, kokanee, an important component of the food web, have provided both a prey base, enhancing the growth of predatory fishes, and a fishery for over 60 years (Wydoski and Bennett 1981).

Predation rates have been estimated by laboratory experiments, field observations, and bioenergetic modeling (Eby et al. 1995). Bioenergetic modeling is a valuable tool used to examine predator-prey relationships, including predator demand and prey abundance, incorporating effects of spatial, temporal and biological variation (Brandt and Mason 1994). Bioenergetic modeling may be the most accurate and economical means to estimate annual consumption needs for cohorts or entire populations of certain fish predators (Stewart et al. 1983; Ney 1993; Chipps and Bennett 2000; Madon and Culver 1993). Using measured survival rates of predators and their absolute abundance, spatial and temporal food habit data, and estimates of thermal experience, consumption of kokanee can be calculated using the bioenergetics approach (Beauchamp et al. 1989, 1995).

Evaluating total consumption by the dominant kokanee predators in Lake Pend Oreille and identifying which cohorts pose the highest predation impacts on kokanee will help managers decide whether predator abundance is excessive. Then managers can determine what balance between predators and prey will allow the kokanee population to increase while continuing to provide a trophy fishery for predators.

Objective 3. Estimate kokanee consumed by kamloops, bull trout, and lake trout $\geq$ 406 mm and relative consumption by kamloops, bull trout, lake trout and northern pikeminnow in Lake Pend Oreille, Idaho.

METHODS

The computer model Fish Bioenergetics 3.0 (Hanson et al. 1997) was used to estimate total annual consumption of kokanee by kamloops, bull trout and lake trout $\geq$ 406 mm fork length which are believed to be the dominant kokanee predators in Lake Pend Oreille (Anderson 1978; Pratt 1985; Rieman and Falter 1981). Additionally, a relative comparison of consumption was estimated for kamloops, bull trout, lake trout, and northern pikeminnow annually/1,000 fish. Consumption was estimated by fitting a known growth curve. Metabolism, swimming speed, egestion, and excretion parameters for kamloops, bull trout, and lake trout were obtained from the model; lake trout were used as a surrogate for bull trout and steelhead for kamloops (Hanson et al. 1997). Parameters used in the model and estimated from Lake Pend Oreille fish predators included population estimates of each predatory cohort, mortality estimates, weight at age estimates, temperatures available to fish throughout the year, and dietary composition.

Specific modeling used by Fish Bioenergetics 3.0 is described in detail in Hanson et al. (1997; Appendix Table 3.1) and summarized here:

$C = C_{max} * p * f(T)$

Where:C = specific consumption rate

C_{max}= maximum specific feeding rate

p = proportion of maximum consumption

f(T) = temperature dependence function

T = water temperature (°C)

$C_{max} = CA * W^{CB}$

Where:W = fish mass

CA = intercept of the allometric mass function

CB = slope of the allometric mass function.

Annual consumption rates of kokanee by individual age cohorts of kamloops, bull trout, and lake trout $\geq$ 406 mm were estimated in terms of grams of kokanee consumed, and 95% confidence intervals were calculated using the population estimates (Objective 1). Numeric losses were converted from grams of kokanee consumed, using the mean weight of age 2 kokanee (1998; 37 g/kokanee) from population estimates made the same year by IDFG. The mean length of age 2 kokanee corresponded with the size of kokanee most commonly consumed by predator fishes (Objective 2). Total consumption estimates for each cohort of kamloops, bull trout, and lake trout $\geq$ 406 mm were related to kokanee production and yield. Production is defined as biomass added to the population, and yield refers to the total biomass lost from the population (Ricker 1975). Kokanee production and yield estimates were obtained from IDFG 1998 estimates of kokanee population abundance and kokanee growth based on hydroacoustic sampling (M. Maiolie, Idaho Department of Fish and Game, unpublished data).

I interpreted P-values for simulations from kamloops, bull trout, lake trout, and northern pikeminnow as presented in the literature (Hanson et al. 1997).

I evaluated the sensitivity of the model to each of the species specific variables over a

12 month period by varying each parameter by +/-10% while keeping all other variables fixed and comparing results to those using the average values. Variables used to evaluate sensitivity of the model included mortality, percent kokanee in diet, temperature, and energy density of kokanee.

Kamloops

Consumption rates in 1998 were estimated for kamloops with the bioenergetic model using steelhead as a surrogate (Hanson et al. 1997). I based model simulations of consumption on estimates of population abundance, mortality, and growth (Objective 1), diet (Objective 2), and thermal history from kamloops in Lake Pend Oreille. Energy used for gamete production, migration, and spawning was not considered. Consumption simulations began on January 1 (simulation day 1) and ended December 31 the same year for ages 4 to 9 kamloops. Monthly averages of diet were used for simulations of all cohorts. Kokanee consumption by age 4 kamloops began on day 100 to compensate for the estimated time necessary for age 4 kamloops to attain predatory length of 406 mm (4.5 years). Diet composition for months when no stomach samples were collected (December – March) was calculated by averaging the dietary items from the surrounding months. Energy values of prey items ranged from 2,742 joules/g wet weight (wt) for *Chironomids* to 7,887 joules/g wet wt for terrestrial invertebrates (Table 3.1). Energy content for each prey item was assumed

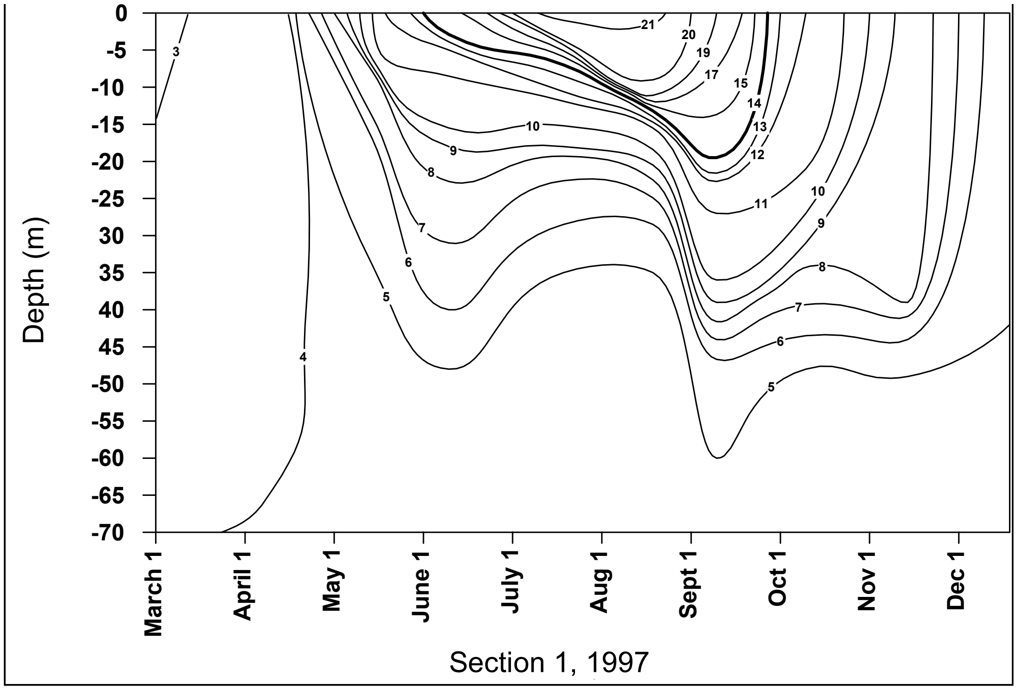
Table 3.1. Energy values for various prey items found in kamloops, bull trout, lake trout, and northern pikeminnow in Lake Pend Oreille, 1997-1998.

Insects	Energy values (joules/g wet wt.)	Citation
Chironomidae	2,742	Cummins and Wuycheck (1971)
Ephemeroptera	see below	used mean value for aquatic invertebrates
Hymenoptera (ants)	see below	used mean value for terrestrial invertebrates
Average aquatic invertebrates	3,178	Cummins and Wuycheck (1971)
Average terrestrial invertebrates	7,887	Cummins and Wuycheck (1971)
Salmonid fishes		
Kokanee	5,221	Beauchamp et al. (1989)
Rainbow trout	5,764	Hanson et al. (1997)
Lake trout	5,776	Stewart et al. (1983)
Bull trout	5,776	Stewart et al. (1983)
Whitefish	5,989	Rottiers and Tucker (1982)
Average salmonids excluding kokanee	5,826	average from above
Catostomid fishes		
Largescale sucker	7,524	Used general value for Cyprinidae from Cummins and Wuycheck (1971)
Cyprinid fishes		
Peamouth, Northern pikeminnow, and Redside shiner	6,703	Petersen and Ward (1999)
Centrarcid fishes		
Yellow perch	4,186	Hanson et al. (1997)
Other		
Opossum shrimp	3,474	Hanson et al. (1997)
Sculpin	5,439	Cummins and Wuycheck (1971)
Decapods	4,506	Cummins and Wuycheck (1971)
Mollusca	2,010	Cummins and Wuycheck (1971)
Plant food	2,558	Cummins and Wuycheck (1971)

constant throughout the year. I assumed kamloops inhabited their preferred temperatures (13° C; Scott and Crossman 1973) when available similar to Brandt and Kirsch (1993) and temperatures nearest that at other times. I used temperature profile data collected by IDFG personnel at 1 m depth intervals between the surface and 60 m to determine monthly temperatures available to fish (Figures 3.1 and 3.2). Consumption rates, metabolism, swimming speed, egestion, and excretion parameters were assumed similar to those for steelhead in the model (Hanson et al. 1997).

Bull trout

Consumption rates in 1998 were estimated for bull trout with the bioenergetic model using lake trout as a surrogate similar to methods used by Beauchamp (University of Washington, pers. comm.). I based model simulations of prey consumption on estimates of population abundance, mortality, and growth (Objective 1), diet (Objective 2), and thermal history from bull trout in Lake Pend Oreille. Energy used for gamete production, migration, and spawning was not considered. Consumption simulations began on January 1 (simulation day 1) and ended December 31 the same year. Results from the diet analysis (Objective 2) were pooled, and the average annual aggregate of dietary items was compared to diets of bull trout in similar systems (Objective 2) and the relative abundance of fishes captured during the gillnet effort (Objective 1). A weighted mean of dietary items was then used in the model for bull trout consumption (ages 6 to 12): kokanee (74.0%), whitefish (13.85%), peamouth (7.29%), northern pikeminnow (2.92%), bull trout (0.97%), lake trout (0.49%), insects (0.24%), and opossum shrimp (0.24%).



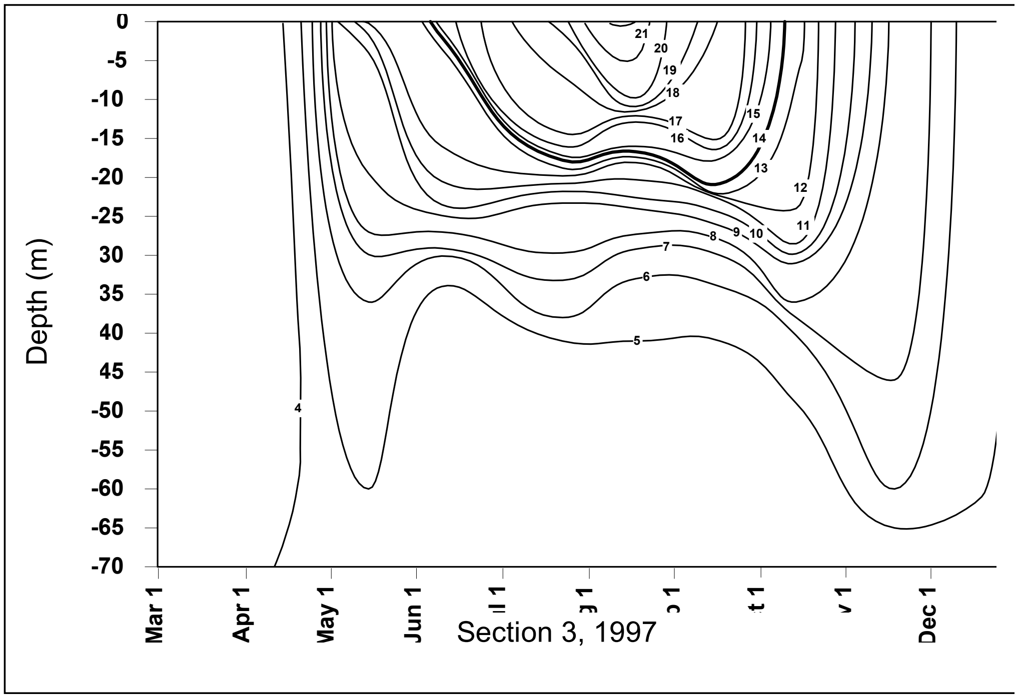
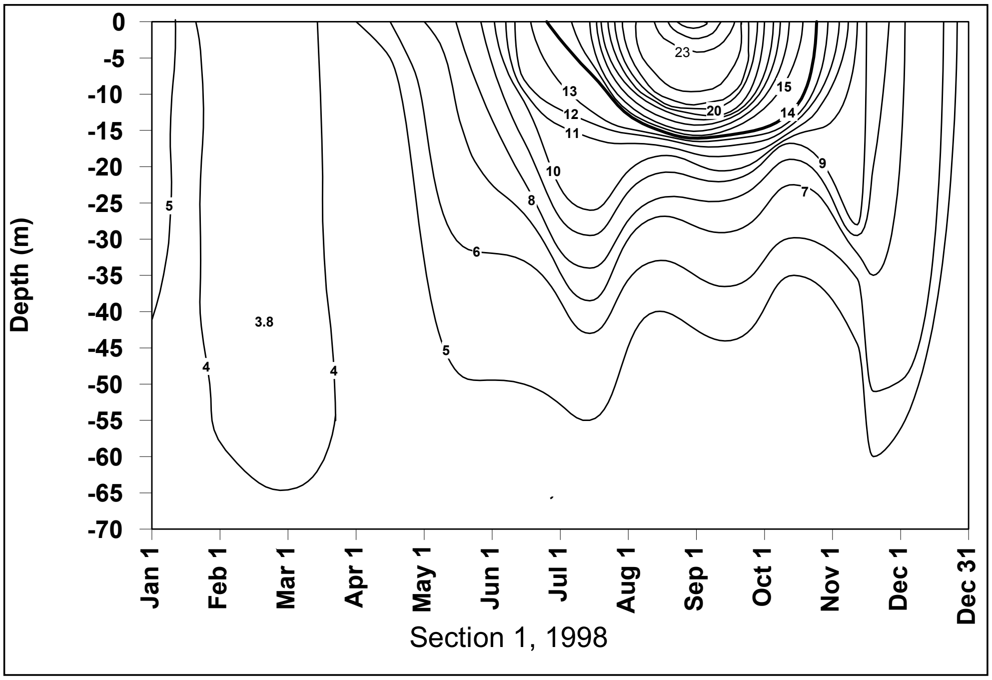
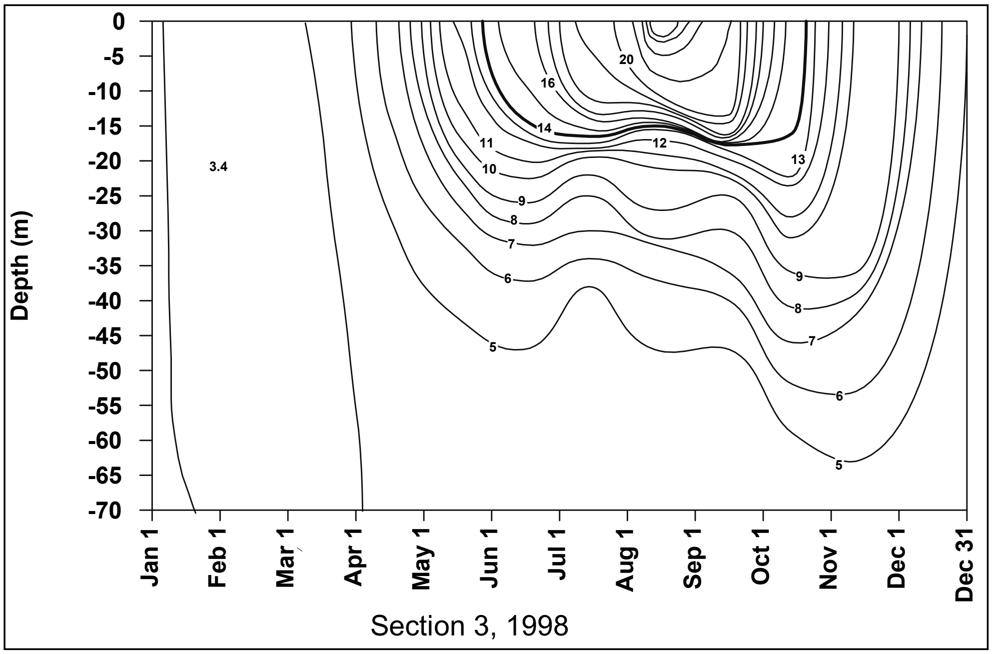


Figure 3.1. Isopleths of water temperatures (°C) from sections 1 and 3 Lake Pend Oreille, Idaho, 1997 (see Figure 1.1).



Section 1, 1998



Section 3, 1998

Figure 3.2. Isopleths of water temperatures (°C) from sections 1 and 3 Lake Pend Oreille, Idaho, 1998 (see Figure 1.1).

Energy values of prey items ranged from 3,178 joules/g wet wt (mean for aquatic insects) to 6,703 joules/g wet wt for peamouth and northern pikeminnow (Table 3.1), and energy content for each prey item was assumed constant throughout the year. I assumed bull trout inhabited their preferred temperatures (12 - 13 °C; Scott and Crossman 1973; D. Beauchamp, University of Washington, pers. comm.) when available similar to Brandt and Kirsch (1993) and temperatures nearest that at other times. I used temperature profiles collected monthly by IDFG personnel (Figures 3.1 and 3.2). Consumption rates, metabolism, swimming speed, egestion, and excretion parameters were those used for lake trout in the model.

Lake trout

Consumption rates in 1998 were estimated for lake trout with the bioenergetic model (Hanson et al. 1997). I based model simulations of prey consumption on estimates of population abundance, mortality, and growth (Objective 1), diet (Objective 2), and thermal history from lake trout in Lake Pend Oreille. Energy used for gamete production, migration, and spawning was not considered. Consumption simulations began on January 1 (simulation day 1) and ended December 31 the same year for lake trout ages 6 to 11. Monthly averages of diet were used for simulations of all cohorts. Kokanee consumption by age 6 lake trout began on day 255 to compensate for the estimated time necessary for age 6 lake trout to attain predatory length of 406 mm (6.75 years). Diet composition for months when no stomach samples were collected (March) was calculated by averaging the dietary items from the surrounding months. Energy values of prey items ranged from 3,178 joules/g wet wt (mean for aquatic insects) to 7,887 joules/g wet wt for terrestrial invertebrates (Table 3.1), and energy content for each prey item was assumed constant throughout the year. I assumed lake trout inhabited their preferred temperatures (10 °C; Scott and Crossman 1973) when available similar to Brandt and Kirsch (1993) and temperatures nearest that at other times. I used temperature profiles collected monthly by IDFG personnel (Figures 3.1 and 3.2). Consumption rates, metabolism, swimming speed, egestion, and excretion parameters were those used for lake trout in the model.

Northern Pikeminnow

Consumption rates in 1998 were estimated for northern pikeminnow with the parameters defined by Petersen and Ward (1999) for the bioenergetic model. I based model simulations of consumption on estimates of mortality and growth (Objective 1), diet (Objective 2), and thermal history from northern pikeminnow in Lake Pend Oreille. Energy used for gamete production, migration, and spawning was not considered. Consumption simulations generally began on January 1 (simulation day 1) and ended December 31 the same year. Monthly averages of diet were used for simulations of all cohorts. Diet composition for months when no stomach samples were collected (December-February) was calculated by averaging the dietary items from the surrounding months. Energy values of prey items ranged from 2,558 joules/g wet wt for 'plant items' to 7,887 joules/g wet wt for terrestrial invertebrates (Table 3.1), and energy content for each prey item was assumed constant throughout the year.

I assumed northern pikeminnow inhabited their preferred temperatures (21.5 °C; Petersen and Ward 1999) when available similar to Brandt and Kirsh (1993) and temperatures nearest that at other times. I used temperature profiles collected monthly by IDFG personnel (Figures 3.1 and 3.2). Consumption rates, metabolism, swimming speed, egestion, and excretion parameters were estimated by Petersen and Ward (1999) for Fish Bioenergetics 3.0.

RESULTS

Bioenergetic modeling indicated that in Lake Pend Oreille kamloops, bull trout, and lake trout collectively consumed more than 153.5 metric tons-mt (65%) of the 235.2 mt of kokanee produced (e.g. biomass gained/yr) 95% CI: [105.4 mt**,** 286.3 mt] in 1998 accounting for 73% of the kokanee biomass lost. Kamloops constitute 82% of the pelagic predator biomass and consumed 53% of the annual kokanee production, whereas bull trout (14%) consumed 10%, and lake trout (4%) consumed 2%.

Kamloops

Bioenergetic modeling predicted kamloops $\geq$ 406 mm (ages 4 to 9) consumed 196.0 mt of prey in 1998. Kamloops consumed nearly 126.3 mt of kokanee followed by ‘other-salmonids’ (41.7 mt), cyprinids (21.7 mt), insects (4.7 mt) and opossum shrimp (2.1 mt). P-values for all cohort simulations ranged between 0.27 and 0.43 (Table 3.2). Monthly prey consumption by all cohorts ranged from 6.7 mt (February) to 23.8 mt (August). Kamloops ages 7 to 9 (> 676 mm) consumed 102.6 mt of prey, whereas kamloops ages 4-5 (384 to 592 mm) consumed 65.5 mt. Kamloops age 6 (593 to 675 mm) consumed 28.2 mt, considerably less than age 7 (37.3 mt).

Age 4 kamloops (384 to 494 mm fork length) consumed the highest quantity of prey (37.6 mt) kokanee (21.4 mt),‘other-salmonids’ (7.5 mt), and other items (Figure 3.3). Monthly prey consumption for age 4 kamloops ranged from 1.2 mt (March) to 4.6 mt (October). Estimated food consumed by other cohorts decreased proportionally (Appendix Table 3.2), although biomass of kokanee consumed did not. Kokanee consumption by kamloops $\geq$ 406 mm ranged from 18.4 mt (age 5) to 24.6 mt (age 7).

Table 3.2. P-values recorded from bioenergetic modeling of piscivorous cohorts for kamloops, bull trout, lake trout and northern pikeminnow from Lake Pend Oreille, Idaho, 1997-1998.

Kamloops

Age	P-value
4	0.32
5	0.27
6	0.32
7	0.43
8	0.42
9	0.40

Lake trout

Age	P-value
7	0.45
8	0.66
9	0.50
10	0.53
11	0.48
12	0.48

Bull trout

Age	P-value
6	0.46
7	0.39
8	0.35
9	0.34
10	0.32
11	0.31
12	0.29

Northern pikeminnow

Age	P-value
6	0.31
7	0.23
8	0.24
9	0.22
10	0.27
11	0.26

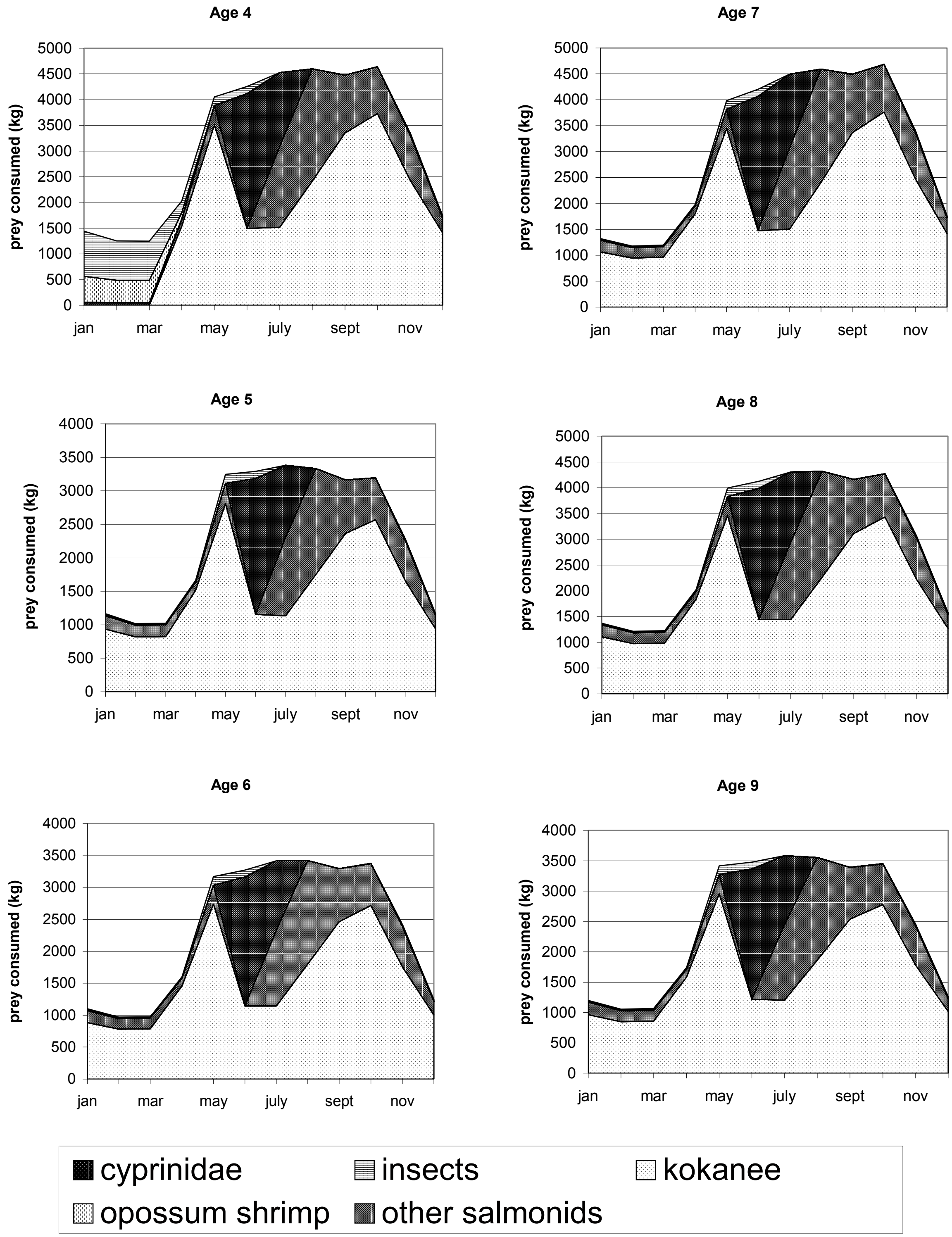


Figure 3.3. Estimated consumption (kg) of prey items by kamloops ages 4 to 9 in Lake Pend Oreille, Idaho, 1998.

Modeling predicted kamloops ≥ 406 mm consumed more kokanee biomass than bull trout and lake trout > 406 mm and northern pikeminnow ≥ 315 mm for 1,000 fish in 1998. Kamloops ≥ 406 mm in Lake Pend Oreille consumed an estimated 126.3 mt of kokanee (3,412,465 kokanee) in 1998 95% CI: [87.3 mt**,** 228.0 mt]. Kamloops 406 to 592 mm

consumed similar biomass of kokanee as kamloops 593 to 864 mm (93.7 mt vs 102.6 mt). Age 7 kamloops consumed more kokanee in October (3.8 mt) than any other cohort throughout the year.

My sensitivity analysis for kamloops indicated that a 10% increase of kokanee in diet resulted in a 14.0% change in kokanee consumption, fewer effects were seen for changes in temperature (11.9%), mortality (-9.9%), and energy value of kokanee (-6.0 %). A 10% decrease resulted in proportionally similar changes.

Bull trout

Bioenergetic modeling predicted bull trout ≥ 406 mm (age 6 to 12) consumed 30.4 mt of prey in 1998. Bull trout consumed nearly 22.5 mt of kokanee followed by whitefishes (4.2 mt), peamouth (2.2 mt), northern pikeminnow (1.0 mt), bull trout (0.3 mt), lake trout (0.2 mt), catostomids (0.1 mt), and insects (0.1 mt). P-values for all cohort simulations ranged between 0.29 and 0.46 (Table 3.2). Monthly prey consumption by all cohorts ranged from 1.1 mt (February) to 4.0 mt (October). Bull trout ages 6 and 7 (406-549 mm) consumed 9.1 mt of prey, whereas bull trout age 8 (550 to 617 mm) consumed 4.0 mt. Bull trout ages 9 to 12 (618 to 889 mm) consumed 9.4 mt. Estimated food consumed by other cohorts decreased proportionally (Figure 3.4).

Age 7 bull trout (475 to 549 mm) consumed the highest quantity of prey (6.4 mt): kokanee (4.7 mt), whitefishes (1.0 mt), and other items (Appendix Table 3.3). Monthly prey consumption for age 7 bull trout ranged from 0.2 (February) mt to 1.0 mt (October).

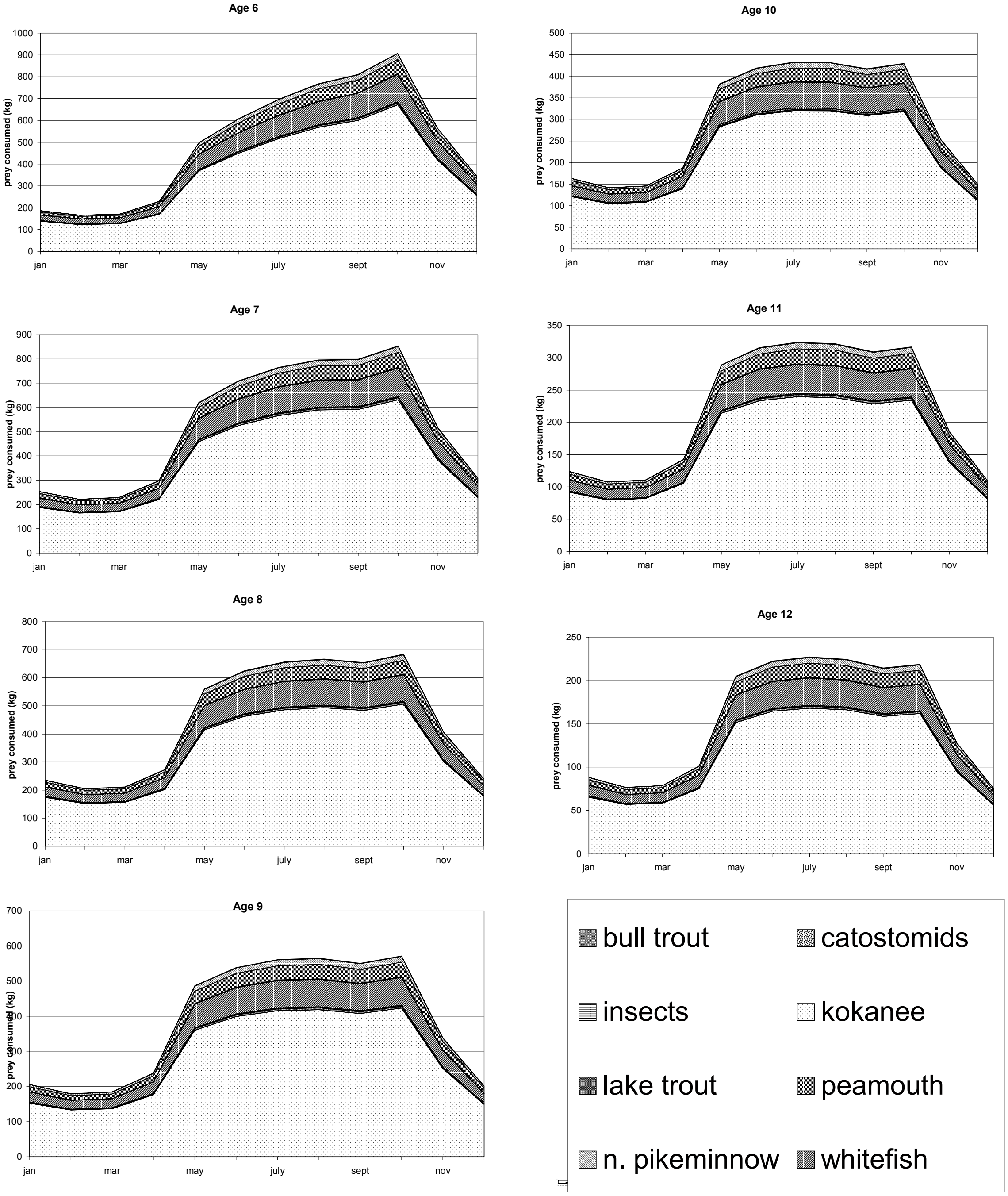


Figure 3.4 Estimated consumption (kg) of prey items by bull trout ages 6 to 12 in Lake Pend Oreille, Idaho, 1998.

Modeling predicted bull trout ≥ 406 mm consumed more kokanee biomass than lake trout ≥ 406 mm and northern pikeminnow ≥ 315 mm, for 1,000 fish in 1998. Bull trout ≥ 406 mm in Lake Pend Oreille consumed an estimated 22.5 mt of kokanee (608,825 kokanee) in 1998 95% CI: [15.3 mt, 42.5 mt]. Bull trout 406 to 549 mm consumed similar biomass of kokanee as bull trout 618 to 889 mm (9.1 mt vs 9.4 mt). Age 7 bull trout consumed more kokanee in October (0.63 mt) than any other cohort throughout the year.

My sensitivity analysis indicated a 10% decrease in mortality resulted in a 15.8% change in total annual consumption of kokanee; fewer effects were seen for changes in diet (-11.3%), temperature (-0.5%), and energy value for kokanee (7.8%). A 10% increase in mortality resulted in a –13.6% change in total annual consumption of kokanee; fewer effects were seen for changes in diet (11.6%), temperature (3.7%), and energy value of kokanee
(-6.7%).

Lake trout

Bioenergetic modeling predicted lake trout ≥ 406 mm (age 6 to 11) consumed 6.8 mt of prey in 1998. Lake trout consumed nearly 4.7 mt of kokanee followed by cottids (0.9 mt), unidentified salmonids (0.5 mt), peamouth (0.1 mt), catostomids (0.03 mt), insects (0.01 mt), opossum shrimp (0.4 mt), and centrarchids (0.002 mt). P-values for all cohort simulations ranged between 0.45 and 0.66 (Table 3.2). Monthly prey consumption for all cohorts ranged from 0.4 mt (February) to 0.8 mt (May). Lake trout age 6-7 (363-492 mm) consumed 4.1 mt of prey, whereas lake trout age 8 (493 to 563 mm) consumed 1.2 mt. Lake trout ages 9 to 11 (564 to 700 mm) consumed 1.3 mt. Estimated food consumed by other cohorts decreased proportionally (Figure 3.5).

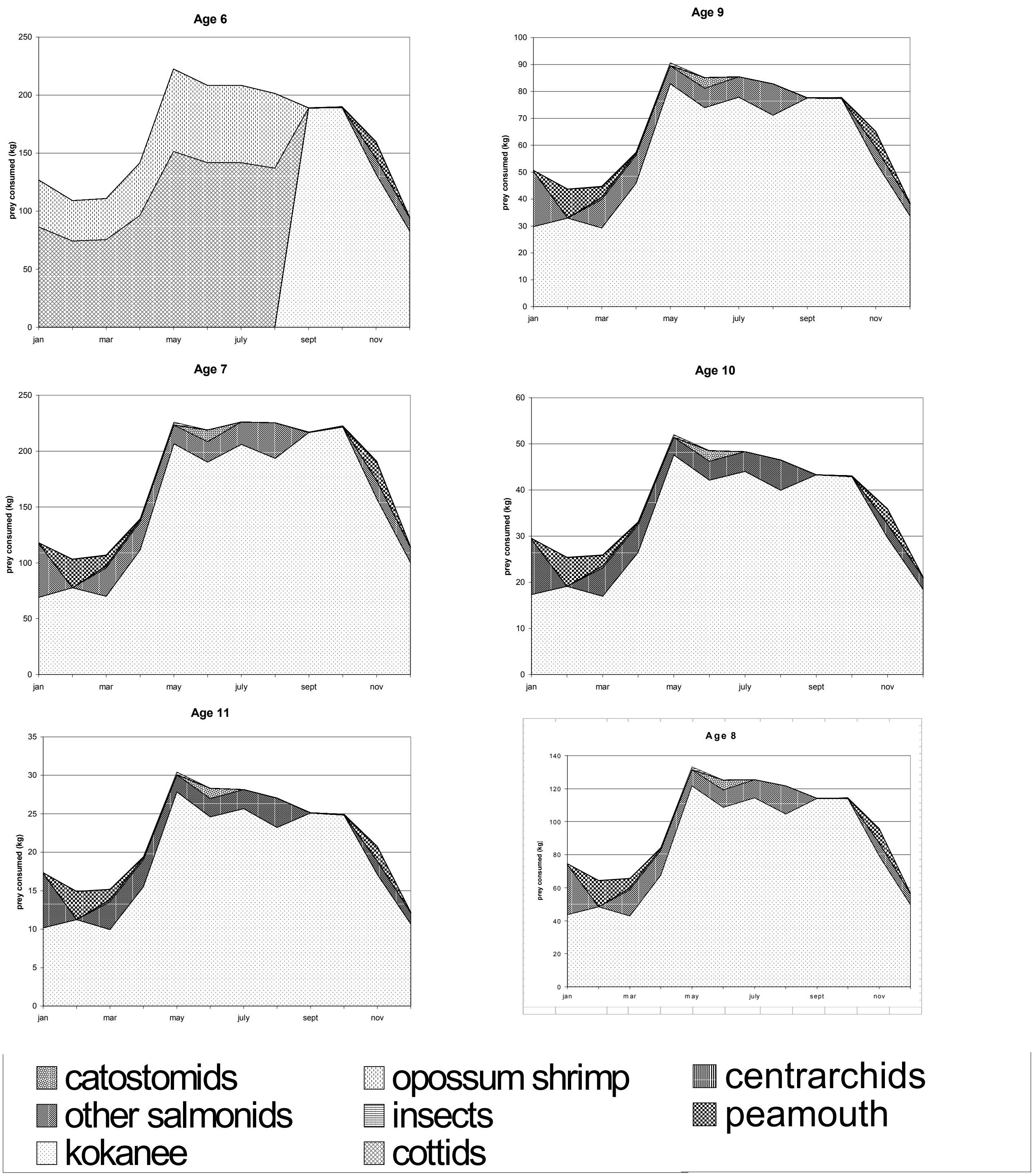


Figure 3.5. Estimated consumption (kg) of prey items by lake trout ages 6 to11 in Lake Pend Oreille, Idaho, 1998.

Age 7 lake trout (427 to 492 mm) consumed the highest quantity of prey (2.1 mt): kokanee (1.8 mt), unidentified salmonids (0.22 mt), and other items (Appendix Table 3.4). Monthly prey consumption by age 7 lake trout ranged from 0.1 mt (February) to 0.23 mt (July).

Modeling predicted lake trout ≥ 406 mm consumed less kokanee biomass than kamloops and bull trout ≥ 406 mm and more than northern pikeminnow ≥ 315 mm for 1,000 fish in 1998. Lake trout ≥ 406 mm in Lake Pend Oreille consumed an estimated 4.7 mt of kokanee (127,642 kokanee) in 1998 95% CI: [2.8 mt, 15.8 mt]. Lake trout 406-492 mm consumed more kokanee than the collective total of lake trout ≥ 493 mm (2.4 mt vs 2.3 mt). Age 7 lake trout consumed more kokanee in October (0.2 mt) than any other cohort throughout the year.

My sensitivity analysis indicated a 10% decrease in mortality resulted in a 23.0% change in total annual consumption of kokanee, fewer effects were seen for changes in diet (-10.0%), temperature (-4.0%), and energy content (9.5%). A 10% increase in mortality resulted in a –17.7% change in total annual consumption of kokanee; fewer effects were seen for changes in diet (8.1%), temperature (4.5%), and energy content (-7.9%).

Northern Pikeminnow (Relative Predation)

Bioenergetic modeling predicted northern pikeminnow ≥ 315 mm (ages 6 to 11) consumed 1.2 mt of prey/1,000 fish in 1998. Northern pikeminnow consumed nearly 0.47 mt of kokanee followed by decapods (0.34 mt), plants (0.14 mt), insects (0.14 mt), rainbow trout (0.03 mt), redside shiner (0.02 mt), molluscs (0.02 mt), northern pikeminnow (0.01 mt), and other crustaceans, peamouth, bull trout, whitefish, and cottids (< 0.001 mt). P-values for all cohort simulations ranged between 0.22 and 0.31 (Table 3.2). Monthly prey consumption/ 1,000 individuals ranged from 0.001 mt (March) to 0.24 mt (October). Age 6 northern pikeminnow (315 to 355 mm total length) consumed the highest quantity of prey (0.22 mt), consuming decapods (0.1 mt), kokanee (0.09 mt), and other items (Figure 3.6).

Monthly prey consumption for age 6 northern pikeminnow ranged from 0.002 mt (March) to 0.05 mt (October). Estimated food consumed by other cohorts decreased proportionally (Appendix Table 3.5). Kokanee consumption by northern pikeminnow ranged from 0.90 mt (age 8) to 0.06 (age 11)/1,000 individuals in 1998. Modeling predicted northern pikeminnow $\geq$ 315 mm consumed fewer kokanee (0.47 mt) for 1,000 fish in 1998 than kamloops (8.6 mt), bull trout (1.8 mt), and lake trout (2.6 mt) $\geq$ 406 mm. Northern pikeminnow $\geq$ 315 mm in Lake Pend Oreille consumed 12,683 kokanee in 1998/1,000 fish. Northern pikeminnow 315 to 426 mm (TL) consumed similar biomass of kokanee as northern pikeminnow 427 to 514 mm (0.26 mt vs 0.20 mt). Age 8 northern pikeminnow consumed more kokanee in July (0.024 mt) than any other cohort throughout the year.

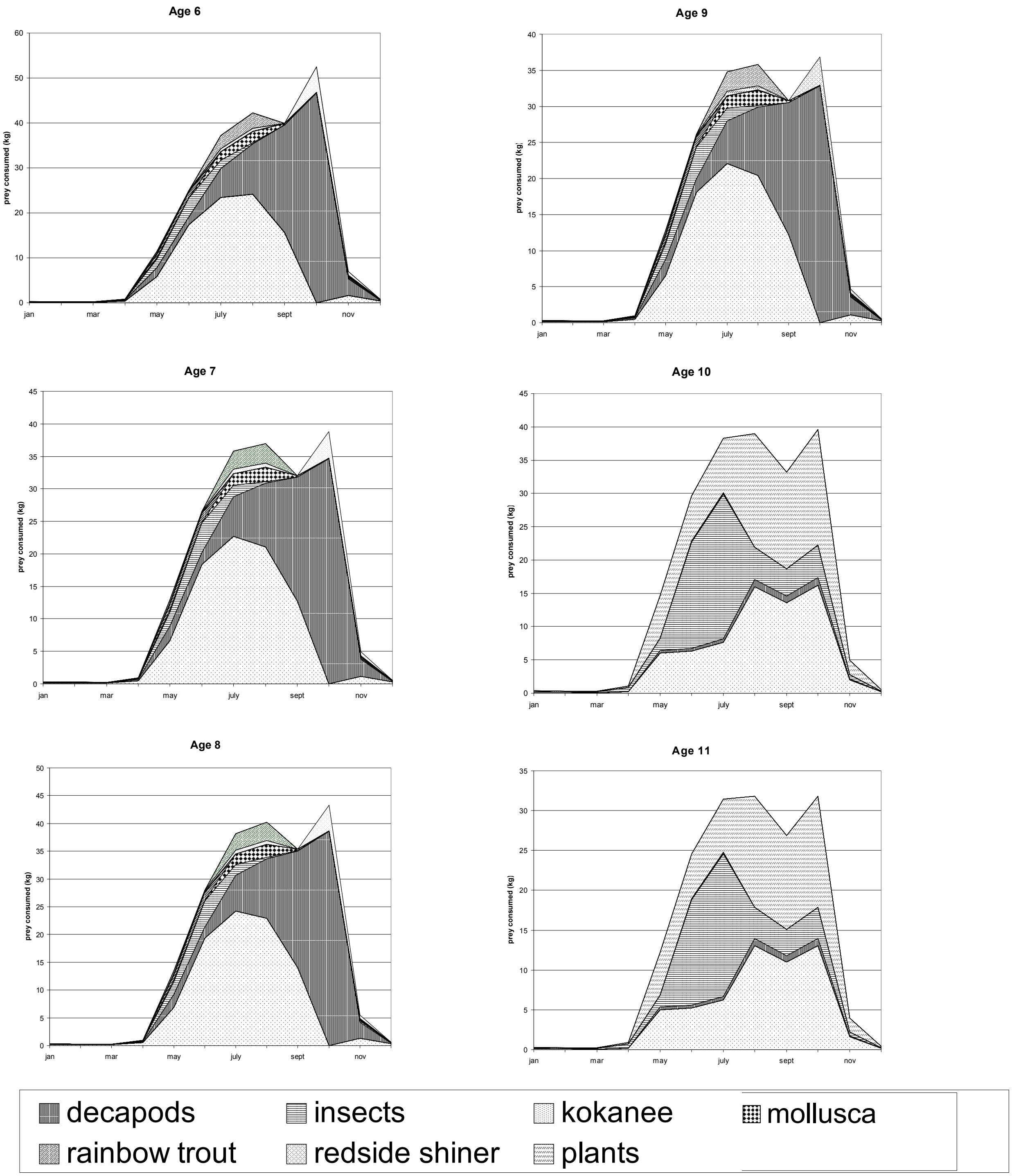


Figure 3.6. Estimated consumption (kg) of prey items by northern pikeminnow ages 6 to 11 based on 1,000 fish annually in Lake Pend Oreille, Idaho, 1998.

DISCUSSION

I feel the application of bioenergetic modeling to predict predator consumption based on species specific parameters estimated from Lake Pend Oreille (population estimates, diets, growth, mortality, and available temperatures) provided an accurate assessment of predator/prey dynamics. Numerous other investigators have used this model to estimate prey consumption for bull trout (Beauchamp et al. 1995); coho, chinook, steelhead, lake trout and brown trout (Rand and Stewart 1998); lake trout (Eby et al. 1995; Stewart et al. 1983;Yule and Luecke 1993); chinook and lake trout (Goyke and Brandt 1993); coho, chinook, and lake trout (Stewart and Ibarra 1991); and walleye (Lyons and Magnuson 1987).

Kokanee consumption by salmonid predators and northern pikeminnow is generally highest in October and lowest during the winter, similar to consumption by piscivorous-sized steelhead in Lakes Ontario and Michigan (Rand et al. 1993). I hypothesize that consumption varies seasonally primarily because of water temperatures. In Lake Pend Oreille, October is generally when the thermocline breaks down (Idaho Department of Fish and Game, unpublished) and temperatures preferred by most salmonids are distributed throughout the lake apparently providing higher foraging efficiency.

Younger piscivorous cohorts of predatory fishes (kamloops ages 4 to 7; bull trout ages 6 to 8; lake trout ages 6 to 7; and northern pikeminnow ages 6 to 8) consume more kokanee/yr than the cumulative total of their older cohorts, similar to trends observed for lake trout in Lake Champlain, Vermont (LaBar 1993). I hypothesize that younger cohorts collectively consume more prey because population biomass and growth are highest for younger piscivorous cohorts.

Kamloops (82% of the predator biomass) consumed 53% of the 1998 kokanee production compared to that for bull trout (14% of the predator biomass), which consumed 10% of the kokanee production. Lake trout comprised 4% of the predator biomass and consumed 2% of the kokanee production. Biomass estimates were not made for northern pikeminnow because population abundance was not estimated. Although northern pikeminnow ≥ 315 mm regularly consumed kokanee (24% of the annual diet; Objective 2), they constituted a small proportion of the population relative to fish < 315 mm (Figure 1.2). Predator fishes totaled 2.68 kg/ha (1.26 predators/ha), whereas kokanee (age 1 to 4) totaled 11.34 kg/ha (222 prey/ha). I estimated total biomass/ha of kamloops, bull trout, and lake trout ≥ 406 mm was approximately 24% that of kokanee, providing Y:C ratios of 4.23. Using total weight of prey species (Y) and total weight of predator species (C) Swingle (1950) made predictions about the 'balanced' state of predators relative to prey. He suggested that Y:C ratios between 1 and 3 are 'desirable' and ratios between 1 and 5 are balanced; however, if ratios are < 5 other factors must be examined in addition to the Y:C ratios in order to differentiate between balanced and unbalanced populations.

An alternative indicator of fluctuating prey abundance is to examine changes in size of prey consumed. For example, shifts to smaller prey by predatory salmonids have been used as an indicator of declining prey abundance (Stewart and Ibarra 1991). Previous research on Lake Pend Oreille has shown only minor differences in sizes of prey consumed among years of high and low kokanee abundances (Objective 2). Additionally, Rieman and Myers (1991) observed that kokanee predators in other Idaho lakes prefer smaller kokanee, although they are capable of consuming prey up to 50% of their length. Furthermore, Juanes (1994) concluded that predatory fishes will consistently select smaller prey when given a choice. The growth of predators also has been used as an indicator of prey abundances (Kitchell and Crowder 1986). Growth rates of kamloops and bull trout have declined over the last 20 years (Pratt 1985; Hoelscher 1992) probably as a result of reduced kokanee numbers. However, Eby et al. (1995) and Mittelbach and Osenberg (1994) concluded that growth rates are a poor indicator of prey abundance.

My estimates of kokanee consumption in Lake Pend Oreille were high according to other authors (Stewart et al. 1981; Rand and Stewart 1998; Rieman and Myers 1991). I estimated that 65% of the kokanee production and 73% of the yield was consumed by predatory salmonids in 1998. Assuming similar consumption to 1998, kokanee predation by salmonid predators ranged from 51% to 79% of production and 43% to 73% of yield from 1996-1999 (M. Maiolie, Idaho Department of Fish and Game, pers. comm.). In Lake Michigan, predator-prey interactions were thought to destabilize when bioenergetic modeling estimated 20-33% of the prey base was consumed by fish predators (Stewart et al. 1981), and the pelagic prey base was unable to recover when consumption exceeded 50% of the annual production (Rand and Stewart 1998). Rieman and Myers (1991) used bioenergetic modeling to predict kokanee/predator consumption ratios on different systems in Idaho, suggesting that consumption exceeding 50% of the annual production would pose a high risk of collapsing a kokanee population. They further speculated that biomass of predators should be between 2 and 10% of the prey biomass. My estimates identify the predator biomass as 24% of the prey biomass in Lake Pend Oreille (1998). Popova (1978) estimated that in any given ecosystem predaceous fishes comprise approximately 30% of the total fish production and generally consume the same amount. These indications from other investigators suggest that predator/prey ratios in Lake Pend Oreille are high and close to exceeding a level that would allow a sustaining kokanee population.

My sensitivity analysis predicted effects of mortality, temperature, diet, and energy density of prey on consumption among species. Estimating consumption by kamloops was influenced most by diet and least by energy value of prey, whereas bull trout and lake trout consumption was influenced most by mortality and least by water temperature. I believe the influence of sensitive parameters was minimal, however, the range of influence appeared to be correlated to population abundance. P-values ranged from 0.22 to 0.66. Hanson et al. (1997) suggests that P-values less than the theoretical maximum consumption rate (P-value = 1) may indicate that prey is limited because predators need to forage more frequently to obtain the observed growth rates.

I collected and analyzed the most extensive dietary analysis performed to date on Lake Pend Oreille fishes. Results from this analysis corroborate my bioenergetics modeling. Although previous dietary studies have been limited, general dietary items and their relative importance were similar to mine (Objective 2). To strengthen my diet analysis for bull trout, I compared my results to diets of bull trout in similar systems. My results were similar to those of comparable systems that sampled more fish, thus I feel confident using my diet analysis from Lake Pend Oreille bull trout. Every effort was made to accurately identify prey items; however, in some cases consumed fish were only able to be identified as 'unidentified salmonids' (Objective 2). Many of these 'unidentified salmonids' were likely kokanee, which if incorporated into the kokanee component of the diet would have increased the estimated total annual consumption of kokanee.

Dietary items used in this analysis may have been affected by sampling, as most samples were collected by angling. Studies in other systems have shown higher percentages of particular food items in angler caught fish than those collected by other methods (Eby et al. 1995). However, in Lake Pend Oreille percentages of dietary items in the various predators were similar to those from other systems or previous Lake Pend Oreille studies (Objective 2). Relying on angler participation to collect stomach samples limited or precluded collecting samples during extended periods of poor weather or fishing closures (December-March). Using months prior to and following these periods to estimate prey consumed during the winter season, I believe, provided the most representative results. Yule and Luecke (1993) calculated seasonal aggregate percentages for dietary items of lake trout similarly in Flaming Gorge Reservoir, WY. Prey consumption during the winter is greatly reduced as a result of low metabolic activity, and errors associated with my estimation methods would be minor. My sensitivity analysis predicted that varying diet +/- 10% can influence consumption estimates by -11% to 14% for all species of fish predators examined.

Another possible source of error in the consumption estimates could come from water temperatures. I assumed that fish would select their preferred temperatures when available (thermal regulation) similar to Brandt and Kirsch (1993). Water temperatures used by fishes are thought to be dictated by available temperature, preferred temperature, and acclimation to changing conditions (Stewart et al. 1983). I believe that profiles recorded by IDFG represented the most accurate water temperature data available. Estimating exact thermal habitat used by pelagic fishes was not feasible, although my sensitivity analysis predicted that varying water temperature +/- 10% can influence consumption estimates by -10% to 12% for all species of fish predators examined.

I explored several techniques to determine the most accurate estimate of mortality, including the use of length frequency, age frequency, and population estimates. Based on observed growth and age structure of each predator population, I concluded that length or age frequency provided the best estimates of mortality. Comparing my mortality estimates to those previously recorded in Lake Pend Oreille provided similar results. My sensitivity analysis predicted that varying mortality +/- 10% can influence consumption estimates by
-17% to 23% for all species of fish predators examined, although this range of influence appears to be directly correlated to the population abundance.

My estimates of predator abundance could have influenced estimates of consumption. My estimates of predatory salmonids in Lake Pend Oreille are the only known estimates for Lake Pend Oreille. Several factors could have influenced my population estimates of each predatory fish examined. Population estimates may not have included all recaptured fish due to tag loss or failure of anglers to report recaptures, thereby overestimating abundance estimates. Conversely, hooking mortality would have underestimated abundance estimates. More precise population estimates could be calculated for lake trout by increasing numbers of marked and recaptured fish.

I acknowledge that energy densities of prey vary throughout a year, thus influencing estimates of consumption. No information regarding these changes was available for prey items found in Lake Pend Oreille, therefore, I assumed that energy densities were constant throughout the year. My sensitivity analysis predicted that varying the energy density of prey (kokanee) +/- 10% can influence consumption estimates by -8% to 10% for all species of fish predators examined.

Another factor that can influence the assessment of predators on prey is the abundance estimates of prey. Hydroacoustic and trawling surveys are performed annually on Lake Pend Oreille following strict protocols and provide the best indication of year to year changes. Both methods show similar downward trends in kokanee abundance, however, neither survey was designed to show seasonal changes in prey abundance. Trawling estimates tend to underestimate prey abundances, which if used would show higher consumption rates at low prey abundances similar to observations by Brandt et al. (1991). Kokanee production and yield estimates used in this study were based on hydroacoustic estimates.

MANAGEMENT IMPLICATIONS

Salmonid predators are a depensatory mortality agent (Stewart et al. 1981), directly affecting the abundance, distribution, and age or size structure of prey (Crowder et al. 1994). As weak year classes of kokanee appear, they are subject to increasingly high predation pressure. Low recruitment by particular cohorts, coupled with stochastic increases in mortality may result in precipitous kokanee declines. One potential management response would be to encourage rapid and high exploitation of predatory salmonids and to carefully monitor the results to better manage in the future (Stewart et al. 1981).

Because of the current deleteriously low abundance of the kokanee population in Lake Pend Oreille, weak upcoming spawning classes, and the possibility of stochastic events (such as flooding), strong management actions are supported. Although predation may not be the catalyst for the kokanee declines, predatory fishes may limit the opportunity for kokanee to reach recovery goals. My consumption estimates have identified specific cohorts of each examined predator that are the most damaging to kokanee. The opportunity for management efforts in Lake Pend Oreille to remove kokanee predators is limited. Bull trout are a threatened species, and the daily harvest limit in 1999 (4 fish) for lake trout was rarely caught (anecdotal evidence 1997-1998), leaving the greatest opportunity for predator removal on kamloops. Kamloops are presently managed as a trophy fishery (2 fish over 20 inches, daily limit). My research indicates age 4 kamloops (409 to 520 mm total length) consume a substantial amount of kokanee (21.4 mt). Under existing management regulations in 1999, kamloops must be a minimum of 508 mm (total length) to harvest. Therefore, the most predacious cohort would not be affected by current angling regulations. Furthermore, my sensitivity analysis for kamloops indicated that annual consumption was most influenced by abundance of kamloops $\geq$ 406 mm. Therefore, I would recommend a management regulation to allow the harvest of all kamloops especially those age 4 and older. Based on my results, management recommendations currently proposed by IDFG for the year 2000 include opening the kamloop harvest for 6 fish daily, any size. Additionally, IDFG is now encouraging anglers to harvest legal kamloops that previously might have been released. Angler surveys during recent fishing derbies show an increased harvest of kamloops compared to past derbies (Idaho Department of Fish and Game, unpublished). Ironically, management recommendations in 1981 also stressed the need to keep the abundance of kamloops at a minimum until kokanee numbers increased (Ellis and Bowler 1981). The kokanee harvest is currently set at a 25 fish daily limit. Management recommendations proposed by IDFG for the year 2000 have also included closing the kokanee fishery. Both reductions in kokanee harvest and increased harvest of salmonid predators have the potential to increase kokanee abundance. Salmonid predators in Lake Pend Oreille are currently removing a substantial portion of kokanee production from the lake. Considering the current low kokanee abundance and level of consumption by predator fishes, fish predators could prevent the kokanee population from increasing or at worst push it to lower levels.

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Appendix Table 3.1. Parameter models used in Fish Bioenergetics 3.0 (Hanson et al. 1997).

Consumption = metabolism + wastes + growth

metabolism = respiration + active metabolism + specific dynamic action
wastes = egestion + excretion
growth = somatic growth + gonad production

Metabolism equations

Respiration = $RA * W^{RB} * f(T) * ACTIVITY$

where:

RA	intercept of the allometric mass function
W	fish mass
RB	slope of the allometric mass function
f(T)	temperature dependence function (Stewart et al. 1983)
ACT	activity multiplier (Kitchell et al. 1977)

Specific dynamic action = SDA * (C -F)

where:

SDA	specific dynamic action
C	specific consumption rate
F	specific egestion rate

Waste equations

Equation set 1 (Kitchell et al. 1977)
Egestion = FA * C

where:

FA	constant proportion of consumption
C	consumption

Excretion = UA * (C - F)

where:

UA	constant proportion of consumption
C	consumption
F	Egestion

Equation set 2 (Elliott 1976)
Egestion = $FA * T^{FB} * e^{(FG*p)} * C$

where:

FA	constant proportion of consumption
T^{FB}	ceofficient of water temperature dependence of egestion
$e^{(FG*p)}$	coefficient for feeding level dependence (P-value) of egestion
C	consumption

Equation set 3 (Stewart et al. 1983)
Egestion = PF * C

where:

PF	(PE - 0.1)/0.9) * (1 - PFF) + PFF
PE	$FA * T^{FB} * e^{FG*p}$
PFF	sum of (PREY (n) * DIET (n)) for n=1 to number of prey
C	Consumption

Excretion = $UA * T^{UB} * e^{(UG*p)} * (C - F)$

where:

UA	defined in equation set 1
T^{UB}	defined in equation set 1
$e^{(UG*P)}$	defined in equation set 2

Growth

Estimated on a site specific level as defined in Objective 3.

Appendix Table 3.2. Estimated consumption (metric tons-mt) of prey items by kamloops (ages 4 to 9) in Lake Pend Oreille, Idaho, 1998.

Cohort (years)	Range (length)	Prey items	Quantity of prey (mt)	Cumulative prey (mt)
4	384-494	kokanee	21.40	21.4
		other salmonids	7.50	28.9
		cyprinidae	4.20	33.1
		opossum shrimp	1.60	34.7
		insects	3.00	37.7
5	495-592	kokanee	18.40	18.4
		other salmonids	5.90	24.3
		cyprinidae	3.13	27.4
		opossum shrimp	0.10	27.5
		insects	0.32	27.8
6	593-675	kokanee	18.70	18.7
		other salmonids	6.10	24.8
		cyprinidae	3.10	27.9
		opossum shrimp	0.09	28.0
		insects	0.30	28.3
7	676-734	kokanee	24.60	24.6
		other salmonids	8.10	32.7
		cyprinidae	4.00	36.7
		opossum shrimp	0.11	36.8
		insects	0.36	37.2
8	735-815	kokanee	23.60	23.6
		other salmonids	7.70	31.3
		cyprinidae	3.90	35.2
		opossum shrimp	0.10	35.3
		insects	0.40	35.7
9	816-865	kokanee	19.60	19.6
		other salmonids	6.30	25.9
		cyprinidae	3.30	29.2
		opossum shrimp	0.10	29.3
		insects	0.27	29.6
	Total		196.28	

Appendix Table 3.3. Estimated consumption (metric tons-mt) of prey items by bull trout (ages 6 to 12) in Lake Pend Oreille, Idaho, 1998.

Cohort (years)	Range (length)	Prey items	Quantity of prey (mt)	Cumulative prey (mt)
6	401-474	kokanee	4.400	4.40
		bull trout	0.058	4.46
		lake trout	0.029	4.49
		whitefish	0.824	5.31
		catostomid	0.014	5.33
		peamouth	0.434	5.76
		n. pikeminnow	0.174	5.93
		insects	0.014	5.95
7	475-549	kokanee	4.710	4.71
		bull trout	0.062	4.77
		lake trout	0.031	4.80
		whitefish	0.882	5.69
		catostomid	0.015	5.70
		peamouth	0.464	6.16
		n. pikeminnow	0.186	6.35
		insects	0.015	6.37
8	550-617	kokanee	4.010	4.01
		bull trout	0.053	4.06
		lake trout	0.026	4.09
		whitefish	0.751	4.84
		catostomid	0.013	4.85
		peamouth	0.395	5.25
		n. pikeminnow	0.158	5.41
		insects	0.013	5.42
9	618-685	kokanee	3.421	3.42
		bull trout	0.045	3.47
		lake trout	0.022	3.49
		whitefish	0.640	4.13
		catostomid	0.011	4.14
		peamouth	0.337	4.48
		n. pikeminnow	0.135	4.61
		insects	0.011	4.62
10	686-753	kokanee	2.629	2.63
		bull trout	0.018	2.65
		lake trout	0.034	2.68
		whitefish	0.492	3.17
		catostomid	0.009	3.18
		peamouth	0.259	3.44
		n. pikeminnow	0.104	3.55
		insects	0.009	3.55
11	754-821	kokanee	1.967	1.97
		bull trout	0.026	1.99
		lake trout	0.013	2.01
		whitefish	0.368	2.37
		catostomid	0.006	2.38
		peamouth	0.194	2.57
		n. pikeminnow	0.078	2.65
		insects	0.006	2.66
12	822-889	kokanee	1.378	1.38
		bull trout	0.018	1.40
		lake trout	0.009	1.41
		whitefish	0.258	1.66
		catostomid	0.004	1.67
		peamouth	0.137	1.80
		n. pikeminnow	0.054	1.86
		insects	0.005	1.86
	Total		30.428	

Appendix Table 3.4. Estimated consumption (metric tons-mt) of prey items by lake trout (ages 6 to11) in Lake Pend Oreille, Idaho, 1998.

Cohort (years)	Range (length)	Prey items	Quantity of prey (mt)	Cumulative prey (mt)
6	363-426	kokanee	0.5900	0.59
		other salmonids	0.2500	0.84
		catostomids	0.0000	0.84
		centrarchids	0.0000	0.84
		peamouth	0.0100	0.86
		cottids	0.9040	1.76
		opossum shrimp	0.4300	2.19
		insects	0.0010	2.19
7	427-492	kokanee	1.8200	1.82
		other salmonids	0.2100	2.04
		catostomids	0.0130	2.05
		centrarchids	0.0010	2.05
		peamouth	0.0050	2.06
		opossum shrimp	0.0020	2.06
		insects	0.0040	2.06
8	493-563	kokanee	1.0100	1.01
		other salmonids	0.0300	1.13
		catostomids	0.0100	1.14
		centrarchids	0.0050	1.15
		peamouth	0.0300	1.18
		opossum shrimp	0.0010	1.18
		insects	0.0020	1.18
9	564-626	kokanee	0.6900	0.69
		other salmonids	0.0900	0.77
		catostomids	0.0050	0.78
		centrarchids	0.0004	0.78
		peamouth	0.0200	0.80
		opossum shrimp	0.0010	0.80
		insects	0.0020	0.80
10	627-699	kokanee	0.3900	0.39
		other salmonids	0.0500	0.44
		catostomids	0.0030	0.44
		centrarchids	0.0002	0.44
		peamouth	0.0010	0.44
		opossum shrimp	0.0003	0.44
		insects	0.0010	0.44
11	700-773	kokanee	0.2300	0.23
		other salmonids	0.0300	0.25
		catostomids	0.0020	0.26
		centrarchids	0.0001	0.26
		peamouth	0.0070	0.26
		opossum shrimp	0.0002	0.26
		insects	0.0010	0.26
	Total		6.8522	

Appendix Table 3.5. Estimated consumption (kg) of prey items by northern pikeminnow (ages 6 to 11)/1,000 fish in Lake Pend Oreille, Idaho, 1998.

Cohort (years)	Range (length)	Prey item	Quantity of prey (kg)	Cumulative prey (kg)
6	315-355	kokanee	89.3216	89.32
		bull trout	0.0038	89.33
		whitefish	0.0011	89.33
		cottidae	0.0005	89.33
		decapoda	96.1982	185.53
		insects	8.7316	194.26
		molluscs	5.3635	199.62
		n. pikeminnow	2.1996	201.82
		other crustacea	0.1965	202.02
		peamouth	0.1472	202.16
		plant food	1.8532	204.02
		rainbow trout	7.1118	211.13
		redside shiner	6.5114	217.64
7	356-391	kokanee	83.8639	83.86
		bull trout	0.0037	83.87
		whitefish	0.0011	83.87
		cottidae	0.0005	83.87
		decapoda	76.8831	160.75
		insects	9.1038	169.86
		molluscs	4.9199	174.78
		n. pikeminnow	2.3661	177.14
		other crustacea	0.1891	177.33
		peamouth	0.1478	177.48
		plant food	1.7366	179.22
		rainbow trout	6.5673	185.78
		redside shiner	4.7438	190.53
8	392-426	kokanee	89.9639	89.96
		bull trout	0.0040	89.97
		whitefish	0.0012	89.97
		cottidae	0.0006	89.97
		decapoda	84.6144	174.58
		insects	9.6046	184.19
		molluscs	5.2948	189.48
		n. pikeminnow	2.4862	191.97
		other crustacea	0.2018	192.17
		peamouth	0.1570	192.33
		plant food	1.8616	194.19
		rainbow trout	7.0575	201.25
		redside shiner	5.2953	206.54
9	427-449	kokanee	81.5935	81.59
		bull trout	0.0036	81.60
		whitefish	0.0011	81.60
		cottidae	0.0005	81.60
		decapoda	73.6046	155.20
		insects	8.9403	164.14
		molluscs	4.7707	168.91
		n. pikeminnow	2.3328	171.25
		other crustacea	0.1846	171.43
		peamouth	0.1450	171.58
		plant food	1.6868	173.26
		rainbow trout	6.3682	179.63
		redside shiner	4.4874	184.12
10	450-500	kokanee	68.6209	68.62
		whitefish	0.0002	68.62
		decapoda	4.6878	73.31
		insects	54.9533	128.26
		other crustaceans	0.3612	128.62
		plant food	73.2543	201.88
11	501-515	kokanee	55.8957	55.90
		whitefish	0.0001	55.90
		decapoda	3.8184	59.71
		insects	45.1199	104.83
		other crustaceans	0.2979	105.13
		plant food	59.6699	164.80
	Total		1165.5085	

The Lake Pend Oreille Aquatic Macrophyte Community and its Response to Higher Winter Water Levels

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Final Report
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Abstract

This study compares the species composition, biomass, and the influence of substrate composition on an aquatic macrophyte community in the meso-oligotrophic Lake Pend Oreille, Idaho under two winter drawdown regimes. Mean dry aquatic macrophyte biomass significantly increased in the drawdown zone (1.4 – 3.5 m) from 39.9 $g \cdot m^{-2}$ under a 3.5 m drawdown in 1990 to 99.2 $g \cdot m^{-2}$ and 103.7 $g \cdot m^{-2}$, respectively under 2.1 m drawdowns in 1998 and 1999. Mean aquatic macrophyte biomass deeper than 3.5 m did not significantly increase, suggesting the increased biomass in the drawdown zone can at least partially be attributed to decreased winter mortality. Myriophyllum sibiricum, Chara spp., and Potamogeton richardsonii dominated the aquatic macrophyte community under the 3.5 m winter drawdown, while Chara spp., P berchtoldii, and P. crispus dominated under higher winter water levels. The exotic Myriophyllum spicatum was present at one sample station and most prevalent in depths between 3.9 – 5.1 m. M. spicatum attained mean *maximum* densities in excess of 900 $g \cdot m^{-2}$ by August, 1999 (one year after it was first observed). Logistic regression indicated a higher probability of finding clay and cobble substrates in the drawdown zone. On these clay substrates, there were significantly lower densities of aquatic vegetation (17.9 $g \cdot m^{-2}$) than on sand (86.6 $g \cdot m^{-2}$) or silt (129.0 $g \cdot m^{-2}$) substrata and few plants were observed on cobble substrata.

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Introduction

Drawdowns can greatly influence the distribution, density, and species composition of aquatic macrophyte communities. Drawdowns may directly influence aquatic vegetation through exposure of both above-ground vegetation and beneath-ground root and rhizome systems to desiccation, under either freezing or hot conditions (Cooke 1980). Indirect effects of drawdowns include alteration of physical habitat through the formation of frost heaves on de-watered sediments and subsequent mechanical damage to root systems (Renman 1989) as well as de-watering and consolidation of exposed substrates (Cooke 1980). Water level fluctuations may also influence substrate particle size distribution (Gracia Prieto 1995). Sediment particle size is an important factor in determining the distribution of aquatic macrophytes (Unni 1977, Anderson 1978, Sand-Jensen and Sondergaars 1979) by controlling the availability of root attachment surfaces, intra-sediment chemistry, and nutrient dynamics (Anderson and Kalff 1988).

The response of aquatic macrophyte communities to seasonal de-watering (lake drawdown) has been the focus of many studies (Lantz et al. 1964, Hunt and Jones 1972, Nichols 1975a, Wilcox and Meeker1991). However, most studies have emphasized the use of drawdown as a lake management technique to control nuisance aquatic vegetation (Mathis 1965, Manning and Sanders 1975, Nichols 1975b, Goldsby et al. 1978, Cooke 1980, Tazik et al. 1982) and as a result, have taken place in meso-to eutrophic systems (Cooke and Gorman 1980, Siver et al. 1986). Fewer studies have taken place in meso-oligotrophic or oligotrophic water bodies (Rorslett 1985, Hellsten and Riihimaki 1996), or studied effects of higher winter water levels on an aquatic macrophyte community after exposure to multiple winter drawdowns.

The importance of aquatic macrophytes to the autotrophic community of freshwater lakes and rivers has been well-established (Hutchinson 1975, Horne and Goldman 1994). Aquatic macrophyte communities influence both physical and biogeochemical lake processes. Carpenter and Lodge (1986) provide a comprehensive review of the role of submersed macrophytes in lake ecosystems including; (1) physical processes, such as light extinction, water flow, substrate accretion and composition, and temperature; and (2) biogeochemical processes, such as oxygen production/consumption, dissolved inorganic and organic carbon cycling, and sediment-water nutrient dynamics. Aquatic macrophytes also serve as a food source and provide habitat for littoral fauna (Soszka 1975, Weaver et al. 1997). Aquatic macrophytes may reach nuisance densities as lake enrichment becomes more prevalent. These nuisance levels of aquatic vegetation may hinder water-based recreation and become aesthetically unpleasing (Tarver 1980, Falter and Burris 1996). Therefore, any anthropogenic changes to the lake littoral zone (*i.e*. lake level manipulations) and subsequently to the aquatic macrophyte community are of both ecological and economic importance.

The objectives of this study were to:

1. Describe Lake Pend Oreille’s littoral sediment and water column pysico-chemistry;
2. Describe the aquatic macrophyte community in Lake Pend Oreille and its response to an experimental increase in winter lake elevation from 625 m

(typified by 1990 winter drawdown) to 626.7 m msl (typified by 1998-99 winter drawdown);

(3) Compare overall biomass of aquatic vegetation in the drawdown zone (the depths of the littoral zone from 0 m to 3.5 m) and in the permanently wetted depths of the littoral zone (depths greater then 3.5 m) in 1990 vs. 1998-99;

(4) Describe composition of the aquatic macrophyte community under both drawdown regimes (1990 and 1999); and

(5) Investigate relationships between substrate particle size, depth, and macrophytes in 1999.

Site Description

Lake Morphometry

The meso-oligotrophic Lake Pend Oreille lies in the glacially formed Purcell Trench in the panhandle of northern Idaho. Approximately 90% of the surface-water inflow and close to 90% of the total nitrogen and phosphorus loads to Lake Pend Oreille are from the Clark Fork River (Frenzel 1993), draining much of Montana west of the Continental Divide, into the northeast corner of the lake (Fig. 1). Lake Pend Oreille is divided into several basins: the deep relatively poorly flushed southern end with a mean hydraulic retention time greater than 10 years (Falter et al. 1992); the deep central basin with its steep shorelines; the shallow northern basin (mean hydraulic retention time less than 1 year; Hoelscher et al. 1993); and the lake’s shallow outlet arm. Lake morphometry is an important factor influencing the spatial distribution of aquatic macrophytes in Lake Pend Oreille.

Lake Pend Oreille proper is a 383 km^2 (94641 acres) lake with mean and maximum depths of 164 m (538 ft) and 357 m (1171 ft), respectively (USGS 1996). It is Idaho's largest and deepest lake. Shoreline length of the lake proper is approximately 310 km with a maximum width of 10 km and low ratios of littoral area/lake volume to pelagic area/lake volume. The lake's outlet arm is the Pend Oreille River, exiting from the northwest corner of the lake. Mean and maximum depths of the outlet arm are 7.4 m and 48 m, respectively. Shoreline length of the outlet arm is about 152 km (USGS 1996). The outlet arm is impounded by Albeni Falls Dam on the Washington-Idaho border. Lake Pend Oreille is an important recreational and residential water body for the area, supporting moderate shoreline development on the northern half of the main lake and the outlet arm as well as seasonally heavy recreational use.

Lake Pend Oreille lies in a 59324 km^2 watershed. Major bedrock types in the watershed are Belt series and Kaniksu batholith (Savage 1965). Much of the watershed is forested (83% of the watershed) consisting mainly of coniferous tree species (Hoelscher et al. 1993). Developed lands (barren and impervious surfaces) in the early 1990's accounted for approximately five percent of the watershed, while agriculture and grazing comprised smaller percentages of total watershed use (EWU 1991). Population growth around Lake Pend Oreille is steadily increasing from about 15587 in the 1960's to 26622 in 1990 and a projected population of 35081 by 2010 (Hoelscher et al. 1993).

History of Winter Lake Drawdowns on Lake Pend Oreille

From 1966 to 1994, an annual winter drawdown controlled by the Albeni Falls outlet dam lowered lake water levels 3.0 m to 3.7 m (lake elevation of 625 m mean sea level (msl)) from mid-November through April, for spring flood control and winter power production. Maximum summer water level has been controlled at 628.6 m msl from 1952 to the present. The Idaho Department of Fish and Game (IDF&G) had concerns that winter drawdowns of 3.5 m were de-watering much of the preferred spawning substrate for winter lake-spawning kokanee (Onchorhynchus nerka). These concerns prompted experimental winter drawdowns of 2.1 m (higher winter lake levels of 626.3 m - 626.7 m msl rather than 625 m) in an effort to enhance kokanee spawning gravel and survival. The IDF&G also wanted to determine whether higher winter water levels would improve over-winter survival of warmwater fishes (*e.g.*, pumpkinseed (Lepomis gibbosus), black crappie (Pomoxis nigromaculatus), and largemouth bass (Micropterus salmoides)) in the outlet arm of Lake Pend Oreille by providing additional littoral habitat. These fishes prefer habitat of shallow waters with zero velocity, and dense vegetation. Over-winter fish habitat for these fishes had been consequently limited by winter drawdown (Dupont 1994). Any increase in aquatic macrophyte densities in these backwater areas as a result of higher winter water levels could increase available winter habitat and habitat complexity.

Materials and Methods

Sample Stations

Nineteen stations on the outlet arm and on Lake Pend Oreille proper were sampled for aquatic macrophytes in 1998 and 1999 (winter drawdown of 2.1 m). Six stations located on the outlet arm and the northern-most basin of the lake had earlier been sampled for aquatic macrophytes in 1990 (winter drawdown of 3.5 m). Drawdown regime analysis is restricted to the six stations with data in all three of these years (Fig. 1). The six sample stations were River Kilometer (RK) 0.8, 4.4, 18.5, and 26.6 on the outlet arm, and Kootenai and Sunnyside Bays. These sites are conducive to macrophyte growth (shallow depths and well-lit, fine substrate) and therefore most likely to respond to higher winter water levels.

Sediment and Water Physico-Chemistry

Sediment

To describe lake sediment chemistry, we sampled lake sediments at eight sample stations in July, 2000 in Lake Pend Oreille (LPO) proper and its outlet arm. LPO proper stations included Bottle, Ellisport, Idlewilde, and Scenic Bays. Outlet arm stations were RK 0.8, 4.4, 18.5, and 26.6. Three to nine replicate sediment samples were obtained at each site using a Petite Ponar Dredge (225 cm^2). Samples were cleaned of all vegetation, placed in storage containers, and stored in the dark on ice until processing. Analyses were performed at the Analytical Sciences Laboratory, University of Idaho. Analyses included the determination of sediment total phosphorus, percent nitrogen, percent organic carbon, percent carbon, and percent organic matter.

Water Column Physico-Chemistry

We measured selected physical and chemical water quality variables at all 19 stations in July-September, 1998 and July-October, 1999. A complete list of variables measured is in Tables 1 and 2. We also measured total phosphorus and nitrate-nitrogen at all 19 sample stations in July-October, 1999 as follows. Three replicate water samples were taken at each station using a 2-liter Kemmerer water sampler. Samples were placed in a 1-liter Cubitainer, fixed with 2 ml H_2SO_4 and stored in the dark on ice until processing. Quality Assessment/Quality Control (QA/QC) analyses included field and laboratory spikes. Field spikes were obtained by retrieving duplicate water samples from six randomly selected stations (three for nitrate-nitrogen and three for total phosphorus each month). One water sample was divided into two 1 l cubitainers. One cubitainer was spiked while the other was used as a control. Nitrate-nitrogen was determined according to Standard Methods Procedure 4500-N.B, and total phosphorus was determined according to Standard Methods Procedure 4500-P.C (APHA 1992).

Aquatic Macrophyte Collection and Laboratory Analysis

Aquatic macrophytes were sampled August 1990 and July through September in 1998 and 1999. Therefore, aquatic macrophyte data used in the drawdown regime analysis were restricted to samples collected in August (the period of maximum macrophyte biomass) in all three sampling years. Using a bathymetric map of Lake Pend Oreille and its outlet arm (USGS 1996), sample stations were established along the depth contours of the littoral zone. Depth zones were designated A through D as follows: A = 0 m (full summer level) – 1.4 m depth; B = 1.4 m – 3.5 m; C = 3.5 m – 7.0 m; and D = 7.0 m – 11.0 m depth. Samples were taken along a transect running perpendicular to the shoreline at increasing depths until all strata were sampled. We collected plants in 1990 with a Peterson Dredge (900 cm^2), taking four to eight replicate plant samples from each stratum per site. A Petite Ponar Dredge (225 cm^2) was used in 1998 and 1999 to obtain eight replicate plant samples from each stratum per site.

Plant samples obtained in 1990 and 1999 were carefully washed to remove any detritus, sediment, and epiphytic algae. Samples were then separated and identified to species. Plant identification followed the manual Flora of the Pacific Northwest (Hitchcock and Cronquist 1973). The Standard Methods Procedure (10400 D.3) for oven dry weight (ODW as $g \cdot m^{-2}$) or biomass, was used to obtain percent species composition by weight and total ODW per grab by depth to estimate areal biomass (APHA 1992). Total areal biomass per grab was determined for aquatic macrophytes sampled in 1990, 1998, and 1999. All mean biomass values include grabs in which no plants were collected (*e.g.*, if eight grabs were retrieved and 3 grabs contained no plants then 3 zero values were entered when computing mean biomass).

Substrate Composition Data Collection

Substrate particle size was visually determined for each plant grab using the modified Wentworth Scale (Hynes 1972). This scale classifies substrate ranging from clay-sized (< 0.004 mm) to boulder-sized (>256 mm) particles. Other qualitative physical properties such as sediment consolidation and color were also recorded.

Statistical Analysis

Sediment

We used analysis of variance (ANOVA) to evaluate overall between-site differences in measured sediment parameters. The Ryan-Einot-Gabriel-Welsch Multiple Range Test was used for multiple comparisons among sites. Sediment nutrient values were log-transformed prior to analysis to meet statistical assumptions (Kleinbaum et al. 1998).

Aquatic Macrophytes

Aquatic Macrophyte Community Dynamics. Mean aquatic macrophyte biomass values for the 19 selected sample stations are reported to describe temporal and spatial patterns of aquatic macrophyte biomass in Lake Pend Oreille proper and its outlet arm. Percent species dominance was calculated for 1999 sample stations. Statistical analyses of mean biomass values were not performed due to the inability to accommodate homogeneity of variance. Percent dominance was calculated by pooling the species data for each station as follows:

$$\text{Percent dominance} = \left(\frac{n}{N}\right) \times 100 \qquad (1)$$

where ‘n’ is the total biomass of a given species and ‘N’ is the total biomass of all individual samples.

Drawdown Regime Analysis. To analyze the aquatic macrophyte community response to higher winter water levels we divided the littoral area into two zones, drawdown and permanently wetted. The drawdown zone was defined as the depths of the littoral zone that were previously de-watered during winter drawdowns of 3.5 m and now permanently wetted under higher winter water levels (winter drawdown of 2.1 m). The drawdown zone encompassed the depths between 1.4 m to 3.5 m.

Aquatic macrophyte biomass in the permanently wetted areas of the littoral zone (depths greater than 3.5 m) were analyzed to determine the temporal response of the aquatic macrophyte community in areas not de-watered during either drawdown regimes. This depth stratum had never been subjected to winter drawdown, and therefore served as a control to determine if an observed increase in biomass occurred over the entire littoral zone or only in the drawdown zone.

Between-year and among-site differences in mean aquatic macrophyte biomass in the drawdown zone and in the permanently wetted depths of the littoral were evaluated using analysis of variance (ANOVA). The Ryan-Einot-Gabriel-Welsch Multiple Range Test was used for multiple comparisons among years. Aquatic macrophyte biomass values were log-transformed prior to analysis to meet statistical assumptions (Kleinbaum et al. 1998). To take into account differences in sampling areas (dredge size of 900 cm^2 in 1990 and 225 cm^2

in 1998-99) between years, 1998 and 1999 biomass measurements were given 1/4 the weight (variance weighting) of the 1990 biomass measurements prior to the analysis. Sample stations were not randomly selected because of the need to ensure the areas analyzed were suitable macrophyte habitat; therefore, inferences based on statistical analyses cannot be made to the entire lake and pertain only to specific stations.

Community composition and diversity. Due to the inherent difficulty in analyzing multi-species community data (Smith et al. 1990), several methods were used to compare community composition in the drawdown zone in 1990 and 1999. Species percent dominance was calculated as described above. Percent frequency was calculated by pooling the species data for all six sites for 1990 and 1999 as follows:

$$\text{Percent frequency} = \left({}^{f}\!/_{F} \right) \times 100 \qquad (2)$$

where ‘ f ’ is the number of samples in which a given species was recorded and ‘F’ is the total number of samples. Percent dominance is based on abundance (biomass) whereas percent frequency is based on the number of samples in which a species was recorded.

Kulczynski’s Index of Disimilarity (CAP 1999) was used to compute station dissimilarity values to define temporal variation in species composition and abundance between sample stations in 1990 and 1999. Rare species (frequency of occurrence less than 5% in both years) were deleted from the data matrix prior to analysis, as these occurrences can usually be attributed to chance rather than to an indication of ecological conditions (Gauch 1982). Aquatic macrophyte biomass for each species was averaged over replicate samples for each sample station to reduce variation (Gauch 1982) and later used as abundance values in the computation. Abundance data were double-square-root transformed (McRae et al. 1998) to allow less abundant species to contribute to between-site dissimilarities.

Dissimilarity values were calculated as follows:

Kulczynski's Index of Dissimilarity: Djk = $1-\left(\frac{1}{2}\left(\frac{W}{A}+\frac{W}{B}\right)\right)$ (4)

where A is the sum of species abundance's at station j, B is the corresponding value at station k, and W is the sum of the minimum values for each species when comparing both stations. Computed values are on a scale from 0 to 1 where a dissimilarity value of 1 would indicate completely different community composition and abundance between stations j and k, and a dissimilarity value of 0 would indicate identical community composition and abundance between stations j and k.

The Kulczynski's Dissimilarity matrix was then used in cluster analysis using Ward's Minimum Variance method. Standard Euclidean distance measures were not used in the cluster analysis due to poor performances of these measures (Ludwig and Reynolds 1988). The hierarchical clustering method was used to produce a dendrogram showing any meaningful clustering of stations. For example, if 1990 sample stations clustered together but separately from 1999 stations, then community structure would be different between these years indicating different macrophyte communities between the two drawdown regimes.

Substrate Composition

To elucidate relationships between substrate composition, depth and aquatic macrophyte biomass we classified each plant grab’s sediment content into one of five substrate categories. Each grab was classified as either (1) “clay “; (2) “silt”; (3) “sand”; (4) “gravel”; or (5) “cobble”.

Binary logistic regression analysis was performed to determine if depth was a significant predictor of substrate. The probability of observing a substrate particle size class at a given depth can then be determined for any significant relationships as follows:

$$\mathrm{P}(\mathit{substrate}) = \exp^{\left(\hat{b}_o + \hat{b}_1 x\right)} \Big/ 1 + \exp^{\left(\hat{b}_o + \hat{b}_1 x\right)} \qquad (5)$$

where $\hat{b}_0$ and $\hat{b}_1 x$ are coefficients derived from logistic regression and ‘exp’ is e raised to the given power.

No aquatic macrophytes were found on “gravel” or “cobble” substrate classes. Therefore only mean aquatic macrophyte biomass on “clay”, “silt”, and “sand” substrate classes were compared using ANOVA and the Ryan-Einot-Gabriel-Welsch Multiple Range Test for pair-wise comparisons. Aquatic macrophyte biomass values were log-transformed prior to analysis to accommodate homogeneity of variance. All statistical analyses were performed using the SAS GLM and LOGISTIC procedures (SAS Institute Inc. 2000) and STATISTICA (Statistica for the Macintosh 1994) computing software.

Results

Sediment and Water Physico-Chemistry

Sediment

Lake sediment chemistry analyses determined that total sediment phosphorus ranged from 395.0 $\mu g \cdot g^{-1}$ - 1563.3 $\mu g \cdot g^{-1}$. Scenic Bay had significantly higher total phosphorus (1563.3 $\mu g \cdot g^{-1}$) than other stations (Table 3). Mean percent nitrogen ranged from 0.0 % at RK18.5 to 0.4 % at Bottle and Idlewilde Bays. Mean percent organic carbon ranged from 0.8 % at RK18.5 to 7.5 % at Scenic Bay; mean percent carbon ranged from 0.7 % at RK18.5 to 8.4 % at Scenic Bay; and mean percent organic matter ranged from 1.4 % to 12.9 % at RK18.5 and Scenic Bay, respectively.

Water Column Physico-Chemistry

Lake Pend Oreille is a meso-oligotrophic water body characterized by moderately high water clarity and low nutrient concentrations. Mean secchi depth ranged from 5.6 m - 12.0 m in August, 1998 and from 3.8 m - 8.9 m in August, 1999. Mean total phosphorus and nitrate-nitrogen concentrations at selected sample stations in August, 1999 ranged less than 7 $\mu g \cdot l^{-1}$ (detection limit) - 7 $\mu g \cdot l^{-1}$ and from 21.5 $\mu g \cdot l^{-1}$ - 40.25 $\mu g \cdot l^{-1}$, respectively (Tables 1 and 2).

Mean percent recovery (QA/QC) for total phosphorus and nitrate-nitrogen field spikes were 101.8% and 74.1%, respectively. Mean percent recovery for laboratory spikes of total phosphorus and nitrate-nitrogen were 90.8% and 94.5%, respectively.

Aquatic Macrophytes

Aquatic Macrophyte Community Dynamics

Mean aquatic macrophyte biomass from the 19 selected sample stations on Lake Pend Oreille proper and its outlet arm ranged from 0.0 g·m^{-2} at Warren Island to 276.0 g·m^{-2} at RK0.8 in 1998 and from 0.0 g·m^{-2} at Maiden Rock to 188.7 g·m^{-2} at RK16.1 in 1999 (Fig. 2 and 3). Mean aquatic macrophyte biomass declined from northern lake stations (*e.g.*, CFR and BOT) to southern lake stations (*e.g.*, IDL and SCE) in both years. No apparent trend in biomass was observed in the outlet arm.

Twenty-five macrophyte species from 14 families were present in Lake Pend Oreille proper and its outlet arm in 1999 (Table 4). Two dominant species in the outlet arm and Lake proper stations in July, 1999 were Potamogeton crispus (comprising 47% and 32% of the community in the outlet arm and Lake proper, respectively) and Elodea spp. (comprising 17% and 22% of the community in the outlet arm and Lake proper, respectively). In August, the two dominant species in the outlet arm were Elodea spp. and P. crispus (each comprising 26% of the macrophyte community). Myriophyllum sibiricum dominated (40%) the aquatic macrophyte community in the outelt arm stations in September. In August and September, the two dominant species in the Lake Pend Oreille proper stations were Chara spp. and P. berchtoldii (comprising 26% and 22% in August and 31% and 27% in September, respectively**;** Fig. 4).

Drawdown Regime Analysis

Mean dry aquatic macrophyte biomass, in the drawdown zone (1.4 m - 3.5 m), significantly increased ($p = 0.01$) from 39.9 g·m^{-2} in 1990 to 99.2 g·m^{-2} and 103.7 g·m^{-2} in 1998 and 1999, respectively (Fig. 5A). Mean aquatic macrophyte biomass among stations and stations×time interaction were not significant ($p = 0.23$ and 0.08, respectively); therefore, we investigated the effects of time on biomass independently of site. Mean aquatic macrophyte biomass in the permanently wetted littoral (depths greater than 3.5 m) were not significantly different ($p = 0.72$) in 1990 (70.3 g·m^{-2}) when compared to 1998 and 1999 (185.0 g·m^{-2} and 157.1 g·m^{-2}, respectively; Fig. 5B).

Community Composition and Diversity

Community composition changed in the drawdown zone in 1990 when compared to 1999 (Table 5). The four dominant aquatic macrophytes in 1990 were Myriophyllum sibiricum (30.1%), Chara spp. (29.3%), Potamogeton richardsonii (23.9%), and P. foliosus (6.3%). In 1999, Chara spp. (27.4%), P. berchtoldii (25.3%), P. crispus (23.6%), and Elodea spp. (12.7%) (E. canadensis and E. nutallii) dominantated the drawdown zone. Community composition in the described drawdown zone does not include the exotic Myriophyllum spicatum. This species was abundant at RK 0.8 in 1999 (maximum densities exceeded 900 g·m^{-2} oven dry weight) in depths between 3.9 – 5.1 m; however, it occurred less frequently and at lower densities in the 1.0 – 3.5 m depth range which includes the described drawdown zone (1.4 – 3.5 m).

The dominant species frequency of occurrence also changed between years. For example, in 1990, the three dominant aquatic macrophyte species also occurred most frequently. In 1999, however, Elodea spp. occurred more frequently (47.9%) than P. crispus (8.3%). All other macrophyte species comprised small proportions of the community. Potamogeton crispus, P. praelongus, and Drepanocladius were not found in 1990 in depths between 1.4 m and 3.5 m; however, they were present in depths below 3.5 m in 1990. These three species were present between 1.4 m and 3.5 m in 1999 after 3 years of higher winter water levels. Potamogeton zosteriformis was not found in 1990, but was present in the 1.4 – 3.5 m drawdown zone in 1999. Potamogeton robbinsii was present in the drawdown zone in 1990 and absent in 1999. Ceratophyllum demersum, Tillaea aquatica, and P. pectinatus were major species that showed no or little response to a change in winter water levels.

Cluster analysis of Kulczynski's dissimilarity values revealed two meaningful clusters (Fig. 6). Most stations within a year (stations under a similar drawdown regime) tended to cluster together. Shannon's H` Diversity Index was also calculated for each station in 1990 and 1999. Index calculations were based on the total number and biomass of species present at each station. Mean Shannon's H` Index did not significantly differ between 1990 and 1999 (*t*-test, p = 0.64).

Substrate Composition

Results of the binary logistic regression indicated that depth was a significant predictor of four of the five-substrate categories (Table 6). Silt was the only non-significant category (p = 0.12). The probability of observing "clay" and "cobble" increased as depth decreased; whereas, the probability of observing "gravel" and "sand" decreased as depth decreased (Fig. 7).

Mean aquatic macrophyte biomass was significantly lower ($p < 0.0001$) on "clay" substrate types (mean dry biomass = 17.9 $g \cdot m^{-2}$) compared to "silt" and "sand" substrate classes which had mean aquatic macrophyte biomass of 129.0 $g \cdot m^{-2}$ and 86.6 $g \cdot m^{-2}$, respectively (Fig. 8).

Discussion

Sediment and Water Physico-Chemistry

Sediment

Lake sediments play a large role in nutrient cycling and dynamics in many lakes and reservoirs (Horne and Goldman 1994). Heathwaite (1994) demonstrated that increased human development often leads to an increase in sediment and nutrient export from land to adjacent waterbodies and these changes are reflected in lake sediments. Lake Pend Oreille is phosphorus-limited (Woods 1993); therefore, any potential sources of phosphorus (*i.e.*, sediments) can potentially contribute to biological productivity. However, aerobic sediment conditions in Lake Pend Oreille retain sediment phosphorus in a biologically unavailable form (*i.e.,* as ferric phosphate). Total mean sediment phosphorus measured in Lake Pend Oreille ranged from 395 $\mu g \cdot g^{-1}$ at Idlewilde Bay to 1563.3 $\mu g \cdot g^{-1}$ at Scenic Bay, July, 2000. These values are likely influenced by the degree of human development at these two bays. Idlewilde Bay is located on a state park and as a result, has little human development. Scenic Bay however, is located on a town (Bayview, Idaho) and has a significant amount of housing development, house docks, and intense boating activity that may have contributed to the observed differences. Except for Scenic Bay, total phosphorus (TP) concentrations in Lake Pend Oreille are similar to those reported by Rattray et al. (1991) for the oligotrophic Lake Taupo, New Zealand (TP range = 234 – 700 $\mu g \cdot g^{-1}$). However, they are lower than the range reported by Ostrofsky (1987) for 66 lakes in the eastern U.S. representing a broad range of lake types from oligotrophic to eutrophic (TP range = 1329 – 9212 $\mu g \cdot g^{-1}$).

Water Column Physico-Chemistry

Due to its deep aerobic water column acting as a nutrient trap (Falter et al. 1992), Lake Pend Oreille is able to dilute much of the effects of the sizeable nutrient loading from the Clark Fork River. Nutrient concentrations (total phosphorus and nitrate-nitrogen) and water transparency (secchi depth) in Lake Pend Oreille proper appear not to have changed from 1990 through 1999. Mean total phosphorus and nitrate-nitrogen concentrations at selected sample stations in August, 1999 ranged less than 7 $\mu g \cdot l^{-1}$ (detection limit) to 7 $\mu g \cdot l^{-1}$ and 21.45 $\mu g \cdot l^{-1}$ - 40.25 $\mu g \cdot l^{-1}$, respectively. Mean concentrations of total phosphorus in Lake Pend Oreille proper in 1989-90 ranged from 5 $\mu g \cdot l^{-1}$ - 10 $\mu g \cdot l^{-1}$ (Woods 1993). Summer secchi depth readings in Lake Pend Oreille proper ranged from about 5.0 - 11.0 m in 1989-90 (Woods 1993). Mean summer secchi depth ranged from 5.6 - 12.0 m in August, 1998 and from 3.8 - 8.9 m in August, 1999. Low secchi depth readings observed by Woods (1993) were measured during spring runoff when turbid inflows entered the lake *via* the Clark Fork River and were not due to an increase in biological production.

Aquatic Macrophytes

Aquatic Macrophyte Community Dynamics

Mean aquatic macrophyte biomass (oven dry weight (ODW)) from the 19 selected sample stations on Lake Pend Oreille proper and its outlet arm ranged from 0.0 $g \cdot m^{-2}$ at Warren Island to 276.0 $g \cdot m^{-2}$ at RK0.8 in 1998 and from 0.0 $g \cdot m^{-2}$ at Maiden Rock to 188.7 $g \cdot m^{-2}$ at RK16.1 in 1999. The lack of aquatic plants at Warren Island and Maiden Rock are likely a function of lake morphometry (littoral slope) and substrate. Both stations were characterized by steep littoral slopes and a substratum dominated by medium to large cobble. The lack of root-attachment surface and low nutrient levels in coarse substrates (Barko and Smart 1986) likely limited macrophyte colonization at these sites.

Higher densities of aquatic macrophytes in sample stations located at the northern end of the lake were also influenced by lake morphometry and the Clark Fork River. The northern lake area has a shallower mean depth, a more gradual littoral slope, and receives an annual spring influx of fine sediments and nutrients from the Clark Fork River providing high quality aquatic macrophyte habitat compared to southern lake areas.

Common species in Lake Pend Oreille and its outlet arm included Potamogeton spp., Elodea, spp., Chara spp., and Myriophyllum spp. Falter and Olson (1990) found similar aquatic macrophyte species in Lake Pend Oreille proper and its outlet arm in 1989-90 which included M. sibiricum, Chara spp., Potamogeton spp., and Elodea canadensis.

Drawdown Regime Analysis

Mean aquatic macrophyte biomass (ODW) in the drawdown zone significantly ($p = 0.01$) increased from 39.9 $g{\cdot}m^{-2}$ in 1990 to 99.2 $g{\cdot}m^{-2}$ and 103.7 $g{\cdot}m^{-2}$ in 1998 and 1999, respectively. This overall increase in aquatic macrophyte biomass in the drawdown zone showed increased survival and spatial expansion of aquatic macrophytes into depth strata under the new regime of year-round submersion with higher winter water levels. We found no significant increase in aquatic macrophyte biomass in the permanently wetted littoral (deeper than 3.5 m) that supports this hypothesis. The lack of significant increase in biomass in the permanently wetted littoral suggests that the observed increase in aquatic macrophyte biomass in the drawdown zone was not due to site enrichment or any other physico-chemical changes that may have occurred between 1990 and 1998-99. Improvements in residential and commercial wastewater treatment systems surrounding the lake may have decreased potential site enrichment in higher density developments around the lake. For example, there has been a decrease in the number of shoreline residences with septic systems impacting the lake since 1977 (Lawlor 1993). And recently, a three-lagoon sewage collection and treatment system was developed for the north-east area of the lake that eliminated several more residential and commercial septic tank systems, thereby reducing potential nutrient leaching into the lake.

The increase in aquatic macrophyte biomass in the drawdown zone under higher winter water levels might be expected in relatively deep lakes with high transparency. Higher water levels increase the amount of available habitat and light does not rapidly become a limiting factor so a net increase of littoral volume ensues. Conversely, higher water levels may reduce the standing crop of aquatic macrophytes in shallower water bodies with low transparency. In these latter systems, high water levels can increase sedimentation, and decrease light penetration through wave re-suspension of sediments (Woltemade 1997), thereby reducing available habitat for aquatic vegetation. Lake Pend Oreille is clearly a lake in the former category.

Community Composition and Diversity

Higher winter water levels have a species-specific effect on aquatic macrophyte communities. Different species have different tolerances to de-watering and exposure to dry conditions (Hudon 1997). Different community composition would therefore be expected under different levels of winter drawdown. Three of the four dominant species present under higher winter water levels were either absent (P. crispus) or represented a very minor proportion of the macrophyte community (Elodea spp. and P. berchtoldii) in the 1.4 m - 3.5 m drawdown depth zone in 1990. Elodea spp. primarily spreads *via* stem fragmentation whereas P. crispus propagates primarily from dormant apices (turions; Nichols and Shaw 1986). Wave action and anthropogenic disturbances (*e.g.*, boat traffic) may lead to the dispersal of these vegetative structures into newly created habitat. The spatial expansion of these species from 1990 to 1998-99 into the new permanently wetted littoral zone may have been facilitated *via* the propagation of vegetative reproductive structures. Furthermore, these two species can overwinter as evergreen plants under ice cover, and grow quickly with spring warming (Nichols and Shaw 1986), thereby obtaining an advantage early in the growing season when competing for light. Hestand and Carter (1975) also documented shifts in dominant species under higher water levels following an overwinter drawdown. Hellsten and Riihimaki (1996) found different aquatic plant species composition in the regulated Lake Ontojarvi compared to the unregulated Lake Lentua. Average winter drawdown in Lake Ontojarvi was about 3.4 m. The aquatic macrophyte community in Lake Ontojarvi was comprised of species that had adapted to the level of disturbance caused by lake regulation.

Chara spp. was the only dominant member of the drawdown zone under both drawdown regimes in Lake Pend Oreille. Charophytes are often pioneering species and their oospores will remain viable after extended periods of dry and freezing conditions (Proctor 1967, Bates and Smith 1994). These characteristics may account for its dominance both in the exposed area of the littoral zone after overwinter drawdown (1990) and its continued dominance with higher winter water levels in Lake Pend Oreille (1999). The movement of P. crispus, P. praelongus, and Drepanocladius from the permanently wetted littoral (depths > 3.5 m) into the drawdown zone with higher winter water levels, suggests that the earlier 3.5 m winter drawdown limited the shoreward distribution of these taxa. In 1999, P. crispus occurred less frequently than Elodea spp. although the former was a more dominant species (occurred in higher densities) in the community. This is likely because P. crispus was found in dense monospecific stands, while, Elodea spp. occurred in more samples, but at lower densities.

Some species showed no response to higher winter water levels. C. demersum represented a small (0.4%) but constant proportion of the community under both drawdown regimes. Since C. demersum lacks true roots, currents and wave action can move it between depth zones and as a result, it will be relatively unaffected by winter drawdowns and subsequent increases in winter water levels. Nichols (1975a) also found C. demersum show no response to overwinter drawdown and no preference to water level in the Chippewa Flowage, Wisconsin. However, Hestand and Carter (1975) found a disappearance of C. demersum upon refilling of shallow Lake Ocklawaha following a 1.5 m overwinter drawdown from September to February. Lake morphometry, winter conditions, and species mix likely influence the response of individual species to higher water levels. For example, the Chippewa Flowage is a large reservoir with interconnected bays. Isolated areas of the reservoir experience different water level changes as surface water connection with the flowage is cut off. As a result, some areas experience less than a 2 m drawdown while other areas experience up to a 9 m drawdown. The areas that experience relatively stable water levels apparently provide refugia for populations of aquatic plants. Whereas Lake Ocklawaha, a shallow reservoir in central Florida, has the entire lake littoral area affected by water level fluctuations, thereby reducing the chance of shallow water refugia. Hestand and Carter (1975) further noted that plant cover of Hydrilla verticillata increased following winter drawdown. Hydrilla may have acted synergistically, through competition for resources, with winter drawdown to reduce densities of C. demersum.

Cluster analysis indicated that different aquatic macrophyte communities were present in the drawdown zone in 1990 compared to 1999. These communities differed in community composition and overall biomass (as described above). I believe that biomass of species present (overall increase in biomass in the drawdown zone) and species composition (spatial expansion of species into the new permanently wetted littoral under higher winter water levels) both contributed to the dichotomy of the two communities. However, with such extreme spatial heterogeneity of aquatic plant communities (France 1988), I do expect that a few sample stations would cluster with stations under a different drawdown regime.

Substrate Composition

Logistic regression showed the probability of observing “clay” and “cobble” decreased as depth increased and the probability of observing “gravel” and “sand” increased as depth increased. With water level fluctuation, finer particles will be transported before large particles (Horne and Goldman 1994), therefore increasing the probability of leaving cobble-sized particles in the drawdown zone. The higher probability of finding cobble substrates in shallow water in this study reduced the amount of available plant habitat in the drawdown zone.

Substrate composition was influenced by both overwinter drawdown and by the dominant bottom morphology of sample stations in this study. The increased probability of observing clay and cobble substrate types in shallow depths are likely a direct result of years (since 1966) of exposing littoral sediments to drying and desiccation.

Four of the six sample stations were located in the outlet arm of Lake Pend Oreille. The outlet arm has some lotic characteristics, having unidirectional flow (velocities up to 8 $cm\cdot s^{-1}$; Dupont 1994) and the presence of an old river channel as the deepest area (thalweg). As depth, current velocity, and slope increase in the thalweg, the substrate shifts to a sand and gravel composition because these larger substrate particles are less likely to be moved by the current. Falter et al. (1991) also cited the direct effects of morphometry and velocity on substrate deposition and accumulation as limiting factors of aquatic macrophyte colonization in the Pend Oreille River, Washington immediately downstream of Lake Pend Oreille. Carlson (1995) compared aquatic macrophyte densities in two sloughs in the Pend Oreille

River, Washington and concluded that lower aquatic macrophyte densities in one slough was primarily a function of morphometry (*i.e*., steeper littoral slope).

Highest biomass was found on silt and sand substrates for two likely reasons (1) the probability of observing sand increased as depth increased; therefore, plants on this substrate were removed from effects of wave action and winter drawdown; and (2) low nutrient levels and limited nutrient diffusion rates in coarse substrates such as gravel (Barko and Smart 1986). Anderson and Kalff (1988) found that silt substrate supported significantly higher biomass than did sand or organic sediments and that these three categories all supported higher biomass than gravel. Madsen and Adams (1989) found maximal aquatic macrophyte biomass on silt substrata in a eutrophic stream (Badfish Creek, Wisconsin). Aquatic macrophyte densities were low on gravel and lowest on sand. Badfish Creek was dominated by P. pectinatus, a species also found in Lake Pend Oreille.

Ecological and Management Implications

Years of winter drawdown have altered the physical habitat for aquatic macrophytes in many areas of Lake Pend Oreille through sediment alterations such as consolidation, erosion, and depositional processes. Sediment consolidation occurs as exposed flocculent sediments dry out and compact. For example, Plotkin (1979) conducted a series of artificial lake drawdowns on experimental lakes. After 6 weeks desiccation, exposed sediment in all test lakes were consolidated and sediment depth decreased by 50%. The sediments in the test lakes remained firm 6 months after refilling. This consolidation can influence aquatic plant growth. For instance Plotkin (1979) noticed slower growth rates of Elodea densa in the compacted sediments compared to flocculent sediment. Our study did not directly measure sediment consolidation; however, consolidated clay sediments were common in shallower depths (*i.e*., the drawdown zone) and these sediments provided relatively poor aquatic plant habitat.

Increasing the permanently wetted littoral area through higher winter water levels has led to an overall increase in aquatic macrophyte density and resulted in the spatial expansion of species from deep-water communities to shallow-water communities in Lake Pend Oreille. The spatial complexity and abundance of the resulting plant community will benefit aquatic and semi-aquatic biota which utilize these vegetated littoral areas. For example, yellow perch (Perca flavescens) are often more dominant in dense, species-rich vegetation beds that are structurally complex (Weaver et al. 1997). Liter (1991) collected fish densities up to 5.2 fish$\cdot$m^{-2} in heavily vegetated areas while sampling with pop nets in the Pend Oreille River, Washington, and concluded that heavily vegetated areas were important fish habitats, especially for juvenile centrarchids. Aquatic macrophyte communitites in the Pend Oreille River, Washington also contained higher density and diversity of zooplankton species than in adjacent open waters (Carlson 1995). For example, Carlson (1995) determined mean zooplankton densities measured in aquatic macrophyte beds to be 43 organisms$\cdot l^{-1}$ in late August compared to 3 organisms$\cdot l^{-1}$ in adjacent open water.

These backwater areas also represent important fish habitat in the outlet arm of Lake Pend Oreille (Dupont and Bennett 1991). Dupont (1994) concluded that many warmwater fishes in the outlet arm of Lake Pend Oreille are limited by overwintering habitat, primarily vegetated areas of low velocity. The observed increase in aquatic plant densities may increase the amount of overwintering habitat and possibly increase winter survival of the warmwater fish community. Furthermore, aquatic macrophytes provide an important substrate for aquatic invertebrates (Soszka 1975) and therefore can increase the food supply for species that forage in these areas. The dominant macrophyte species found under higher winter water levels in Lake Pend Oreille represent important habitat and food sources for migratory waterfowl. For example, turions and seeds produced by P. crispus and E. canadensis are important food for many waterfowl species (Rogers and Breen 1980, Nichols and Shaw 1986).

In managing Lake Pend Oreille, a balance must be attained between improving littoral habitat (providing a diverse aquatic macrophyte community) versus the possibility of nuisance aquatic plant growth (dense monospecific stands) as a result of high winter water levels. Extremely dense aquatic plant growth not only impedes recreation (Hestand and Carter 1975), but also decreases bass (Micropterus salmoides) growth rates as a result of decreased forage efficiency (Engel 1987).

Development of the Exotic Myriophyllum spicatum (Eurasian watermilfoil)

The invasive, nonindigenous species (Myriophyllum spicatum L.) was first observed in Albeni Cove on the outlet arm of Lake Pend Oreille in the summer of 1998. The patchy distribution of M. spicatum in the 1.0 – 3.5 m depth range and subsequent exclusion from the drawdown regime analysis should not minimize the effects this species can have on surrounding littoral habitats. For example, mean *maximum* densities within monospecific plant beds exceeded 900 $g \cdot m^{-2}$ oven dry weight by August, 1999. These densities are higher than values reported for milfoil in the Pend Oreille River, Washington, which reached densities near 600 $g \cdot m^{-2}$ (Getsinger et al. 1997). This species has the potential to spread rapidly throughout this system. For instance Eurasian watermilfoil spread at a rate of 3.7 ha·yr in the Pend Oreille River, Washington immediately downstream of Albeni Falls Dam and has become a severe nuisance throughout this 55 km river reach (Gibbons et al. 1983, Falter et al. 1991). Winter drawdown has been used successfully to control this species (Goldsby and Bates 1978, Siver et al 1986) in some systems; however M. spicatum occurs deeper than 5 m in the outlet arm of Lake Pend Oreille reducing much of the benefit of a 3.5 m winter drawdown as a control method. Possible management of this system could include utilizing a winter drawdown of 3.5 m every few years (since consecutive winter drawdowns have shown to provide little additional macrophyte control compared to the initial drawdown; Nichols 1975b) to control nuisance aquatic vegetation and maximize the available wetted littoral for aquatic biota.

Summary

- Highest mean densities of aquatic macrophytes were found in northern lake stations and declined at mid- and southern lake stations. Aquatic macrophytes most commonly found in Lake Pend Oreille proper and its outlet arm were P. crispus, Elodea spp., M. sibiricum, and Chara spp.
- Mean aquatic macrophyte biomass (oven dry weight) significantly increased in the drawdown zone from 39.9 $g{\cdot}m^{-2}$ in 1990 (winter drawdown of 3.5 m) to 99.2 $g{\cdot}m^{-2}$ and 103.7 $g{\cdot}m^{-2}$ in 1998 and 1999, respectively (winter drawdown of 2.1 m).
- Mean aquatic macrophyte biomass (oven dry weight) in the permanently wetted littoral did not significantly increase from 70.3 $g{\cdot}m^{-2}$ in 1990 when compared to 1998 and 1999 (mean aquatic macrophyte biomass of 185.0 $g{\cdot}m^{-2}$ and 157.1 $g{\cdot}m^{-2}$, respectively). This suggests the observed increased biomass in the drawdown zone can at least partially be attributed to decreased winter mortality from freezing and desiccation under higher winter water levels.
- Two distinct aquatic macrophyte communities existed in the drawdown zone under the two drawdown regimes. Myriophyllum sibiricum, Chara spp., Potamogeton richardsonii, and P. foliosus dominated the aquatic macrophyte community under the 3.5 m winter drawdown, while Chara spp., P berchtoldii, P. crispus, and Elodea spp. dominated under higher winter water levels (winter drawdown of 2.1 m). The spatial expansion of species previously restricted to depths below 3.5 m in 1990 to areas shallower than 3.5 m in 1998 and 1999 contributed to the observed differences in community structure.

- The patchy distribution of M. spicatum in the 1.0 – 3.5 m depth range and subsequent exclusion from the drawdown regime analysis should not minimize the potential effects this species can have on surrounding littoral habitats. Illustrated by the production of large monospecific beds, which attained mean *maximum* densities in excess of 900 $g \cdot m^{-2}$ one year after it was first observed in 1998.
- A higher probability of observing clay and cobble substrate types existed in the drawdown zone than in the permanently wetted littoral. These two substrate types provided relatively poor habitat for aquatic macrophytes. For example, significantly lower densities of aquatic vegetation was observed on clay (17.9 $g \cdot m^{-2}$) substrate types than on silt or sand substrates (mean macrophyte biomass of 129.0 $g \cdot m^{-2}$ and 86.6 $g \cdot m^{-2}$, respectively), and few plants were observed on cobble substrates.
- A 40 % increase in macrophyte biomass in the drawdown zone increased littoral habitat heterogeneity and therefore available overwintering habitat for littoral fishes that utilize these areas.
- Possible management of this system could include utilizing a winter drawdown of 3.5 m every few years to control nuisance aquatic vegetation and maximize the available wetted littoral zone for aquatic biota.

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Figures

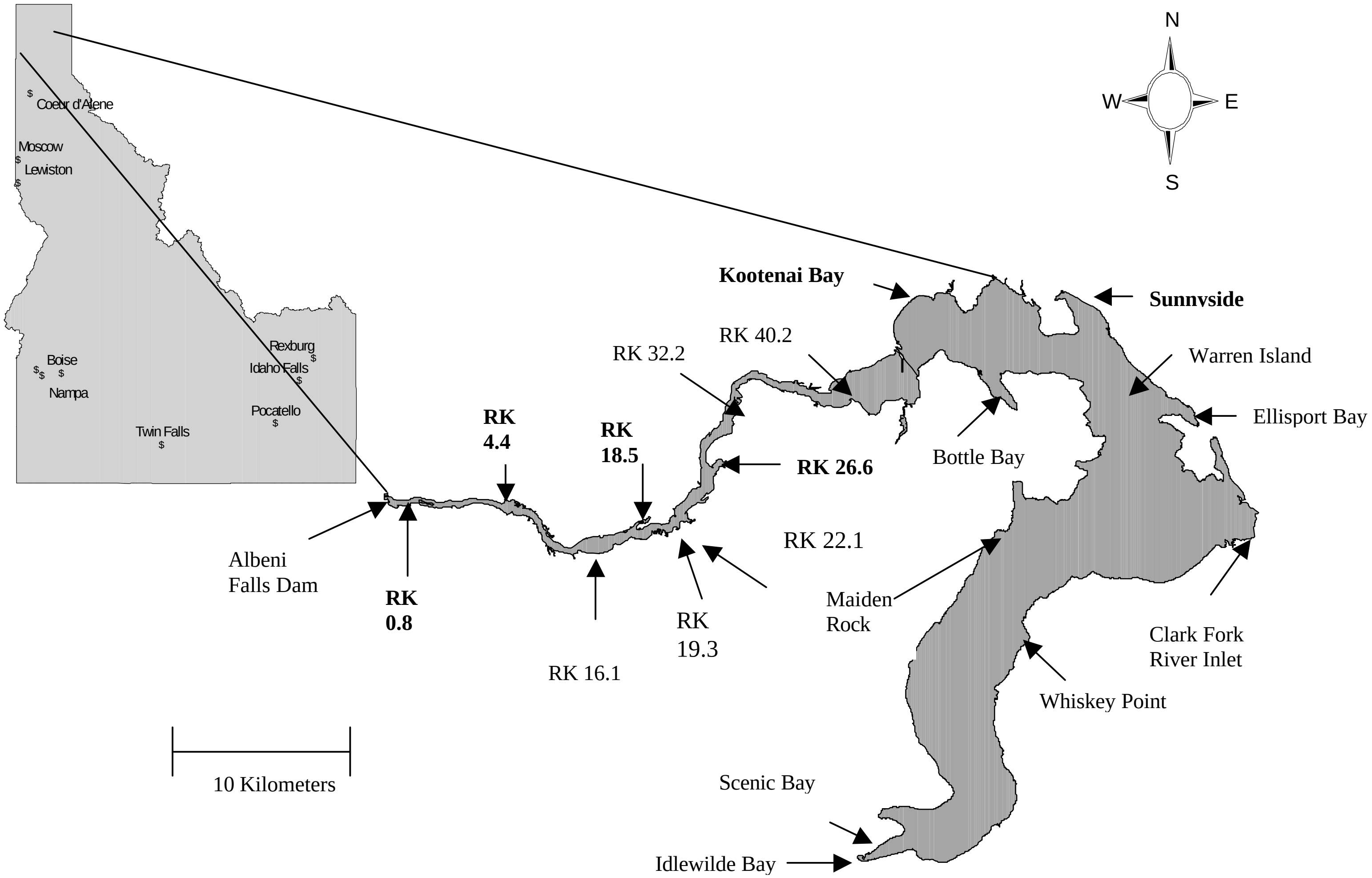


Figure 1.-Aquatic macrophyte sampling stations located on the outlet arm of Lake Pend Oreille and Lake Pend Oreille proper. Stations used in drawdown regime analysis are in bold.

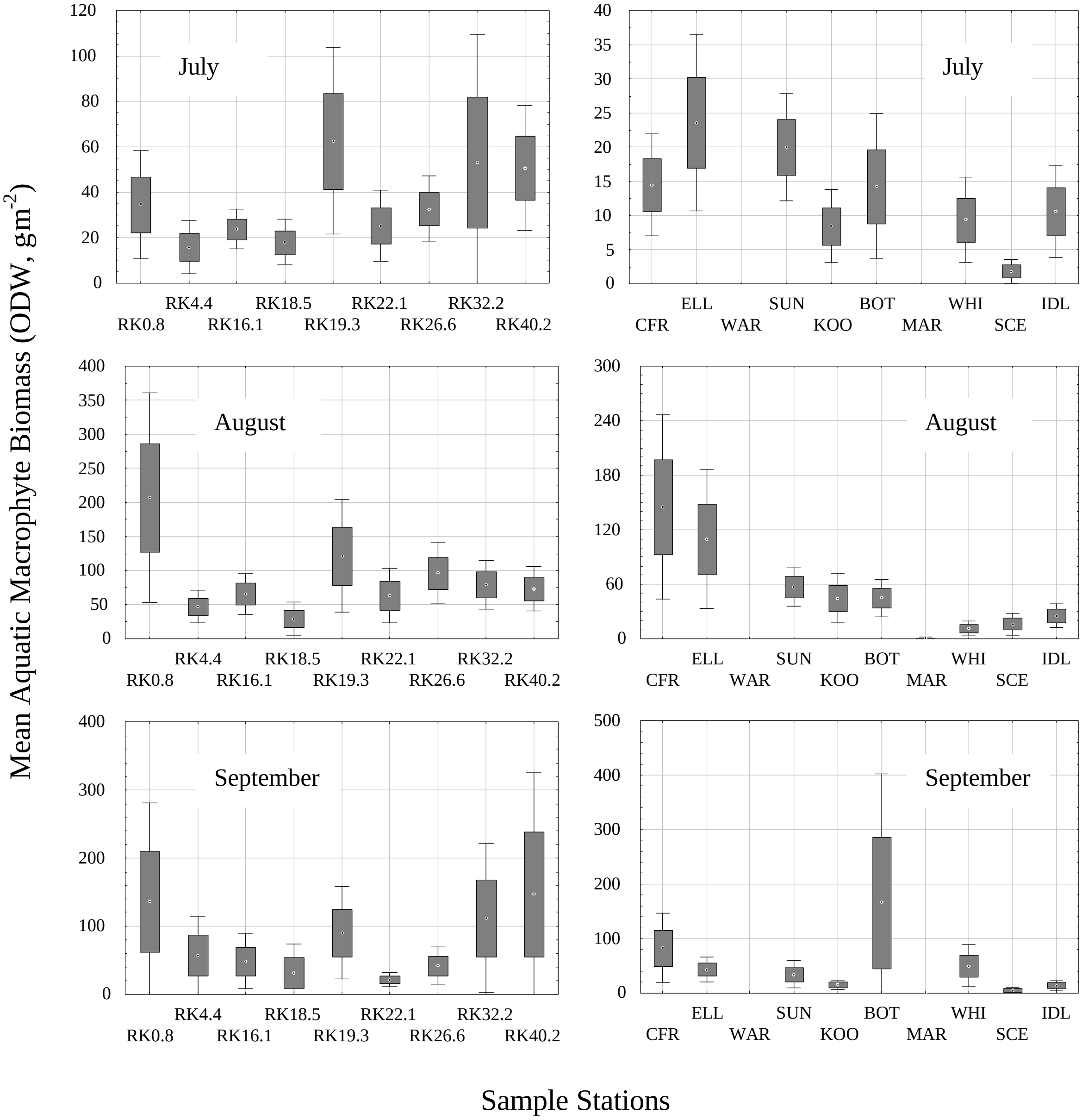


Figure 2.-Mean aquatic macrophyte biomass (oven dry weight (g·m^{-2})) at the 19 selected sample stations on Lake Pend Oreille proper and its outlet arm July, August, September, 1998. The box represents mean ± 1 standard error and the bars represent mean ± 1.96* standard error. CFR = Clark Fork River inlet, ELL = Ellisport Bay, WAR = Warren Island, SUN = Sunnyside, KOO = Kootenai Bay, BOT = Bottle Bay, MAR = Maiden Rock, WHI = Whiskey Point, SCE = Scenic Bay, and IDL = Idlewilde Bay.

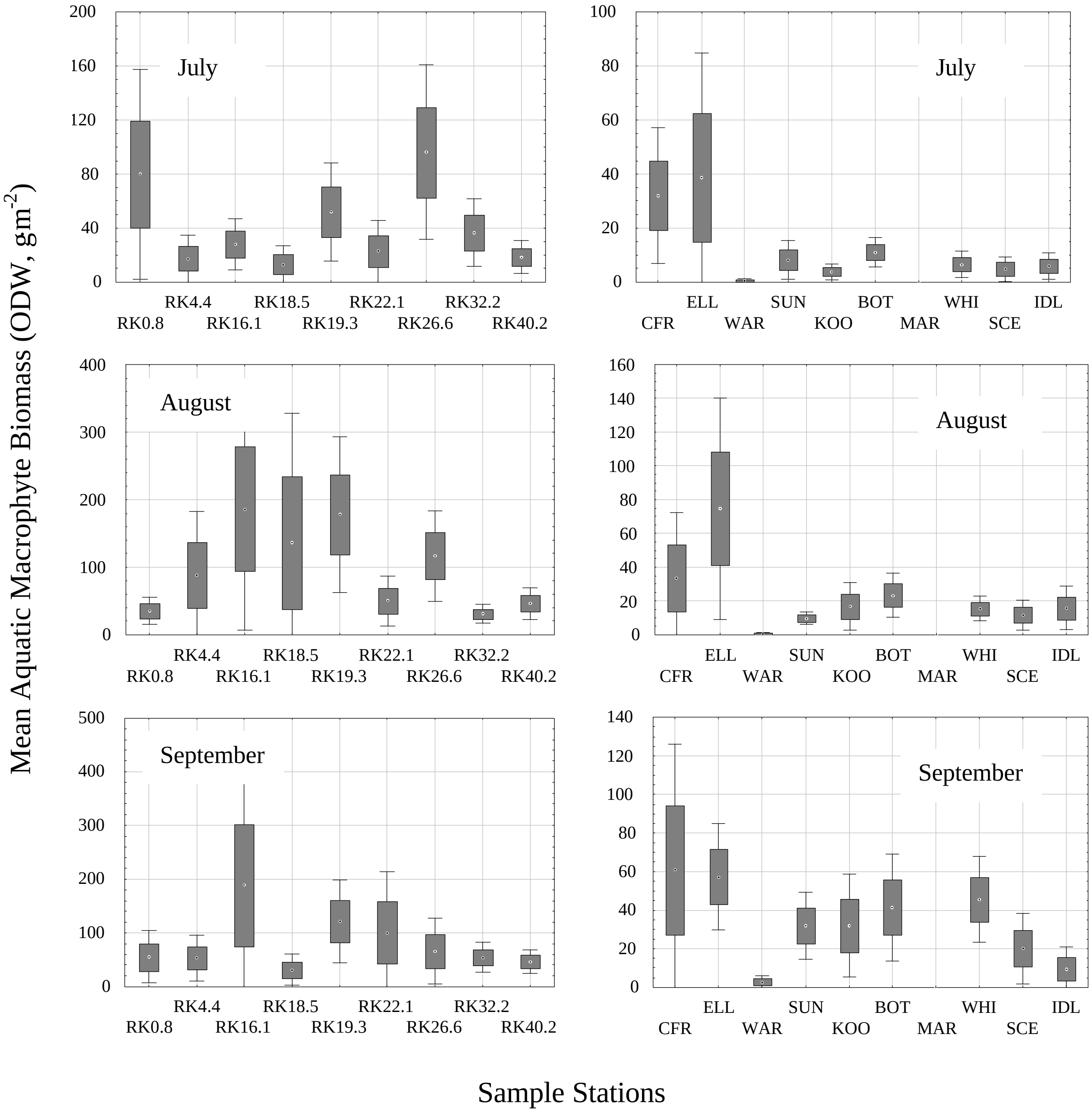
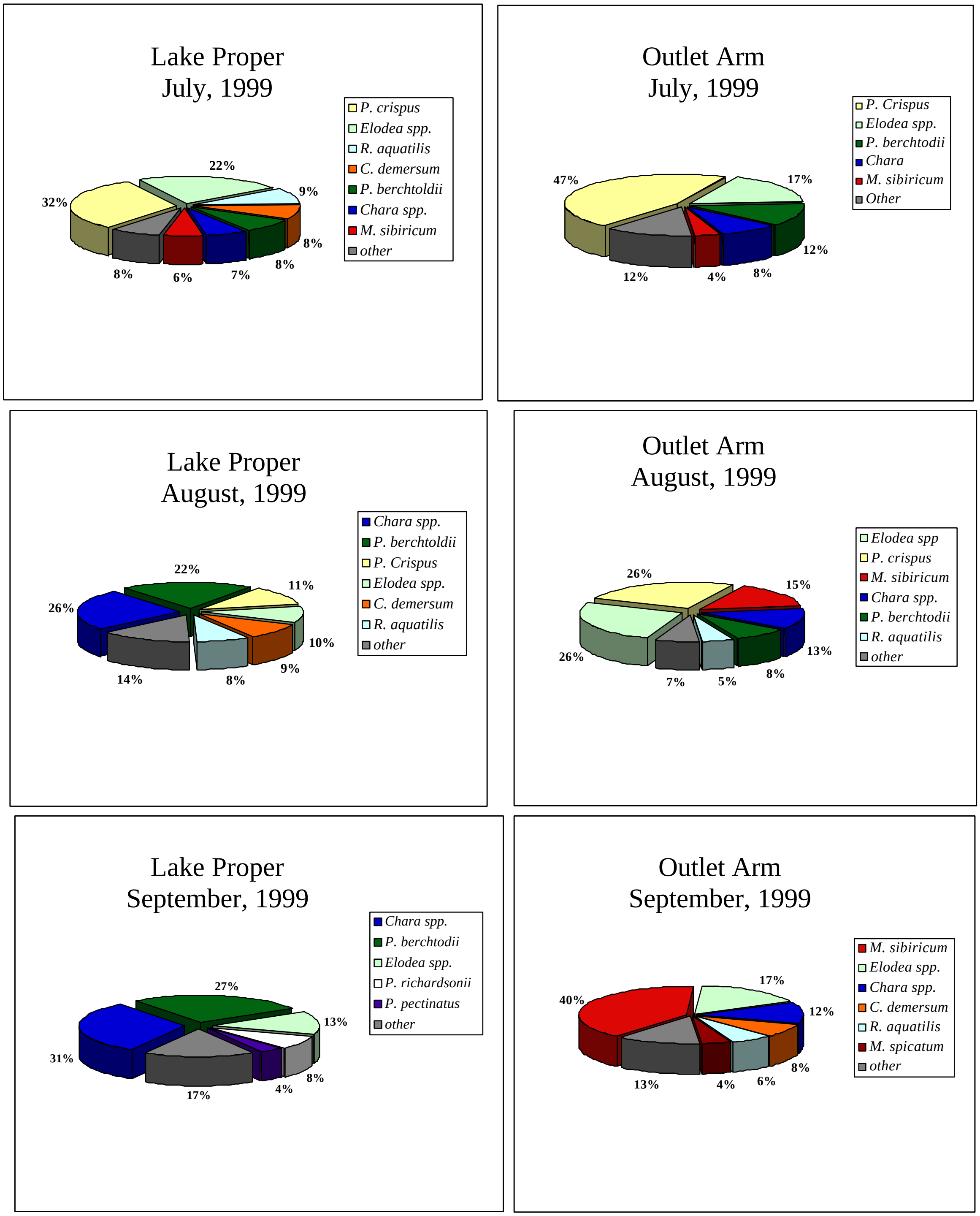


Figure 3.- Mean aquatic macrophyte biomass (oven dry weight (g·m^{-2})) at the 19 selected sample stations on Lake Pend Oreille proper and its outlet arm July, August, September, 1999. The box represents mean ± 1 standard error and the bars represent mean ± 1.96* standard error. CFR = Clark Fork River inlet, ELL = Ellisport Bay, WAR = Warren Island, SUN = Sunnyside, KOO = Kootenai Bay, BOT = Bottle Bay, MAR = Maiden Rock, WHI = Whiskey Point, SCE = Scenic Bay, and IDL = Idlewilde Bay.



Lake Proper July, 1999

Outlet Arm July, 1999

Lake Proper August, 1999

Outlet Arm August, 1999

Lake Proper September, 1999

Outlet Arm September, 1999

Figure 4.-Dominant aquatic macrophyte species from the 19 selected sample stations in Lake Pend Oreille proper and its outlet arm, July, August, September, 1999.

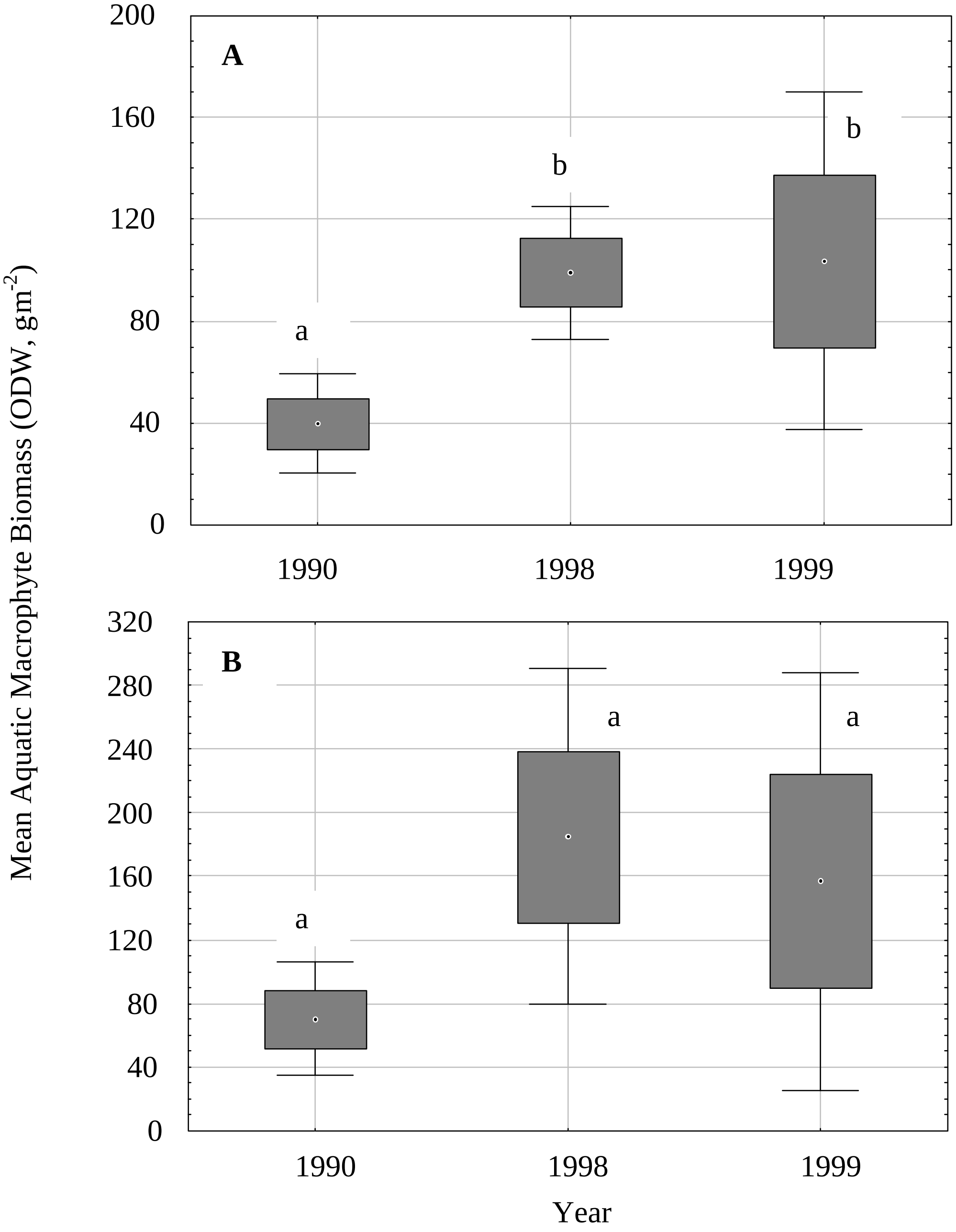


Figure 5.-Mean aquatic macrophyte biomass (oven dry weight ($g{\cdot}m^{-2}$)) in Lake Pend Oreille, Idaho, August 1990, 1998, and 1999 in (**A**) the winter drawdown zone (1.4 m - 3.5 m) and (**B**) the permanently wetted littoral (3.5 m - 7.0 m). The box represents mean ± 1 standard error and the bars represent mean ± 1.96* standard error. Different letters designate significant difference ($p < 0.05$) between mean aquatic macrophyte biomass.

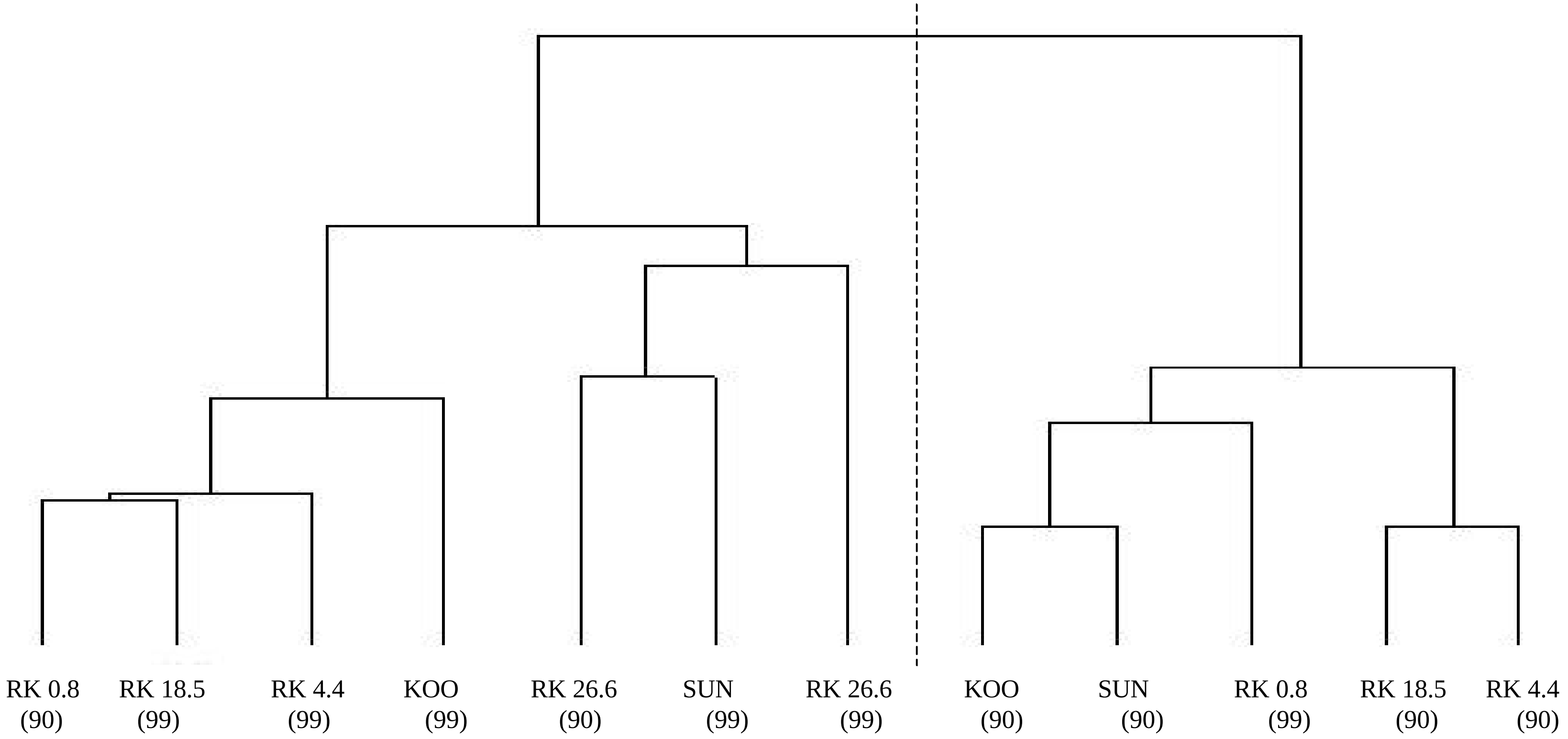


Figure 6.-Dendrogram of sample stations from Kulczynski's dissimilarity distance matrix based on aquatic macrophyte species composition and abundances in the drawdown zone (1.5 m – 3.5 m) for sample stations on the outlet arm of Lake Pend Oreille and Lake Pend Oreille proper, Idaho, August 1990 and 1999. Winter lake drawdown of 3.5 m occurred in 1990 compared to 2.1 m drawdown in 1999. Site code is followed by sample year in parenthesis (RK = River Kilometer, KOO = Kootenai Bay, SUN = Sunnyside). Dashed line represents delineation of clusters.

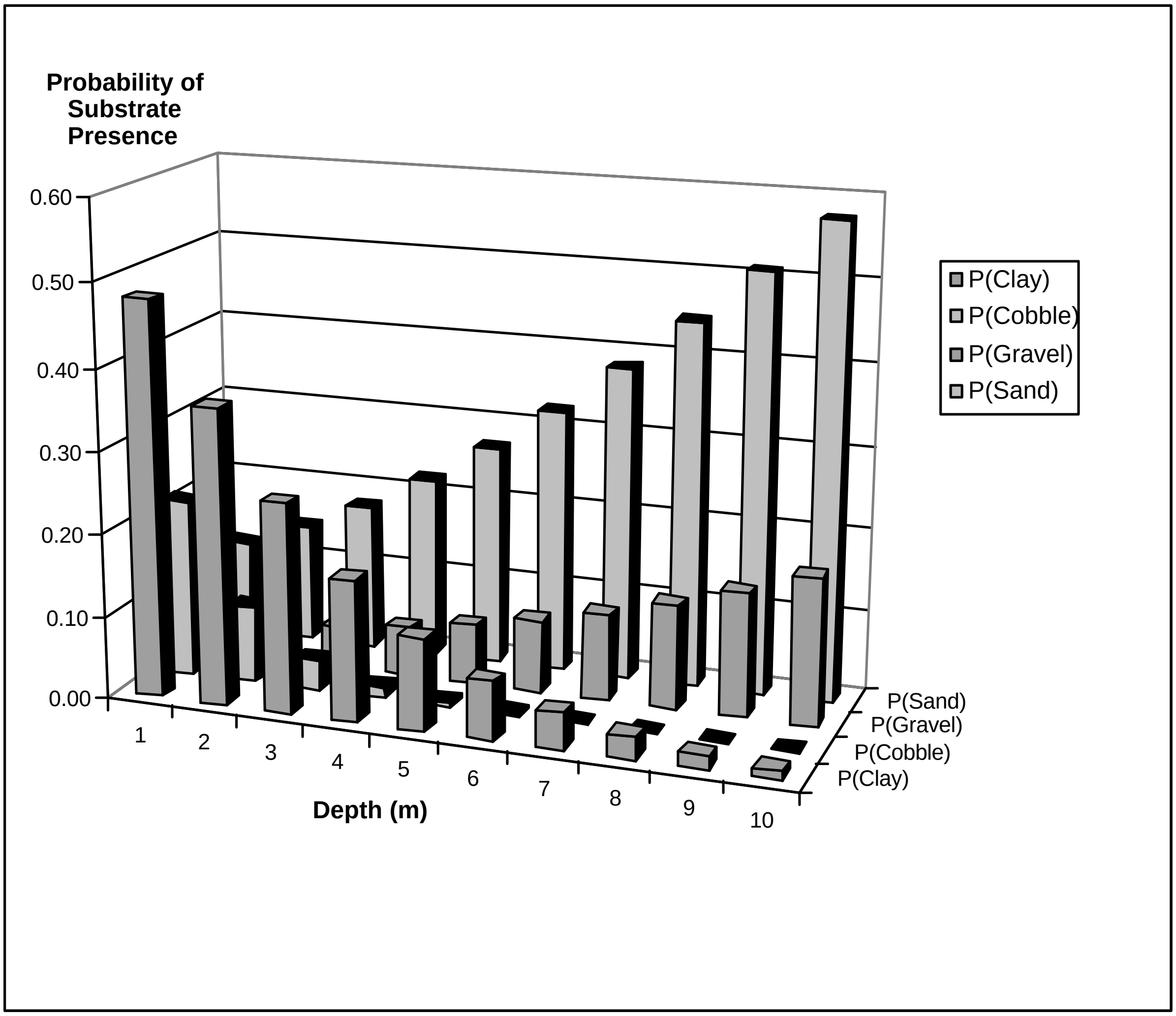


Figure 7.-Probabilities of observing four substrate classes (clay, cobble, gravel, and sand) at various increasing depths from full summer pool for selected sample station on Lake Pend Oreille, Idaho, August 1999.

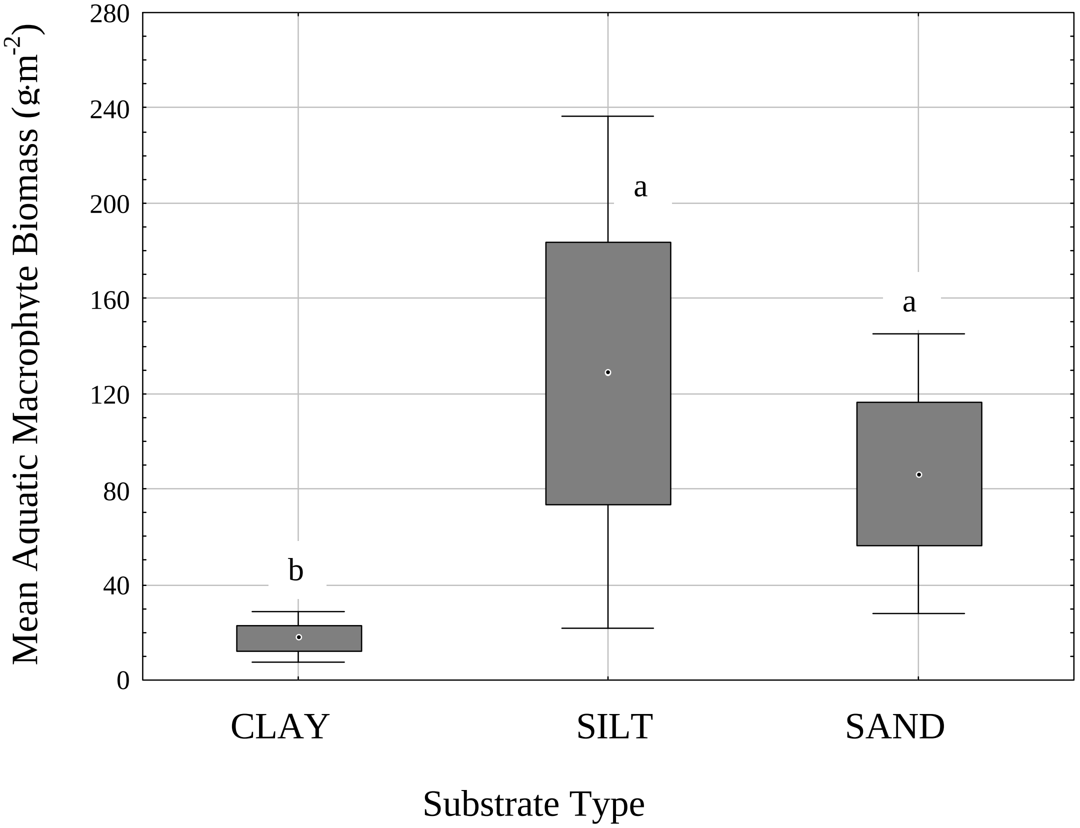


Figure 8.-Mean aquatic macrophyte biomass (oven dry weight ($g \cdot m^{-2}$)) on three substrate classes in Lake Pend Oreille, Idaho, August 1999. The box represents mean ± 1 standard error and the bars represent mean ± 1.96* standard error. Different letters designate significant difference ($p < 0.05$) between mean aquatic macrophyte biomass.

Tables

Table 1.- Selected physico-chemical water quality variables from Lake Pend Oreille proper and its outlet arm July – September, 1998.

Site	Date	Secchi Depth (m)	Mean Temperature (C)	Mean Conductivity (u siemens)	Alkalinity (mg·l^{-1} CaCO$_3$)	Site	Date	Secchi Depth (m)	Mean Temperature (C)	Mean Conductivity (u siemens)	Alkalinity (mg·l^{-1} CaCO$_3$)
Clark Fork	JUL	3.4	20.6	*	*	**RK 40.2**	JUL	2.7	20.6	*	*
	AUG	10.1	23.4	*	*		AUG	8.4	24.1	*	*
	SEP	8.5	22.0	175.0	79.0		SEP	7.9	23.1	186.0	78.0
Site Mean		**7.3**	**22.0**	*	*	**Site Mean**		**6.3**	**22.6**	*	*
Ellisport Bay	JUL	4.1	21.1	*	*	**RK 32.2**	JUL	3.4	20.4	*	*
	AUG	10.8	24.0	*	*		AUG	8.6	23.9	*	*
	SEP	7.8	22.1	175.0	79.0		SEP	7.0	22.6	186.0	76.0
Site Mean		**7.5**	**22.4**	*	*	**Site Mean**		**6.3**	**22.3**	*	*
Warren Island	JUL	5.6	19.8	*	*	**RK 26.6**	JUL	4.0	20.9	*	*
	AUG	11.3	23.8	*	*		AUG	8.5	24.5	*	*
	SEP	11.3	22.1	188.0	80.0		SEP	4.1	22.4	181.0	78.0
Site Mean		**9.4**		*	*	**Site Mean**		**5.5**	**22.6**	*	*
Sunnyside Bay	JUL	3.8	20.0	*	*	**RK 22.1**	JUL	3.0	21.3	*	*
	AUG	11.5	23.5	*	*		AUG	7.3	24.1	*	*
	SEP	9.5	21.9	181.0	79.0		SEP	4.6	22.3	179.0	78.0
Site Mean		**8.3**	**21.8**	*	*	**Site Mean**		**5.0**	**22.6**	*	*
Bottle Bay	JUL	4.3	20.5	*	*	**RK 19.3**	JUL	3.6	21.6	*	*
	AUG	8.8	23.5	*	*		AUG	8.3	23.8	*	*
	SEP	9.0	22.3	178.0	71.0		SEP	4.8	22.3	179.0	79.0
Site Mean		**7.3**	**22.1**	*	*	**Site Mean**		**5.6**	**22.6**	*	*
Kootenai Bay	JUL	3.4	20.5	*	*	**RK 18.5**	JUL	3.9	22.3	*	*
	AUG	10.6	23.2	*	*		AUG	8.5	23.7	*	*
	SEP	9.3	22.2	184.0	81.0		SEP	4.9	22.4	287.0	78.0
Site Mean		**7.8**	**22.0**	*	*	**Site Mean**		**5.8**	**22.8**	*	*
Maiden Rock	JUL	4.9	15.1	*	*	**RK 16.1**	JUL	3.6	20.8	*	*
	AUG	13.5	23.6	*	*		AUG	8.5	23.8	*	*
	SEP	11.3	21.7	191.0	79.0		SEP	4.5	22.4	183.0	77.0
Site Mean		**9.9**	**20.1**	*	*	**Site Mean**		**5.5**	**22.3**	*	*
Whiskey Point	JUL	6.4	19.8	*	*	**RK 4.4**	JUL	3.9	21.1	*	*
	AUG	12.0	22.9	*	*		AUG	5.6	23.4	*	*
	SEP	13.3	21.5	181.0	79.0		SEP	4.6	22.2	200.0	79.0
Site Mean		**10.6**	**21.4**	*	*	**Site Mean**		**4.7**	**22.2**	*	*
Scenic Bay	JUL	6.0	13.7	*	*	**RK 0.8**	JUL	3.6	21.4	*	*
	AUG	11.5	23.6	*	*		AUG	7.0	23.2	*	*
	SEP	12.4	21.6	181.0	79.0		SEP	4.6	21.9	232.0	75.0
Site Mean		**10.0**	**19.6**	*	*	**Site Mean**		5.1	22.2	*	*
Idlewilde Bay	JUL	5.0	13.2	*	*						
	AUG	7.8	22.7	*	*						
	SEP	11.8	22.1	190.0	78.0						
Site Mean		**8.2**	**19.3**	*	*						

Table 2.- Selected physico-chemical water quality variables, total phosphorus, and nitrate-nitrogen concentrations from Lake Pend Oreille proper and its outlet arm July – October, 1999. One standard deviation is shown in parenthesis for total phosphorus and nitrate-nitrogen where applicable.

Site	**Date**	**Secchi Depth** (m)	**Mean Temperature** (C)	**Mean Dissolved Oxygen** ($mg \cdot l^{-1}$)	**Mean Conductivity** (u siemens)	**Alkalinity** ($mg \cdot l^{-1}$	**pH**	**Mean Total Phosphorus** ($ug \cdot l^{-1}$)	**Mean Nitrate-Nitrogen** ($ug \cdot l^{-1}$)
Clark Fork	JUL	2.5	14.6	9.8	168.9	69.0	7.9	<7	69.9 (45.0)
	AUG	6.1	18.5	9.5	168.0	80.0	7.9	<7	25.2 (3.2)
	SEP	7.1	17.4	9.3	170.0	77.5	6.6	<7	27.9 (1.1)
	OCT	6.0	11.9	9.9	170.0	83.0	*	8.31 (3.3)	26.2 (4.5)
Site Mean		**5.4**	**15.6**	**9.6**	**163.7**	**77.4**	**7.7**	**<7**	**37.3**
Ellisport Bay	JUL	3.3	15.7	10.0	167.9	72.0	8.0	<7	38.8 (47.1)
	AUG	7.0	20.1	9.8	169.4	76.0	8.0	<7	39.7 (19.5)
	SEP	8.0	18.9	9.1	211.0	77.0	7.0	<7	23.3 (3.9)
	OCT	7.9	12.2	9.8	149.0	81.0	*	<7	27.1 (2.5)
Site Mean		**6.5**	**16.7**	**9.7**	**174.3**	**76.5**	**7.8**	**<7**	**32.2**
Warren Island	JUL	3.5	14.9	10.0	171.0	68.0	7.9	<7	16.4 (1.7)
	AUG	7.7	18.6	9.3	169.8	76.0	7.9	<7	21.4 (7.7)
	SEP	9.8	19.2	9.0	176.0	79.0	6.9	<7	25.5 (3.0)
	OCT	8.1	12.3	9.9	150.5	84.0	*	<7	19.9 (4.5)
Site Mean		**7.3**	**16.2**	**9.5**	**166.8**	**76.8**	**7.7**	**<7**	**20.8**
Sunnyside Bay	JUL	3.5	15.7	9.6	222.8	43.0	7.1	<7	24.1 (6.1)
	AUG	5.6	17.9	9.9	153.4	74.0	7.2	<7	23.2 (4.0)
	SEP	8.8	18.7	8.8	171.3	73.0	6.7	<7	26.9 (1.3)
	OCT	7.9	12.2	9.8	147.0	81.0	*	<7	22.5 (4.9)
Site Mean		**6.5**	**16.1**	**9.5**	**173.6**	**61.8**	**7.0**	**<7**	**24.2**
Bottle Bay	JUL	3.9	15.3	9.9	162.2	67.0	7.5	<7	70.0 (45.2)
	AUG	6.6	18.1	9.5	198.1	77.0	7.3	<7	22.8 (2.4)
	SEP	6.0	18.8	8.9	171.5	82.0	7.0	<7	29.5 (5.3)
	OCT	7.8	11.9	9.8	147.5	81.5	*	<7	18.9 (3.2)
Site Mean		**6.1**	**16.0**	**9.5**	**169.5**	**76.9**	**7.3**	**<7**	**35.3**
Kootenai Bay	JUL	3.6	16.2	10.0	192.2	72.0	7.9	<7	25.4 (8.3)
	AUG	6.3	20.1	9.4	163.9	75.0	7.6	<7	22.4 (11.0)
	SEP	8.7	19.0	9.0	176.9	75.0	6.8	<7	24.8 (2.7)
	OCT	5.9	11.8	10.2	139.4	80.0	*	<7	28.2 (1.7)
Site Mean		**6.1**	**16.8**	**9.6**	**168.1**	**75.5**	**7.6**	**<7**	**25.2**
Maiden Rock	JUL	5.6	15.8	9.9	142.2	59.0	6.8	<7	43.0 (48.6)
	AUG	8.9	20.3	9.3	171.8	80.0	7.2	<7	25.1 (12.6)
	SEP	*	17.5	9.4	170.0	76.0	6.5	<7	24.2 (2.0)
	OCT	10.1	12.3	10.0	145.5	80.5	*	<7	26.5 (3.5)
Site Mean		**8.2**	**16.5**	**9.6**	**157.4**	**73.9**	**6.9**	**<7**	**29.7**
Whiskey Point	JUL	4.4	14.2	10.1	159.7	76.0	8.0	7.2 (1.6)	47.6 (42.4)
	AUG	8.6	18.7	10.1	165.8	79.0	7.9	<7	30.0 (6.7)
	SEP	8.1	17.6	9.3	172.5	75.0	6.7	<7	27.1 (2.2)
	OCT	10.4	12.2	9.8	148.0	80.5	*	8.2 (2.2)	22.4 (1.7)
Site Mean		**7.9**	**15.7**	**9.8**	**161.5**	**77.6**	**7.8**	**<7**	**31.8**
Scenic Bay	JUL	4.5	15.7	9.9	169.1	76.0	8.0	<7	47.3 (41.0)
	AUG	8.6	20.7	9.1	175.7	82.0	7.9	<7	20.0 (2.9)
	SEP	8.5	17.0	9.5	168.0	75.0	6.7	<7	21.0 (5.9)
	OCT	8.9	12.1	9.9	142.0	82.0	*	<7	25.0 (7.5)
Site Mean		**7.6**	**16.4**	**9.6**	**163.7**	**78.8**	**7.8**	**<7**	**29.2**
Idlewilde Bay	JUL	5.1	14.7	10.1	144.2	78.0	7.2	<7	70.9 (53.4)
	AUG	7.9	20.8	9.2	177.6	78.0	7.9	<7	40.3 (14.8)
	SEP	7.1	16.6	9.5	170.0	74.5	6.8	<7	43.5 (36.3)
	OCT	10.2	11.9	9.9	142.5	80.0	*	<7	23.8 (1.5)
Site Mean		**7.6**	**16.0**	**9.7**	**158.6**	**77.6**	**7.5**	**<7**	**44.6**

Table 2 con't.- Selected physico-chemical water quality variables, total phosphorus and, nitrate-nitrogen concentrations from Lake Pend Oreille proper and its outlet arm July – October, 1999. One standard deviation is shown in parenthesis for total phosphorus and nitrate-nitrogen where applicable.

Site	**Date**	**Secchi Depth**	**Mean Temperature**	**Mean Dissolved Oxygen**	**Mean Conductivity**	**Alkalinity**	**pH**	**Mean Total Phosphorus**	**Mean Nitrate-Nitrogen**
		(m)	(C)	(mgl^{-1})	(u siemens)	(mgl^{-1} $CaCO_3$)		(ugl^{-1})	(ugl^{-1})
RK 40.2	JUL	3.4	16.5	9.7	188.0	69.0	8.0	<7	14.9 (6.0)
	AUG	4.1	20.5	9.1	166.9	75.0	7.7	<7	32.3 (4.5)
	SEP	6.1	18.7	9.3	175.6	73.5	6.7	<7	26.1 (2.4)
	OCT	7.4	11.1	10.1	146.5	81.0	*	<7	24.5 (0.6)
Site Mean		**5.3**	**16.7**	**9.5**	**169.3**	**74.6**	**7.7**	**<7**	**24.5**
RK 32.2	JUL	2.8	16.2	9.6	180.0	67.0	8.0	<7	22.2 (10.4)
	AUG	4.1	20.5	9.1	166.9	74.0	7.9	<7	26.2 (1.2)
	SEP	5.8	18.7	9.1	172.9	75.5	6.7	<7	28.7 (2.3)
	OCT	7.1	11.2	10.1	143.0	82.0	*	<7	25.7 (0.9)
Site Mean		**4.9**	**16.7**	**9.5**	**165.7**	**74.6**	**7.1**	**<7**	**25.7**
RK 26.6	JUL	3.3	14.9	9.6	168.9	69.0	7.3	<7	73.5 (45.1)
	AUG	3.8	20.2	9.2	163.7	72.5	7.0	<7	30.9 (3.3)
	SEP	7.1	18.5	8.7	170.5	73.0	6.6	7.7 (2.7)	24.8 (15.4)
	OCT	6.4	11.2	10.3	148.3	81.0	*	7.1 (2.2)	23.7 (0.8)
Site Mean		**5.1**	**16.2**	**9.5**	**162.9**	**73.9**	**7.1**		**38.2**
RK 22.1	JUL	3.3	15.2	9.5	172.6	67.0	7.6	<7	43.5 (46.4)
	AUG	3.9	20.7	9.3	163.7	76.0	7.6	<7	29.2 (2.6)
	SEP	5.9	19.0	8.7	169.0	73.0	6.7	<7	26.2 (3.3)
	OCT	6.7	11.1	10.4	144.0	79.0	*	<7	21.8 (0.9)
Site Mean		**4.9**	**15.6**	**9.5**	**162.3**	**73.8**	**7.5**	**<7**	**30.2**
RK 19.3	JUL	3.1	15.8	9.4	248.9	66.0	7.8	7.5 (1.6)	20.5 (1.8)
	AUG	4.3	20.8	9.2	170.8	72.0	7.9	<7	29.7 (6.7)
	SEP	5.9	19.8	8.7	177.5	74.0	6.9	9.8 (1.1)	27.8 (2.8)
	OCT	6.4	11.1	10.3	142.0	80.0	*	9.3 (4.2)	29.9 (12.4)
Site Mean		**4.9**	**16.9**	**9.4**	**184.8**	**73.0**	**7.7**	**7.5**	**27.0**
RK 18.5	JUL	3.4	15.8	9.4	176.6	70.0	7.7	<7	66.3 (46.4)
	AUG	4.0	21.1	9.3	171.8	70.0	7.8	<7	29.4 (2.3)
	SEP	6.9	20.0	8.8	173.5	74.0	6.2	<7	34.8 (13.4)
	OCT	6.2	11.3	10.5	144.0	78.0	*	<7	17.8 (3.1)
Site Mean		**5.1**	**17.1**	**9.5**	**166.5**	**73.0**	**7.6**	**<7**	**37.1**
RK 16.1	JUL	3.0	15.7	9.5	167.4	70.0	7.6	7.1 (4.9)	45.1 (43.5)
	AUG	3.8	21.1	9.2	171.2	74.0	7.6	<7	26.9 (0.3)
	SEP	4.6	20.2	8.8	177.0	73.0	6.9	<7	26.9 (6.6)
	OCT	5.8	11.3	10.4	140.5	79.5	*	<7	23.8 (2.5)
Site Mean		**4.3**	**17.1**	**9.5**	**164.0**	**74.1**	**7.5**	**<7**	**30.7**
RK 4.4	JUL	3.4	16.7	9.5	402.5	70.0	7.5	7.3 (3.3)	44.9 (38.8)
	AUG	3.9	20.5	9.0	165.2	72.0	7.5	7.0 (4.6)	27.8 (8.4)
	SEP	4.0	20.0	8.7	176.5	73.0	7.0	<7	35.2 (1.5)
	OCT	5.6	11.5	10.4	142.3	79.0	*	11.4 (5.1)	30.4 (16.2)
Site Mean		**4.2**	**17.2**	**9.4**	**221.3**	**73.5**	**7.4**	**7.3**	**34.6**
RK 0.8	JUL	3.4	16.0	9.3	230.6	67.0	7.2	<7	42.8 (44.3)
	AUG	3.9	20.5	9.3	173.3	72.0	7.5	<7	26.8 (0.4)
	SEP	5.2	19.6	8.1	168.5	72.0	7.5	<7	33.9 (1.1)
	OCT	6.2	11.1	10.1	131.4	76.0	*	<7	18.3 (1.5)
Site Mean		**4.7**	**16.8**	**9.2**	**176.0**	**71.8**	**7.4**	**<7**	**30.5**

Table 3.-Mean selected sediment chemical values for eight sample stations on Lake Pend Oreille proper and its outlet arm, July, 2000. One standard deviation is shown in parentheses. Mean values with the same superscripted letter within a given column are not significantly different ($p > 0.05$).

Sample Station	Mean Total Phosphorus ($\mu g \cdot g^{-1}$)	Mean Percent Nitrogen (%)	Mean Percent Organic Carbon (%)	Mean Percent Carbon (%)	Mean Percent Organic Matter (%)
Bottle Bay	577.8 (56.5) ^{bc}	0.4 (0.1) ^{a}	5.6 (1.0) ^{a}	5.6 (1.5) ^{a}	9.6 (1.7) ^{a}
Ellisport Bay	546.7 (90.3) ^{bc}	0.3 (0.1) ^{abc}	3.8 (1.9) ^{ab}	3.6 (1.9) ^{ab}	6.5 (3.2) ^{ab}
Scenic Bay	1563.3 (1422.9) ^{a}	0.2 (0.2) ^{abc}	7.5 (6.0) ^{a}	8.4 (7.1) ^{a}	12.9 (10.3) ^{a}
Idlewilde Bay	395.0 (27.4) ^{c}	0.4 (0.2) ^{ab}	5.8 (1.8) ^{a}	6.1 (2.8) ^{a}	9.9 (3.2) ^{a}
RK 0.8	611.1 (113.4) ^{bc}	0.1 (0.1) ^{dc}	1.8 (1.9) ^{bc}	1.9 (2.6) ^{bc}	3.1 (3.2) ^{bc}
RK 4.4	790.0 (88.8) ^{b}	0.1 (0.1) ^{bcd}	1.9 (1.2) ^{bc}	1.7 (1.1) ^{bc}	3.3 (2.1) ^{bc}
RK 18.5	483.3 (192.4) ^{c}	0.0 (0.0) ^{d}	0.8 (0.5) ^{c}	0.7 (0.6) ^{c}	1.4 (0.9) ^{c}
RK2 6.6	545.0 (97.1) ^{bc}	0.2 (0.1) ^{abc}	2.9 (1.3) ^{ab}	2.7 (1.2) ^{ab}	5.0 (2.3) ^{ab}

Table 4.-Aquatic macrophyte species collected from the 19 selected sample stations on Lake Pend Oreille proper, Idaho and its outlet arm, 1998 and 1999. Mean percent organic content of oven dry weight biomass is included for July, August, and September, 1999. One standard deviation is shown in parentheses where applicable.

Species	**Mean Percent Organics (July)**	**Mean Percent Organics (August)**	**Mean Percent Organics (September)**	**July-September Mean**
Callitrichaceae (Water-starwort Family)				
Callitriche marginata Torr.	93.2 (--)	95.8 (--)	87.2 (5.9)	92.1
Ceratophyllaceae (Hornwort Family)				
Ceratophyllum demersum L.	84.3 (4.9)	87.1 (3.3)	83.6 (5.0)	85.0
Characeae (Stoneworts)				
Chara spp.	58.8 (14.6)	56.8 (19.9)	44.5 (11.8)	53.4
Nitella spp.	56.5 (1.3)	59.4 (16.1)	47.9 (8.8)	54.6
Crassulaceae (Stonecrop Family)				
Tillaea aquatica L.	86.1 (4.2)	87.6 (3.9)	81.2 (8.2)	85.0
Elatinaceae (Waterwort Family)				
Elatine triandra	92.9 (4.1)	Not found	Not found	--
Hippurisaceae (Mare's-tail family)				
Hippuris montana Ledeb.	78.4 (7.0)	Not found	82.7 (5.2)	80.55
Hydrocharitaceae (Frog's-bit Family)				
Elodea canadenis Rich. in Michx.	82.6 (6.1)	82.1 (2.1)	80.7 (4.8)	81.8
E. Nuttallii (Planch.) St. John	81.2 (4.9)	83.3 (2.6)	73.9 (--)	79.5
Haloragaceae (Water-milfoil Family)				
M. sibiricum (Fern.) Jeps.	83.2 (3.2)	84.2 (2.8)	87.0 (6.2)	84.8
Myriophyllum spicatum L.	80.8 (--)	85.2 (3.3)	86.4 (3.5)	84.1
Isoetaceae (Quillwort Family)				
Isoetes spp.	74.0 (9.0)	73.3 (12.4)	70.2 (8.6)	72.5
Najadaceae (Water-nymph Family)				
Najas flexilis (Willd.) Rost. & Schmidt	85.9 (7.9)	84.0 (6.6)	81.1 (4.8)	83.7
Potamogetonaceae (Pond Weed Family)				
Potamogeton berchtoldii Fieb.	85.0 (4.8)	86.0 (5.3)	84.6 (7.1)	85.2
P. crispus L.	86.7 (3.4)	86.2 (2.6)	93.7 (3.8)	88.9
P. foliosus Raf.	81.3 (--)	Not found	Not found	--
P. gramineus L.	86.0 (5.7)	83.6 (6.5)	83.9 (7.3)	84.5
P. pectinatus L.	84.7 (4.5)	86.6 (3.5)	85.3 (4.1)	85.5
P. praelongus Wulf.	89.7 (1.8)	84.6 (2.9)	77.2 (--)	83.8
P. richardsonii (Bennett) Rydb.	85.6 (4.9)	88.2 (3.6)	85.1 (3.9)	86.3
P. robbinsii Oakes	81.9 (5.6)	85.1 (2.5)	88.2 (16.7)	85.1
P. zosteriformis Fern.	86.6 (7.2)	89.6 (2.4)	92.5 (2.4)	89.6
Ranunculaceae (Buttercup Family)				
Ranunculus aquatilis L.	86.6 (3.1)	84.2 (2.6)	85.5 (4.3)	85.4
Zannichelliacaea (Horned Pondweed Family)	87.8 (5.3)	75.8 (--)	84.9 (7.2)	82.8
Zannichellia palustris L.				
Bryophytes				
Drepanocladius spp.	62.4 (13.3)	46.8 (7.9)	56.4 (9.4)	55.2

Table 5.-Percent dominance and percent frequency of aquatic macrophyte species in the drawdown zone (1.4 m – 3.5 m depth) from the six selected sample stations on the outlet arm of Lake Pend Oreille and Lake Pend Oreille proper, Idaho.

Species	**1990 Percent Dominance**	**1990 Percent Frequency**	**1999 Percent Dominance**	**1999 Percent Frequency**
Ceratophyllaceae (Hornwort Family)				
Ceratophyllum demersum L.	0.4	8.7	0.4	4.2
Characeae (Stoneworts)				
Chara spp.	29.3	60.9	27.4	54.2
Crassulaceae (Stonecrop Family)				
Tillaea aquatica L.	0.0	4.4	0.0	2.1
Hydrocharitaceae (Frog's-bit Family)				
Elodea canadenis Rich. in Michx.	1.8	17.4	12.7	47.9
E. Nuttallii (Planch.) St. John				
Haloragaceae (Water-milfoil Family)				
Myriophyllum sibiricum (Fern.) Jeps.	30.1	26.1	1.7	8.3
**M. spicatum* L.				
Isoetaceae (Quillwort Family)	2.0	8.7	0.2	14.6
Isoetes spp.				
Najadaceae (Water-nymph Family)				
Najas flexilis (Willd.) Rost. & Schmidt	0.1	13.0	0.0	4.2
Potamogetonaceae (Pond Weed Family)				
Potamogeton robbinsii Oakes	0.3	4.6	0.0	0.0
P. pectinatus L.	2.0	4.4	2.1	14.6
P. crispus L.	0.0	0.0	23.6	8.3
P. zosteriformis Fern.	0.0	0.0	0.3	4.2
P. praelongus Wulf.	0.0	0.0	0.0	2.1
P. richardsonii (Bennett) Rydb.	23.9	30.4	0.5	6.3
P. pusillus L.	0.0	8.7	0.0	0.0
P. berchtoldii Fieb.	0.5	8.7	25.3	58.3
P. gramimeus L.	1.4	8.7	0.1	8.3
P. foliosus Raf	6.3	4.4	0.0	0.0
Ranunculaceae (Buttercup Family)				
Ranunculus aquatilis L.	1.9	13.0	5.6	16.7
Bryophytes				
Drepanocladius spp.	0.0	0.0	0.0	4.2
Others	0.0	0.0	0.0	2.1

* M. spicatum did not occur frequently in the 1.0 – 3.5 m depth range and therefore was not represented in samples between 1.4 - 3.5 m depths (drawdown zone) in 1999. However this species was present at sample station RK0.8, first having appeared in Lake Pend Oreille in July, 1998.

Table 6.- Depth (m) as a predictor of substrate particle size class ($\hat{b}_0$ and $\hat{b}_1 x$ are coefficients derived from binary logistic regression; α = 0.05).

Substrate Class	$\hat{b}_0$	$\hat{b}_1$	**p-value**
Clay	0.4225	- 0.4984	< 0.0001
Silt	-0.8984	0.0797	0.12
Sand	- 2.936	0.2594	< 0.0001
Gravel	- 3.5624	0.2045	.03
Cobble	- 0.2986	- 0.9881	0.004

Prediction of Potential Eurasian Watermilfoil Habitat in Lake Pend Oreille, Idaho

Abstract

The exotic aquatic macrophyte Eurasian watermilfoil was first observed in Albeni Cove on the outlet arm of Lake Pend Oreille, in August, 1998. We conducted a systematic random sampling of Eurasian watermilfoil throughout the cove to describe relationships between milfoil biomass and depth. These data, along with substrate composition, were used in a geographic information system (GIS) to predict the amount of potential Eurasian watermilfoil habitat in this system. This information was then used to suggest management options for future milfoil control programs. We also conducted physico-chemical measurements in the water column (light and dissolved oxygen profiles, pH, and total alkalinity) in and adjacent to the Eurasian watermilfoil bed to assess effects of this species on the surrounding physical and chemical environment. Light attenuated rapidly beneath the canopy reaching levels below 1 % incident at about 1.5 m that likely contributed to the formation of monospecific stands of milfoil in Albeni Cove. A significant relationship was found between milfoil density and depth. A model describing the relationship between milfoil biomass and depth along with a substrate grid was used in a GIS to quantify possible habitat. Approximately 39% (1438 ha) of the outlet arm area is likely Eurasian watermilfoil habitat. Management of milfoil in this system could include the use of herbicides, hand harvesting, and mechanical harvesting. Contact herbicides may be effective in backwater areas of zero current velocity, hand harvesting can be used to remove isolated, low density colonies. Systemic compounds or mechanical harvesting may be utilized in areas where current is present and densities are high.

Introduction

In 1998, Eurasian watermilfoil (Myriophyllum spicatum L.) was discovered in Lake Pend Oreille, Idaho at Albeni Cove (River Kilometer 0.8), just upstream of Albeni Falls Dam (Fig. 9). Milfoil has been present in the Pend Oreille River immediately downstream of Albeni Falls Dam since 1976, and this area was a possible source of fragments. Eurasian watermilfoil has the potential to spread rapidly in clear, lentic waters of the Pend Oreille system. For example, Eurasian watermilfoil spread at a rate of 3.7 ha·yr in the Pend Oreille River and has become a severe nuisance throughout the river (Gibbons et al. 1983a, Falter et al. 1991, WDE 1993).

Lake Pend Oreille proper is a 383 km^2 (94640 acres) meso-oligotrohic lake with mean and maximum depths of 164 m (538 ft) and 357 m (1171 ft), respectively (USGS 1996). The lake’s outlet arm is the Pend Oreille River, exiting from the northwest corner of Lake Pend Oreille. Mean and maximum depths of the outlet arm are 7.4 m (24 ft) and 48 m (157 ft), respectively with a shoreline length of 152 km (94 mi.; USGS 1996). The outlet arm is impounded by Albeni Falls Dam on the Washington-Idaho border and controls water levels of the entire lake. An annual winter drawdown from mid-November through May of 2.3 m (7.5 ft) to 3.5 m (11.5 ft) is implemented primarily for spring flood control and winter power production.

The objectives of this study were to:

1. Identify likely habitat for milfoil colonization on the outlet arm of Lake Pend Oreille using a GIS to integrate Eurasian watermilfoil biomass, water depth, and substrate composition;
2. Describe apparent physico-chemical effects of Eurasian watermilfoil on the surrounding environment; and
3. Develop and recommend management options to control the spread of milfoil in this system.

Ecology of Eurasian Watermilfoil

Eurasian Watermilfoil Distribution and Growth Forms

Eurasian watermilfoil is a submersed, perennial, aquatic angiosperm that was introduced into the United States near Chesapeake Bay in the late 1880's. Since its introduction, Eurasian watermilfoil has spread across the United States and become one of the most troublesome submersed aquatic plants in North America (Smith and Barko 1990). Nuisance growths of Eurasian watermilfoil (hereafter also referred to as milfoil) restrict water-based recreation through the development of dense surface canopies (Nichols 1975, Wile 1978) and create aesthetically displeasing lake littoral zones.

Biology of Eurasian Watermilfoil

Eurasian watermilfoil is a member of the Haloragaceae (watermilfoil family). This submersed perennial aquatic herb is essentially evergreen which overwinters as root-stocks forming no specialized overwinter structures such as turions (Smith and Barko 1990). Milfoil has a pillar-like growth form (vertical clumpings of 10-40 stems per clump) early in the growing season (Budd et al. 1995), but as water temperature and photoperiod increase, long stems are produced that can exceed 10 m in length. These stems are covered with finely dissected leaves arranged in whorls of 3 to 6, usually 4 per node (Hitchcock and Cronquist 1973, Aiken et al. 1979). Leaf outline is feather-like with 14 – 24 pairs of leaflets (Aiken et al. 1979). Stems branch once reaching the water surface form dense surface canopies. The formation of these dense surface canopies interferes with water-based recreation and can decrease the diversity of littoral vegetation (Madsen et al. 1991). Once canopy formation begins, leaves low on the stem senesce leaving only the surface canopy foliated.

Milfoil possesses several structural and physiological adaptations that allow it to be a superior competitor:

(1) The location of photosynthetic tissue near the water surface;

(2) C_4- fixation similarities (*i.e.*, a bicarbonate (HCO^{-3}) uptake mechanism analogous to the C_4-dicarboxylic acid pathway where CO_2 is actively transported to the site of the Calvin Cycle with a subsequent decarboxylation) (Hutchinson 1975);

(3) The ability to survive under low light (1-2% of surface light);

(4) An opportunistic use of nutrients (nutrient uptake from the most available source, whether sediments or the water column); and

(5) A life history that tolerates cool weather (the ability to overwinter as the entire plant and grow under ice; Nichols and Shaw 1986), and very rapid growth throughout the growing season out-competing native vegetation (Gibbons et al. 1983a).

Nutrient Dynamics

Milfoil communities are affected by surrounding sediment and water column nutrient concentrations (Nichols and Keeney 1976, Rattray et al. 1991). The addition of nitrogen to sediments has been shown to result in a 30-40% increase in milfoil biomass (Anderson and Kalff 1986). Eurasian watermilfoil colonies also affect surrounding nutrient dynamics *via* nutrient uptake, translocation, and release upon senescence and decomposition (Smith and Barko 1990, Nichols and Keeney 1973, Carignan 1985). DeMarte and Hartman (1974) concluded that ^{32}P was actively translocated from the roots of M. sibiricum to the shoot system and subsequently released to the surrounding water. Smith and Adams (1986) also demonstrated the importance of roots in transferring phosphorus from lake sediments into plants and concluded that roots accounted for 73% of total plant phosphorus uptake (shoot uptake accounted for 27%). During their experiment, phosphorus efflux from live milfoil shoots to the water was low. However, high efflux occurred during decay, illustrating the importance of phosphorus release upon senescence. Bristow and Whitcombe (1971) reported that most (59%) of the phosphate measured in stems of milfoil was derived from sediment, demonstrating the importance of sediment composition to growth of rooted aquatic macrophytes that derive nutrients primarily from lake sediments. Nutrient release may be an important component influencing pelagic phytoplankton community composition and abundance in fall (Brooker and Edwards 1975, Malthus et al. 1990). Landers (1982) reported that senescing mifoil beds produced about 18% of the annual total phosphorus load and a significant amount of nitrogen to an Indiana reservoir. Additionally, significant increases in phytoplankton and periphyton biomass (indicated by Chl *a*) were measured in response to the pulses of nutrient release from milfoil decay.

Effects on Benthic Macro Invertebrates and Fishes

Ecological effects of nuisance growths include the decline of native aquatic vegetation under dense milfoil canopies (Madsen et al. 1991) and lower aquatic invertebrate densities (essential food for many fishes and semi-aquatic organisms) within milfoil beds (Sloey et al. 1997). For example, Keast (1984) found five important taxa of fish prey invertebrates to be three to seven times more abundant in a Potamogeton-dominated community than in a milfoil-dominated community. In the same study, three to four times as many fish were found feeding in the benthos beneath the indigenous macrophyte bed when compared to beneath the milfoil plant community. However, Liter (1991) found higher fish densities in vegetated sloughs when compared to the main reservoir while sampling with pop nets in Box Canyon Reservoir on the Pend Oreille River, Washington. These vegetated sloughs in Box Canyon Reservoir are largely composed of milfoil (Falter et al. 1991) and contained fish densities of up to 5.2 fish $\cdot m^{-2}$ (Liter 1991). Lyons (1989) speculates that environmental degradation caused by the invasion of milfoil into Lake Mendota, Wisconsin, contributed to the extinction of eight species of small littoral fishes and consequently a reduction in prey abundance for larger fishes. Other effects include a possible decrease in foraging efficiency of littoral fishes through an increase in habitat complexity (difficulty of piscivorous fishes locating prey) and light reduction (Diehl 1988) as well as altering fish spawning site distribution (Keast 1984). Engel (1987) documented a shift in prey item occurrence in largemouth bass as the density of aquatic macrophytes (Potamogeton spp., Ceratophyllum demersum, Spirogyra, and others) increased. For example, bass and bluegill (Lepomis macrochirus) under age III utilized aquatic plant beds early in the year (low plant densities) while feeding on aquatic invertebrate larvae. As aquatic plant densities increased, bluegill in those areas shifted to feed on zooplankton and finally to aquatic plant tissue at maximum plant densities. Largemouth bass, however, began feeding on fish prey as plant densities increased, but encountered difficulties penetrating dense macrophyte beds in search for prey. Dibble and Harrel (1997) also found piscivory to be more prevalent in largemouth bass contained in milfoil enclosures than those contained in common pondweed-dominated enclosures. Diets of largemouth bass contained in the pondweed enclosures consisted primarily of macroinvertebrates. Dibble and Harrel (1997) hypothesized that differences in plant architecture were responsible for these differences in diet. For example, the frequency of vertical and horizontal interstices was higher in the pondweed communities (increased frequency of microhabitat for aquatic invertebrates) relative to milfoil communities (Dibble and Harrel 1997). This enhanced spatial complexity in the pondweed communities may increase the abundance of prey items and therefore benefit the foraging efficiency of littoral fishes.

Controlling Factors

The mechanisms of colonization and factors that affect the dispersal of milfoil have received a great deal of attention due to the profound impact milfoil invasion can have on a waterbody and surrounding ecosystems. Factors influencing the distribution of Eurasian watermilfoil on a large spatial scale include water column total phosphorus and Carlson's Index (Madsen 1998). Milfoil dominance increases as water column total phosphorus levels increase from oligotrophic (< 10 ug$\cdot$l^{-1}) to mesotrophic (< 30 ug$\cdot$l^{-1}) and then declines as total phosphorus levels exceed 50 ug$\cdot$l^{-1}. Carlson's Index (1977; TSI) is based on Secchi depth, chlorophyll *a* (ug$\cdot$l^{-1}), and total phosphorus concentrations. Lakes are then classified on a scale ranging from 0 to 100 based on these parameters. According to Carlson's Index, milfoil dominates in oligo-mesotrophic to moderately eutrophic waterbodies (TSI 35-70) (Madsen 1998).

Factors affecting milfoil within-lake distribution include water depth and substrate composition (Peltier and Welch 1969, Spence and Chrystal 1970, Anderson 1978, Spence 1982, Chambers and Kalff 1985, Duarte et al. 1986, Sheldon 1994, Middelboe and Markager 1997). The low nutrient concentrations and limited rates of nutrient diffusion found in coarse substrates provide poor habitat for macrophyte growth (Barko and Smart 1986, Aiken and

Picard 1980). Milfoil prefers substrates that range from 6 to 18% organic matter and sediment textures from 12 to 36% fine particles (< 0.5 mm diameter). However, it can be found on substrates from 0 to 32% organic matter and on sediment textures from 0 to 40% fine particles (Nichols 1994).

Higher levels of organic matter in sediments seem to retard milfoil growth (Barko 1983), largely as a result of changes in pH, redox potential, and the evolution of growth inhibiting gases (*e.g.*, hydrogen sulfide and ammonia) from eutrophic sediments (Horne and Goldman 1994). Depth also limits within-lake distribution of milfoil. Milfoil is most commonly found in depths of 1-3 m, but is commonly found in depths greater than 6 m and in depths of up to 10 m in waterbodies with high transparency (Boylen et al. 1996, Aiken et al. 1979). Poor light penetration can limit the distribution of milfoil to shallower waters (Nichols and Rogers 1997). Freezing and desiccation of milfoil plants on dewatered sediments in regulated lakes and rivers also limit the littoral distribution of milfoil colonies (Stanley 1976).

Eurasian Watermilfoil Propagation

Eurasian watermilfoil can spread rapidly within and between water bodies. Intra-lake colonization is primarily achieved through fragment production (both auto and allofragmentation) and/or clonal expansion which is mostly accomplished *via* stolon growth (Madsen and Smith 1997, Kimbel 1982). Fragment production and dispersal are likely responsible for the spread of milfoil across North America (Smith and Barko 1990). Boat movements between infested and non-infested water bodies facilitate inter-lake fragment dispersal (Williams 1993). Johnstone et al. (1985) found the plant distribution of five nonindigenous aquatic plants that spread vegetatively to be significantly associated with boating and fishing activities. Seed production does occur; however, it is less important than vegetative reproduction (Aiken et al. 1979).

Eurasian Watermilfoil Management

Management of milfoil has become a top priority for many agencies across the United States. To manage aquatic systems, several tools have been developed to study the spatial distribution of organisms and analyze relationships between environmental variables and biotic systems. Geographic information systems (GIS) are becoming increasingly popular in many biophysical sciences, including the aquatic sciences for this purpose (Lehmann and Lachavanne 1997). For example, Jensen et al. (1992) used GIS to develop a model for predicting the potential spatial distribution of cattail (Typha latifolia) and waterlilies (Nymphaea odorata) based on five biophysical criteria. Welch and Remillard (1988) used remote sensing in conjunction with GIS to monitor water quality and distribution of aquatic macrophytes in a South Carolina lake. Narumalani et al. (1997) used logistic multiple regression and GIS to determine the probability of macrophytes occurring at various water levels in a cooling reservoir in South Carolina. Many other studies (Koutnik and Padilla 1994, Janauer 1997, Williams and Lyons 1997, Gottens et al. 1998) pertaining to the management of aquatic ecosystems have also used GIS to assist in the analysis, modeling, and mapping of the spatial distributions of aquatic systems and their communities. GIS also facilitates the transfer of information between organizations and between organizations and the public and therefore represents a powerful tool in aquatic resource management.

Control techniques include the use of herbicides (both contact and systemic herbicides), rotovation, benthic barriers, benthic dredging, biological control agents (*e.g.*, the weevil Euhrychiopsis lecontei), and microbial control agents (*e.g.*, the fungus Mycoleptodiscus terrestris) (Richardson 1975, Wile 1978, Cooke and Gorman 1980, Nichols 1984, Sneh and Stack 1990, Verma and Charudattan 1993, Nelson 1996, Getsinger et al. 1997, Newman et al. 1997, Sutter and Newman 1997). Analysis of a water body with respect to potential areas of colonization and system-specific characteristics that may influence the effectiveness of control measures should be carried out prior to implementation of such control measures (Van Vierssen 1993) due to the wide variety of techniques available.

Eurasian watermilfoil was first observed in the outlet arm of Lake Pend Oreille in August, 1998. Milfoil beds in Albeni Cove were chemically treated in late August, 1998 in an attempt to reduce densities and prevent the spread of this species up the outlet arm and into Lake Pend Oreille proper. Chemical treatment consisted of applying two contact herbicides Aquathol ® (endothall (7-oxabicyclo (2,2,1) heptane-2, 3-dicarboxylic acid) and Reward ® (diquat (6,7-dihydrodipyrido[1,2-a:2',1'-c] pyrazinediium ion)) to 34 acres of water. The Bonner County (Idaho) Weed Control and Waterways Department performed the application.

Materials and Methods

Eurasian Watermilfoil Sampling and Laboratory Analysis

We used systematic random sampling design to describe milfoil densities in Albeni Cove in relation to depth. Thirty transects, 27.5 m apart, beginning at the west end of the cove and extending to the eastern-most point of the cove. The first transect sampled was randomly selected. Every third transect was sampled from that point until the entire bay was sampled. Five samples were obtained between 0 – 10 m depths on each sampled transect. Samples were labeled, stored on ice, and frozen upon returning from the field. Biomass (oven dry weight (ODW, $g \cdot m^{-2}$)) and species composition were determined for each sample following Standard Methods Procedure 10400 D.3 (APHA 1992).

The watermilfoil bed in Albeni Cove was also sampled in August, 1998 (pre-chemical treatment) and again in August, 1999 (post-chemical treatment) to obtain *maximum* biomass estimates. A Petite Ponar dredge (225 cm^2) was used to obtain four replicate plant grabs from the entire bed in 1998 and three in 1999. The dredge was positioned towards the center of the milfoil bed to ensure the edge of the bed was not sampled. Depth (m) and substrate type (clay, silt, sand, gravel, and cobble) were recorded for each grab. Biomass (oven dry weight (ODW, $g \cdot m^{-2}$)) was determined for each sample following Standard Methods Procedure 10400 D.3 (APHA 1992).

Eurasian Watermilfoil Site Limnology

Solar radiation extinction was measured with a LI-COR LI-250 (LI-COR ®,Lincoln NE) light meter in or near the center of the milfoil bed and outside of the milfoil bed from the water surface to lake bottom. A dissolved oxygen profile was obtained using a YSI model 55/25 (YSI Inc., Yellow Springs, OH) dissolved oxygen meter both within and adjacent to the milfoil bed. Electrical conductivity was taken using a YSI model 33 S-C-T. Alkalinity and pH were measured as follows: (1) water samples were taken using a 2-liter Kemmerer water sampler; (2) samples were retrieved at mid-depth near the center of the milfoil bed and; (3) three replicate water samples for the determination of pH and total alkalinity (mg $CaCO_3 \cdot l^{-1}$) were stored in full BOD bottles, and placed on ice until processing that evening (replicates were not obtained from outside the milfoil bed). Alkalinity was determined by the titration method according to Standard Methods procedure 2320.B (APHA 1992). Mean percent species composition by weight was also determined using data obtained from the *maximum* biomass samples. Together, those data were used to determine apparent effects milfoil has on the surrounding aquatic macrophyte community.

GIS Database Development

Bathymetry

A digitized bathymetric map of the outlet arm was obtained from the U. S. Geological Survey (USGS). To generate this map, the USGS measured depths at 62 bathymetric sections on the outlet arm using a calibrated video depth sounder. Depth and locations were digitized onto a base map of the shoreline that had been generated from 7.5-minute USGS topographic maps (USGS 1996).

Substrate Composition

A polygon coverage containing the dominant substrate types in the outlet arm of Lake Pend Oreille was obtained from Dupont (1994, Fig. 10). The substrate coverage was converted into a 10-m raster grid. The assumption was made that substrate particle size distribution had not changed significantly over time from that identifies in 1994.

Statistical Analysis

Eurasian Watermilfoil Biomass and Depth

Regression analysis was used to determine the relationship between water depth (m) and biomass of milfoil (ODW, $g \cdot m^{-2}$). Biomass values were log-transformed prior to analysis to accommodate homogeneity of variance (Kleinbaum et al. 1998). Substrate composition was not included in the regression analysis due to insufficient replication on the various substrate types; however, substrate composition was used in the GIS modeling process. All statistical analyses were performed using SAS GLM (SAS Institute Inc. 2000) or STATISTICA® (Statistica for the Macintosh 1994) computing software.

GIS Analysis

The bathymetric map contained discrete depth values (*i.e.*, every contour line had a measured depth value, but the area between contour lines did not have depth values). In order to generate a map consisting of continuous depth values, we converted the bathymetric coverage into a TIN (Triangulated Irregular Network) model. The TIN was then converted into a 10 m cell-sized raster grid. All coverage and grid manipulations were performed using various commands and modules in ArcInfo v. 7.2.1 and ArcView v. 3.2 (ESRI, Environmental Systems Research Institute).

The model describing the relationship between milfoil biomass and depth in Albeni Cove was applied to the depth grid to generate predicted densities of milfoil for each cell in the grid based on its depth value (Fig. 11). Substrate and biomass grids were then combined using the CON statement in ArcInfo. The CON function is a conditional statement that is evaluated on a cell-by-cell basis. For example, substrate cells were given the value from the predicted biomass grid if the substrate was “clay,” “silt,” or “sand” and given a value of “zero” if the substrate was “gravel” or “cobble,” since milfoil was absent from all gravel and cobble substrate types sampled. This allowed a final estimation of likely available habitat taking into account substrate composition and depth. These predicted biomass values were then used as indicators of suitable milfoil habitat. We assumed that a higher predicted biomass was indicative of more suitable habitat since aquatic macrophytes can be used as bioindicators of suitable habitat (Nichols and Buchan 1997, Nichols 1994).

Results

Eurasian Watermilfoil Site Limnology

Light rapidly attenuated under the dense milfoil canopy from 17, 000 LUX at the surface to 40 LUX at 3.25 m (outlet arm bottom, Fig. 12). Only 0.59% of surface solar radiation was present at 2 m depth. Light attenuated from 16,000 LUX to 4,300 LUX at 3.25 m in open water adjacent to the milfoil canopy.

Daytime dissolved oxygen in the milfoil bed was at 115% saturation ($9.8\ mg{\cdot}l^{-1}$) at the surface and declined to 80% saturation ($6.8\ mg{\cdot}l^{-1}$) at the sediment-water interface (Fig. 13). Dissolved oxygen adjacent to the milfoil bed was at 90% saturation ($8.1\ mg{\cdot}l^{-1}$) at the surface and 91% saturated ($8.2\ mg{\cdot}l^{-1}$) at 3.25 m. Mean water-column temperature (°C) and conductivity (μsiemens) inside the milfoil bed were 19.8 and 147, respectively. Water-column temperature (°C) and conductivity (μsiemens) outside the milfoil bed were 20.5 and 173.3, respectively. Mean alkalinity inside the milfoil bed was 73.0 mg $CaCO_3{\cdot}l^{-1}$ and mean pH was 7.3. Alkalinity outside the bed was 72.0 mg $CaCO_3{\cdot}l^{-1}$ and pH was 7.5 (Table 10).

Milfoil was the dominant species present in the *maximum* biomass samples comprising 84% mean species composition by weight. Elodea canadensis, Ceratophyllum demersum, and Ranunculus aquatilis comprised a minor proportion of the most dense milfoil beds with 10%, 5%, and 1% mean species composition, respectively.

GIS: Predicted Available Habitat

The relationship between milfoil biomass and depth predicted that approximately 52% (2098 ha) of the outlet arm area was suitable habitat. Suitable habitat was defined as any area predicted to contain any densities of milfoil. This definition is broad, but given the coarse resolution of the analysis and the limited number of predictor variables it allows for a liberal estimation of available habitat. Using the relative predicted densities as indicators of habitat quality, approximately 33% (1346 ha) of the predicted milfoil habitat was "low" quality habitat (predicted biomass between 1 – 25 $g \cdot m^{-2}$, ODW), 5% (194 ha) was "moderate" quality habitat (predicted biomass between 26 – 210 $g \cdot m^{-2}$, ODW), and 14% (558 ha) was "high" quality habitat (predicted biomass > 210 $g \cdot m^{-2}$, ODW) (Fig. 11).

Eurasian Watermilfoil Biomass and Depth

Depth was a significant predictor of milfoil density ($p < 0.0001$, $r^2 = 0.57$). We found that a parabola described the relationship between milfoil biomass and depth (Fig. 14).

$$\mathrm{LOG(biomass)} = -2.257 + 2.482(\mathrm{depth}) - 0.330(\mathrm{depth})^2 \qquad (1)$$

Once the model took into account both substrate composition and depth, approximately 39% (1438 ha) of the outlet arm area was predicted as suitable habitat (*i.e.*, was in the depth range of 0 m to 7 m and was not on gravel or cobble substrates).

Approximately 24% (871 ha) was “low” quality habitat, 4% (147 ha) of “moderate” quality, and 11% (420 ha) was “high” quality habitat (Figs. 15 and 16).

Discussion

Eurasian Watermilfoil Biomass and Depth Modeling

The relationship between depth and milfoil biomass in Lake Pend Oreille was approximated by a parabolic curve with a maximum biomass attained near 4 m depth. Lehmann et al. (1994) also found this parabolic relationship between biomass and depth with three pondweed species in Lake Geneva, Switzerland, and used the relationships in modeling submerged macrophyte biomass using GIS. Low biomass in the shallow depths is partially due to the effects of winter drawdown and in many cases may be attributed to disturbance caused by wave action (Schiemer and Prosser 1976, Chambers 1987). The decrease in milfoil biomass deeper than 4 m is related to an increase in littoral slope. As depths approach 6 m, slope increases to the thalweg. Higher slope decreases physical stability of the finer sediments resulting in poor plant habitat (Duarte and Kalff 1986). Low light is often cited (Spence and Chrystal 1970, Duarte et al. 1986) as a limiting factor to the maximum depth of colonization of aquatic macrophytes. However, in this study the light compensation point for photosynthesis (1% of surface light) was deeper (8 m in Albeni cove) than the deepest milfoil communities suggesting that other factors, such as littoral slope and substrate, are controlling the maximum depth of milfoil colonization in this system. Carlson (1995) also concluded that slope and substrate were likely limiting the Eurasian watermilfoil-dominated community in the Pend Orielle River, Washington. Ballesteros et al. (1989) speculated that sediment features were responsible for the lower boundaries of aquatic macrophyte colonization in an oligotrophic lake when irradiance failed to explain the maximum depth of colonization. Irradiance was about 50% well above the compensation point (1%).

Reward ® (diquat) and Aquathol ® (endothall) application in 1998 failed to significantly reduce the *maximum* biomass of Eurasian watermilfoil in Albeni Cove from 1999 maxima (1998 mean maxima = 1119.7 $g \cdot m^{-2}$, 1999 mean maxima = 905.3 $g \cdot m^{-2}$, *t*-test, $p = 0.35$). The ineffectiveness of this application may be due to several factors. The chemical application occurred late in the growing season. Diquat is most effective early in the growing season when plants are actively photosynthesizing (Murphy and Barrett 1993). Furthermore, water velocities in the outlet arm likely limited the contact time of the chemicals in the areas of higher velocity. For example, Newroth (1979) concluded that diquat was ineffective and expensive in large spread treatments of milfoil, especially in lotic systems. Reinert et al. (1985) determined over 90% of granular endothall entered solution 24 h after application. This rapid release rate may reduce its effectiveness in lotic systems (Reinert et al. 1985).

Future management options may include different herbicides and/or mechanical control methods. For example, in the Pend Oreille River, Washington, just west of Albeni Falls Dam, mechanical rotovation was successful in reducing milfoil stem densities. Milfoil stem densities were reduced 63 - 90% immediately following rotovation and remained reduced 25 - 70% the following growing season (Gibbons and Gibbons 1988). Wile (1978) also reduced milfoil stem densities with multiple harvests by a mechanical harvester, and concluded that fish populations were unaffected by harvest activities. Population estimates of warmwater fish species (pumpkinseed Lepomis gibbosus) remained level over the duration of their study in both harvested and nonharvested control areas. However, Wile (1978) did record a direct loss of fish that were trapped in the vegetation upon removal. A loss of approximately 8.9 kg fish per ha lake area harvested. Small (12 to 190 mm) yellow perch (Perca flavescens) were the most numerous species removed accounting for 56% of the total number of fish harvested (Wile 1978). Winter drawdowns also have been successfully implemented to control milfoil populations (Goldsby et al. 1978, Tarver et al. 1978, Cooke 1980, Tarver 1980, Siver et al 1986). However, these studies occurred in enriched water bodies where milfoil is limited to shallow depths and therefore fully exposed during drawdown. Winter drawdown to 3.5 m will not be as successful in the outlet arm of Lake Pend Oreille due to high transparency and the resulting deeper milfoil colonization (depths greater than 5 m). A winter drawdown to 3.5 m would only reduce densities in the shallowest areas of the littoral zone.

Other chemicals that may be considered include systemic compounds such as triclopyr (3,5,6-trichloro-2-pyridinyl-oxyacetic acid) and 2,4-D (2,4-dichlorophenoxy acetic acid). Triclopyr is a selective herbicide that has the potential to remove the nonindigenous dicot milfoil while not affecting native monocots such as Elodea spp. (Sprecher and Stewart 1995). Getsinger et al. (1997) reduced milfoil biomass by 99% (4 weeks after treatment) using triclopyr in a portion of the Pend Oreille River, Washington, between Albeni Falls Dam and Box Canyon dams. Milfoil plants have also been shown to be highly susceptible to 2,4-D. Westerdahl and Hall (1983) determined the threshold concentration required to control milfoil was 0.10 - 0.25 mg·l^{-1}. Diver-operated suction dredging and hand harvesting have been used for milfoil removal in the outlet arm of Lake Pend Oreille in September, 2000. Divers up-rooted the entire plant and placed it into a bag or suction dredge. This procedure effectively removed milfoil shoots and roots; however, long-term effectiveness of this procedure has not yet been determined. Suction harvesting substantially reduced the biomass and percent coverage of milfoil in Lake George, New York, while increasing species richness in the harvested areas a year later (Eichler et al. 1993). Hand harvesting has also been used effectively to reduce densities on small patches of milfoil (Titus 1994).

Eurasian Watermilfoil Site Lminology

The light attenuation under the milfoil canopy illustrates the competitive nature of this species and its ability to shade out native vegetation (Aiken et al. 1979, Madsen 1994). We found that light was reduced below the compensation point below about 1.5 m under the milfoil canopy limiting photosynthesis of indigenous plants and resulting in a monospecific milfoil stand. Milfoil becomes dominant partially as a result of its growth form and its competitive abilities. Falter et al. (1991) reported similar effects of milfoil beds on light penetration in the Pend Oreille River, Washington. Madsen et al. (1991) recorded a decline in the number of native plant species under a dense milfoil canopy. The number of plant species dropped from 20 (under low densities of milfoil) to 9 under a dense milfoil canopy cover. Falter et al. (1991) also reported that milfoil communities dominated some littoral areas in the Pend Oreille River, Washington, accounting for up to 97% of the littoral aquatic macrophyte community. All mechanisms by which milfoil out-competes native species are in need of further investigation.

The dissolved oxygen profile of the Lake Pend Oreille milfoil bed is typical of many aquatic plant communities (Carpenter and Lodge 1986). During daylight hours, photosynthesis near the surface creates supersaturated dissolved oxygen (DO) conditions, while respiration of macrophyte tissue consumes oxygen in deeper waters, especially near the sediment-water interface (Jensen 1989). Frodge et al. (1990) found elevated DO concentrations in the surface canopies of submerged species and lower DO concentrations near the sediments in Keevies Lake and Bull Lake, Washington, and concluded that canopy formation was probably more important than species composition with respect to effects on water chemistry. In our study on the outlet arm of Lake Pend Oreille, water temperature, electrical conductivity, total alkalinity, and pH in the milfoil bed were all similar to those values found in the pelagic zone of the outlet arm. However, Carter et al. (1991) observed pH to be stratified by depth in aquatic macrophyte comunities in the Potomac River with pH associated with decompositional processes in anaerobic benthos. Effects of macrophyte communities on the surrounding water chemistry, however, depends upon the type of waterbody and the size and depth of the system and can be expected to differ between and within lakes and rivers (Carter et al. 1991).

GIS: Predicted Available Habitat and Management

The GIS illustrated the potential spatial extent of milfoil in Lake Pend Oreille using two habitat variables. According to the model, a large proportion (39%) of the littoral area on the outlet arm of Lake Pend Oreille is suitable milfoil habitat (Fig 16.). The amount of potential habitat is likely overestimated due to the spatial scale of the analysis and the limited number of predictors involved in the model. At this scale, the analysis does not take into account the within-bed spatial complexity and patchiness (France 1988). Milfoil populations in oligo to meso-oligotrophic waterbodies often form patches of varying densities and sizes that may be attributed to patchy areas of habitat in these systems and/or the intrinsic growth patterns seen in nutrient-poor environments (Madsen 1994). However, the model gives an indication to the potential impacts this species can have on the outlet arm and potentially on Lake Pend Oreille proper. Future modeling efforts should include more predictor variables such as littoral slope and fetch (as a determinant of wave action). A logistic model could then be developed to determine the probability of milfoil colonization at a given location. Such a model would be valuable for management agencies when they prioritize control efforts to certain areas of a water body. This model also illustrates the need for agencies to develop an effective management plan and to inform the public of the potential effects of this species and the ease with which it is dispersed.

Based on this research, areas on Lake Pend Oreille proper that represent potential habitat for Eurasian watermilfoil (*i.e.*, have suitable depth and substrate) include Scenic and Bottle Bays, the Pack River Delta, and the Clark Fork River Inlet. Another northern lake area is the littoral zone surrounding the Sandpoint public beach. There are fine sediments and shallow depths near the public beach and the presence of public boat ramps provides a vector for its introduction. Middle and southern lake areas contain less potential milfoil habitat due to steep littoral zones and coarse substrates.

Results from literature demonstrate the profound impact Eurasian watermilfoil can have on littoral communities and human recreation. Site-specific management techniques need to be developed to maximize effectiveness and minimize costs. The use of herbicides in conjunction with mechanical harvesting in areas of high use (*e.g.*, boat ramps) may represent an effective means for reducing the rate of milfoil colonization compatible with water-based recreation. However, the elimination of this species by these methods, or any others, is unlikely if not impossible (Gibbons et al. 1983b). Eventually, the milfoil community will naturally decline in abundance (Trebitz et al. 1993). The duration of peak biomass is approximately 10 years; however, the mechanisms responsible for its decline are varied and seem to be a result of multiple interacting factors (Carpenter 1980). Trebitz et al. (1993) also noted an invasion cycle of milfoil dominance in Lake Wingra, Wisconsin. Milfoil dominated Lake Wingra in the 1960's and then declined in the 1970's. While total plant biomass remained similar between those years (between 300 – 400 $g \cdot m^{-2}$), species diversity increased with milfoil persisting at lower densities. Creed (1998) suggested that the native herbivorous weevil (Euhrychiopsis lecontei (Dietz)), whose normal host is northern milfoil (M. sibiricum), may be partly responsible for the decline of Eurasian watermilfoil in many northern states and Canada.

In summary, Eurasian watermilfoil control programs in the outlet arm of Lake Pend Oreille should be developed to take into account the physical and biological limitations present at a given point of infestation. The use of herbicides, hand harvesting, and, mechanical harvesting if necessary, represent viable control options for this system. Contact herbicides may be effective in backwater areas of zero current velocity; whereas, hand harvesting can be used to remove isolated low-density colonies. Systemic herbicides or mechanical harvesting may be utilized in areas where milfoil densities are high and current is present. Since milfoil is now a part of the littoral community in this system, fisheries managers should manage these communities to maximize the use of this new habitat. For example, in some areas channels can be cut through the vegetation to increase the forage efficiency and cover for piscivores by increasing edge effect. More diverse colonies of other aquatic macrophyte species could grow to protect emerging year classes and nursery areas of fish (Engel 1995).

Summary

- A significant relationship was found between Eurasian watermilfoil biomass and depth in the outlet arm of Lake Pend Oreille with a maximum biomass attained near 4 m.
- Approximately 52% (2098 ha) of the outlet arm area was likely Eurasian watermilfoil habitat based on depth alone. Once the GIS accounted for areas consisting of gravel and cobble substrate, approximately 39% (1438 ha) of the outlet arm area was predicted as likely habitat (*i.e.*, was in the depth range of 0 m to 7 m and was not on gravel or cobble substrates).
- Reward ® (diquat) and Aquathol ® (endothall) application failed to significantly reduce the mean *maximum* biomass in 1999 (905.3 $g \cdot m^{-2}$) from1998 maxima (1119.7 $g \cdot m^{-2}$). The ineffectiveness of this treatment may be associated with a single application late in the growing season.
- Eurasian watermilfoil management should be site-specific, allow for the degree of infestation, and take into account the surrounding physical environment.
- Future modeling efforts could include more predictor variables such as littoral slope and fetch (as a determinant of wave action). A logistic model could then be developed to determine the probability of milfoil colonization at a given location.

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Figures

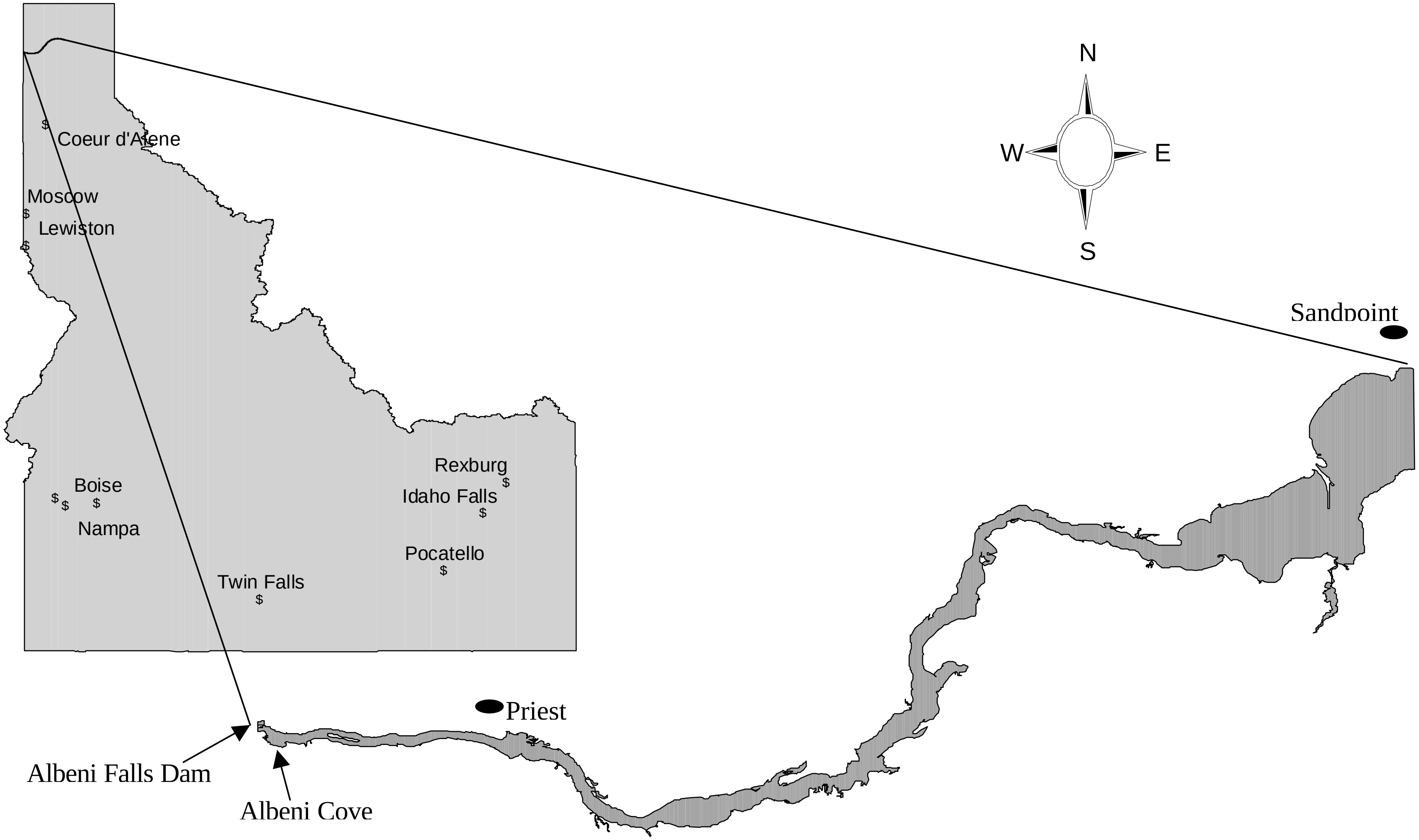


Figure 9.-The outlet arm of Lake Pend Oreille, Idaho. Albeni Falls Dam impounds the outlet arm at the Idaho-Washington border. Eurasian water was discovered in Albeni Cove in August, 1998.

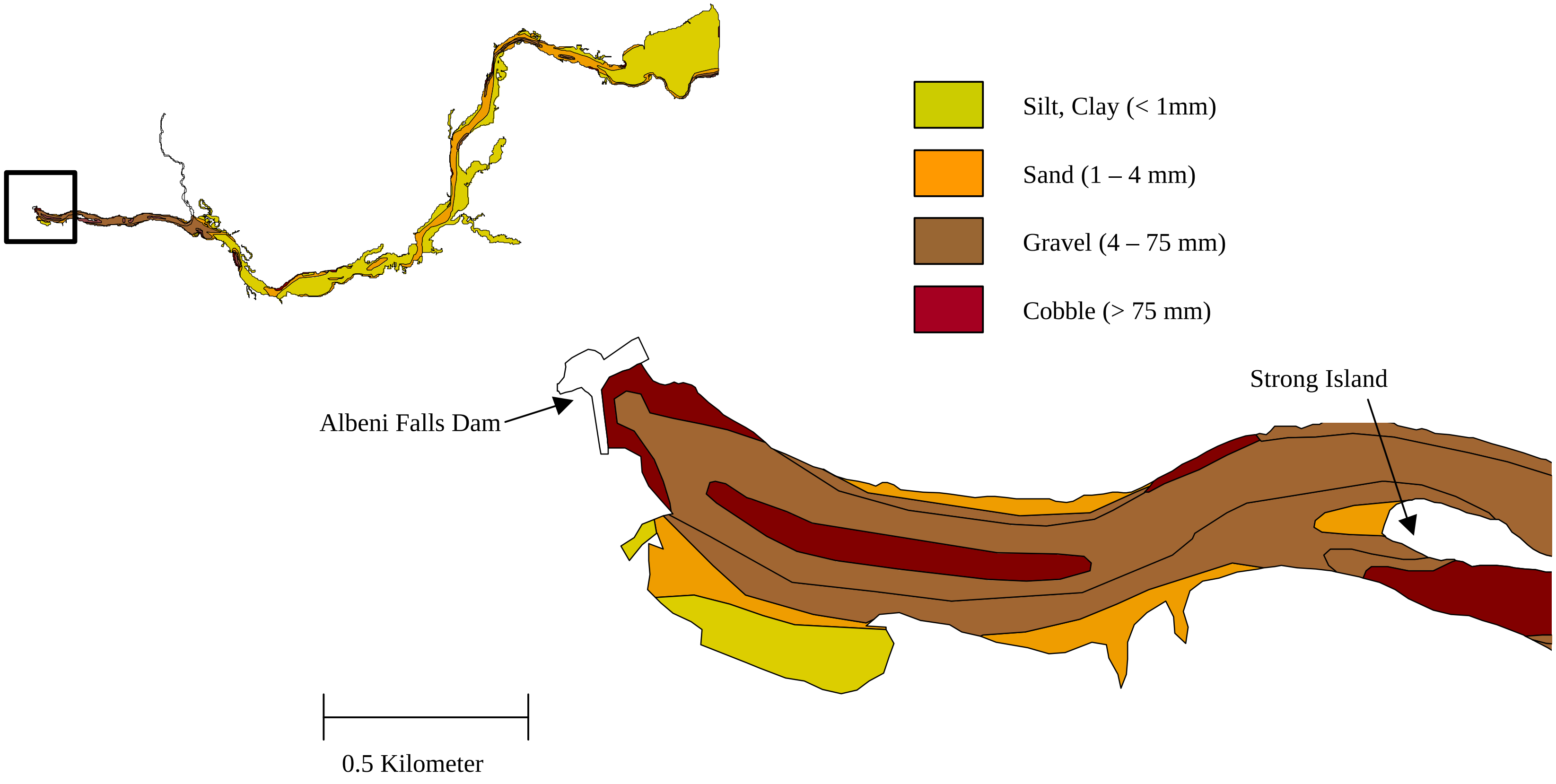


Figure 10.-Substrate composition grid of the outlet arm of Lake Pend Oreille, Idaho. Substrate size classes ranged from clay to boulder-sized substrates (Dupont 1994).

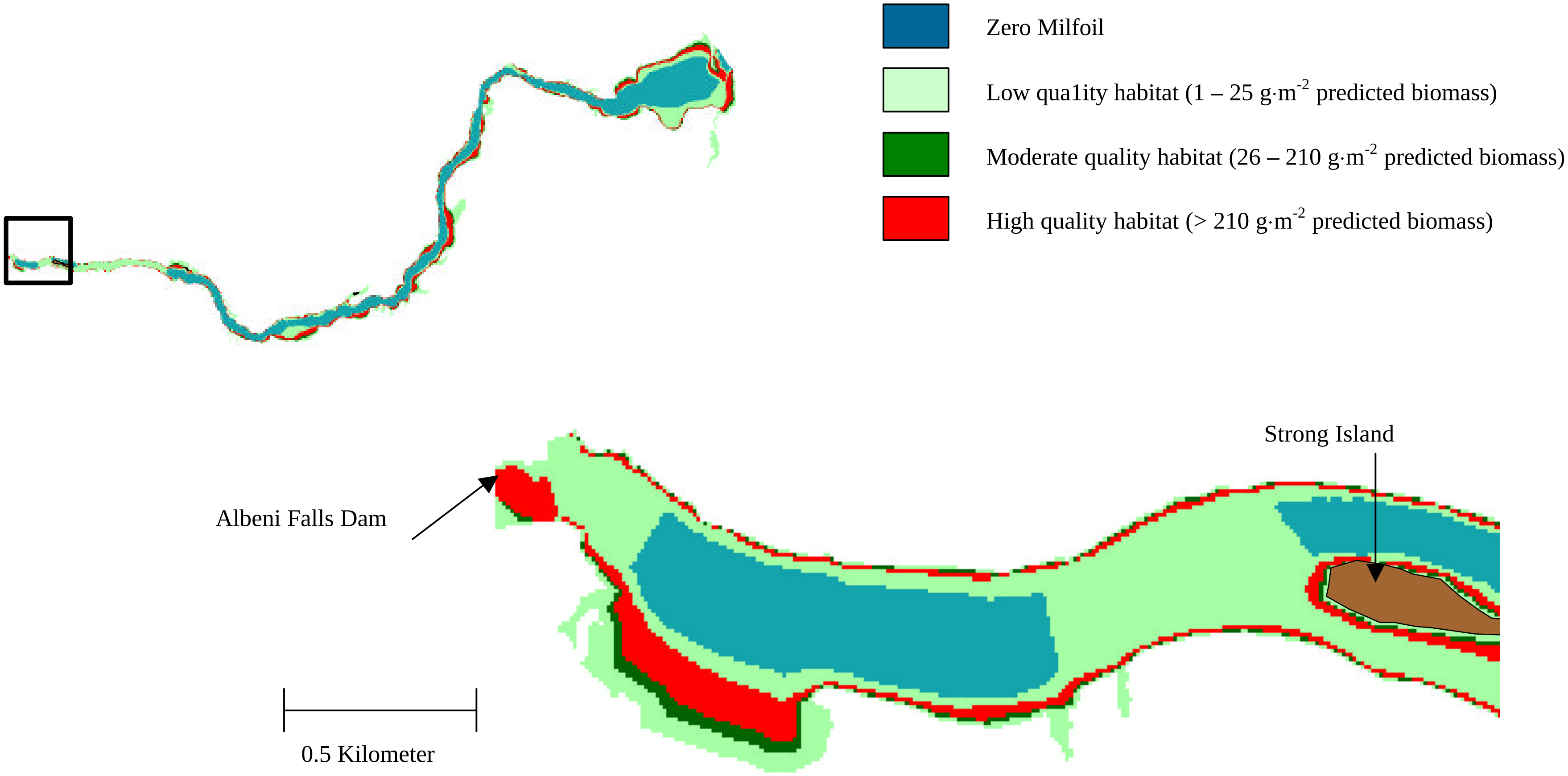


Figure 11.-Predicted milfoil densities based on the depth-density relationship in the outlet arm of Lake Pend Oreille, Idaho, 1999.

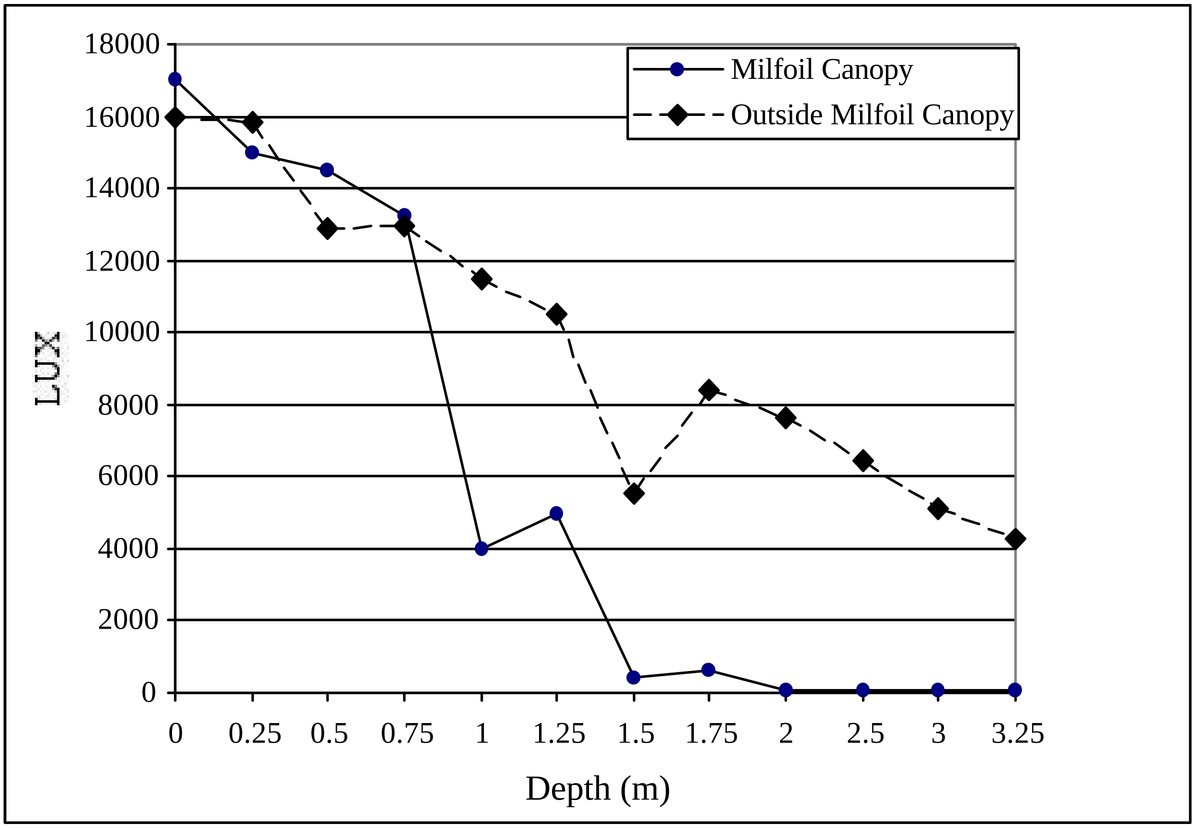


Figure 12.-Light profiles of Eurasian watermilfoil bed (maximum densty of 905.3 g·m^{-2}) compared to open water adjacent to the milfoil bed in Albeni Cove, outlet arm of Lake Pend Oreille, Idaho, 1999.

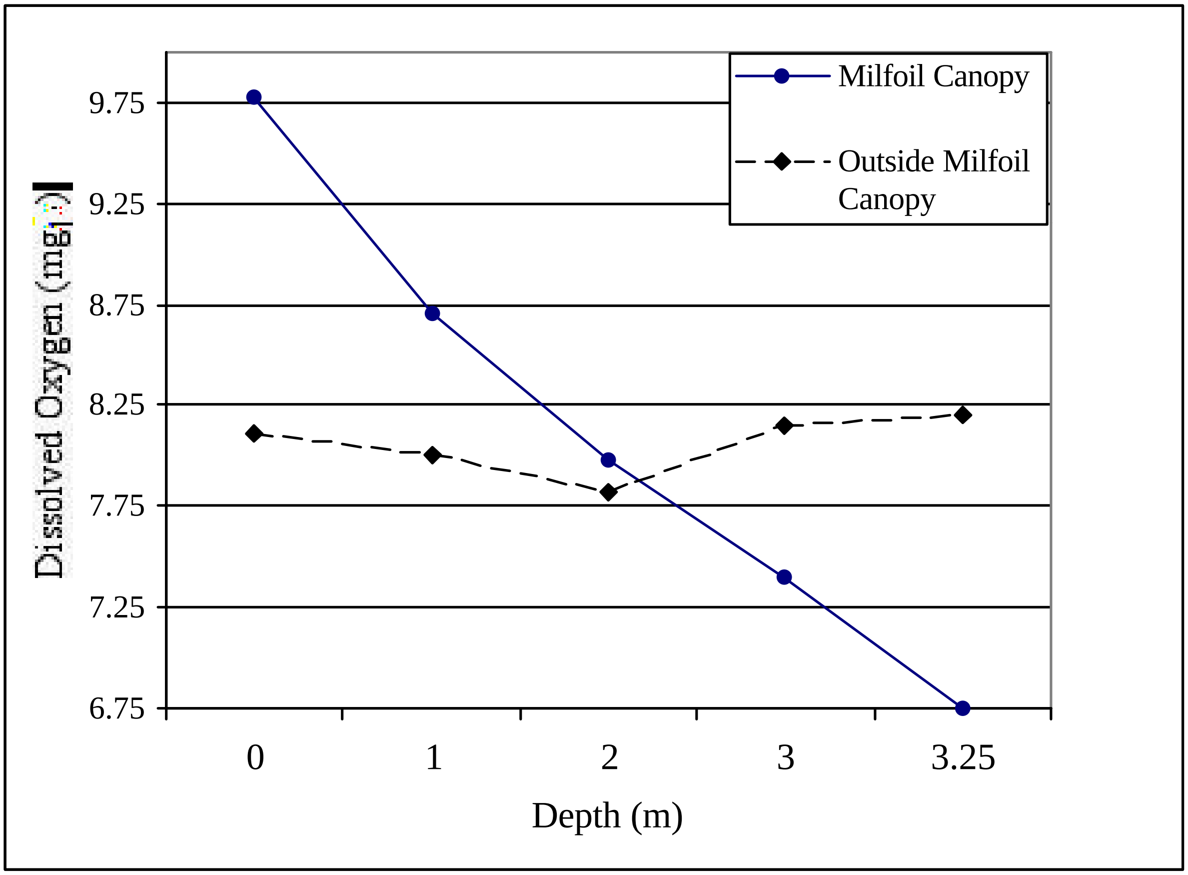


Figure 13.-Dissolved oxygen profiles of of Eurasian watermilfoil bed (maximum densty of 905.3 g·m^{-2}) compared to open water adjacent to the milfoil bed in Albeni Cove, outlet arm of Lake Pend Oreille, Idaho, 1999.

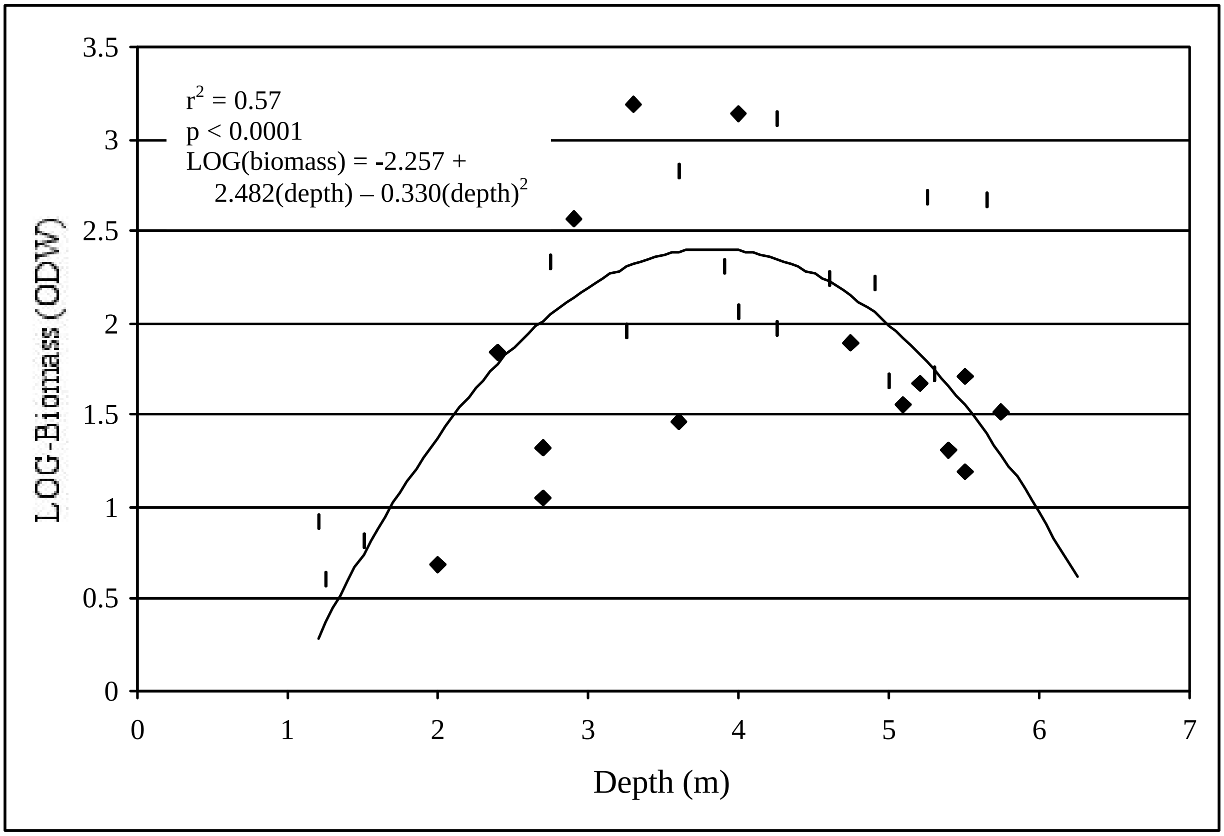


Figure.-14. Log Eurasian watermilfoil biomass (oven dry weight, g·m^{-2}) in relation to depth (m) in Albeni Cove, outlet arm of Lake Pend Oreille, Idaho.

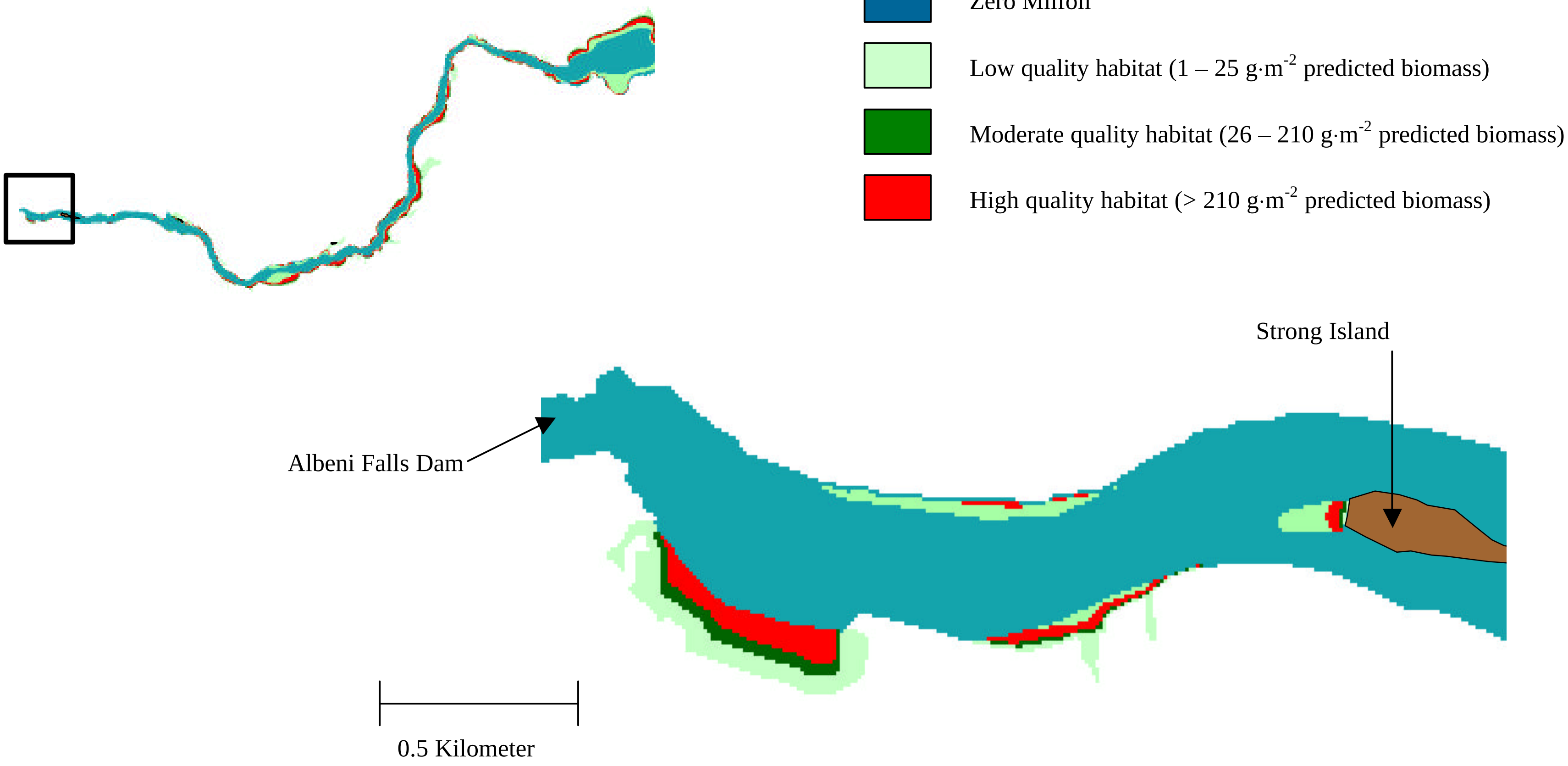
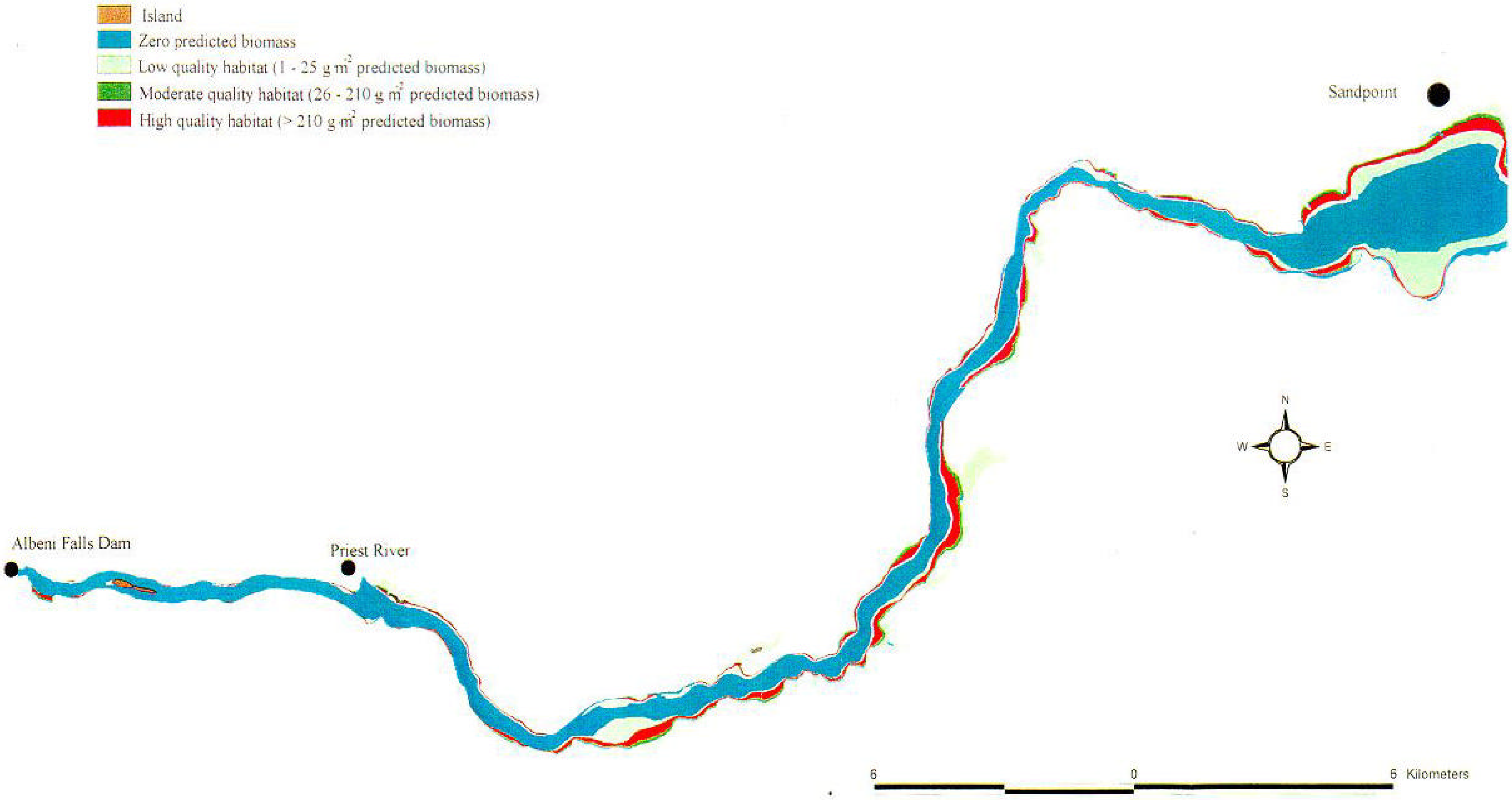


Figure 15.-Predicted densities of Eurasian watermilfoil based on depth and substrate type in the outlet arm of Lake Pend Oreille, Idaho, 1999.


Island
Zero predicted biomass
Low quality habitat (1 - 25 g m^{-2} predicted biomass)
Moderate quality habitat (26 - 210 g m^{-2} predicted biomass)
High quality habitat (> 210 g m^{-2} predicted biomass)
Sandpoint
Albeni Falls Dam
Priest River
N
W
E
S
6
0
6 Kilometers

Tables

Table 7.- Water chemistry parameters measured from in a Eurasian watermilfoil bed and in open water adjacent to the milfoil bed in Albeni Cove on the outlet arm of Lake Pend Oreille, Idaho, 1999.

	Temperature (°C)	Electrical Conductivity (μmhos)	Total Alkalinity (mg CaCO3·l^{-1})	pH
Within milfoil bed	19.8	147.0	73.0	7.3
Open water	20.5	173.3	72.0	7.5

The Fish Community in the Pend Oreille River, Idaho:

Response to Higher Winter Water Levels

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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 Oncorhynchus nerka 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^{o} 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 (χ^2 = 271.94, $P < 0.001$) and 2000 (χ^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 °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 °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 ^{o}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 ^{o} 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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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.

		Stratum 1				Stratum 2				Stratum 3				Total			
	Tropic	Before		After		Before		After		Before		After		Before		After	
Species	group[a]	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

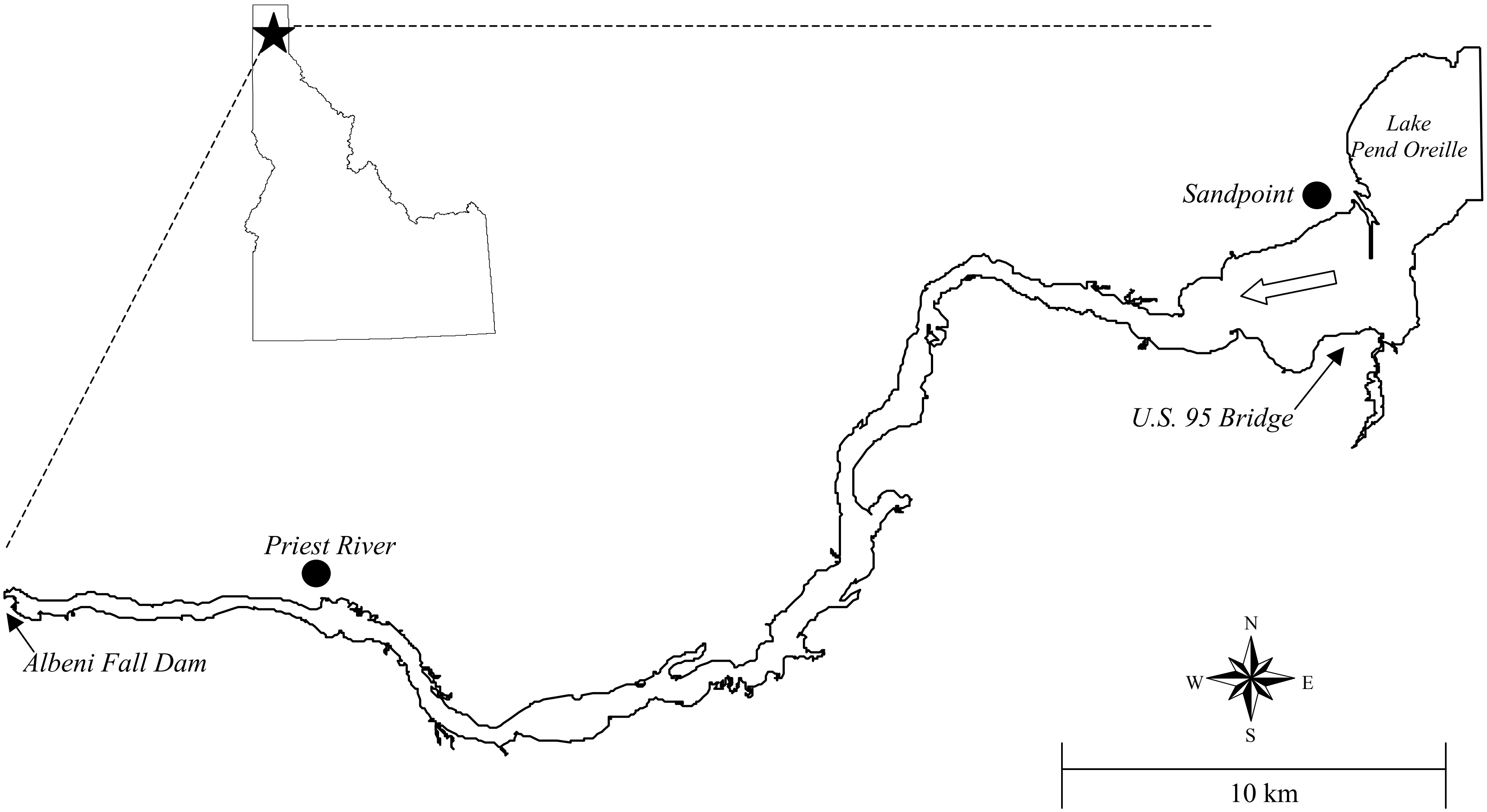


Figure 1. — Study area on the Pend Oreille River, Idaho.

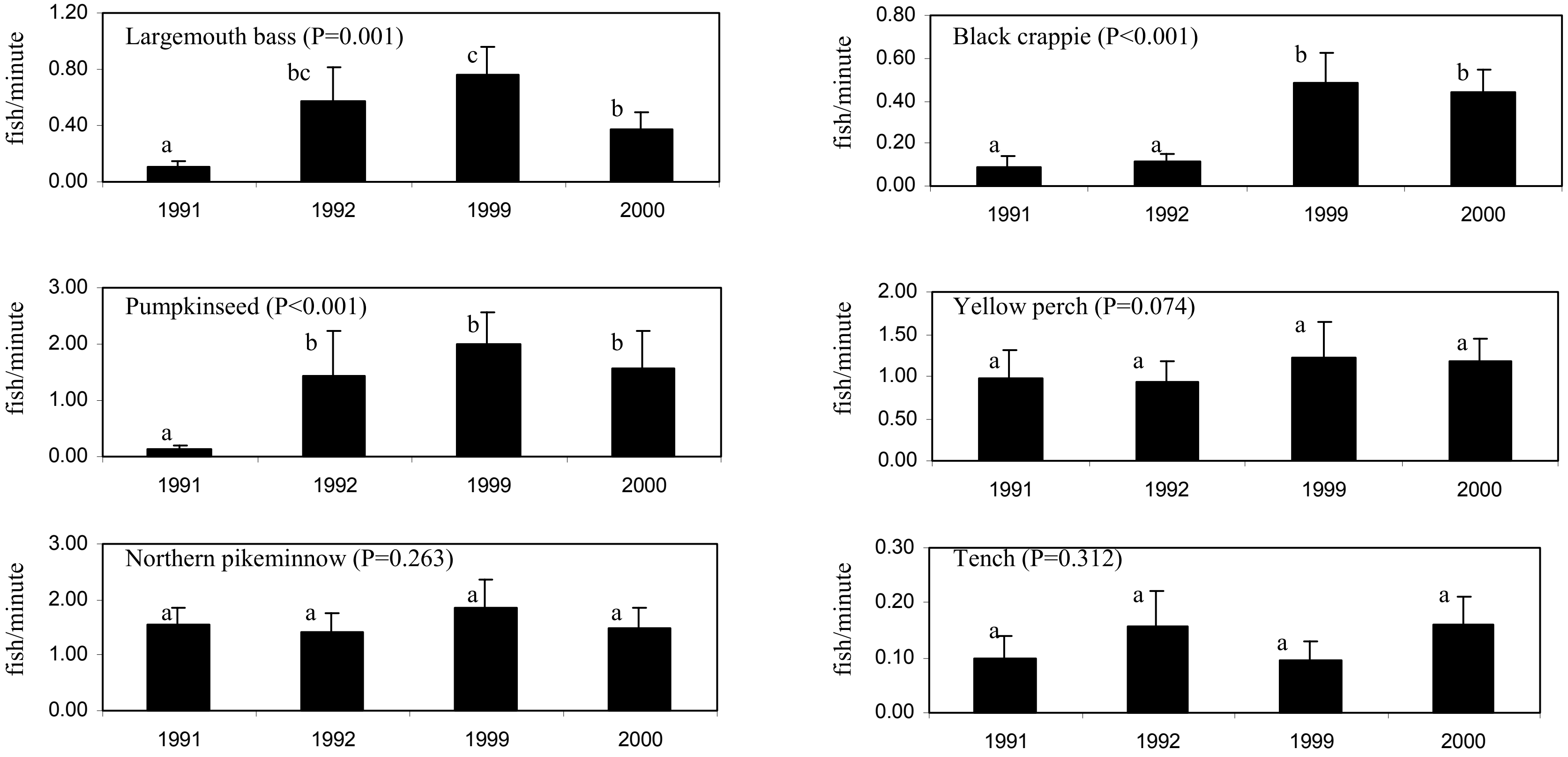


Figure 2. — Catch rates of fishes sampled by electrofishing from the Pend Oreille River before (1991-1992) and after (1999-2000) three years of higher winter water levels. Age-0 fish were not included in the analysis. Error bars represent standard error of mean CPUE. Significant differences ($P < 0.05$) are indicated by alphabetic superscript.

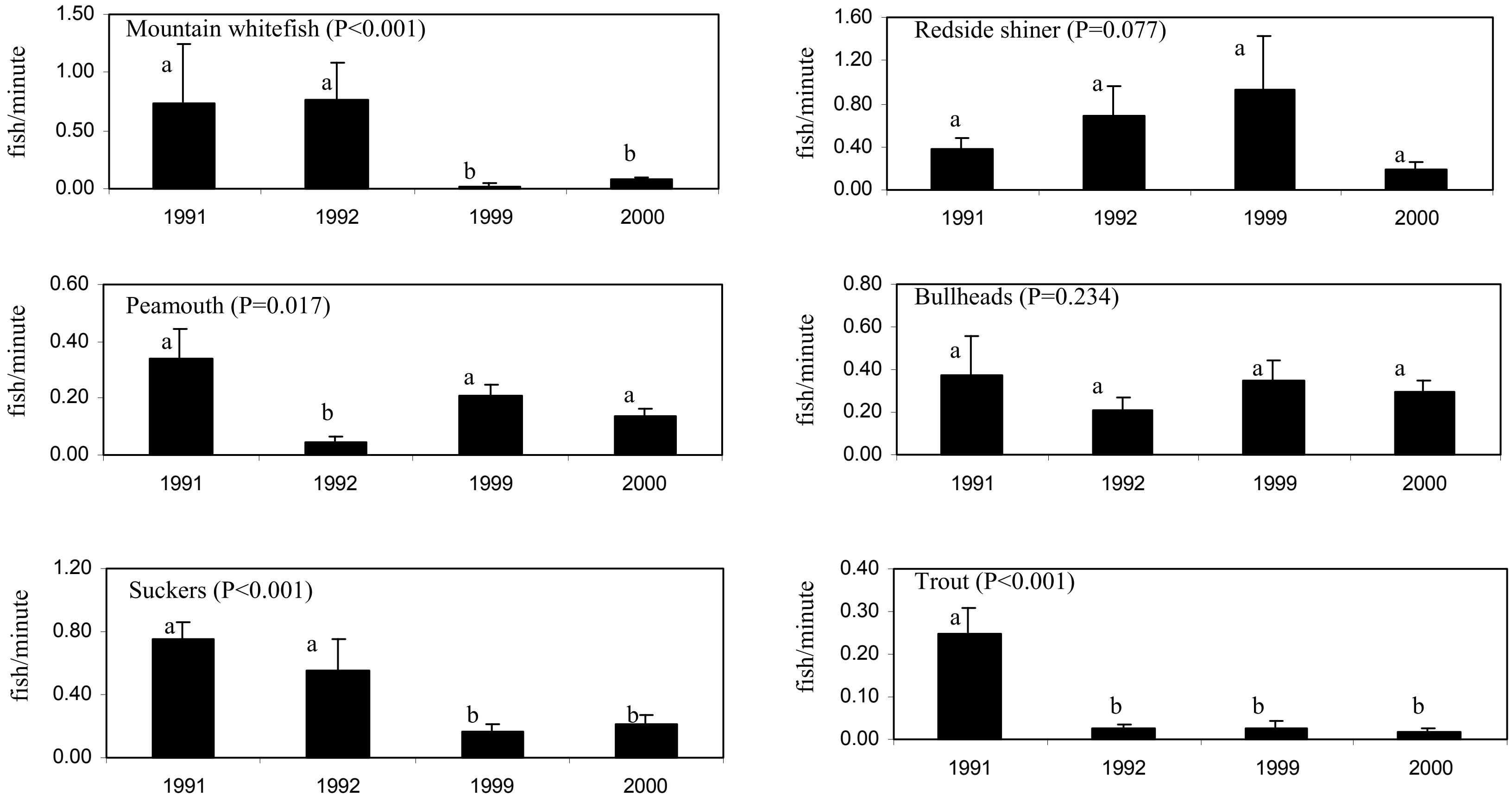


Figure 3. — Catch rates of fishes sampled by electrofishing from the Pend Oreille River before (1991-1992) and after (1999-2000) three years of higher winter water levels. Age-0 fish were not included in the analysis. Error bars represent standard error of mean CPUE. Significant differences ($P < 0.05$) are indicated by alphabetic superscript.

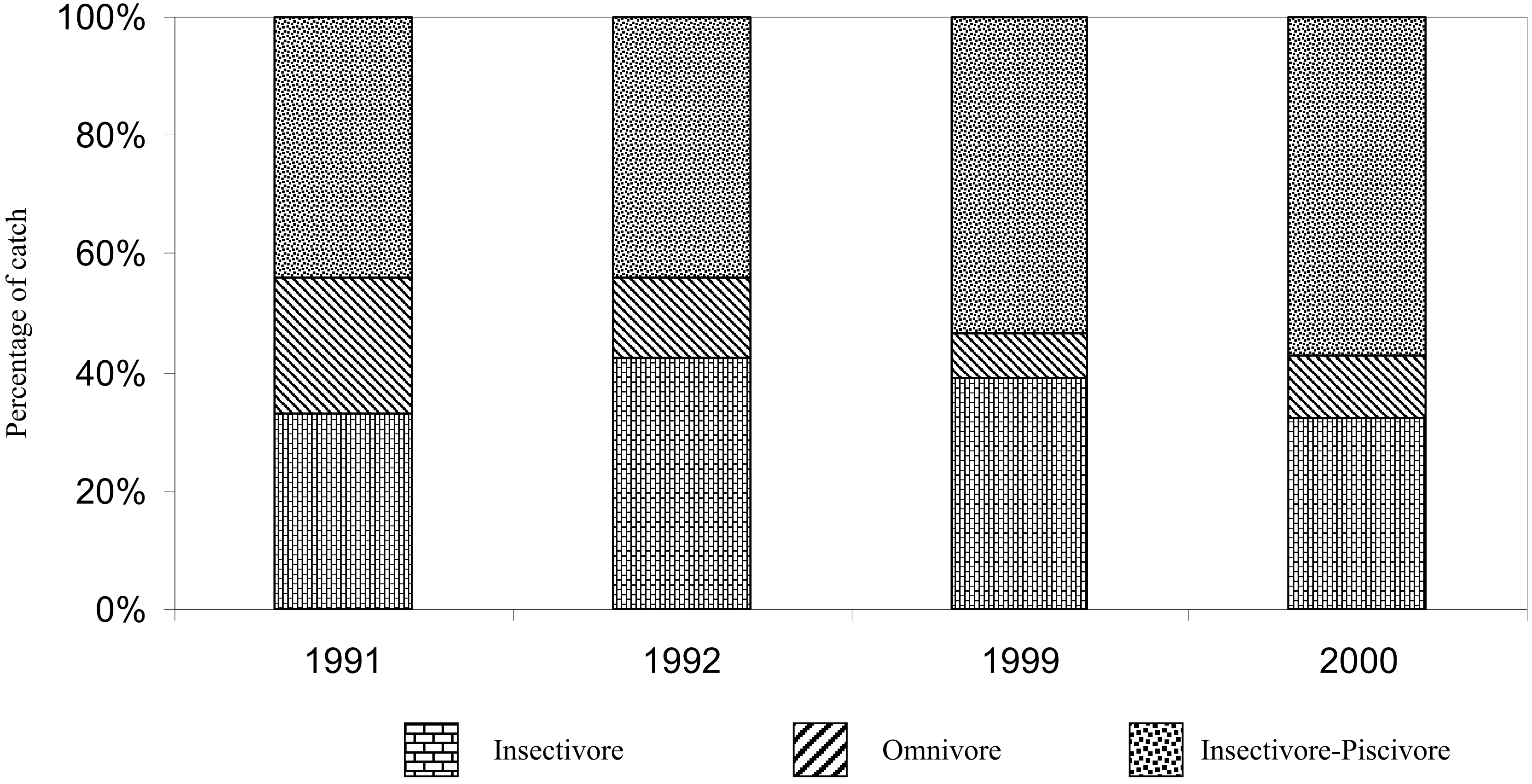


Figure 4 — Percent composition of trophic groups collected in the Pend Oreille River, Idaho before (1991-1992) and after (1999-2000) three years of experimental drawdown.

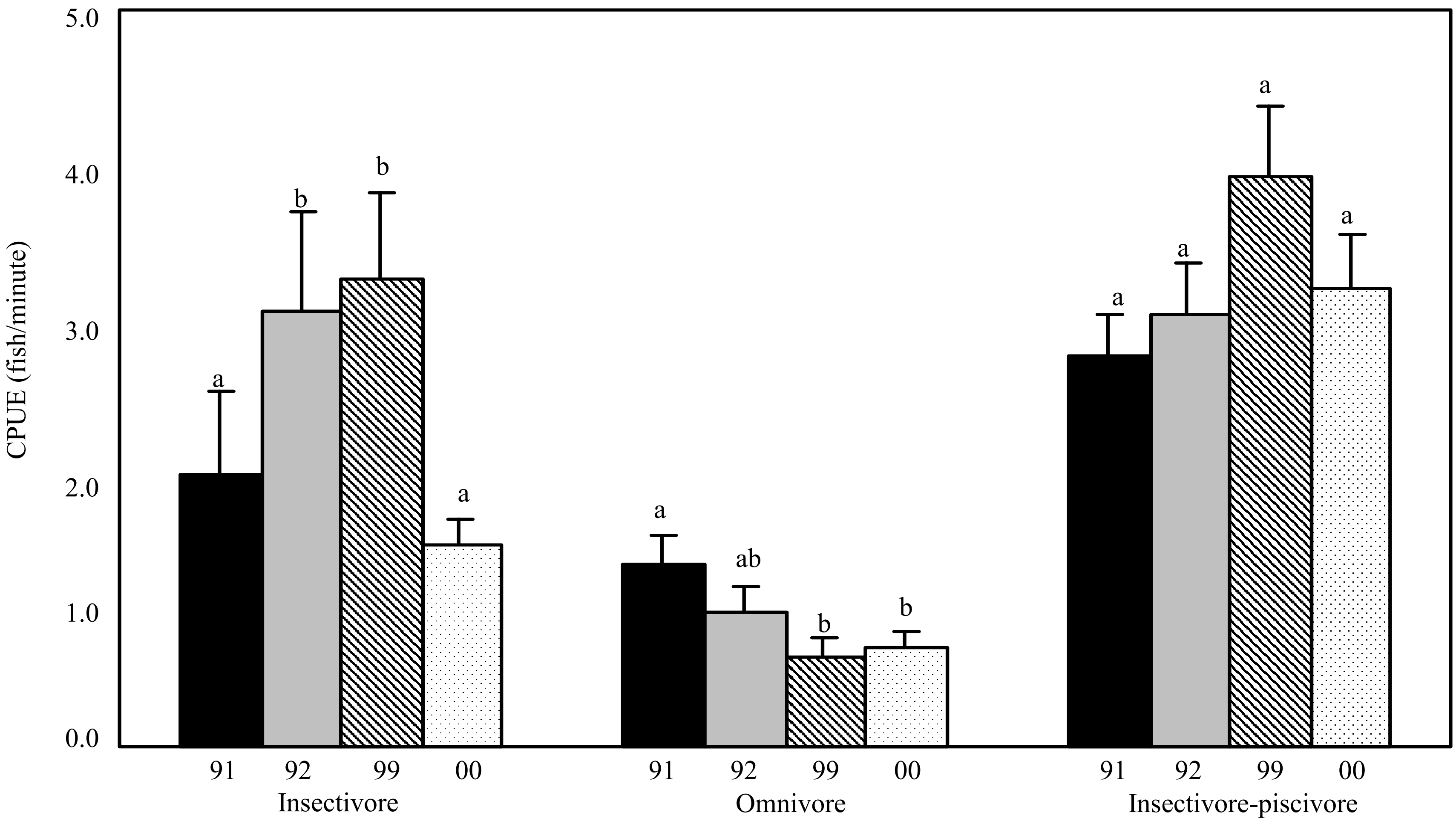
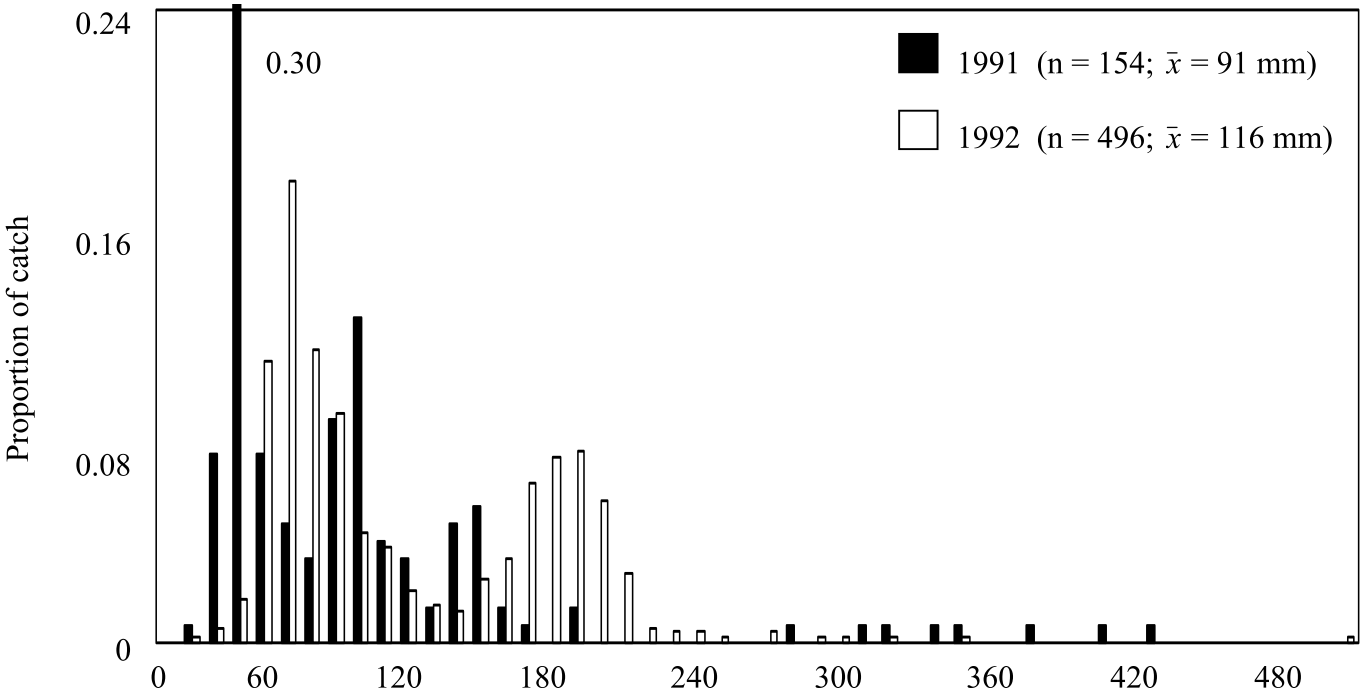


Figure 4a — CPUE of trophic groups (insectivores, omnivores and insectivores-picivores) collected from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of experimental drawdown. Error bar represent standard error of mean CPUE. Significant differences ($P<0.05$) are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



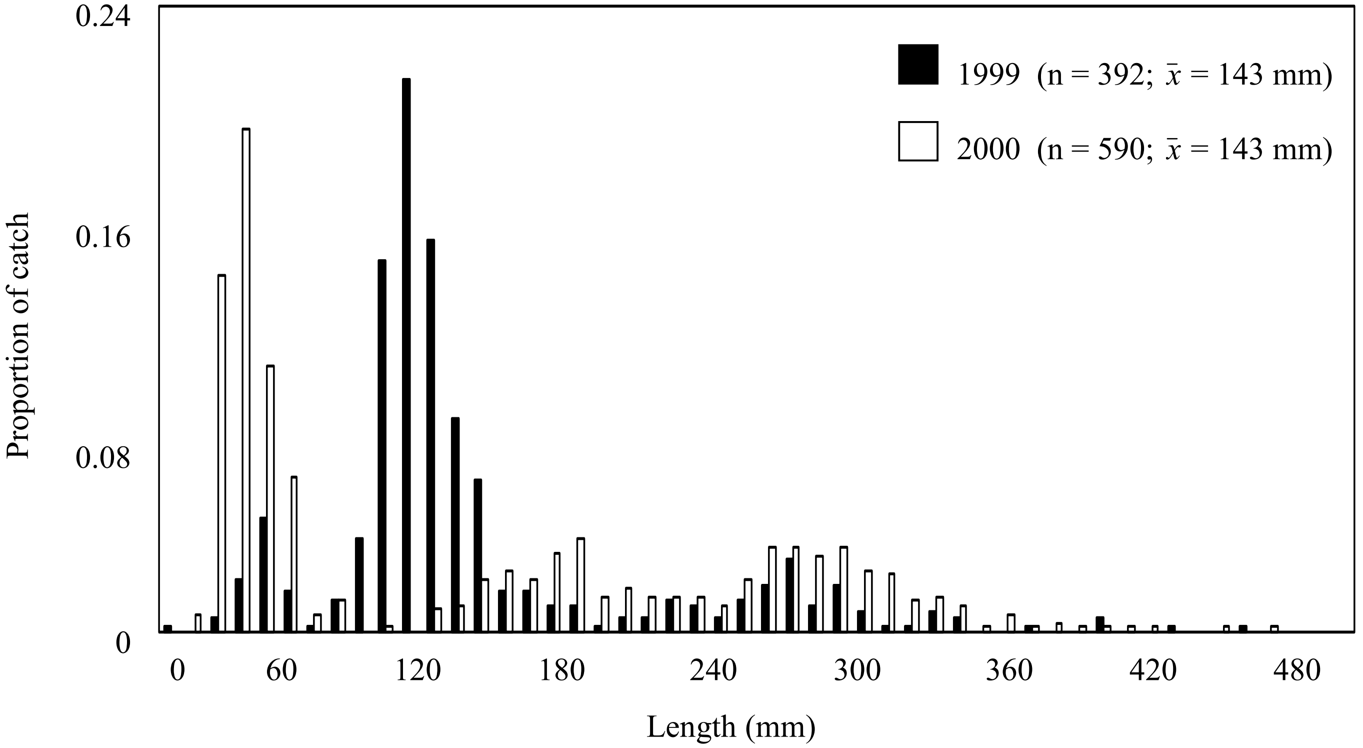


Figure 5. — Length frequencies of largemouth bass collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.

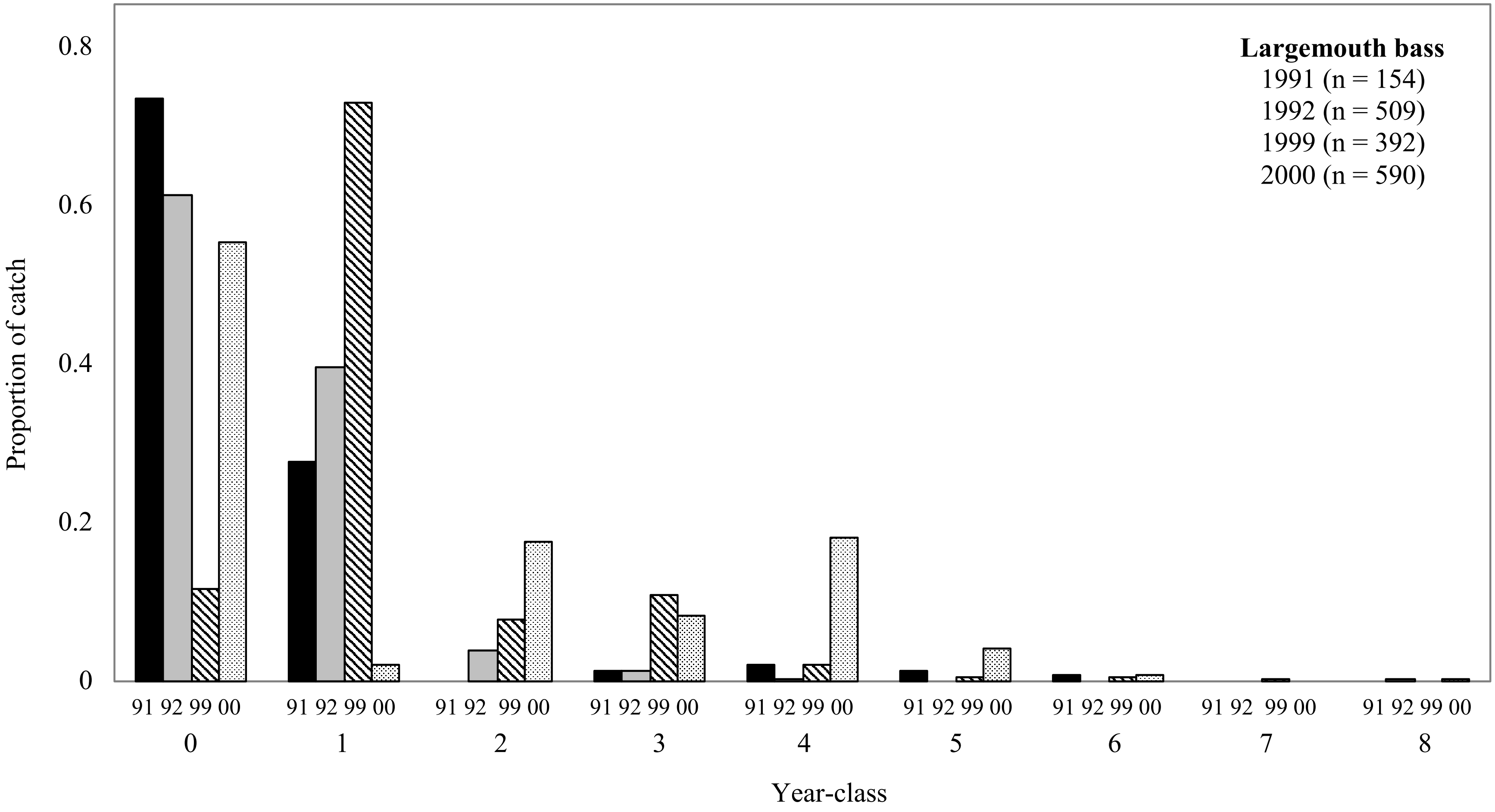


Figure 6. — Age structure of largemouth bass collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.

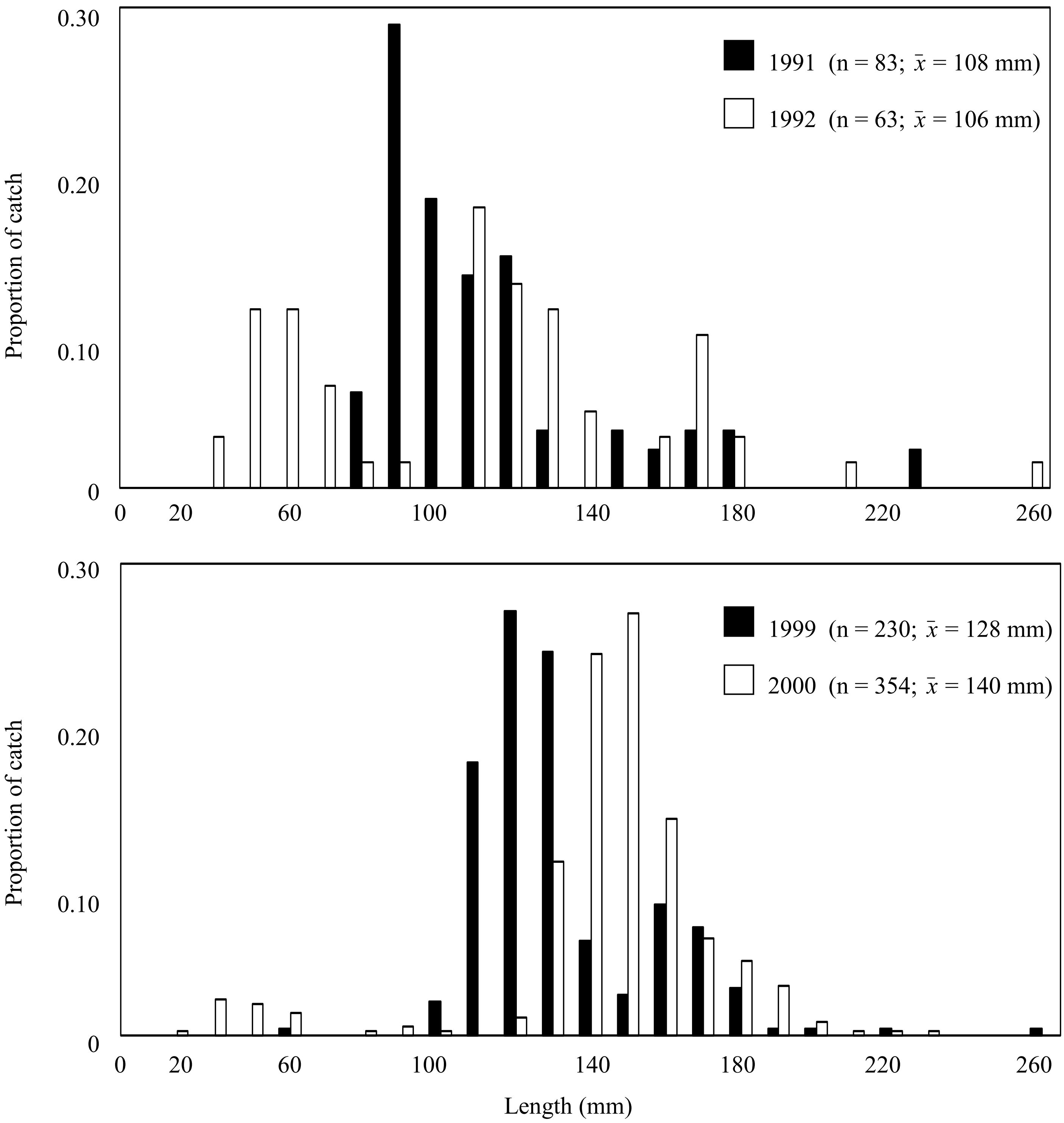


Figure 7. — Length frequencies of black crappie collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.

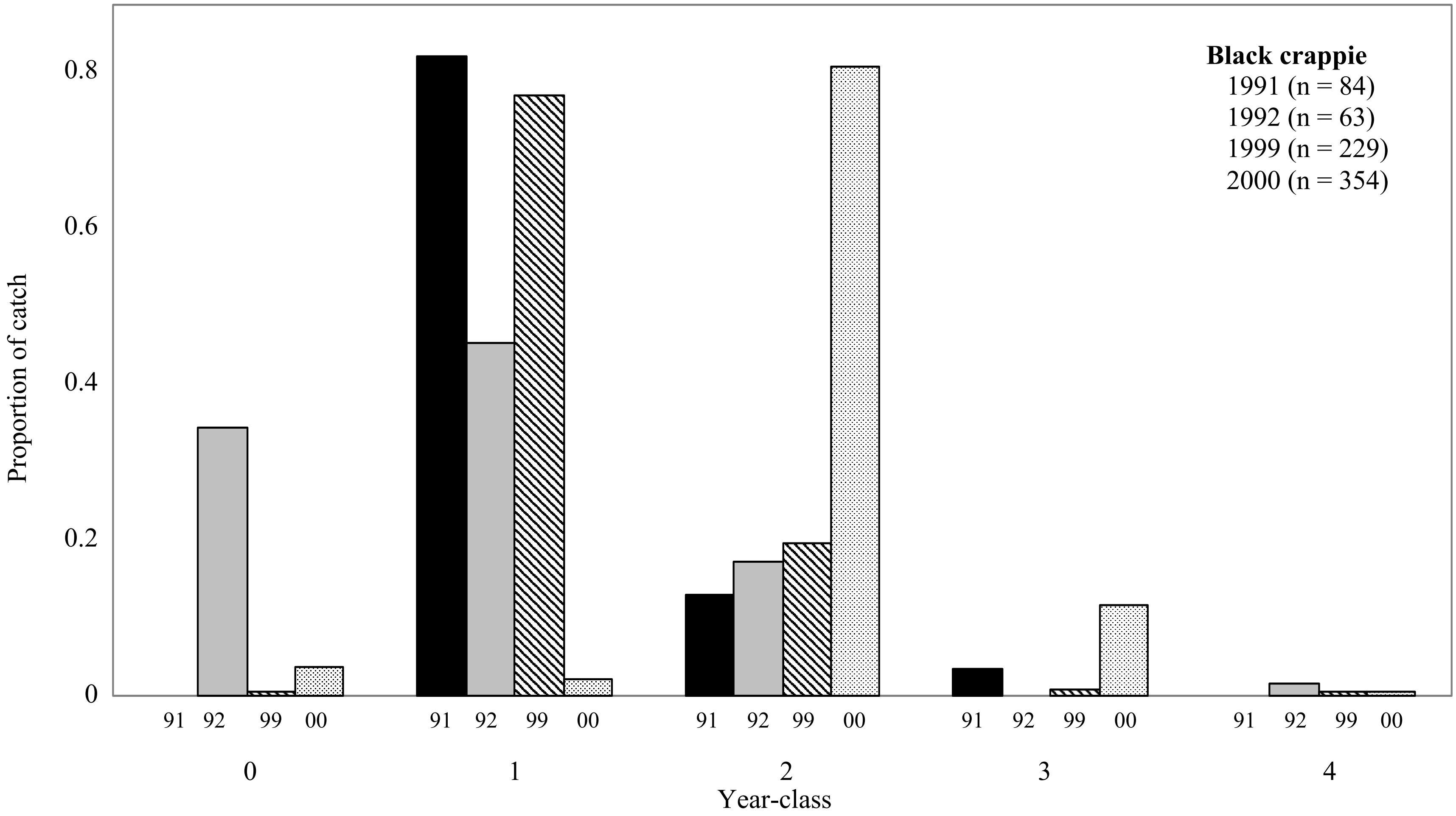


Figure 8. — Age structure of black crappie collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.

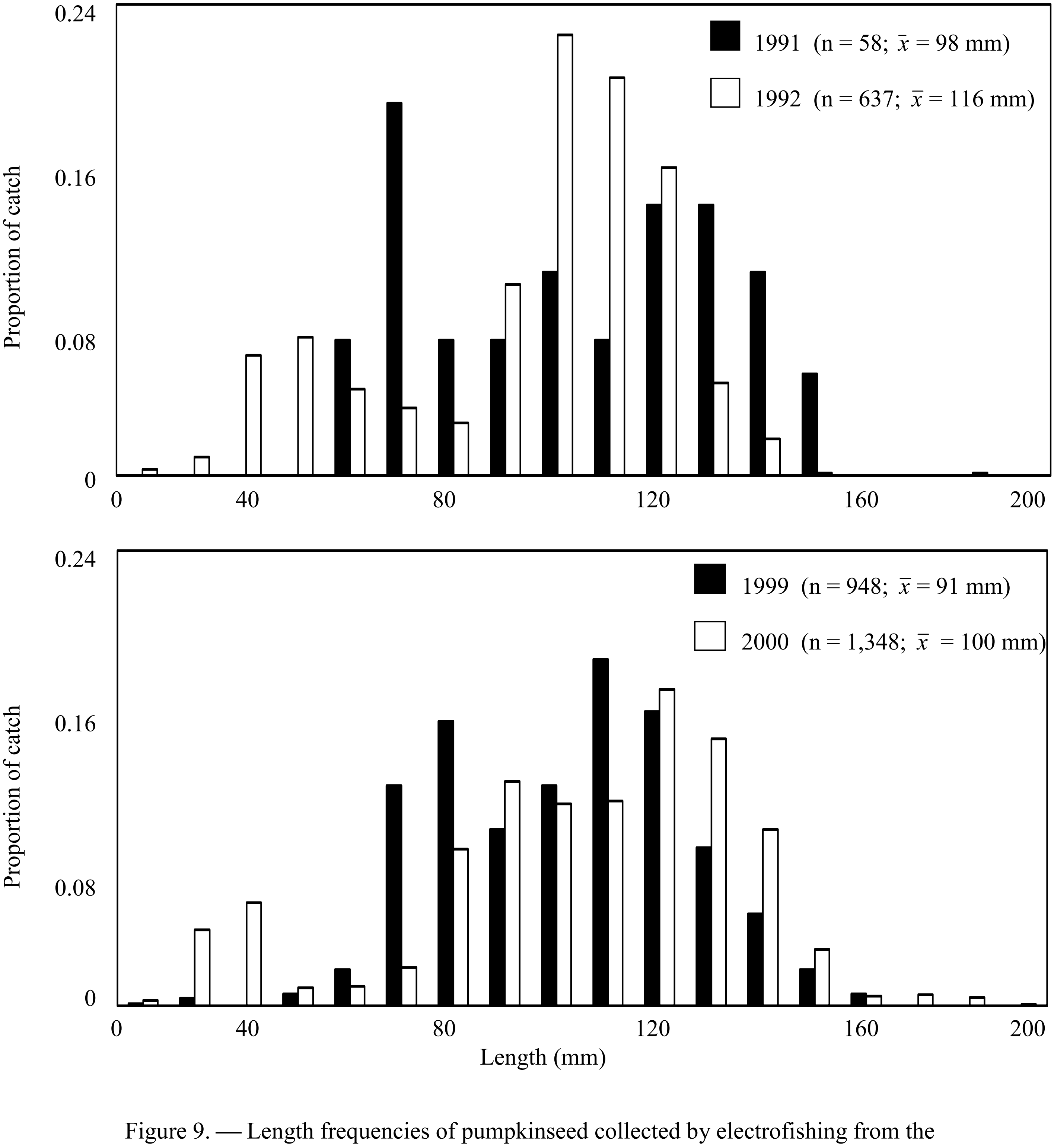


Figure 9. — Length frequencies of pumpkinseed collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.

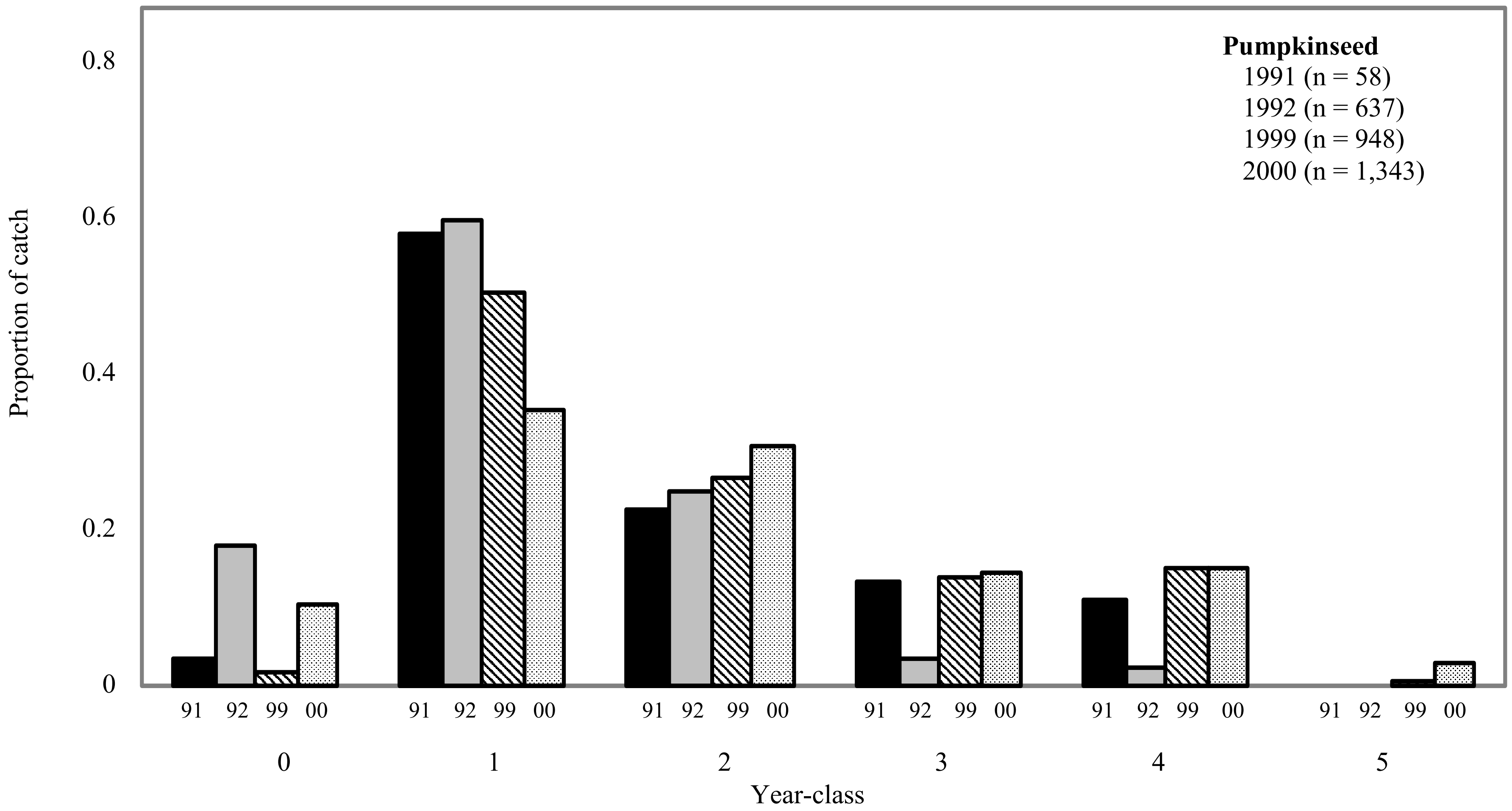


Figure 10. — Age structure of pumpkinseed collected by electrofishing from the Pend Oreille River, Idaho before (1991 - 1992) and after (1999 - 2000) three years of higher winter water levels.

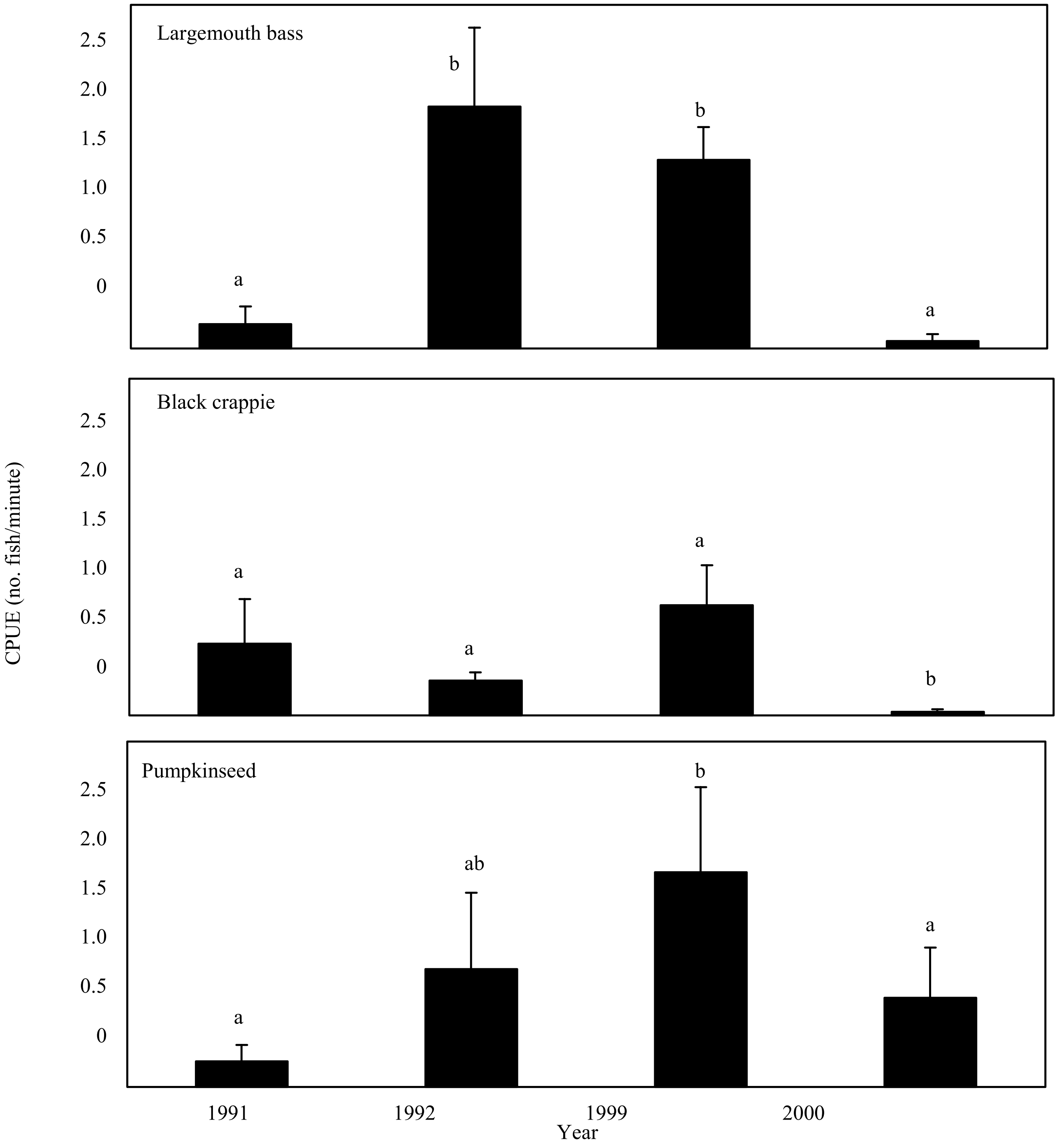


Figure 11. CPUE of age-1 largemouth bass, black crappie, and pumpkinseed collected from in the Pend Oreille River, Idaho, in 1991, 1992, 1999 and 2000. Error bars represent standard error. Significant differences ($P<0.05$) are indicated by alphabetic superscripts.

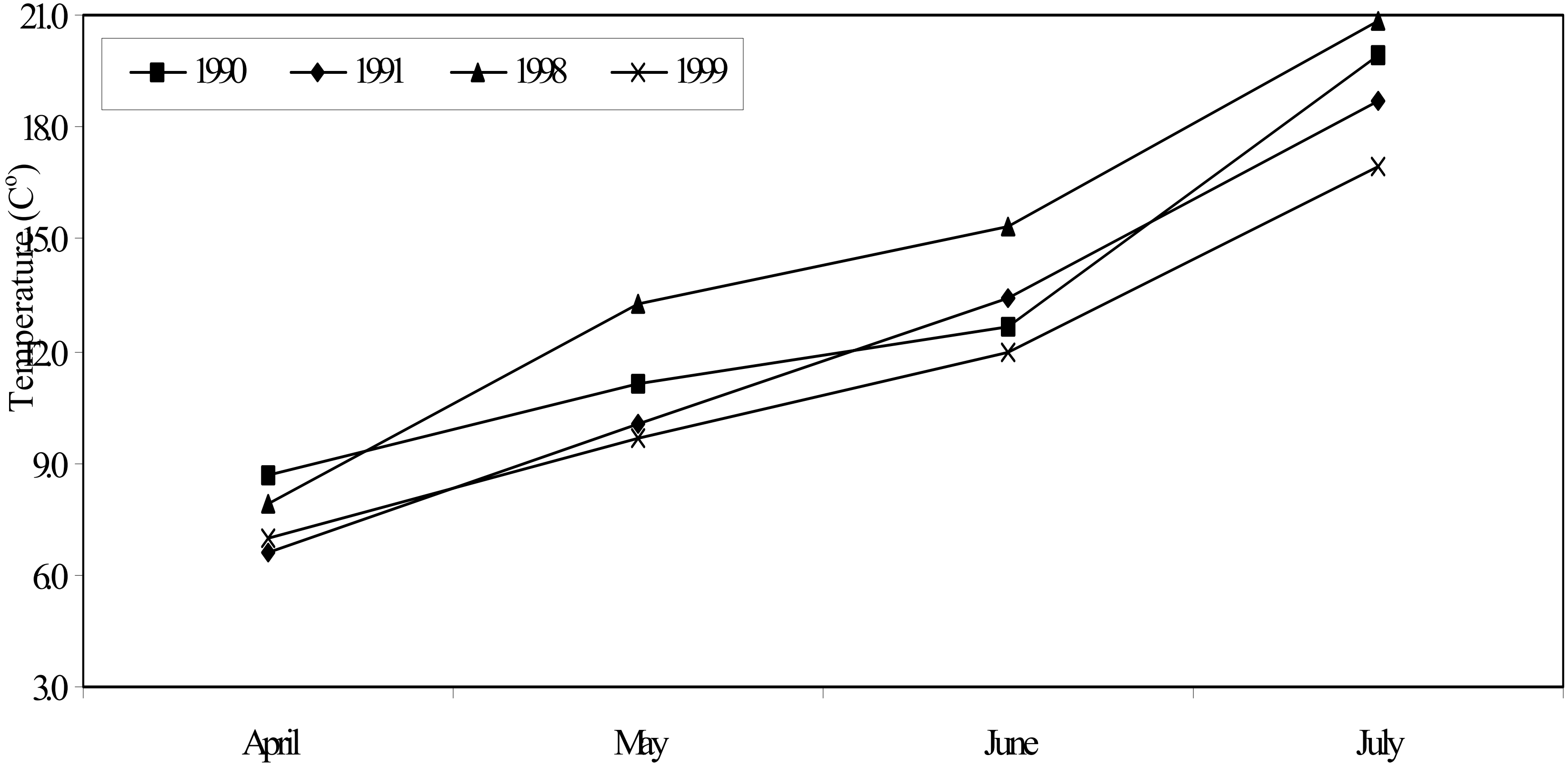


Figure 12.— Mean monthly temperatures during spring months associated with spawning activity and early juvenile development.

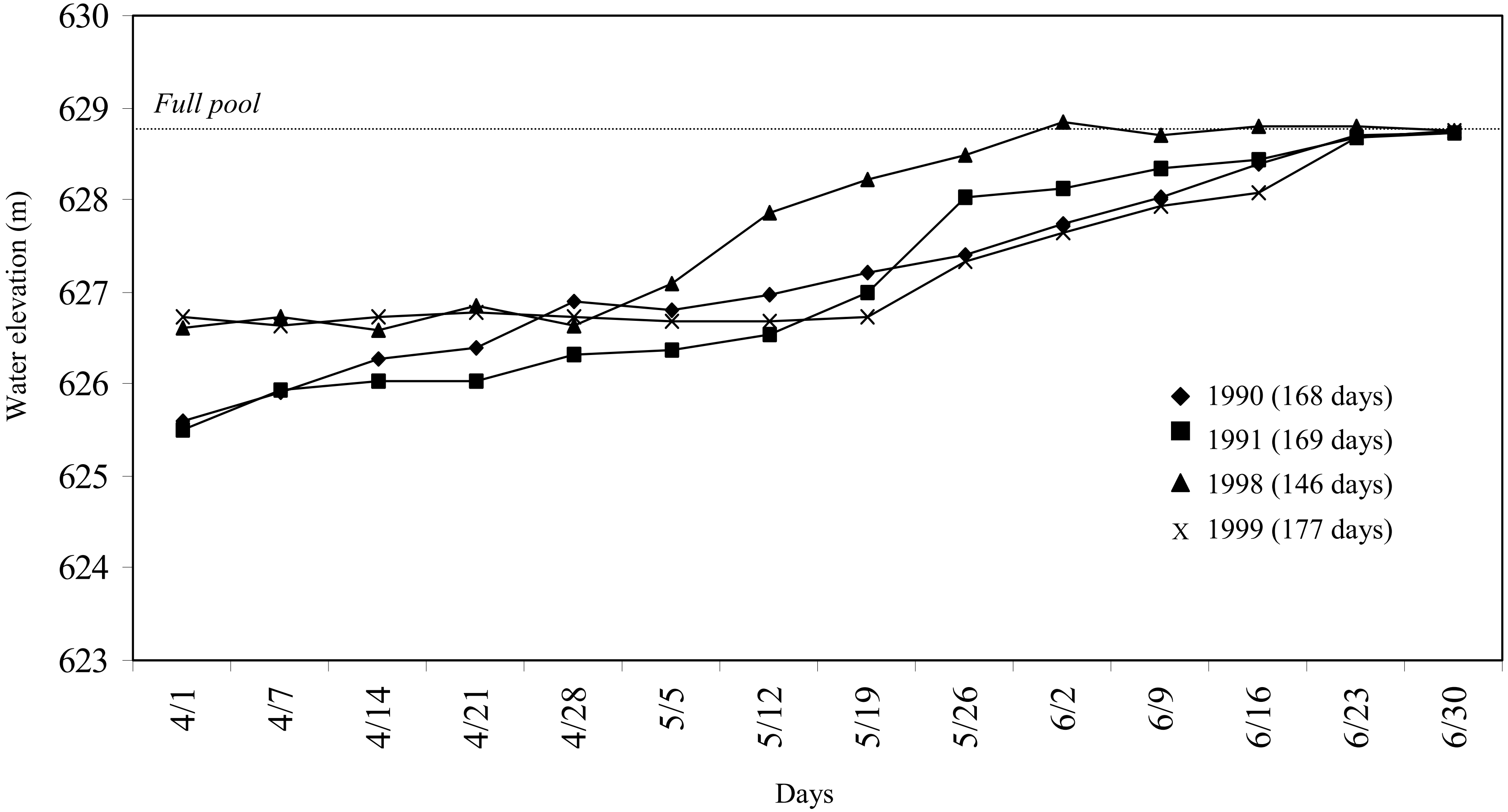


Figure 13.— Water level fluctuations during spawning and early juvenile development. Days refer to the number of days from January first to reach full pool.

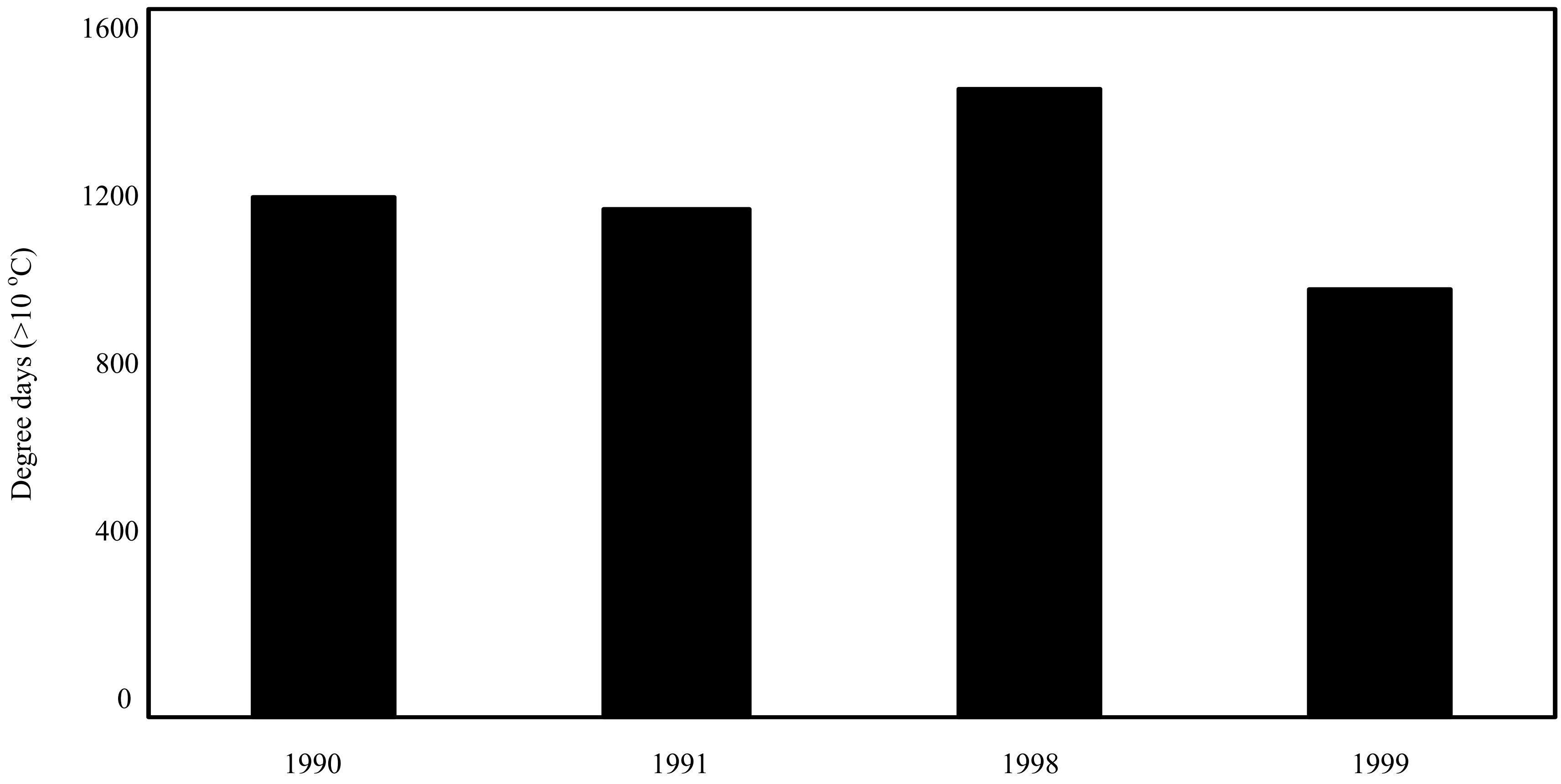


Figure 14.— Length of growing season (as determined by the number of degree-days > 10 °C) associated with the first year of life of age-1 fish.

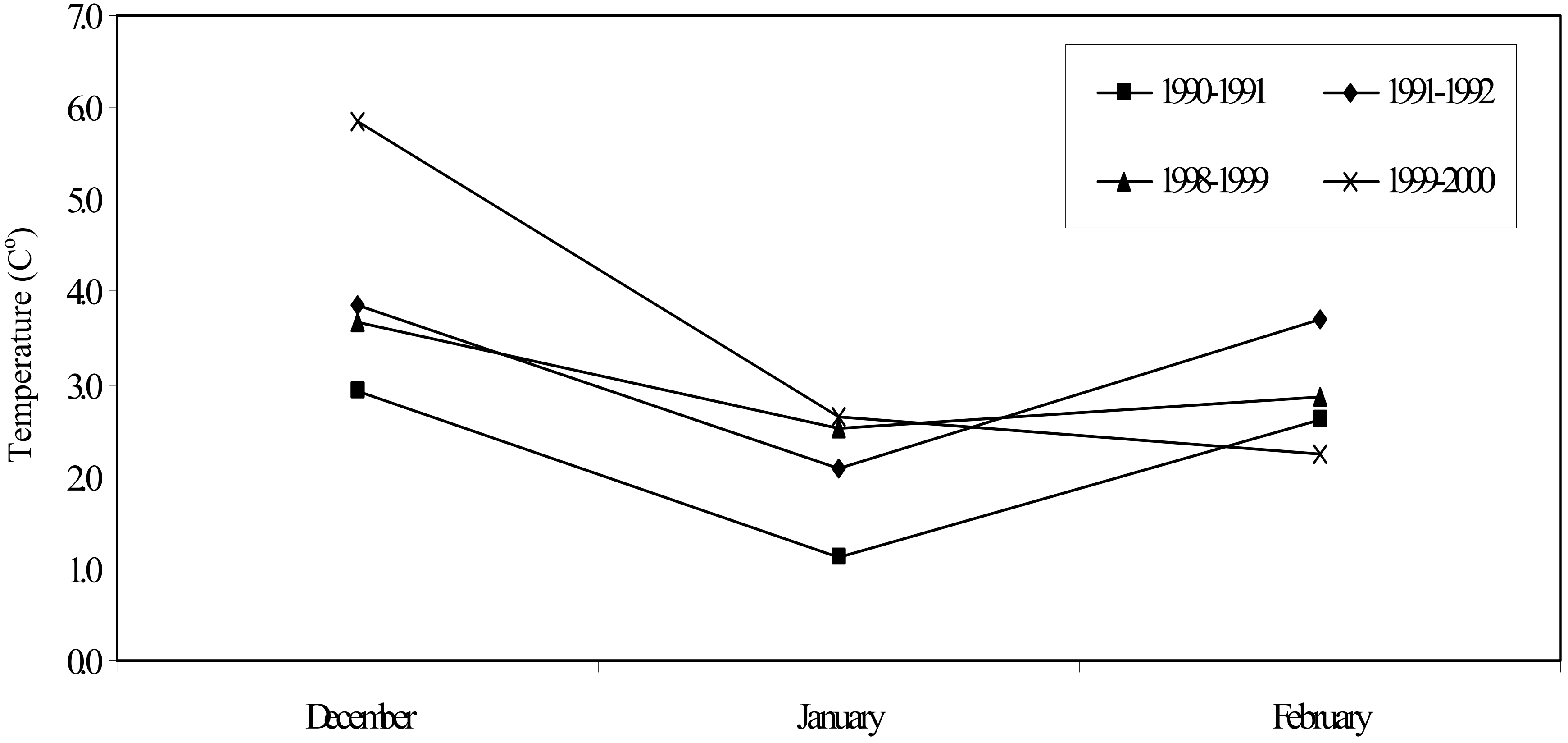


Figure 15.— Mean monthly temperatures during months associated with first over-winter.

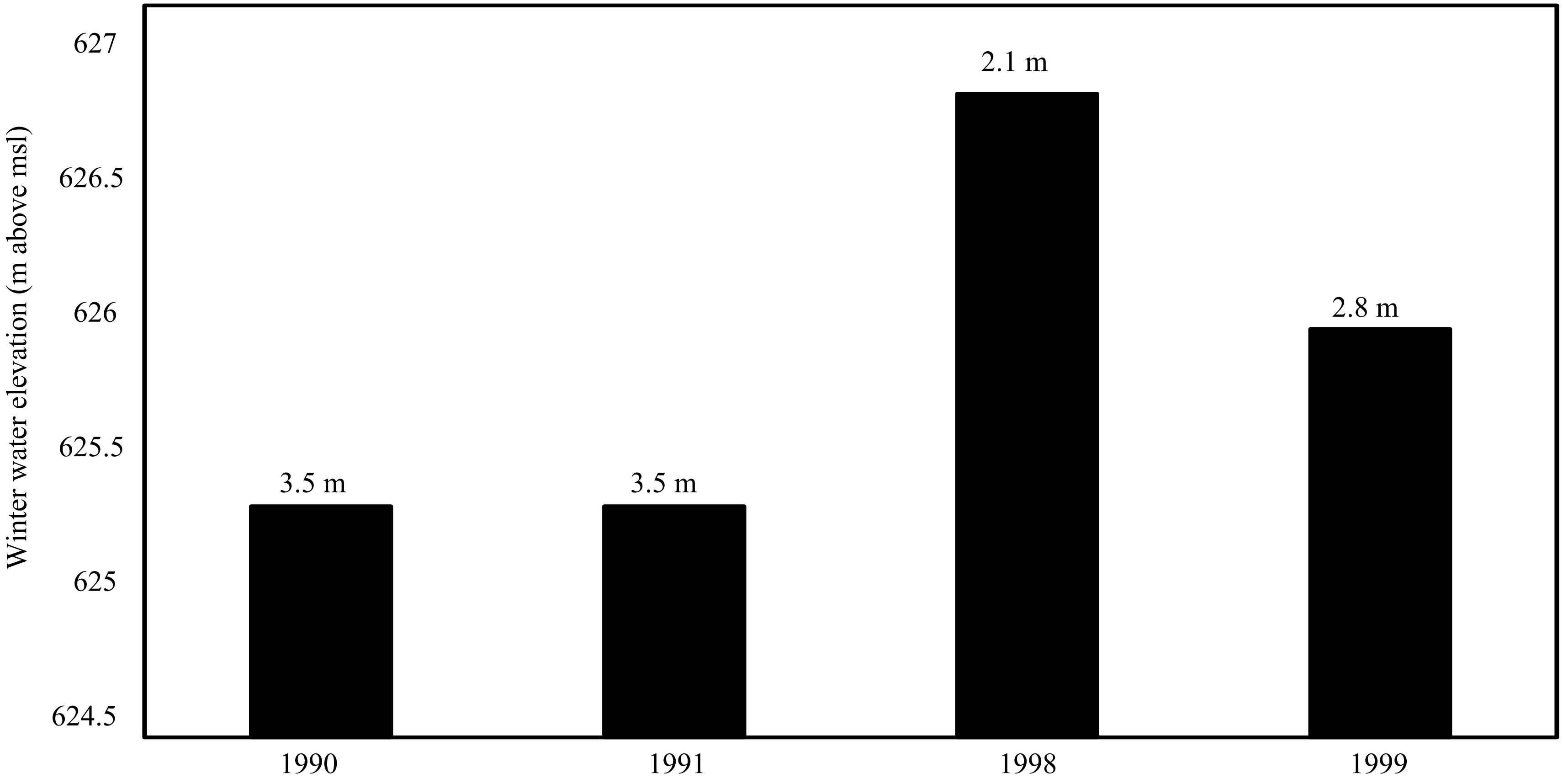


Figure 16.— Winter water elevation (m above msl) experienced with the first winter. Numbers indicate meters below full pool.

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 ^{o} 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 (^{o}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 ^{o} 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 °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 °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 °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

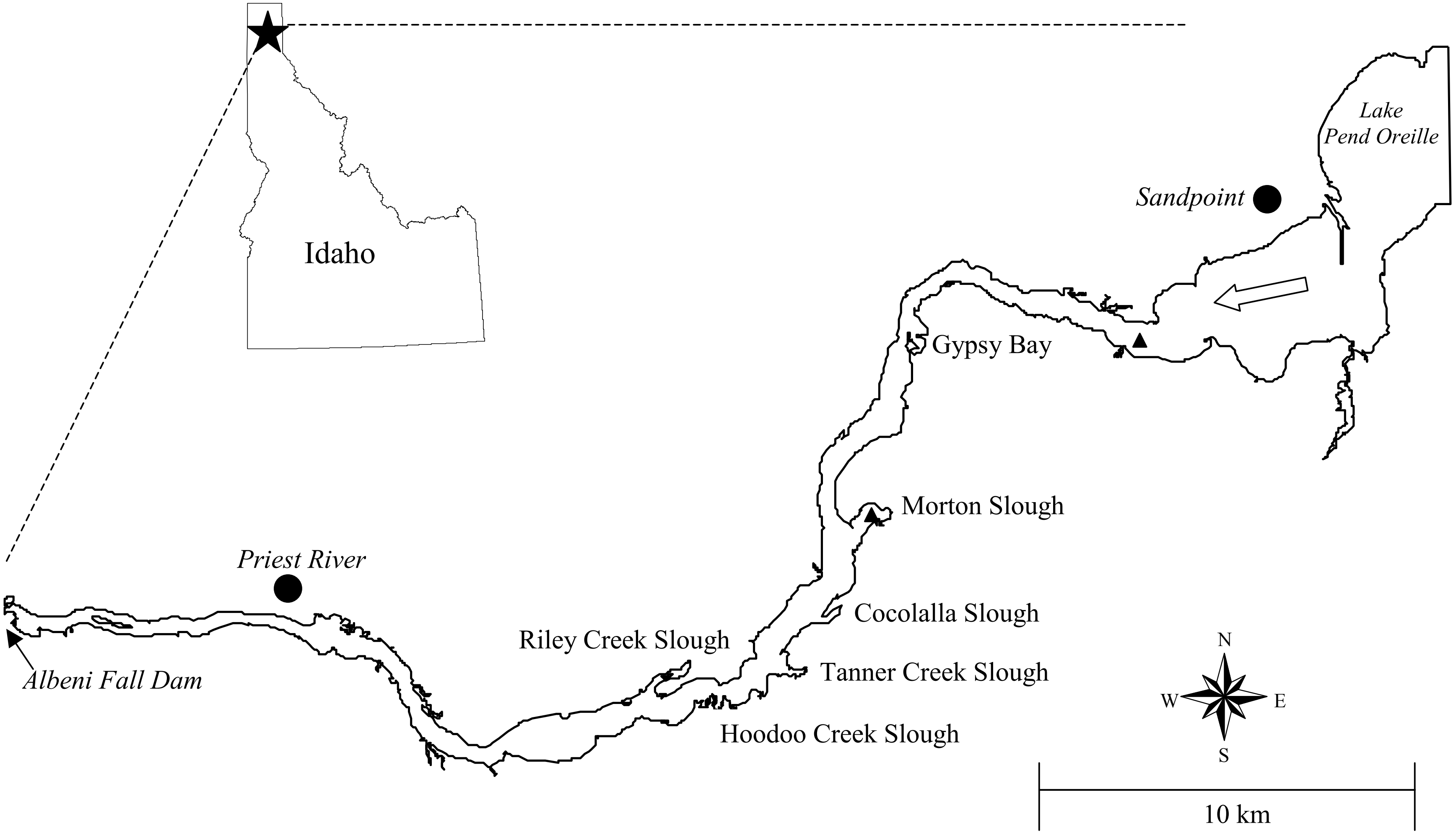

Figure 1. Study area map of the Pend Oreille River including the six primary backwater areas. Triangles (▲) show the locations of the 2 temperature recording stations.

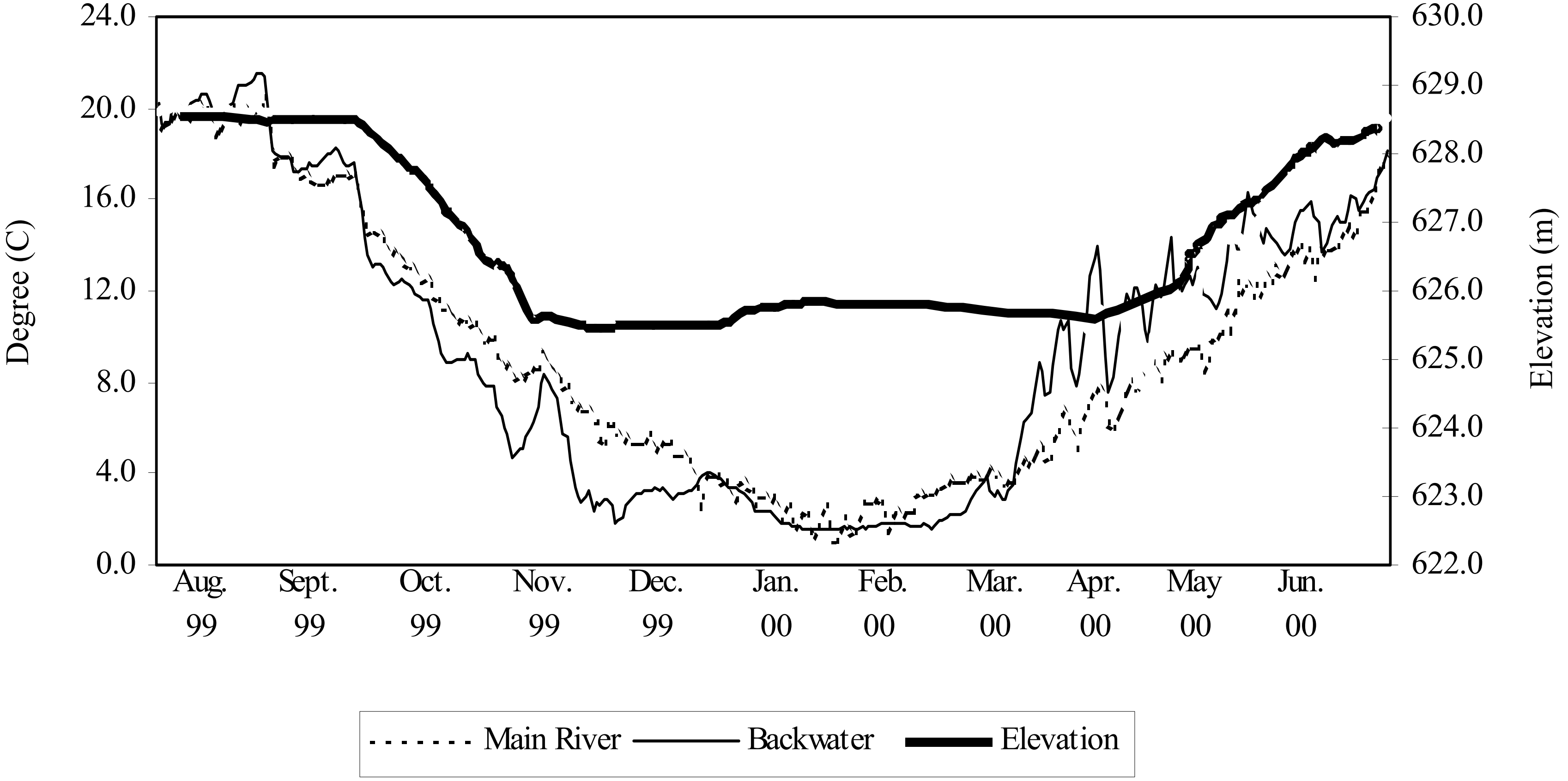

Figure 2. Mean daily water tempratures and water surface elevation from August 1999 to June 2000, in the Pend Oreille River, Idaho.

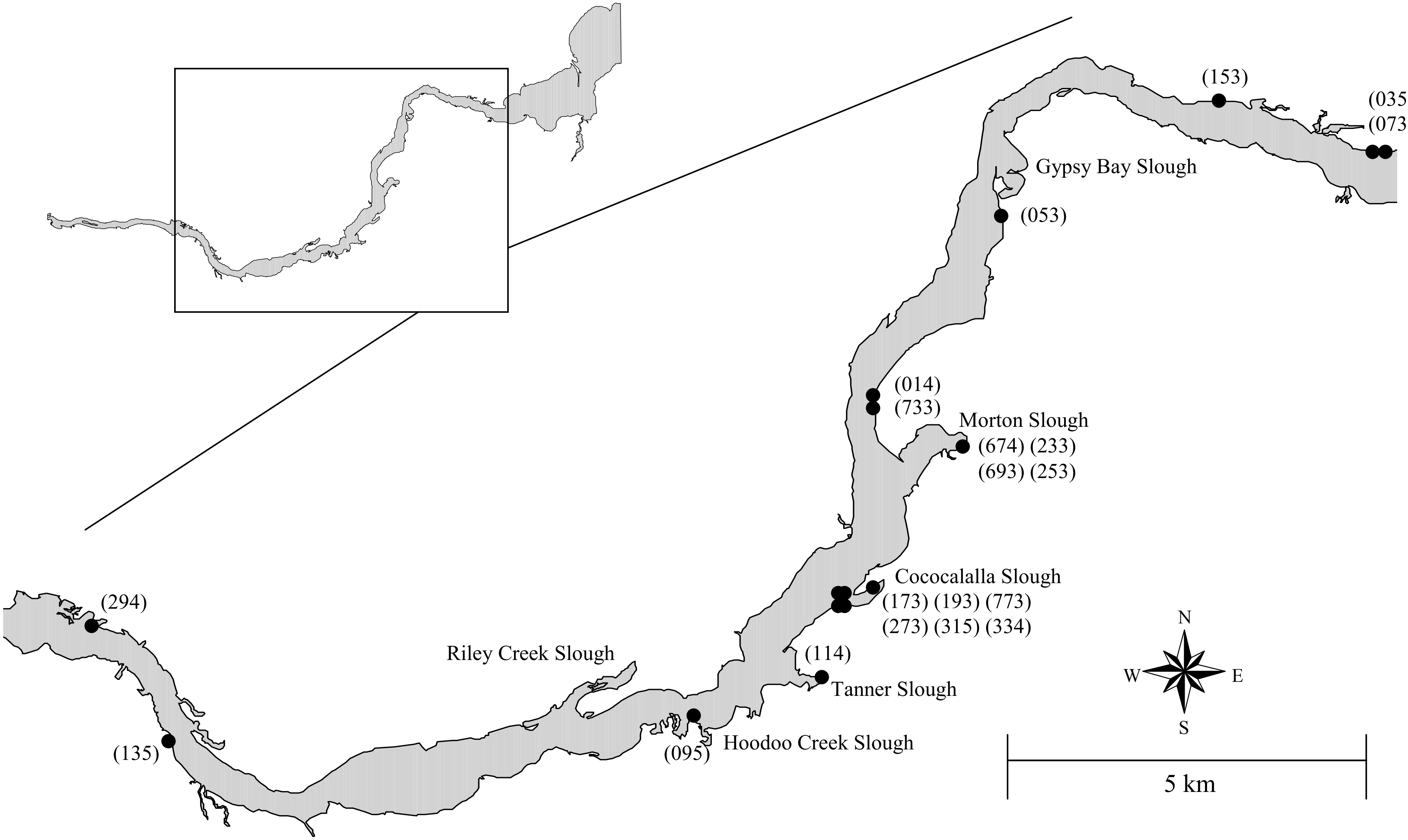

Figure 3. Initial capture locations of 20 radio tagged largemouth bass collected from August 29 to October 19, 1999 in the Pend Oreille River, Idaho. Parentheses contain codes of individual fish.

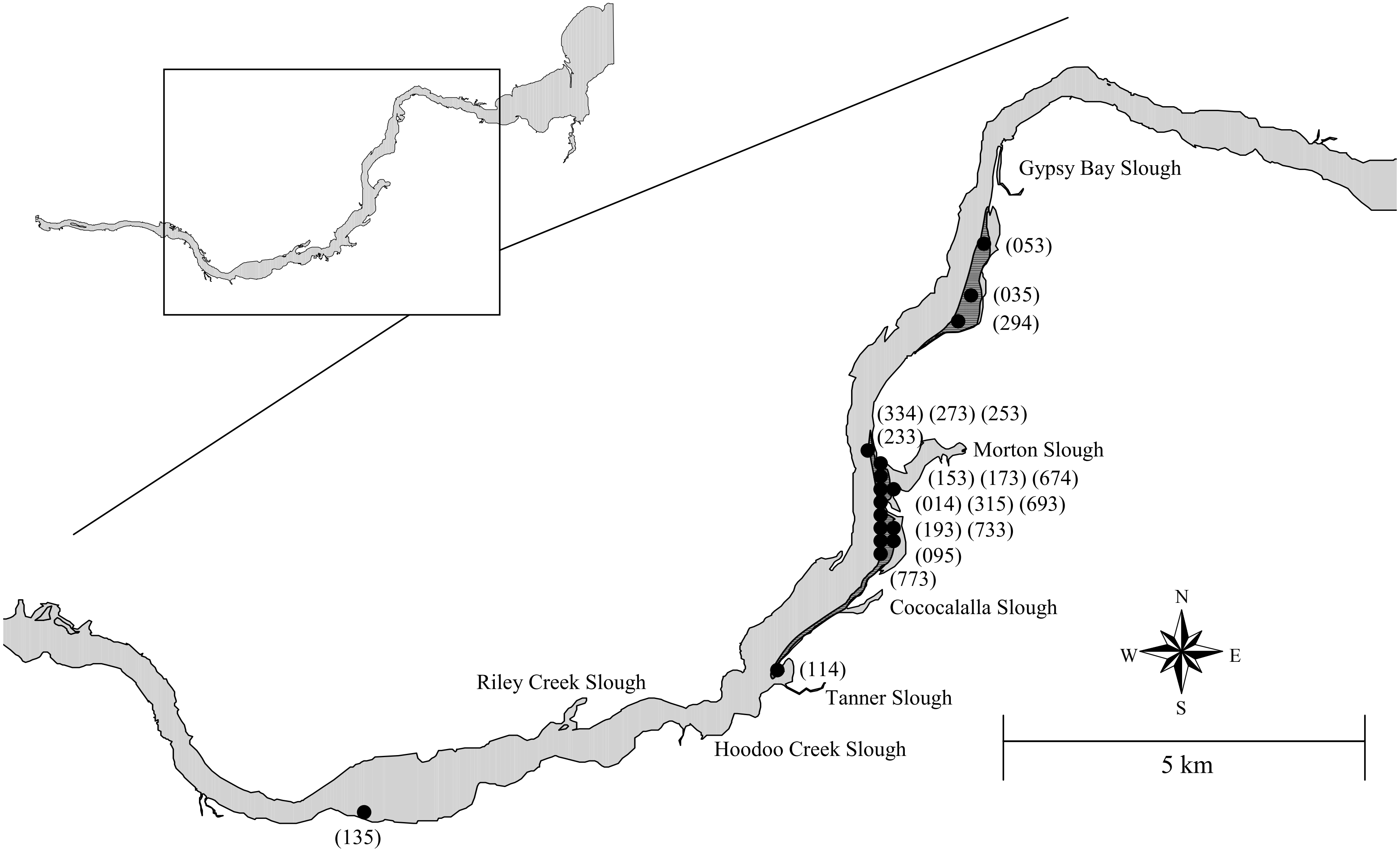

Figure 4. Locations of radio tagged largemouth bass in the Pend Oreille River, Idaho, on November 4, 2000 under 2.9 m winter drawdown conditions. Shaded areas indicate primary wintering areas (PWA) from November 1999 to March 2000.

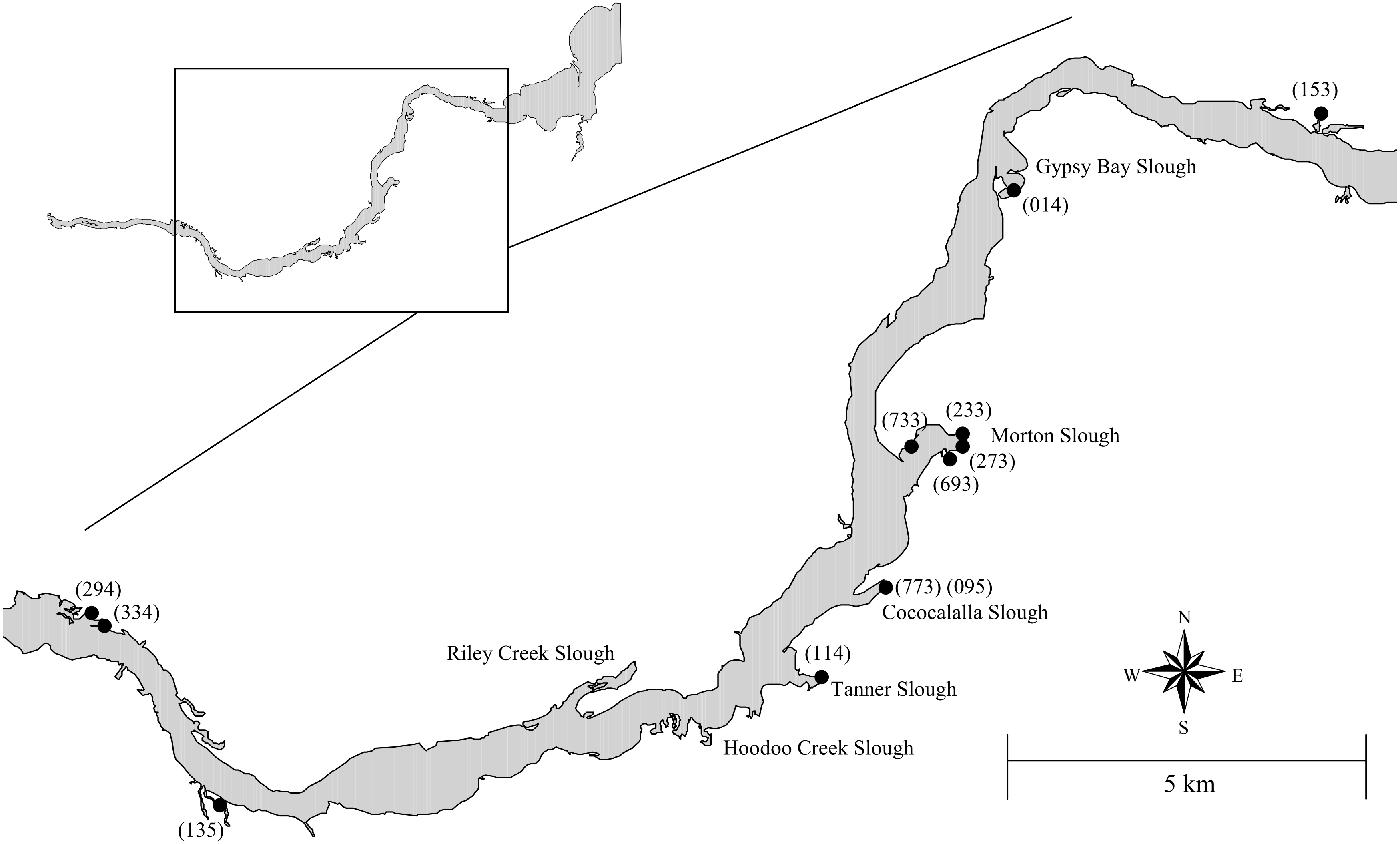

Figure 5. Locations of twelve radio tagged largemouth bass in the Pend Oreille River, Idaho, on 2 June, 2000.

Larval kokanee prey selection and growth

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Abstract: We investigated how springtime zooplankton community changes at Lake Pend Oreille, Idaho, have affected larval kokanee Oncorhynchus nerka (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 Bosmina, the historically important early season food source for larval kokanee. However, culturing of Bosmina proved difficult, so we used the cladoceran Ceriodaphnia dubia. Ceriodaphnia 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 Chlamydomonas 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 Cyclops and Diaptomus (Clarke 1999), but we subsampled our zooplankton collections to verify taxonomic composition.

Growth Experiments

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 Ceriodaphnia 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$\cdot$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 to15 copepods$\cdot$ L^{-1}), those found before Mysis establishment (15 cladocerans to 20 copepods$\cdot L^{-1}$), or an intermediate ratio (8 cladocerans to 17 copepods$\cdot L^{-1}$). 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:

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

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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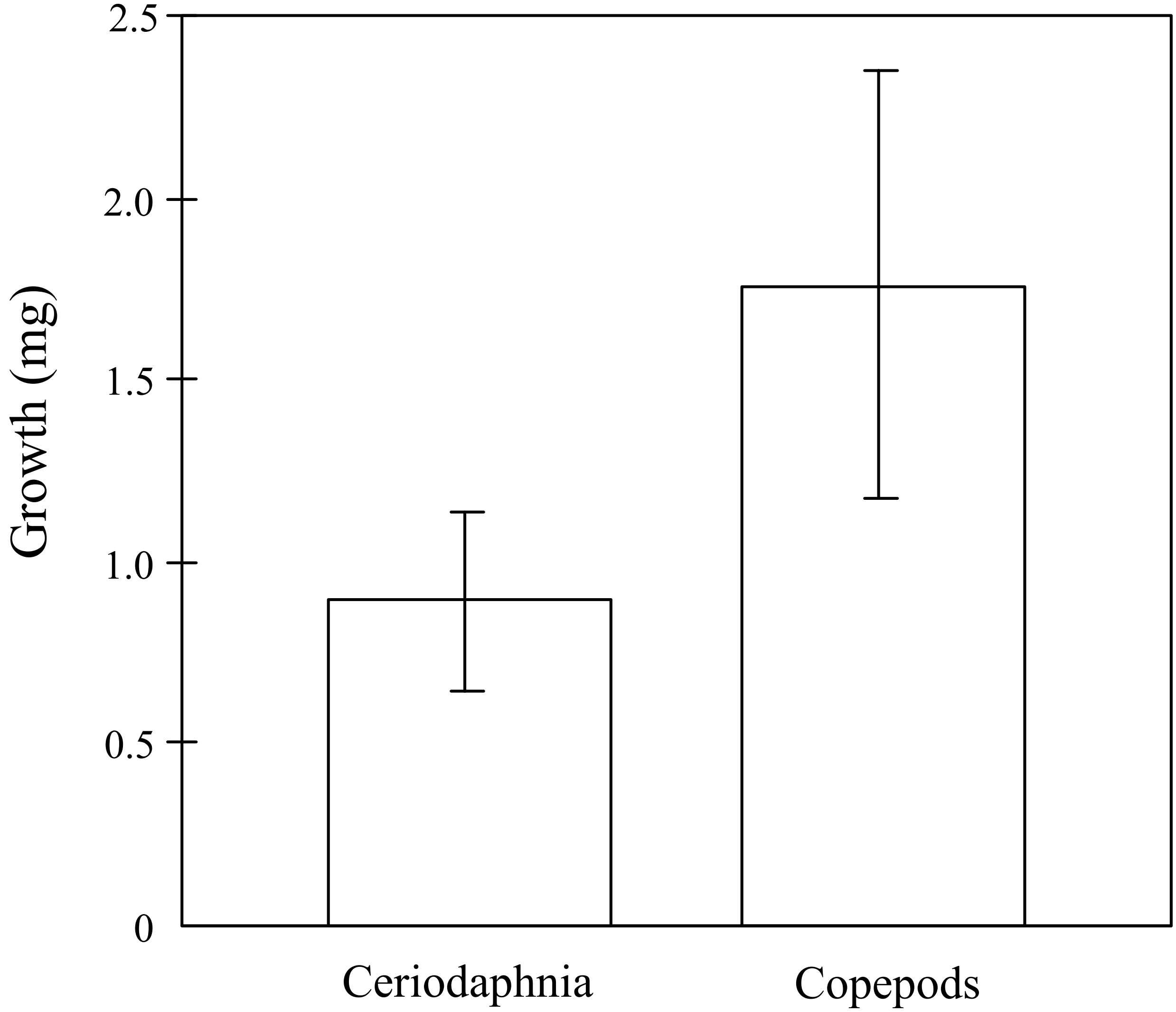

Figure 1. Mean kokanee growth (ending weight - beginning weight) fed either Ceriodaphnia or a mixed copepod diet for ten days. Vertical lines represent one standard error.

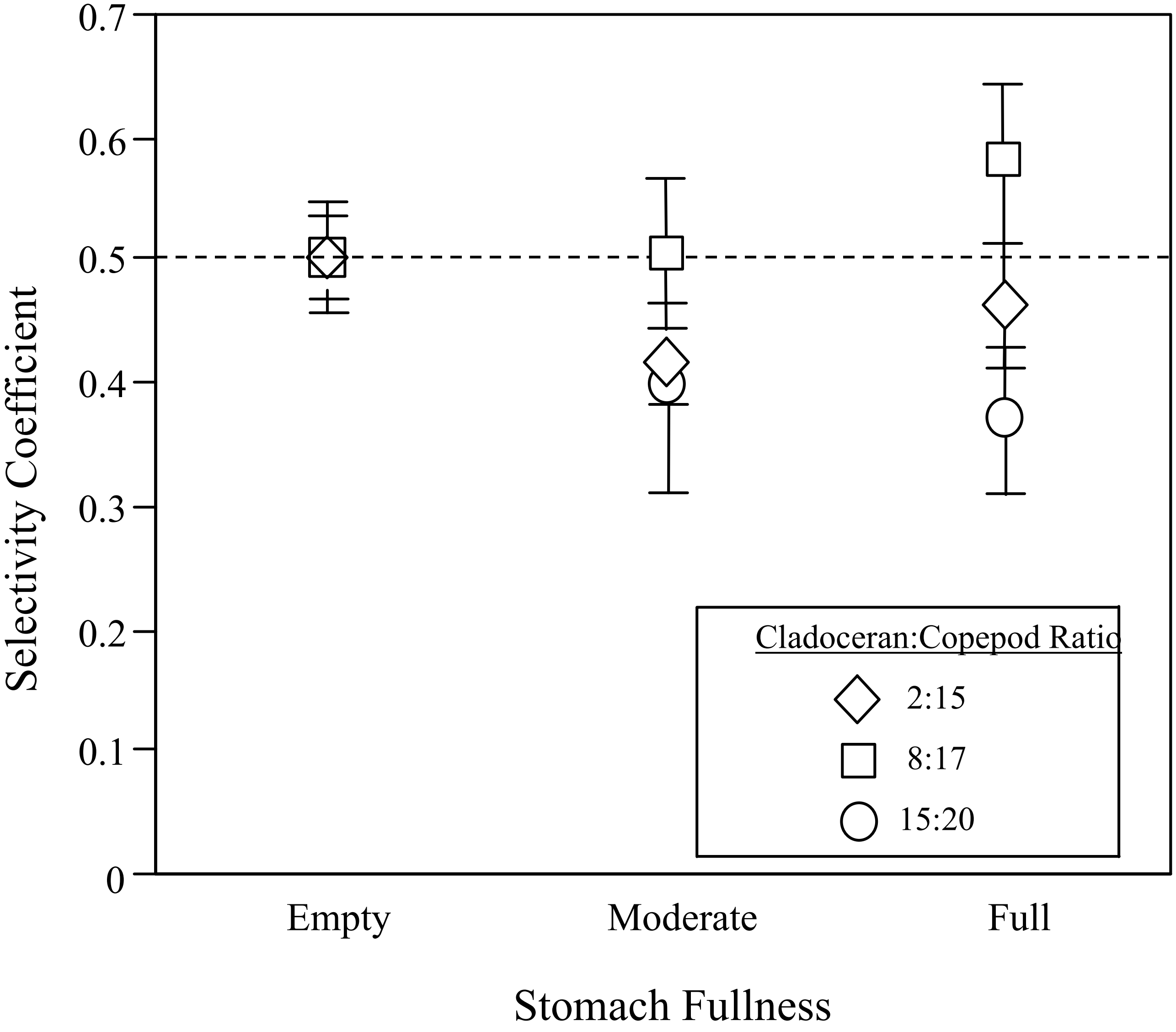

Figure 2. Chesson's selectivity coefficient (α) for kokanee feeding on Diaptomus at one of three relative prey ratios, and at three levels of gut fullness. Dashed line represents random feeding, vertical lines represent one standard error.

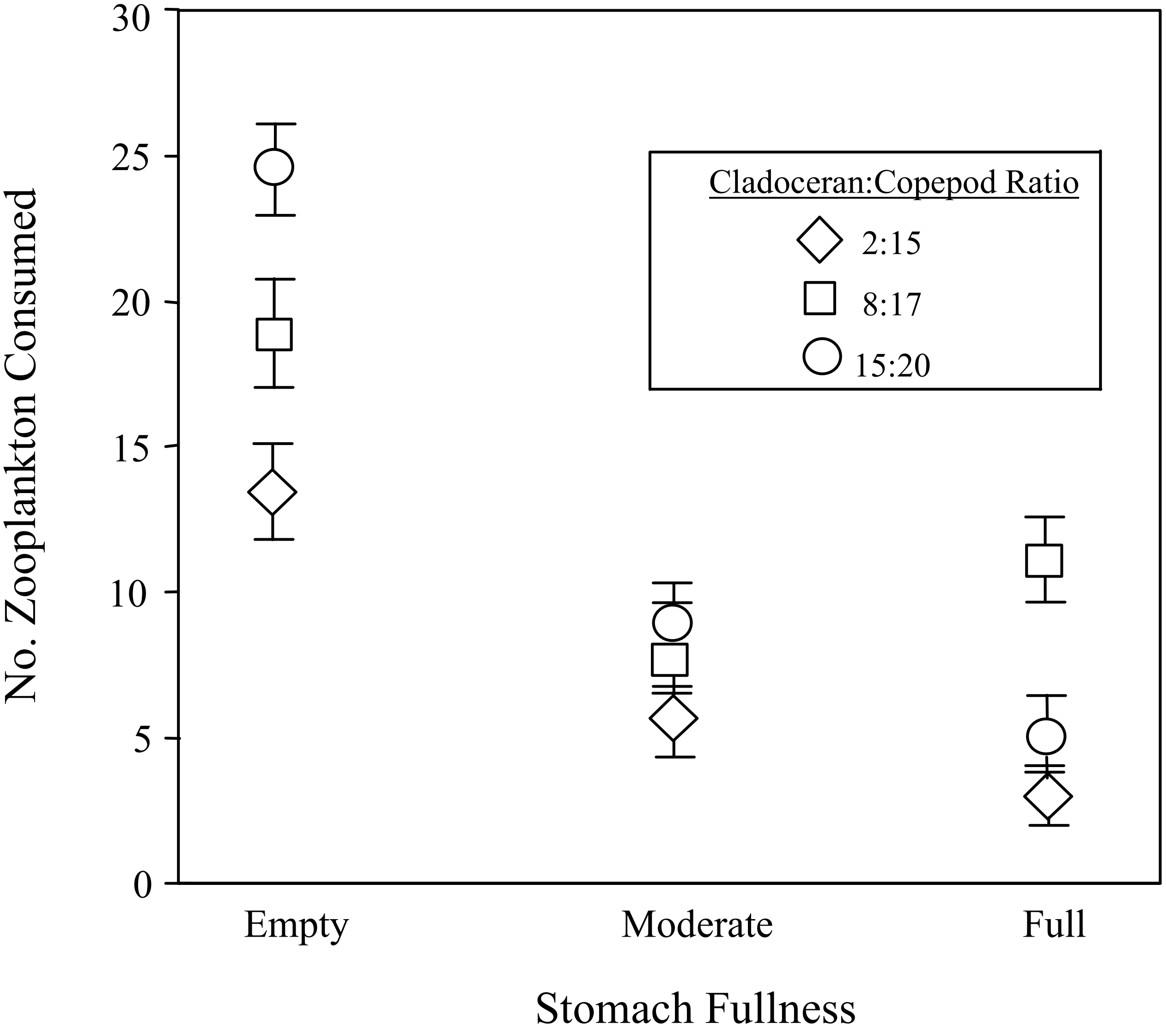

Figure 3. Mean total number of prey items ingested by kokanee feeding at one of three relative prey ratios, and at three levels of gut fullness. Vertical bars represent one standard error.