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EFFECT OF THE OPERATION OF KERR AND HUNGRY HORSE DAMS ON THE REPRODUCTIVE SUCCESS OF KOKANEE IN THE FLATHEAD SYSTEM

TECHNICAL ADDENDUM TO THE FINAL REPORT

Prepared by:

Will Beattie and Joel Tohtz - Project Biologists
Bob Bukantis and Steve Miller - Research Assistants
Montana Dept. Fish, Wildlife, and Parks

Prepared for:

Fred Holm
Bonneville Power Administration
Division of Fish and Wildlife
Bex 3621, Portland. Oregon 97208

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EXECUTIVE SUMMARY

Since 1981, our studies have documented decreases in the kokanee (Oncorhynchus nerka) population from what was formerly the dominant sport fishery in the Flathead system. The original intention of these studies was to assess the impacts of hydroelectric operations at Kerr and Hungry Horse dams, and quantify fisheries losses attributable to their influence in the system. Hydropower operations were found to significantly reduce kokanee recruitment from both river and lakeshore spawning areas. Due primarily to their influence on the timing and amplitude of water level fluctuations, operation of the dams was estimated to reduce adult kokanee spawners in the system annually by as many as 150,000 fish.

Sport harvest also contributed to kokanee losses during these years. Revised total escapement and harvest estimates for 1981 and 1985 indicate that 50 percent or more of kokanee spawners may have been harvested before reproducing in either year. Recruitment to the lake, however, was still quite large. Over 9 million kokanee fry were estimated to have entered Flathead Lake in both 1982 and 1986.

Beginning in 1986, studies were redirected to understanding the effects of Mysis relicta on kokanee populations in the Flathead system. The establishment of M. relicta in Flathead Lake in the early 1980s has drastically altered the lake's zooplankton community. These changes in turn are associated with rapid declines in kokanee spawning escapement. In 1985, total escapement in the Flathead River system was estimated at 147,000 fish. Minimum estimates of kokanee escapement in both 1988 and 1989 are now less than 1000 fish in the entire Flathead system.

We know that M. relicta has been a dominant factor reshaping the ecology of Flathead Lake. Recently, however, it appears that M. relicta is also adjusting to changing conditions in the lake. A third, smallest size class was identified in M. relicta samples from 1986, 1987, and 1988. This size class represents a new generation not previously identified in the life history of M. relicta in Flathead Lake, and occurs as average densities of M. relicta continue to decline. We estimated 52 M. relicta/m^2 from the fall, 1988 census. This density is about equal to M. relicta densities estimated in 1985, and down from peak densities of about 130/m^2 estimated in 1986.

In 1988, total crustacean zooplankton densities were lower in Flathead Lake at three sampling stations than in the two previous years. 1988 peak total densities occurred in July at roughly 11 organisms/liter. Since cladoceran densities were about equal during these years, lower total zooplankton density results from loss of copepods.

A dual-beam hydroacoustic survey of Flathead Lake conducted in 1988 indicates roughly 4.5 million fish greater than 50 mm were living in the lake. A significant portion (over 30 percent) of these fish were associated with the lake bottom. Although species verifications are difficult in a lake this large, 60 to 90 percent of limnetic species sampled in all areas were lake whitefish (Coregonus clupeaformis). Unlike kokanee, lake whitefish numbers are stable or increasing after M. relicta became established. We feel that this response is probably explained by their benthic feeding habits, and ability to use *M. relicta* as a new food item in their diet. Von Bertalanffy growth models for lake whitefish populations before and after *M. relicta* introduction indicate faster growth rates after *M. relicta* was established. Growth coefficients increased from 0.14 to 0.20 following the introduction of the shrimp. Average lake whitefish size in our samples, however, has changed very little.

Since predation by *M. relicta* has reduced zooplankton abundance in Flathead Lake, competition for food between kokanee and lake whitefish has been proposed to explain recent kokanee declines. Although youngest lake whitefish and kokanee are predominantly plankton feeders, no data establish that either species is food limited. If feeding stress exists for kokanee, we believe it must occur at very early stages in their development. All kokanee that we are able to capture are in excellent condition. However, kokanee numbers are very low in the lake, and it is possible that food limitations are responsible for high mortality of fish smaller than we normally capture.

Comparing Flathead Lake with other lakes that have kokanee and recently established *M. relicta* populations, it is clear that the presence of *M. relic-* & alone does not explain kokanee population collapses. Swan Lake, also in the Flathead drainage, has a stable kokanee population, despite abundant *M. relicta*. In part for this reason, we feel that predation by other fish is more likely the dominant factor determining the fate of kokanee populations when *M. relicta* is introduced. Bottom oriented predators that can readily incorporate *M. relicta* are especially implicated in kokanee losses. In most lakes we have examined, the presence of lake trout (*Salvelinus namavcush*) seems especially important in determining whether or not a kokanee population collapse will occur.

Because reestablishing kokanee in the Flathead system is uncertain at this time, management planning must remain flexible. Although efforts to rebuild kokanee populations in Flathead Lake should continue, alternative fisheries compensation programs should be developed. We recommend that these alternatives emphasize native and established species, and focus on protecting and enhancing river spawning and rearing areas, and critical lake habitats. The enhancement of native fish populations through the release of hatchery fish should be included as part of the mitigation program.

INTRODUCTION

This addendum to the Final Report for project 81-S-5 presents results of research on the zooplankton and fish communities of Flathead Lake. The intent of the Study has been to identify the impacts of hydroelectric operations at Kerr and Hungry Horse Dam on the reproductive success of kokanee and to propose mitigation for these impacts. Recent changes in the trophic ecology of the lake, at least in part related to the establishment of Mysis relicta in the system, have reduced the survival of kokanee. In the last three years the Study has-been redirected to identify, if possible, the biological mechanisms which now limit kokanee survival, and to test methods of enhancing the kokanee fishery by artificial supplementation. These studies were necessary to the formulation of mitigation plans. The possibility of successfully rehabilitating the kokanee population, the original mandate of the Study, is in doubt because of change in the trophic ecology of the system.

This report first presents the results of studies of the population dynamics of crustacean zooplankton, upon which planktivorous fish (e.g. kokanee) depend. It has been suggested that food availability may be limiting the survival of kokanee in Flathead Lake, in particular the survival of juvenile fish. Previous work has documented declines in zooplankton abundance that was apparently related to the increased grazing pressure of mysid shrimp. This report also presents trends in M. relicta abundance, including their life history in Flathead Lake and their average density as measured by the fall census in 1988.

A modest effort was directed to measuring the spawning escapement of kokanee in 1988. Because of its relevance to the study, we also report assessments of 1989 kokanee spawning escapement. Hydroacoustic assessment of the abundance of all fish species in Flathead Lake was conducted in November, 1988.

Summary of the continued efforts to document the growth rates and food habits of kokanee and lake whitefish are included in this report. Revised kokanee spawning escapement and harvest estimates, and management implications of the altered ecology of Flathead Lake comprise the final sections of this addendum.

Measurement of the survival rate of juvenile kokanee and the relative survival rates of wild and hatchery-produced kokanee fry, as proposed in the contract extension, have not been possible. Considerable effort was expended in attempting to sample juvenile kokanee in the period following the release of hatchery-raised fry. Either very high mortality or their rapid dispersion to very low overall density in the lake precluded any quantitative sampling of kokanee fry. Final assessment of the success of the supplementation program will be possible in the following years when those fry will reach maturity and begin to contribute to the sport fishery or to spawning escapement.

Appendix D is a bibliography of reports and scientific publications produced from project 81-S-5. Appendix E is a journal article entitled "The effect of the establishment of Mysis relicta on the zooplankton community of Flathead Lake, and coincident decline in the survival of kokanee". This article was accepted for publication in the American Fisheries Society Symposium Series to be published in 1990.

METHODS

Zooplankton Density

Duplicate zooplankton samples were collected with a 0.5 m closing zooplankton net constructed from 80 micron Nitex. The net was retrieved with an electric winch at 0.4 m/sec. Three stations on Flathead bake - Somers Bay (1-5), Lakeside Bay (l-l), and Big Arm (6-4) - were sampled from May 15 to October 1, 1988 (Figure 1). When the lake was not thermally stratified bottom to surface hauls were taken. When the lake was stratified, stage hauls were taken from the bottom to the base of the thermocline and from the base of the thermocline to the surface. When the water column was isothermal or only weakly stratified, bottom to surface hauls were taken. Samples were preserved in the field with 95 percent ethyl alcohol.

Eoischura nevadensis and _Leptodora kindtii_ were counted in five 10 ml samples after concentrating the sample to approximately 90 ml. These large species were counted with a 'dissecting microscope. For the other crustacean zooplankton, samples were diluted to between 130 and 300 ml to facilitate counting. One ml subsamples were dispensed into a Sedgwick-Rafter cell for counting. The following criteria were applied to more efficiently apply counting effort and reduce overall subsampling variance. If a taxon was counted more than 200 times in a subsample, no further counts were made for that taxon. If it occurred 100 to 200 times two counts were made. If it occurred 50 to 100 times three counts were made. A taxon was counted in four subsamples if less than 50 individuals were counted per subsample.

Mysis Census

On September 12 and 13, 1988, _M. relicta_ were collected at 40 stations on Flathead Lake (Figure 1). Sampling stations were proportionately allocated to three depth strata and randomly specified within each stratum. Depth zones were: less than 40 m, 40 to 75 m, and greater than 75 m. These stations represented approximately 45, 30 and 25 percent of the lake surface area, respectively. All samples were taken at least two hours after sunset. We used a 500 micron mesh conical net with a one meter diameter opening. The net was pulled from the bottom to the surface with an electric winch at about 0.4 meters per second. Samples were preserved with 95 percent ethyl alcohol.

We sampled more stations'in 1988 than previous years, without replicating the hauls, to reduce the variance of the estimate of average abundance. Previous surveys indicated that much greater variance in _M. relicta_ density occurs between stations than between replicates taken at the same statiqn.

Measuring the length of antenna1 scales of _M. relicta_ simplifies obtaining length frequencies, once the relationship between scale length and total length is derived. Antenna1 scales were measured under a dissecting microscope with an ocular micrometer. Total length (tip of rostrum to tip of telson) was measured for 124 _M. relicta_. Using least squares linear regression we calculated a linear model relating antenna1 length to total length. The regression was used to convert measured antenna1 scale lengths to estimates of total length. The sex of individual _M. relicta_ was determined when feasible.

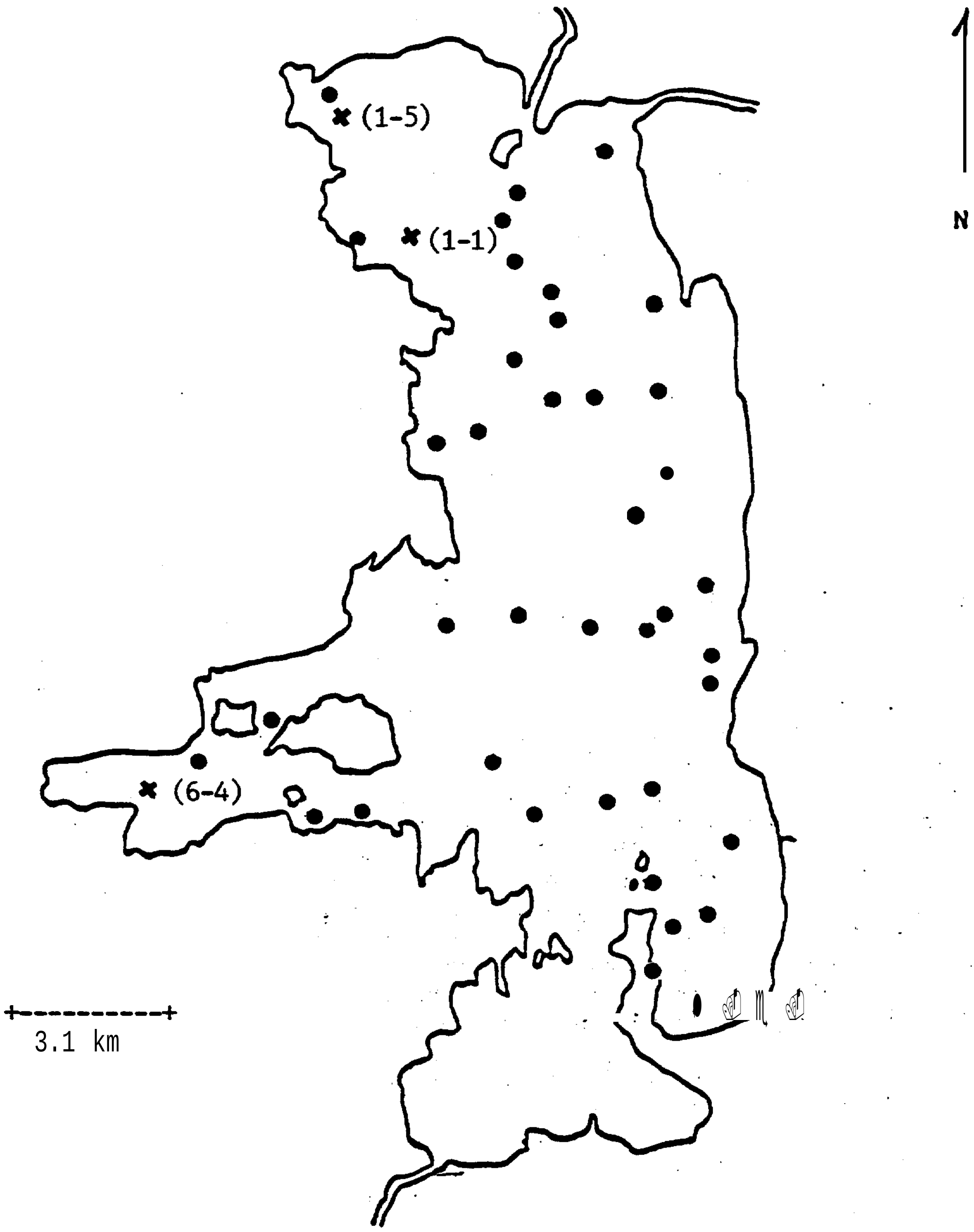

Figure 1. Zooplankton and Mysis sampling stations on **Flathead** Lake in 1988..

Spawning Escapement Surveys

In 1988, spawning kokanee were counted by two snorkelers in McDonald Creek at two week intervals from September 21 to October 18. We flew two aerial surveys of the mainstem and South Fork of the Flathead River on September 22, and October 20. River system surveys. were discontinued when it became apparent that a significant spawning run would not develop. This decision was based on the'timing of the river spawning run in the previous seven years. We also surveyed Flathead Lake shoreline, from Yellow Bay to Skidoo Bay on November 22. We decided not to-conduct more extensive shoreline surveys because escapement was very low.

In 1989, we again limited our spawner surveys because of low escapement. Two aerial surveys of 'the mainstem Elathead River were flown on September 25 and October 18. A snorkel survey was conducted in McDonald Creek on October 17. Eight historically important spawning sites in the mainstem Flathead River were examined for kokanee spawning on November 7. The east shore of Flathead Lake from Woods Bay to Skidoo Bay was surveyed on November 9 and 21.

Because the river and lakeshore surveys were discontinued in both years, escapement estimates must be treated as minimum estimates.

Hydroacoustic Estimation of Fish Abundance

A hydroacoustic survey was conducted on Flathead Lake during the nights of November 4 through 7, 1988. A Biosonics Model 105 dual-beam echosounder was used to obtain estimates of fish abundance and size. The system operated at 420 kHz through 6 and 15 degree transducers mounted in a towing fin. The equipment operated on 110AC volt power from a portable generator aboard the MDFWP research vessel "Bull Trout". The data were collected in digital format on a VCR recording system. Sixteen hours of data were collected along 16 transects (Figure 2). The transects excluded nearshore areas where depth was less than 12.2 m (40 feet). South Bay was also excluded from the sampled area. Measurements of fish density and target strength in 5 m depth strata were made with a Biosonics Model 281 Echo Signal Processor. The volume of water sampled was determined by the dtiration-in-beam technique (Thorne 1988). Since many fish were close to the lake bottom, the target strength of fish within 2 m of the bottom were measured manually with a storage oscilloscope (Thorne 1989).

Fish density (fish/m^3) in each depth stratum for each transect was output from Biosonic's data processing software. Near-bottom fish density was calculated separately from the manually acquired near-bottom data base. Density estimates for each stratum weretransformed and summed over the entire water column to calculate areal density according to the formula:

$$\text{fish}/100\ \text{m}^2 = \sum_{i=1}^{n} [(D_{Li} - D_{Ui})/10](\text{fish}/1000\ \text{m}^3)$$

where D_{Li} 'and D_{Ui} are the lower and upper limits of the depth stratum respectively (Nunnallee 1973).

Fish abundance estimates were derived for nine zones of Flathead Lake (Figure 3) by multiplying average fish density by surface area. Fish densities for each transect within a given zone were weighted by the length of the transect to calculate average density. Transect lengths were measured during sampling with a Signet Mk 267 digital knot log.

Only fish greater than 50 mm were included in the density estimates. We assumed that young-of-the-year fish of all species in Flathead Lake exceeded this threshold by late fall. Target strength frequencies were summarized by depth stratum and transect. Target strength distribution ranged from -59 dB to -22 dB. These target strengths can be approximately converted to fish size according to the Love equation:

$$\text{Target strength (dB)} = 19.1 \log (L) - 0.9 \log(f) - 62$$

where L is fish length (cm), and f is the acoustic frequency.

We detected smaller targets on all of the transects, but these were considered to be mysid shrimp or zooplankton aggregations. We also derived estimates of the abundance of fish larger then 500 mm (-32 dB) in the nine sampling zones, because of interest in the trophy fisheries for bull trout (Salvelinus confluentis) and lake trout in Flathead Lake. These estimates were calculated from the average proportion of targets larger than -33 dB in each stratum applied to the overall abundance estimate. Fish of any discrete size class will return a range of target strengths because of variation in their orientation in the acoustic field. The Love equation is based only on "ideal" target strengths measured when fish are oriented horizontally beneath the acoustic axis. Because this range was not measured for bull trout or lake trout, we did not know the proportion of targets weaker than -32 dB that represented this large size class. Therefore the estimates we present are only minimum estimates of the abundance of fish larger than 500 mm.

Coefficients of variation (CV) were calculated for fish density in four zones - the northwest corner of the lake (Area 1, Figure 2), shoreline areas, limnetic areas, and Big Arm. Cochran (1963) suggested that the variance of a ratio estimator, such as fish density (number/area) could be expressed by:

$$(CV)^2 = C_{yy} + C_{xx} - 2C_{xy}/n$$

where C_{yy} and C_{xx} are the squared coefficients of variation for fish density and length of each transect, arid C_{xy} is covariance of length and density:

$$C_{xy} = \sum_{i=1}^{n} [(y_i - y_x)(x_i - x_x)/(n-1)(y_x)(x_x)]$$

Subscripts i are individual observations; subscripts x are means. The coefficient of variation on overall density is taken as the square root of $(CV)^2$ (Eberhardt 1978).

The species composition of the Flathead Lake fish community was determined from gill net sampling preceding and following the acoustic sampling, i.e. from October 1 to December 22, 1988. Experimental, 1.83 x 38.1 m gill nets were set for 12 to 18 hours on the bottom and midwater at each site. The nets were constructed of equal length panels of 3/4, 1, 1 1/4, 1 1/2, and 2

STRATA	TRANSECTS
1	1 a-e
2	2 b-c
3	3 a-d
4	4 a-c
5	5 a-d
6	6
7	7, 8, 9 a-b
8	10, 13 a-b; 15, 16
9	11, 12, 13

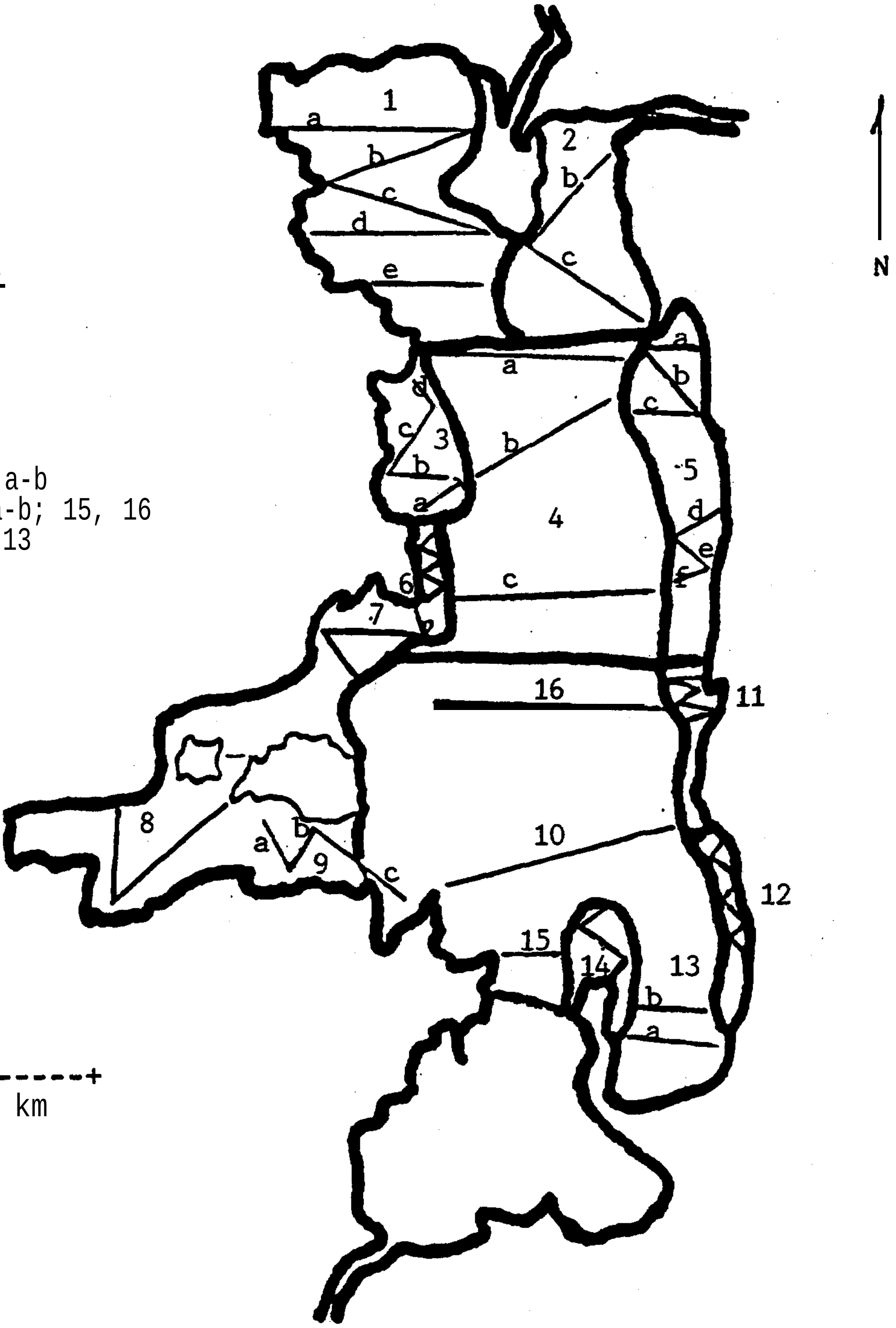

Figure 2. Locations of transects sampled in the 1988 hydroacoustic survey of Flathead Lake. The sampling areas are defined by heavy borders.

inch (bar measure) nylon mesh. 'Monofilament gill nets, 5 x 33 m long and constructed of 3/4 and 1 inch mesh, were also set midwater at some sites. Trawl sampling, primarily in area 1, supplemented the gill net samples. Beattie et al. (1988) described the trawl gear in detail. Because of the logistic difficulty of adequately sampling the fish community of a large lake system within a short period adjacent to the acoustic sampling, we could not quantify the species composition in all areas sampled with the hydroacoustic gear. Gill nets were set in areas, primarily nearshore, of known fish concentrations. We do not fully understand how the species composition of these nearshore concentrations reflects that of the limnetic zone. Some fish species may be more vulnerable to capture in gill nets, but this analysis did not consider size or species selectivity in determining species composition.

Age and Growth

We assessed age and growth of kokanee and lake whitefish from scales routinely taken from all fish captured during the project. Scales were removed from fish bodies below the dorsal fin and above the lateral line, an area recommended for scale studies of both species (Nielson and Johnson 1983). Age was determined from number of annuli. By convention in this report, age is designated by Roman numerals representing number of annuli on a scale. Because no annulus was considered complete unless circuli indicted renewed growth beyond the most recent annulus, all ages are reported as year plus. An age I+ fish, for example, had a single annulus on its scale, and was captured during'its second year of life in the lake. We prepared scales for examination by embedding in acetate using a hydraulic laboratory press and heated plates (Fred S. Carver, Inc.). Scales were pressed at 20000 psi pressure applied for 2.5 minutes. Acetate impressions were projected on a 3M Consultant 114 microfiche reader at different magnifications depending on scale size and convenience in determining scale features. The distance from center of scale focus to annuli and scale edge was measured directly from the projected image. Measurements'were converted to actual distance between annuli and scale radius, for use in back calculations of length at annulus formation. .

Agreement of ages determined'by different readers was assessed when possible using a subsample of same scales from both species (Appendix C). Since age from scales of older fish is subject to greatest interpretive discrepancy, age determinations for lake whitefish were also assessed from Walford growth transformations (Walford 1946), derived from data for earliest year classes (ages O+,I+, and II+). Empirically determined mean lengths at age were compared with same lengths for each age class predicted by' the 'model (Appendix C). Walford growth transformations were also used to determine the appropriateness of a von Bertalanffy growth model (Bertalanffy 1938) to describe pooled lake whitefish samples. The form of the von Bertalanffy equation adopted in this report'is:

$$Lt = loo[1-e^{-K(t-t0)}]$$

where Lt'is length at time t (years), loo is the theoretical ultimate length for fish in the population, K is the von Bertalanffy growth coefficient, and t0 is the time at which growth is theoretically 0. Age VIII+. fish were not included in calculations to avoid bias from very small numbers (2 total in all samples). Theoretical maximum lengths for each population were estimated from Walford lines, with no attempt to iteratively improve the estimates. Remaining terms in the model were estimated from least squares linear regression of $\ln(l_\infty - L_t)$ on age.

Estimates of length at annulus formation were based on proportional increases of body length and scales (Hile 1970). A linear model of this relationship was adopted after least squares regression of scale radius on length at capture for both species showed correlation coefficients greater than 0.93 (Appendix C). The relationship between length at capture (Lc) and distance from scale focus to scale edge (E) was taken to be:

$$Li = (Ai/E)(Lc)$$

where Li is the calculated body length at annulus i, and Ai is the distance from center of scale focus to scale annulus i. Growth of fish prior to establishing scales was estimated from the intercept of least squares regressions of scale edge on length at capture. Final calculated lengths at annuli for kokanee and lake whitefish are based on the modified equation:

$$Li = (Ai/E)(Lc-C) + C$$

where C is the intercept of the scale/body regression.

Average length at capture was determined for each year class available. Mean calculated lengths at annulus formation were compared on a year by year basis when appropriate and possible. Lake whitefish scale samples were also pooled from the late 1980s, and compared with pooled scale samples of lake whitefish collected before the establishment of _M. relicta_ in Flathead Lake. Where probability values are reported, statistics were tested against a null hypothesis of no difference at a 0.05 level of significance.

Growth was estimated from relative change in mean lengths at capture [(length at time t+l)-(length at time t)/length at time t)] for same age fish collected in different sample months, and for all age classes by sample year. Relative increase in mean lengths at annulus formation was used for growth history analysis of individual cohorts, and for comparison with rates derived from actual lengths at capture. Growth parameters for lake whitefish samples collected before and after _M. relicta_ establishment were also assessed from von Bertalanffy estimates developed for each group.

Food Habits

Food habits of kokanee and lake whitefish captured in 1988 were assessed from stomach contents of all fish that retained identifiable food items. Stomachs were removed between the cardiac and pyloric sphincters, with contents extruded into plastic vials containing 95 percent ethyl alcohol as a preservative. Most food items in each stomach were identified and counted directly under a binocular microscope (40x). An exception was made when certain crustacean zooplankton exceeded 200 organisms per stomach, in which case zooplankton numbers were estimated from three 1 ml subsamples in a Sedgwick-Rafter counting chamber for the genera _Daphnia, Bosmina, Diacyclops_ (formerly _Cyclops_), and _Leptodiaptomus_ (formerly _Diaptomus_). To facilitate counting, samples were diluted to provide subsamples of approximately 100 organisms in each chamber. All other food items were identified and counted from the entire sample, regardless of numbers in the stomach.

The proportional contribution of each food item to total numbers of food items ingested was determined for each species by age class and sample month. Because of the limited number of stomach samples from kokanee in 1988, these determinations were not based on mean percentages as was true in previous reports (e.g. Beattie et al. 1988). We were concerned that averaging percentages might exaggerate contribution for food items that occur in many stomachs it low numbers, and obscure contribution of food items less commonly incorporated. Proportions were also examined by length class (50 mm increments) to assess possible bias in food item selectivity that results from fish size rather than chronological age. When no meaningful difference was detected, age class was adopted for convenience in discussion. Age classes were pooled only when no significant differences could be detected in the type and timing of food items ingested.

Because of concern that young kokanee and lake whitefish compete directly for reduced numbers of zooplankton, proportions of Danhnia thorata, Bosmina lonairostris, Diacyclops bicusnidatus-thomasi, Enishura nevadensis, and Leptodiaptomus ashlandii were examined separately against totals of these food items ingested. Diet was also assessed from frequency of occurrence of each food item in all stomachs by total sample, and by month in which fish had been captured.

Zooplankton Selectivity

Selection for D. thorata, B. longirostris, L. ashlandii, E. nevadensis, and D. bicusoidatus-thomasi was assessed by comparing percentages of these food items in stomachs with their corresponding frequency in zooplankton samples from the lake. A Strauss (1979) linear index of selection was calculated to provide a common scale for comparison. For purposes of this report, the index (L) was developed as the difference between unweighted proportions of each zooplankton species in stomach samples and lake zooplankton samples:

$$L = ri - pi$$

where ri is the proportion of species i found in stomachs, and pi is the proportion of species i in the lake. Index values can range from -1 to 1, with random incorporation indicated by 0. In developing the index, stomach samples were pooled separately by month, age class, and the area of the lake in which they were collected.

Estimated sample variance of the index $[s^2(L)]$ is given by:

$$s^2(L) = [ri(1-ri)/\ n_r] + [pi(1-pi)/n_p]$$

where n = numbers of D. thorata measured in stomachs (subscript r) and lake samples (subscript p) respectively. Estimated standard deviation of L was determined as the square root of the estimated variance. Recognizing that gear selectivity (Hamley 1975) precludes truly random fish samples, and that different digestion rates for different size organisms will also influence results (Strauss 1979), in&x values were not interpreted as strict quantifications. Although reported in their quantitative form, we used these values primarily to corroborate qualitative assessments of the degree of diet selection.

To investigate feeding selection for different prey sizes, total carapace lengths (tip of head to base of tail spine) of D. thorata were measured with a binocular microscope (ocular micrometer, 40X) for organisms found in fish stomachs, and in samples from zooplankton monitoring stations in the lake. Average length and length frequency distributions were compared between stomach contents and'lake samples. A linear index of selection was developed for cladocerans less than 0.8 mm, and compared with same index values for larger D. thorata. Stomach samples were chosen from all available age classes of fish captured near zooplankton sampling stations. Date of fish capture and zooplankton collections corresponded as closely as possible. Where a sample contained more than 200 organisms, the first 200 D. thorata encountered were measured in random 1 ml subsamples drawn from the well mixed total sample. Where D. thorata were less than 200, all individuals were measured. Because of the small number of kokanee captured in most 'months, this assessment was limited to samples from the northwest section of-Flathead Lake collected in June and August.

RESULTS

Zooplankton Abundance

Average zooplankton densities of selected species by sample site are tabulated in Appendix A for lake samples collected in 1988 by Montana Department of Fish, Wildlife and Parks personnel. Results reported here are limited to samples from three locations in the western half of Flathead Lake. Additional zooplankton samples from two mid-lake sites were collected by workers at the University of Montana Biological Station (UMBS) as part of a cooperative effort to provide more 'complete characterizations of zooplankton dynamics in the lake. Data from UMBS are not included in this report. For these reasons, we urge caution in extending zooplankton results reported here to large scale inferences about the lake.

Crustacean zooplankton densities were lower in 1988 at station l-l than they were the previous two years (Figure 3). ‘Peak density also occurred later in the season in 1988 than the previous two years.

D. thorata, B. loneirostris, D. bicusnidatus-thomasi and L. ashlandii, declined in abundance. The copepods D. bicuspidatus-thomasi and L. ashlandii showed a greater decline than the cladocerans. The delay in seasonal peak total zooplankton density was primarily a result of the decline in copepod abundance, because both B. longirostris and D. thorata show peak abundance similar in timing or slightly earlier than the previous two years.

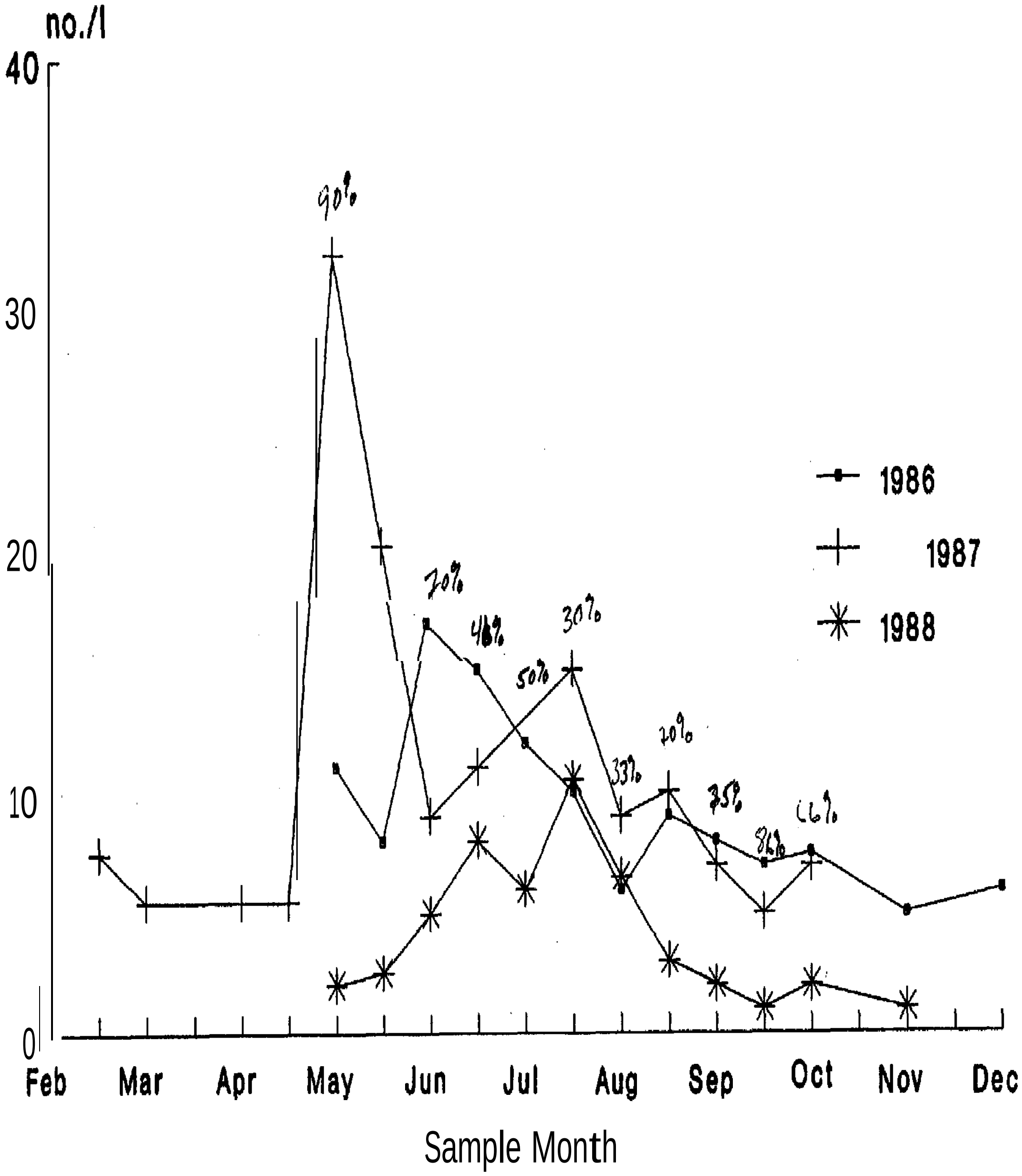

Figure 3. Seasonal trends in total crustacean zooplankton abundance in Flathead Lake in 1986, 1987, and 1988.

We noted the reappearance of two cladoceran species in the 1988 zooplankton. *Daohnia longiremis* was last seen in the 1986 zooplankton in two samples. We saw two individuals in one sample collected at site l-5 on 9 June, 1988. *L. kindtii* disappeared in 1986, but we found quantifiable densities at all three sites sampled in 1988.

L. kindtii was most abundant at station 6-4, and was most abundant in hypolimnetic samples taken at that station. In general, *L. kindtii* was more abundant in the hypolimnion, except at station 1-5 where it was only collected on two dates at relatively low densities in the epilimnion in August, and in a full depth haul in early October.

E. nevadensis occurred at relatively similar low densities at all three sites, except for a relatively large peak density exhibited in the epilimnion during mid-summer at station l-l. Densities were generally higher in the epilimnion than the hypolimnion.

Nauplii occurred at similar densities at all three sampling stations. Densities were consistently higher in the hypolimnion.

Abundance of *L. ashlandii* was roughly similar at all three sites. Highest densities were at site l-l, and site 6-4 was intermediate between the other two. The depth distribution pattern is the opposite of that shown by nauplii, *L. ashlandii* were generally found in highest density in the epilimnion.

The density of *D. bicusnidatus-thomasi* was highly variant, and no consistent pattern was apparent between sites or depth zones.

B. longirostris densities were similar from station to station except for a sharp early summer pulse at station 6-4. The data show evidence of positioning in the water column by *B. longirostris* to some stimulus, possibly temperature. In June, the density of *B. loneirostris* was markedly higher in the epilimnion (Figure 4), whereas in July the situation reversed, especially at station 6-4 (Figure 5). By the end of August, density was again highest in the epilimnion, and continued to increase in the epilimnion relative to the hypolimnion to the end of the sampling period.

D. thorata showed an early summer pulse which was more clearly defined than that of *B. longirostris* (Figure 6). In contrast to *B. lonairostris*, *D. thorata* was almost exclusively epilimnetic in distribution, with the curious exception of site 6-4 where densities in the hypolimnion were only slightly less than densities in the epilimnion.

In general the 1988 data showed similar patterns of abundance among the three sampling sites. However, there are a few notable differences between sites. Peak densities are considerably higher for *D. thorata* and *E. nevadensis* at Lakeside (l-l) than at the other two sites while peak densities for *B. longirostris* are highest for Big Arm (6-4).

The reappearance of *D. lonpiremis* and *L. kindtii* may be due to a decline in predation pressure from *M. relicta*. Densities of *M. relicta* in 1988 were similar to those observed in 1985, about the time these two species disap-

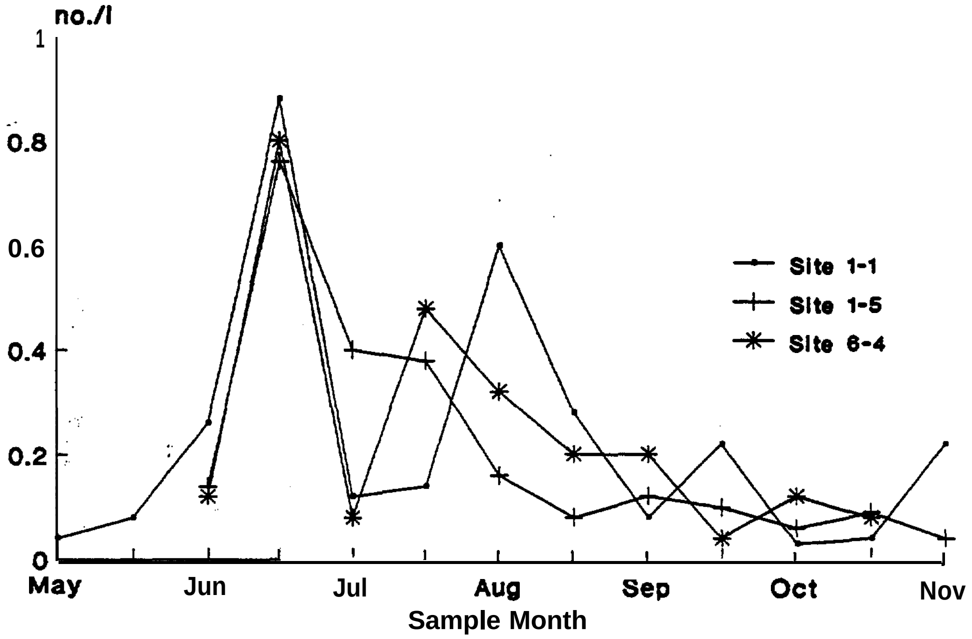

Figure 4. Seasonal trends in the abundance of *Bosmina longirostris* in the epilimnion of Flathead Lake at three zooplankton sampling stations in 1988.

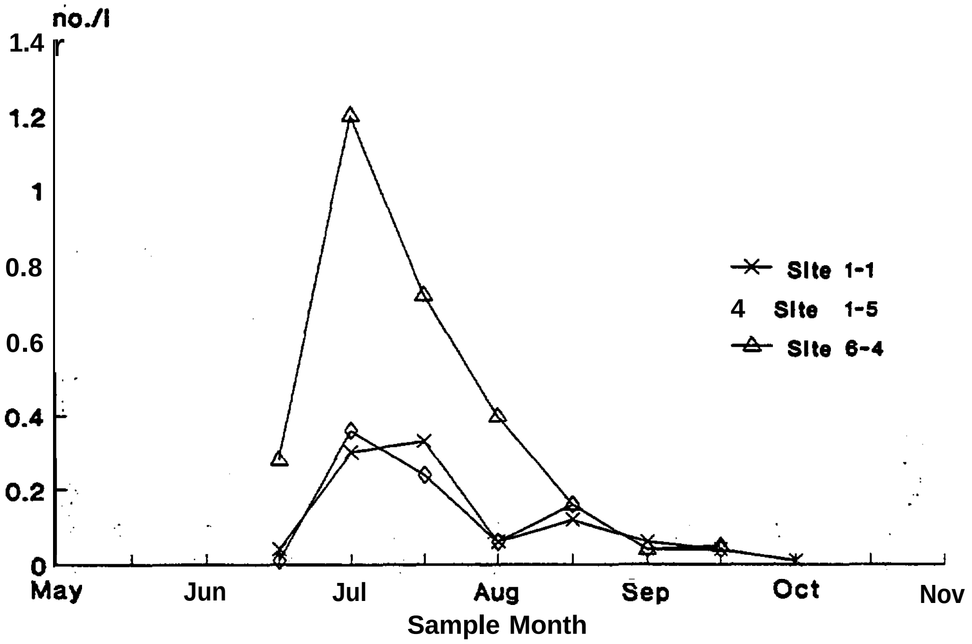

Figure 5. Seasonal trends in the abundance of *Bosmina longirostris* in the hypolimnion of Flathead Lake at three zooplankton sampling stations in 1988.

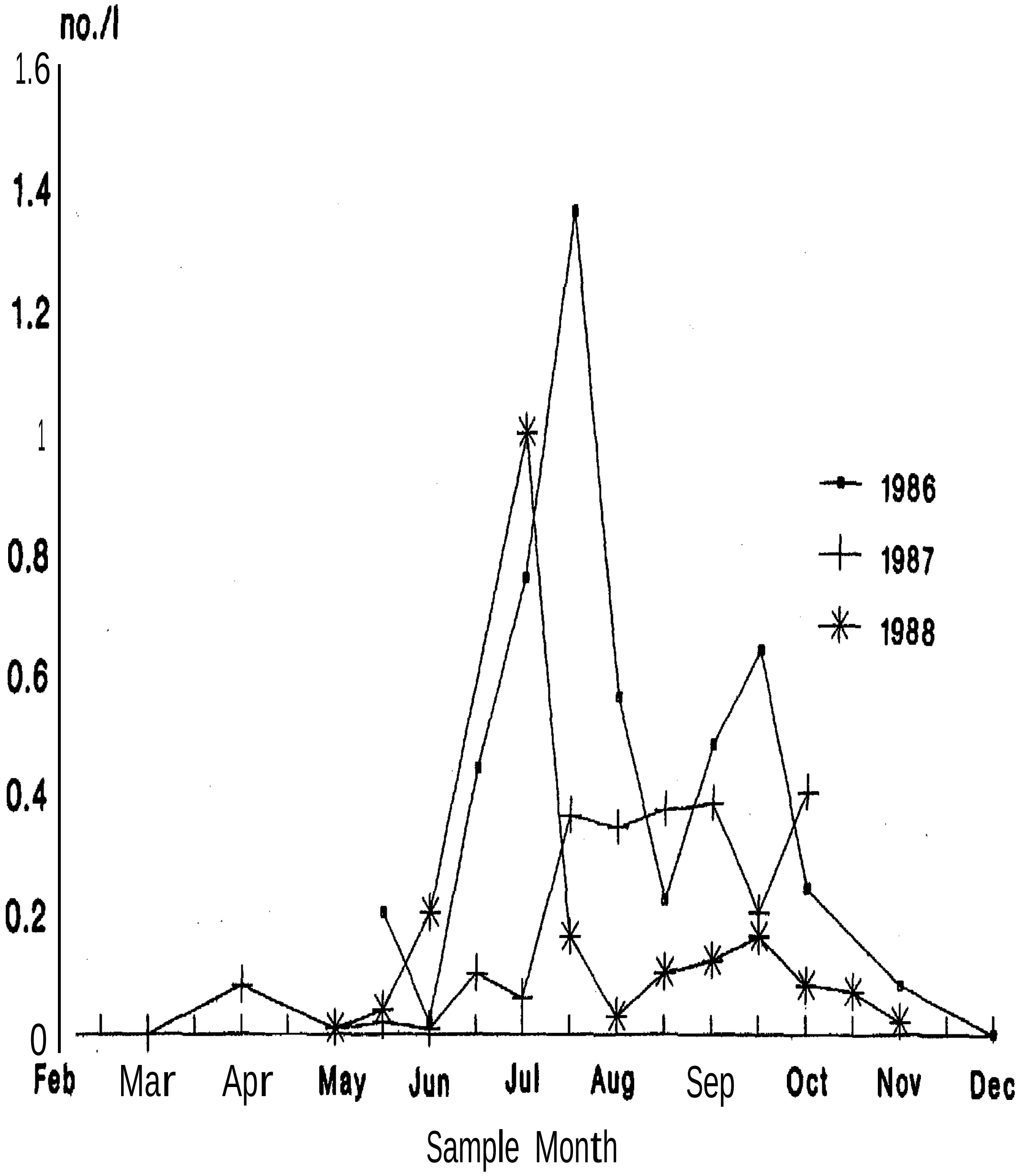

Figure 6. Seasonal trends in the abundance of <u>Daphnia thorata</u> at station 1-1 in Flathead Lake in 1986, 1987, and 1988.

peared from the Flathead Lake zooplankton samples. Cladoceran species such as *B. loneirostris* reappeared in Lake Tahoe samples during periods of depressed *M. relicta* abundance (Threlkeld, 1981).

Because *M. relicta* has declined in Flathead Lake, it would be reasonable to expect that total zooplankton density would increase, especially in light of the reappearance of *B. longirostris* and *L. kindtii*. But total zooplankton density declined in 1988 compared to the previous two years. We have no data on why this occurred. The observed decline may be due to a decrease in zooplankton birth rates due to a decline in primary productivity, or may be related to fish grazing in certain areas of the lake.

Mysis Abundance And Age Structure

ABUNDANCE

M. relicta were first documented in Flathead Lake in 1981 when several individuals were collected while trawling for kokanee in the north end of the lake (Leathe and Graham 1982). Since then the population has risen dramatically until 1986, when it apparently peaked (Figure 7). The past two years have seen a decline, and the fall 1988 population survey indicated an average of about 52 *M. relicta* per square meter of lake surface, or about equal to the 1985 density.

SIZE DIFFERENCES

Regression of total lengths of *M. relicta* on antennal scale lengths produced the relationship:

total *M. relicta* length = 1.47 + 5.78(antennal scale length).

This equation explained 95.77 percent of the variance in the data with $p < 0.01$ for both slope and intercept. We used this equation to estimate total lengths of *M. relicta* sampled in 1986, 1987, and 1988 to compare size differences between years.

Size-frequency histograms were plotted for each site separately for male and female *M. relicta*. The data showed tri-modal, approximately normal distributions (Figure 8). The data which formed the middle mode were separated out. in all cases to perform analyses on between site, sex, and year differences in mean size of *M. relicta*. This was done to meet the assumptions of parametric statistics, and because it represented the most abundant class of *M. relicta* and thus gave us the largest possible sample size for testing.

Analysis of variance showed no significant differences between mean size of *M. relicta* between sites in any year except for the 1986 sample taken at site l-l. At that site male *M. relicta* were significantly smaller than at the other 3 sites tested.

Data from 1987 was used to test whether there was a significant difference in mean size of male and female *M. relicta*. Females were significantly larger than males ($p = 0.00001$). Mean *M. relicta* size was tested for between

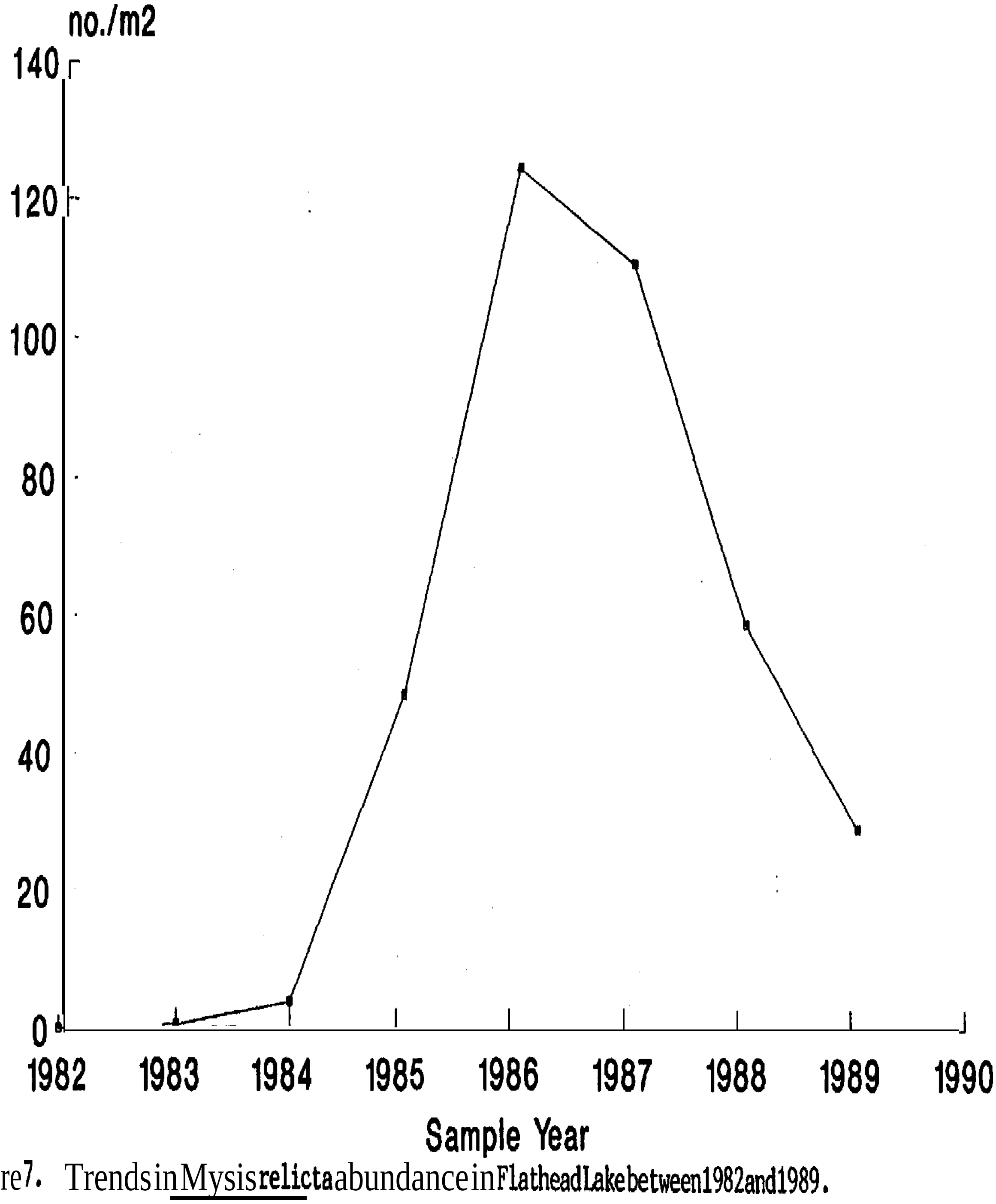

Figure 7. Trends in *Mysis relicta* abundance in Flathead Lake between 1982 and 1989.

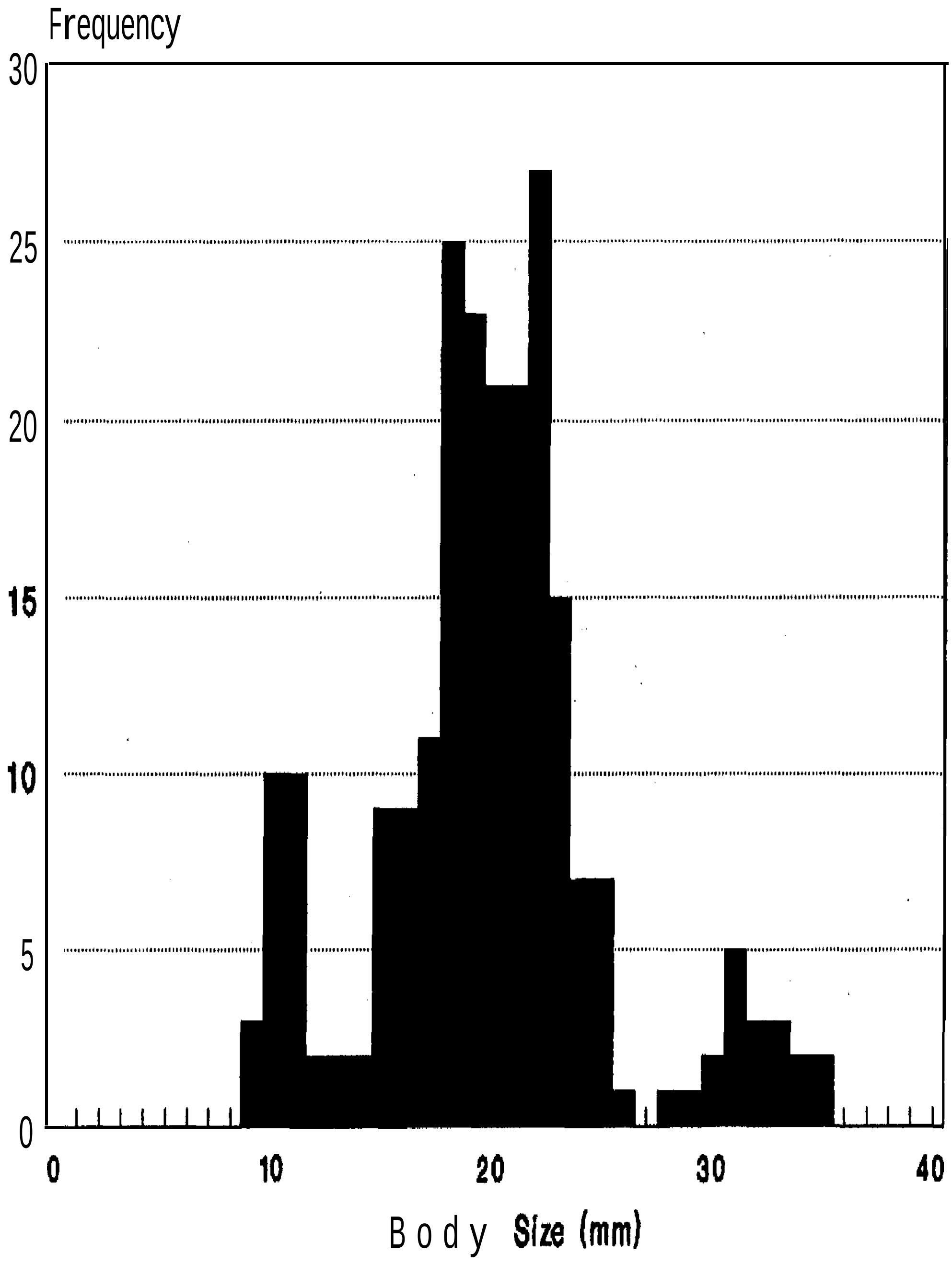

Figure 8. Size frequency histogram illustrating the tri-model distribution of *Mysis relicta* in recent samples from Flathead Lake. Data are from female andimmature individuals captured in May, 1987.

year differences with one-way analysis of variance (Table 1). Both males and females collected in the fall of 1987 were significantly smaller than their counterparts collected in 1986 or 1988 ($p < 0.0001$). M. relicta collected in fall 1986 were not significantly different in size from those collected in fall 1988.

Table 1, Size differences (mm) by.sex for Mysis relicta sampled in 1986, 1987, and 1988.

Year of capture	Male				Female			
	mean	95% CI		n	mean	95% CI		n
1986	9.19	8.97	9.42	133	9.32	9.09	9.54	132
1987	8.20	8.02	8.38	215	8.73	8.56	8.90	227
1988	9.32	9.11	9.53	161	9.59	9.36	9.82	132

MYSIS SIZE FREQUENCY

Each size-group in the size-frequency histograms for M. relicta is composed of both males and females, and apparently represents a distinct age-group.

Flathead Lake M. relicta (at least during the time period 1983 through. 1986) release their young mostly during late winter and early spring and most M. relicta reproduce in the end of their first year with some individuals surviving to reproduce at about two years (Bukantis and Bukantis 1987). The May 1987 histogram shows, three M. relicta age classes. In order of increasing size, they are: recently released young, the parents of those young, and the relatively rare II+ group. As these groups mature into the fall, the rarest, largest size class dies out, the major group which had primarily been responsible for release of the young of the year now becomes the largest size class., and is also relatively rare. The young of the year are the numerical dominants in the fall-and are starting to mature reproductively at that time.

The smallest size class of M. relicta makes a greater contribution to the overall population each' year (Figure 9). Increasing importance of this class may indicate a change from the initial M. relicta life history pattern of a one year life cycle with release of young occurring in late winter and early spring. M. relicta populations are well known for exhibiting differing life history features in different environments (Morgan, 1980). The new size class showing up in Flathead Lake may represent later-released young from parents which require more than one year to produce a brood. Flathead Lake M. relicta may also be exhibiting a life history similar to that of Lake Michigan, where at least some individuals reproduce a second time about 4 months after the initial release of young by.,other individuals in the population (Morgan and Beeton, 1978). Lake Paajarvii in Sweden has M. relicta populations which

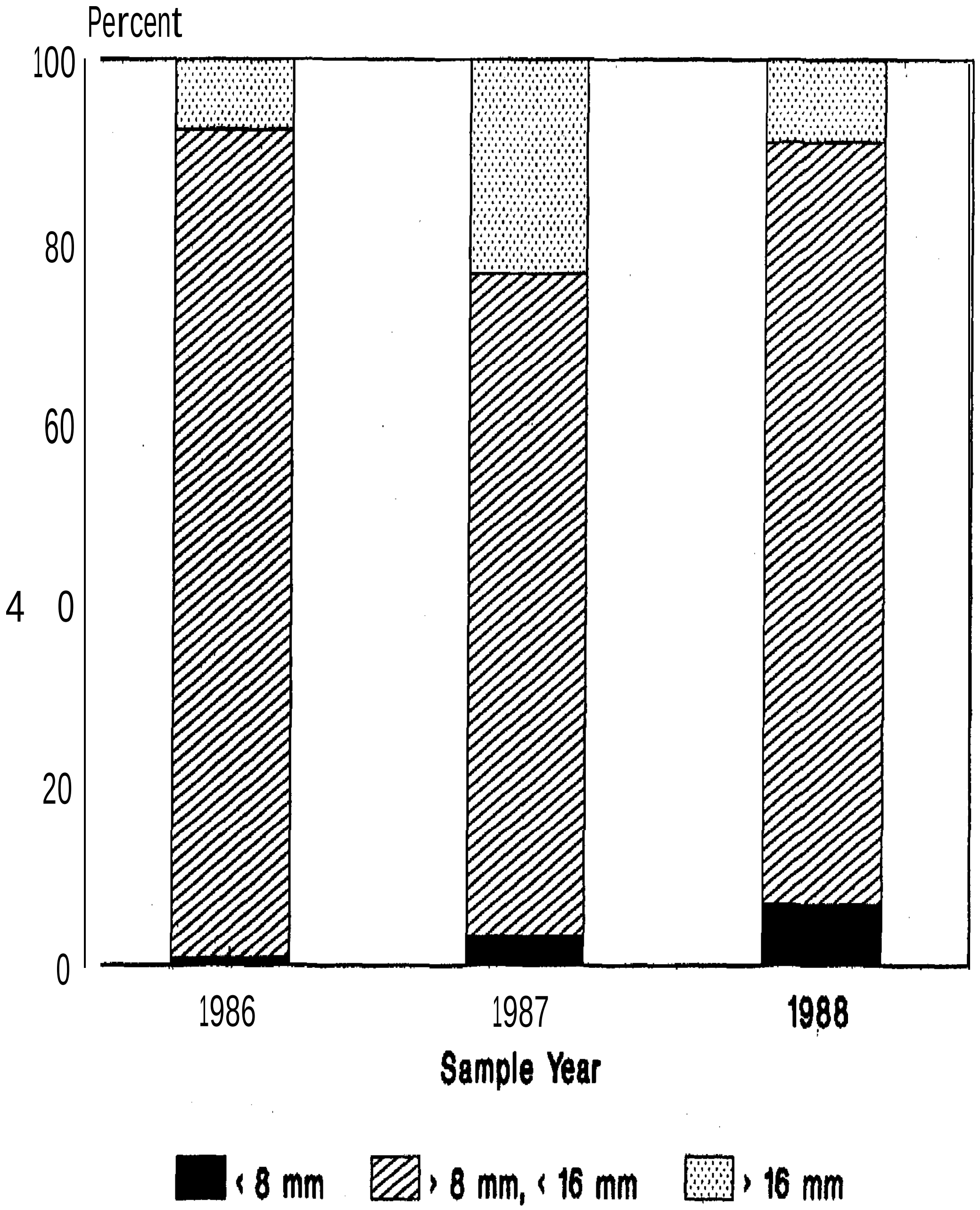

Figure 9. Percent contribution of three size classes of Mysis relicta to total Mysis density in Flathead Lake in 1986, 1987, and 1988.

breed at different times of the year (Hakala, 1978). Perhaps Flathead Lake M. relicta are altering their life history, strategy in response to limiting resources now that the population may have reached its carrying capacity.

The M. relicta population has declined in the last two years. This is due to either a decline in recruitment, possibly from lowered fecundity due to resource limitation, or to an increase in mortality rate, and was likely due to both. Unfortunately, we have no data on fecundity. However we do have a rough estimate of mortality. The largest size class each year represents the survivors-.of the two smallest size classes of the year before. We calculate survivorship estimates of 0.22 for between 1986 and 1987, and 0.055 for between 1987 and 1988. There was an increasing mortality rate on M. relicta, which may have been due to the increasing incidence of M. relicta in the diets of lake. trout, bull trout and lake whitefish.

Spawning Escapement

1988

There were no kokanee spawners observed in McDonald Creek on the first survey date, September 21, 1988. On October 4, 1988 we counted 120 kokanee, and on October 18, 1988 we counted 110 kokanee. In the previous four years the spawning run into McDonald Creek had begun by mid-September, and had peaked by the middle of October.

About 300 to 400 kokanee were observed in the Flathead River, between Columbia Falls and the South Fork confluence, on the first aerial survey on September 22, 1988. We did not observe any schools of kokanee in the river on the last aerial survey on October 20, 1988.

We counted about 25 kokanee redds in Skidoo Bay during the survey of the Flathead Lake shoreline conducted on November 22, 1988. We also counted 30 kokanee in the Swan River, below Bigfork Dam, when we snorkeled that reach on October 12,. 1988.

'Although the 1988 spawning escapement, surveys were not as rigorous as in previous years, the data indicate that the total spawning run in the Flathead system was less than 1000 fish. We had unverified reports of occasional sport harvest of kokanee in Flathead Lake during the summer of 1988, but no significant fishery developed:.

1989

On October 17, 1989; we counted 20 redds in McDonald Creek, evenly distributed above and below Apgar Bridge. Glacier National Parks personnel had observed SO-100 adults near Apgar bridge prior to our survey, but 'we did not see any kokanee in the creek. Cur survey included all of McDonald Creek from the outlet of Lake McDonald to confluence with the Middle Fork of the Flathead River.

We did not see any kokanee schools during the September 25 and October 18, 1989 aerial surveys of the mainstem Flathead River.

We counted 22 redds on November 7, 1989, at "House of Mystery", one of 8 sites examined in the Flathead River that historically have been important kokanee spawning areas. At this same location we saw 3 or 4 kokanee in the river. No other fish or redds were observed.

No kokanee or redds were observed along the Flathead Lake lakeshore, or in the Swan River below Bigfork Dam, during surveys on November 9 and 21, 1989. The only kokanee reported spawning in these areas in 1989 were a few fish observed in the Swan River below Bigfork Dam on December 11.

The 1988 and 1989 escapements are the lowest on record for kokanee in the Flathead system. We believe that predation and competition for a diminished food base probably contributed to increased mortality of kokanee in the last several years, accounting for the very low number of spawners.

Hydroacoustic Assessment of Fish Abundance

We estimated that 4.599 million fish larger than 50 mm were living in Flathead Lake in November, 1988. This figure translates to an overall fish density of 120.2 fish/hectare (48.7 fish/acre). The estimate includes fish species that inhabit the limnetic zone of the lake, i.e. bull trout, lake trout, kokanee, lake whitefish, and pygmy whitefish (Prosonium coulteri). This estimate excludes those species living primarily in the littoral zone, i.e. cutthroat trout (Salmo clarki), yellow perch (Perca flavescens), minnows (Cyprinidae), and suckers (Catostomidae). The extent to which some of these littoral species, e.g. cutthroat trout and northern squawfish (Ptvchocheilus oreaonensis), also inhabit the limnetic zone is not fully understood. But we did not capture these littoral species in gill nets or trawl hauls. Between 1979 and 1983 acoustic estimates of the density of 8 to 14 inch kokanee in Flathead Lake ranged from 15.71 to 22.96 fish per surface acre (Hanzel 1984). It is difficult to compare these historic estimates with the 1988 figure because of differences in acoustic equipment.

Fish density varied from 0.7197 to 2.3762 fish/100 m^2 among the nine strata (Table 2). The highest fish density occurred in the shoreline areas of the east and southern part of Flathead Lake (stratum 9). The lowest average density occurred in Big Arm (stratum 7). Fish density along individual transects ranged from 0.2678 fish/100 m^2 (transect 1D) to 5.2968 fish/100 m^2 (the eastern half of transect 1A). Fish detected within 2 m of the bottom comprised a significant part of the total fish density along all of the transects (Table 3). Fish density and mean target strengths for each transect and depth stratum are tabulated in Appendix B.

Estimating the variance of hydroacoustic estimates of fish abundance is a complex statistical task because variance in sampling volume arid target strength estimates, sampling transects which are not mutually independent, and incomplete knowledge of fish distribution enter into the analysis. We chose instead to present a simple estimates of the coefficient of variation (CV^2) of fish density in four types of habitat. In stratum 1, the northwest corner of Flathead Lake where fish density is highly variable, CV^2 was 0.351, which corresponds to a standard error (SE) of 59.2 percent about the average density. Among all the shoreline strata combines, CV^2 was 0.0435, or a SE of 20.9 percent. In the combined limnetic strata CV^2 was 0.0195 or S.E. of 14.0

Table 2. Average fish density midwater and near-bottom in nine sample strata designated from the 1988 dual-beam hydro acoustic survey of Flathead Lake.

Stratum	Density (fish/100 m^2) Midwater	Bottom	Total
1 --	0.9883	0.4319	1.4202
2	1.1176	0.5435	1.6611
3	0.5080	0.4161	0.9241
4	1.2804	0.1339	1.4143
S	1.1231	0.1585	1.3716
6	0.8879	0.3066	1.1945
7	0.4832	0.2365'	0.7197
8	1.4963	0.2378	I.7341
9	1.9071	0.4691	2.3762

Table 3. Hydroacoustic estimates of midwater, near-bottom, and total fish abundance in nine strata designated from the 1988 dual-beam survey of Flathead Lake.

Stratum	Lake Area (ha)	Number of Fish Midwater	Near-bottom	Total
1	4,353.3	344,749	182,456	527,205
2	2,961.0	281,514	158,806	440,320
3	1,164.6	47,229	48,459	95,688
4	8,348.3	807,834	111,098	918,932
5	2,114.8	173,907	33,520	207,427
6	244.3	19,380	7,328	26,708
7	4,116.6	154,274	97,358	251,632
8	13,828.0	1,581,401	328,077	1,909,478
9	1,120.6	169,236	52,571	221.897
Totals	38,251.S	3,598,904	1,019,673	4,599,287

percent, and in Big Arm, where overall fish density was lowest, CV^2 was .0361, or S.E. of 19.0 percent. These coefficients of variation approximate variance in fish density, but cannot be applied to estimate the confidence intervals about the estimate of total fish abundance.

Net sampling in selected strata indicated that bull trout comprised from 1.3 to 4.8 percent of the limnetic fish community (Table 4). Lake trout made up from 6.7 to 25.0 percent, and lake whitefish from 61.9 to 91.9 percent. We did not collect any lake trout in area 1 (Somers/Lakeside) in the fall, though they were present earlier in the spring and summer. Kokanee were collected only from area 1 and area 9 (Skidoo Bay shoreline), where they comprised 5.6 percent and 14.3 percent of the catch, respectively. If we assume that a large proportion of the kokanee population was aggregated in these two strata, a minimum estimate of the total population would be 65,000 fish. But the probability of kokanee being more widely distributed throughout the lake at very low density suggests that this figure is a very conservative estimate. A much more intensive sampling effort would be required to validate this estimate of kokanee abundance and to estimate the relative abundance of the different age classes of this species. Pygmy whitefish were sampled only in area 1, where they comprised 23.8 percent of the catch. The absence of cyprinids, yellow perch, and catostomids in the fall samples validates our assumption that these species do not comprise a significant part of the limnetic fish community.

Estimates of the abundance of fish over 500 mm long (approximately 5 pounds), based on the distribution of acoustic target strengths, were derived because of increasing interest in the fishery for trophy lake trout and bull trout. Among the nine strata these large fish comprised from 1.4 to 7.6 percent of total fish community. We estimated that 27,700 fish fell into this large size class. This is a minimum estimate because of uncertainty about the range of target strengths returned by large fish (see discussion in Methods.). Net sampling indicated that lake trout were three to six times more abundant than bull trout. This would suggest that at least 23,000 lake trout, five pounds and larger, are present in Flathead Lake. If the sport harvest of trophy lake trout is measured in the future, the estimates of abundance could be useful in assessing harvest-related mortality and in setting.bag limits.

Because we were not able to establish the distribution of young of the year (YOY) and yearling kokanee by trawl surveys, the hydroacoustic survey could not estimate the overall abundance of juvenile kokanee. Considerable effort was expended in attempting to locate juvenile kokanee in the north end of Flathead Lake during the summer and fall of 1988. Juvenile kokanee were found in the areas we sampled in previous years. Very few YOY kokanee were caught, as discussed later in the Food Habits discussion. We did capture yearling fish earlier in the summer in area l-5, but not at the time of the hydracoustic survey.

The total number of kokanee fry reared in four MDFWP hatcheries and planted in Flathead Lake from mid-June to mid-July, 1988 was 2.5 million.' We conclude that these fish either experienced very high mortality during the summer or dispersed into a low overall density. Either result would preclude the consistently successful sampling necessary for estimation of their abundance. In Lake Pend Oreille, Idaho, Bowles (1988) found that less than 15

Table 4. Estimates of the abundance of linmetic species in nine depth strata designated from the 1988 dual-beam hydroacoustic survey of Flathead Lake.

	Number of Fish					
Stratum	Bull Trout (percent)	Lake Trout (percent)	Kokanee (percent)	Lake Whitefish (percent)	Pygmy Whitefish (percent)	Fish >500 mm TL (percent)
1	8,400 (1.6)	0 (0)	33,100 (5.6)	363,800 (69.0)	125,500 (2.4)	3,598 (1.5)
2	18,500 (4.2)	110,100 (2.5)	____ ____	311,700 (70.8)	____ ____	6,554 (3.5)
3	1,200 (1.3)	64,400 (6.7)	____ ____	87,900 (92.0)	____	3,400 (6.9)
4	not verified by species					4,620 (3.8)
5	not verified by species					777 (0.8)
6	350 (1.3)	1,800 (6.7)	____ ____	24,500 (92.0)	____ ____	488 (6.5)
7	7,550 (3.0)	22,900 (9.1)	____ ____	221,200 (87.9)	____	5,455 (4.5)
8	not verified by species					2,615 (0.23)
9	10,550 (4.8)	35,200 (15.9)	31,700 (14.3)	137,350 (61.9)	____	228 (1.4)
Totals	46,550	176,400	64,800	1,146,450	125,500	27,735

percent of YOY kokanee survived their first summer. If mortality of this magnitude occurred in Flathead Lake, it is logical that the survivors in the fall would be extremely difficult to sample quantitatively.

The limited samples of all age classes of kokanee that we have collected in Flathead Lake over the last three years do not indicate that food availability is directly limiting survival. Small changes in the growth rate of yearling fish were documented in 1987. It is possible that decreased food availability is causing starvation mortality, but that the few surviving fish, because of different behavior or distribution, did not show the effect.

We think it more likely that increased predation explains the increase in kokanee mortality observed in the last three years. Juvenile lake trout are known to feed on M. relicta in Flathead Lake. Recruitment of juvenile lake trout may have increased because of the increased availability of M. relicta. Even if the lake trout population is stable, the hydroacoustic estimate of their overall abundance suggests that lake trout predation alone could account for the high mortality of kokanee. Support of this conclusion depends on further quantification of lake trout food habits and distribution, i.e. the age at which lake trout become piscivorous and their predatory impact in the areas of Flathead Lake where hatchery-reared kokanee are released in the summer.

Hatchery supplementation of the kokanee fishery has been limited by brood stock availability and shortage of suitable hatchery facilities. Natural production of kokanee fry in the Flathead system ranged from 10 to 15 million fry in the early 1980's. The three recent adult year class failures, 1986, 1987, and 1988, were recruited from YOY year classes in 1982, 1983, and 1984 that numbered at least ten million. The limiting factor, whether it was related to food availability, competition, or predation, reduced fry-to-adult survival of these strong YOY year classes. Intuitively, it would be highly unlikely for YOY year classes of 2 to 4 million hatchery-reared fry to survive in appreciable numbers, unless for some reason their viability were much higher than that of wild fry. The hatchery releases have been timed to coincide with high food availability in the lake, but our studies have not been able to find any evidence that hatchery-reared fry have improved recruitment in Flathead Lake.

Age and Growth

KOKANEE

We caught 68 kokanee in 1988, while attempting primarily to sample younger fish (age 0+ and I+). Our main sampling objective was to quantify juvenile survival rates in conjunction with recent fry stocking efforts.

All kokanee were captured in the northwest section of Flathead Lake (Area 1, Figure 2), and most fish (60) were caught in mid-water trawls. Kokanee were captured in all months from April through December, but sample size varied considerably (Table 5).

Table 5. Age composition of kokanee collected in 1988 by number captured each month.

Age Class	Month of Canture									Totals
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
0+	2	0	0	0	0	3	0	0	0	5
I+	0	5	28		15	8	0	1	0	48
II+	0	1	10		0	1	2	6	1	12
III+	0	0	0	0	0	1	0	2	0	3
Totals	2	6	29	1	5	13	2	9	1	68

Age 0+ kokanee averaged 97.5 mm total length at capture (SE = 9.31 mm). This average length is larger ($p < 0.01$) than mean lengths of fish captured in either 1986 or 1987 (Beattie et al. 1988), indicating better growth in 1988. However, with similar gear, technique, and sampling effort, we caught many more age 0+ fish in 1986 (30) and 1987 (51). This observation suggests total numbers of age 0+ fish may have declined in 1988.

Age I+ kokanee averaged 155.8 mm total length at capture (SE = 3.90 mm). Mean lengths in samples increased continuously in our summer collections, with largest relative-length increases occurring in July (Figure 10). Growth rate may have been less in August and early September, although the large length increase observed in November suggests kokanee grew rapidly through fall. The small number of age I+ fish caught in most months requires caution interpreting this seasonal growth pattern as typical of kokanee in 1988. The late year trend especially is suspect since sample size is especially small. The summer trend, however, is quite similar to growth patterns identified for age I+ kokanee collected in 1986 and 1987 (Beattie et al. 1988). Rapid length increases in summer correspond to increasing water temperature and abundance of <u>D. thorata</u>. These factors likely contribute to consistent summer growth patterns from year to year.

Age II+ kokanee averaged 229.8 mm total length at capture (SE = 9.69 mm). Seasonal growth trends appear similar to age I+ fish (Figure 10), although no age II+ fish were captured in July or August. September samples again suggest reduced growth rate in early fall. Mean length was larger in October, but unlike age I+ samples, growth rate declined as age II+ fish entered winter months. Since'most (75 percent) kokanee captured later than September were age II+, reduced growth entering winter may more accurately describe seasonal growth patterns in 1988. Less growth in winter would be consistent with historical observations of kokanee during ice covered years in Flathead Lake (MDFWP - unpublished data).

Age III+ kokanee averaged 288.7 mm total length at capture (SE = 6.67 mm). Comparison of mean length at capture with all age groups in 1988 (Figure 11) suggests good growth for each year class, including oldest fish. This possibility is consistent with data that individual kokanee grow well even

Figure 10. Monthly trend in mean length at capture for age 0+ and I+ kokanee caught in 1988,

after the introduction of M. relicta (Hanzel 1984, appendix E). Adult kokanee captured in recent years have been in good physical condition (Hanzel et al 1988), although Beattie et al. (1988) did report growth rate declines for younger fish (age 0+ and I+) between 1986 and 1987.

Comparison of relative growth rates estimated from length at capture, with same rates determined from calculated lengths at annulus formation (Figure 12), suggests growth rate was increasing as age III+ fish continued in their fourth year of life. However, the pattern may not be significant. Variation- in growth rate would be expected each year, and we know from long term data that age III+ and IV+ kokanee in Flathead Lake have not been consistently distinguished from size differences along (Hansel 1984).

We believe' individual kokanee are growing as well or better than before the introduction of M. relicta. If this is a correct assessment, better growth could be explained by decreasing numbers of fish in the population. Strong density dependent growth relationships have been noted for kokanee in the Flathead system for many years, even providing the basis for a model to estimate year class strength from average length of female spawners (Fraley and McMullin 1984). This explanation of recent growth patterns is confounded by simultaneous reductions in available food (Beattie et al. 1985, Beattie and Clancey 1987,. Bukantis and Bukantis 1987, Beattie and Clancey 1988), but kokanee losses are large (e.g. more than 99 percent loss in escapement between 1985 and 1987 - Beattie et al. 1988). Less intraspecific competition for lake resources seems likely, despite declining food abundance.

LAKE WHITEFISH

Four-hundred eighty-three lake whitefish were examined from samples taken in 1986, 1987, and 1988. Lake whitefish were captured in all areas of the lake where sampling was attempted, indicating greater abundance and widespread distribution compared with kokanee. Captures were evenly distributed between net types: 65 five percent of lake whitefish collected were caught in gill nets, the rest were caught in mid-water trawls. Because lake whitefish captures were often an indirect result of sampling for kokanee, most fish (74 percent) were collected in the northwest section of the lake. Sampling became concentrated in this area as the project progressed because it was here that most kokanee coiild be caught.

The oldest lake whitefish captured were VIII+ years, but age composition of all samples is skewed strongly towards much younger ages (Table 6). Approximately 80 percent of fish in combined lake whitefish samples were age III+ or younger. In contrast, age VI+, VII+ and VIII+ fish account for just 6 percent of total numbers collected. Age composition of samples reflects project emphasis to capture young kokanee. Older lake whitefish are not frequently taken in mid-water trawls commonly used to sample kokanee. A complete description of lake whitefish age and growth requires a larger sample of older fish. This deficiency is being compensated in part from other work (University of Montana, M.S. thesis project in progress). Our samples are sufficient 'at this time, however, to 'assess lake whitefish at ages when we feel interactions between species would be most critical to kokanee success.

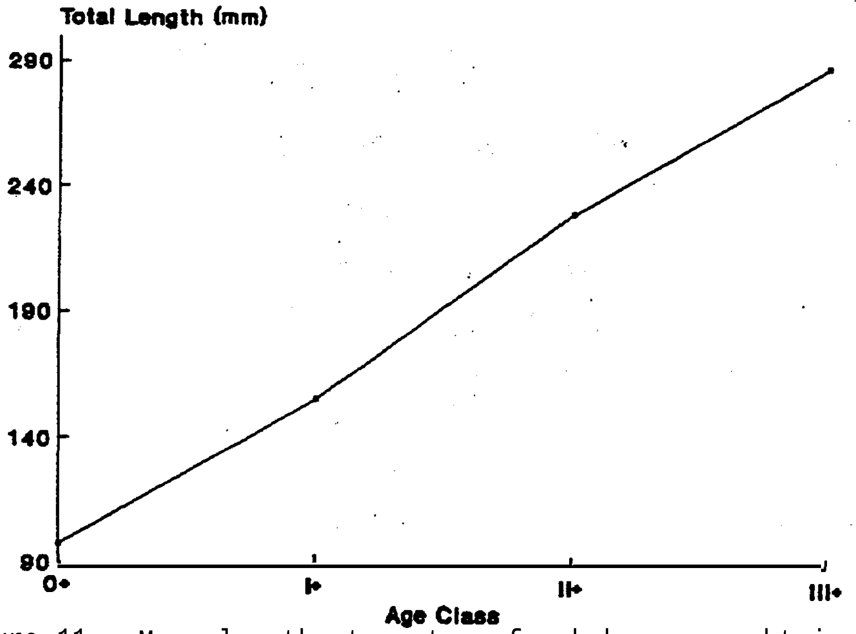

Figure 11. Mean length at capture for kokanee caught in 1988.

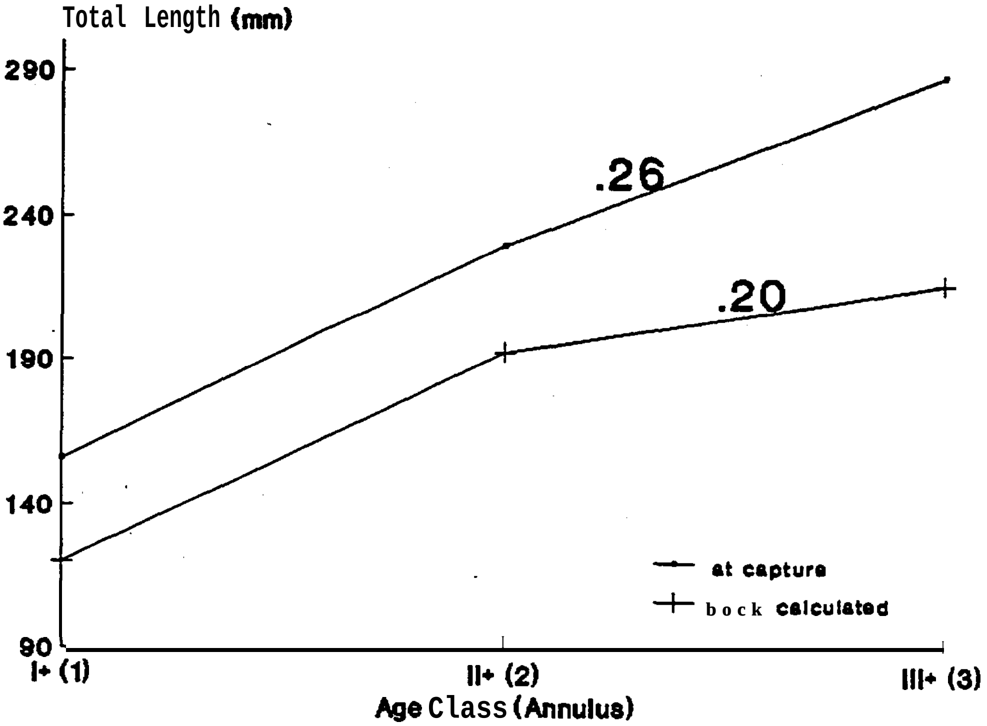

Figure 12. Comparison of mean length at capture and mean length at annulus formation for kokanee caught in 1988.

Table 6. **Age composition of lake whitefish collected in 1986, 1987, and 1988 by number caught each year.**

Age Class	Year of Capture			
	1986	1987	1988	Total
0+	15	29	15	59
I+	38	27	48	113
II+	38	55	38	131
III+	28	12	36	76
IV+	17	13	4	34
V+	15	19	7	41
VI+	14	4	5	23
VII+	3	1	0	4
VIII+	2	1	0	2
TOTALS	170	160	153	483

Mean lengths at capture by age class each year (Figure 13, Table 7) indicate largest growth gains occurred during first four years of life. Growth rate slows after age IV+, the age when lake whitefish in Flathead Lake typically reach maturity (Bjorklund 1953, Hanzel et al. 1989). With three exceptions, mean length at capture was equivalent ($p > 0.05$) for same age classes each year, suggesting very stable growth in the lake. Exceptions include age I+ and II+ fish caught in 1988 which were larger on average ($p < 0.001$) than same age groups captured in either 1986 or 1987, and age IV+ fish caught in 1987 which were larger ($p < 0.015$) than same age fish in 1986.

Comparison of mean lengths at capture pooled by sample months suggests that seasonal growth patterns are quite different for youngest fish (age 0+ and I+) and older sub-adults (age II+ and III+). Mean length increased rapidly for age I+ fish in spring, and both age 0+ and I+ samples indicate rapid growth during summer (Figure 14, Table 8). Average length for age II+ and III+ fish also increased rapidly in spring, but growth rate apparently declined from July into winter months. Our data suggest size selective mortality for older sub-adults in Flathead Lake; indicated by the smaller average lengths in our samples each month (Figure 15, Table 9). Although we believe that gear selectivity probably explains the result, we can not identify any change in our sampling procedures that would introduce this systematic bias. We also can not explain at this time what would cause increased mortality of larger members of a cohort, if,-the phenomenon suggested is a biological reality in the lake..

Recent well documented changes in zooplankton communities in.Flathead Lake (Potter 1978, Bukantis and Bukantis 1987, Beattie et al. 1988) have significant implications for changing food relationships in the lake. However, comparison of mean lengths at annulus formation calculated from pre and post-*M. relicta* scale collections indicates length gains for lake whitefish remain surprisingly similar (Figure 16). Mean calculated lengths at annulus are equivalent ($p > 0.05$) for the same age classes, except that age 0+ and I+ fish are smaller on average ($p < 0.001$) in the 1980s than was true before the introduction of *M. relicta*.

Data from both populations fit the von Bertalanffy model well (Figure 17). Walford growth transformations displayed excellent linear relationships, with correlation coefficients of 0.993141 and 0.991825 respectively for the pre-*H. relicta* samples and samples collected after *M. relicta* was established. Walford lines developed-from these regressions are:

$$\text{Length at age } t+1 = 0.865538(\text{length at age } t) + 83.1161$$

for pre-*M. relicta* samples, and

$$\text{Length at age } t+1 = 0.822379(\text{length at age } t) + 106.772$$

for samples collected after the shrimp was introduced to Flathead Lake.

The equations yield theoretical maximum lengths of 618.14 mm for fish during the late 1960s and 1970, and 601.12 mm for fish in the 1980s. These theoretical lengths appear reasonable compared with recent observations of lake whitefish in Flathead Lake, and suggest little change in growth potential despite recent perturbations in the lake. This does not mean, however, that the lake whitefish population is unaffected in recent years. Smaller size of

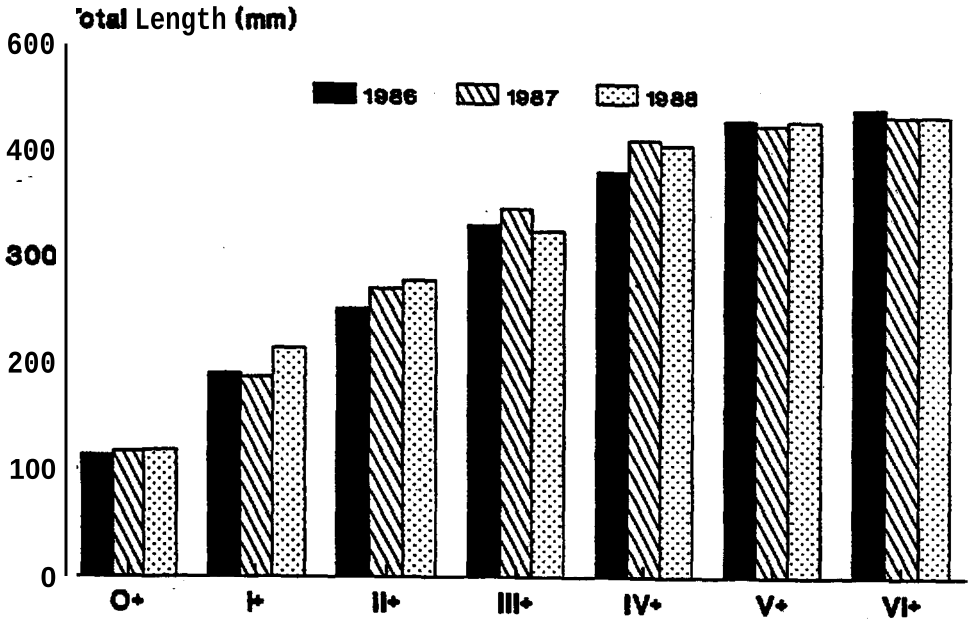

Figure 13. Mean length at capture for lake whitefish captured in 1986, 1987, and 1988.

Table 7. Mean total length at capture (mm) for lake whitefish caught in 1986, 1987, and 1988.

Year of Capture		Age Class						
		0+	I+	II+	III+	IV+	V+	VI+
1986	length	113.5	190.1	252.0	329.6	381.4	428.7	438.9
	(SE)	(5.27)	(3.11)	(4.78)	(5.26)	(8.03)	(4.38)	(4.17)
1987	length	116.7	186.3	270.7	345.1	409.5	423.7	431.5
	(SE)	(3.07)	(3.06)	(3.58)	(7.35)	(6.17)	(10.20)	(26.50)
1988	length	118.2	213.3	277.5	323.6	405.0	427.4	431.2
	(SE	(1.53)	(4.43)	(6.57)	(7.09)	(16.32)	(9.17)	(6.24)

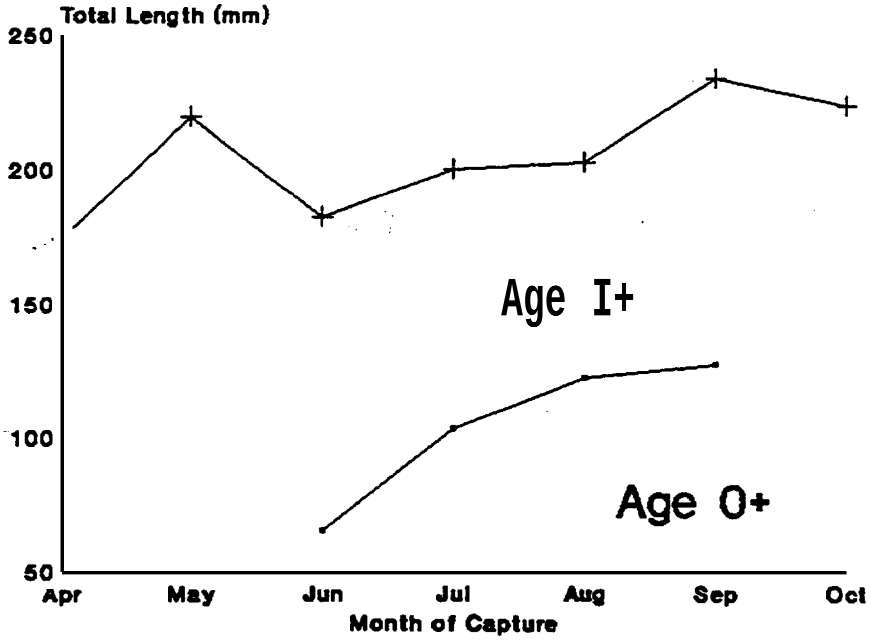

Figure 14. Monthly trend in mean length at capture for age 0+ and I+ lake whitefish caught in 1986, 1987, and 1988.

Table 8. **Mean total length at capture (mm) by sample month: age 0+ and I+ lake whitefish caught 1986, 1987, and 1988.**

Age class		Month of Capture						
		Apr	May	Jun	Jul	Aug	Sep	Oct
0+	length	---	---	65	102.9	122.4	127.2	---
	(SE)	---	---	(5.00)	(3.45)	(1.15)	(3.92)	---
I+	length	173.8	219.0	182.3	200.1	203.1	233.9	224.1
	(SE)	(5.00)	(11.72)	(3.49)	(8.99)	(3.63)	(3.66)	(2.32)
					3	↑		

~~0.5%~~ 6%   4.5%   ~~[illegible]~~

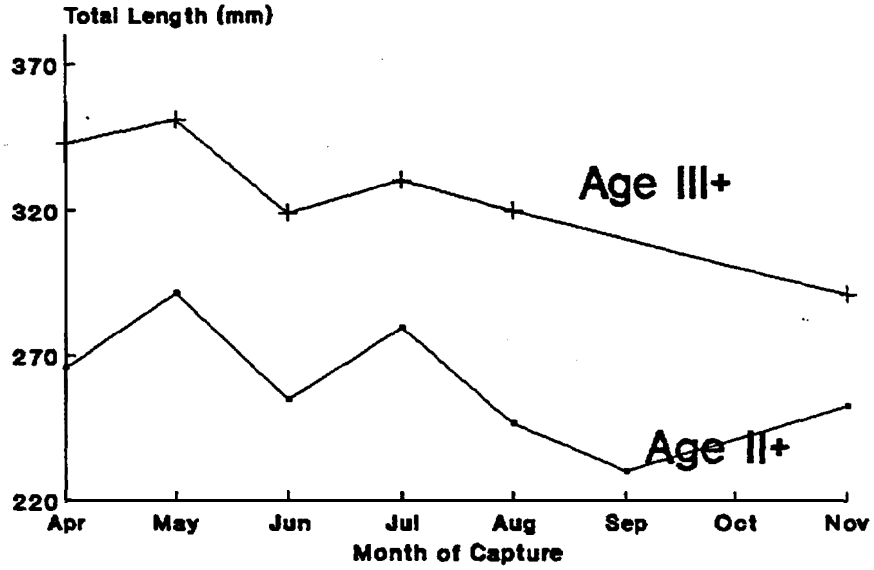

Figure 15. Monthly trend in mean length at capture for age II+ ad III+ lake whitefish caught in 1986, 1987, and 1988.

Table 9. Mean total length at capture (mm) by sample month: age II+ and III+ lake whitefish caught in 1986, 1987, and 1988.

Age Class		Month of Capture							
		Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
II+	length	265.6	291.2	254.8	279.5	246.5	230.0*	——	252.5
	(SE)	(5.05)	(6.33)'	(5.64)	(3.94)	(7.38)	——	——	(4.83)
III+'	length	342.9	351.4	319.0	330.4	320.0	——	——	290.8
	(SE)	(4.86)	(7.64)	(22.18)'	(5.51)	(22.20)	--	——	(9.11)

* Single fish

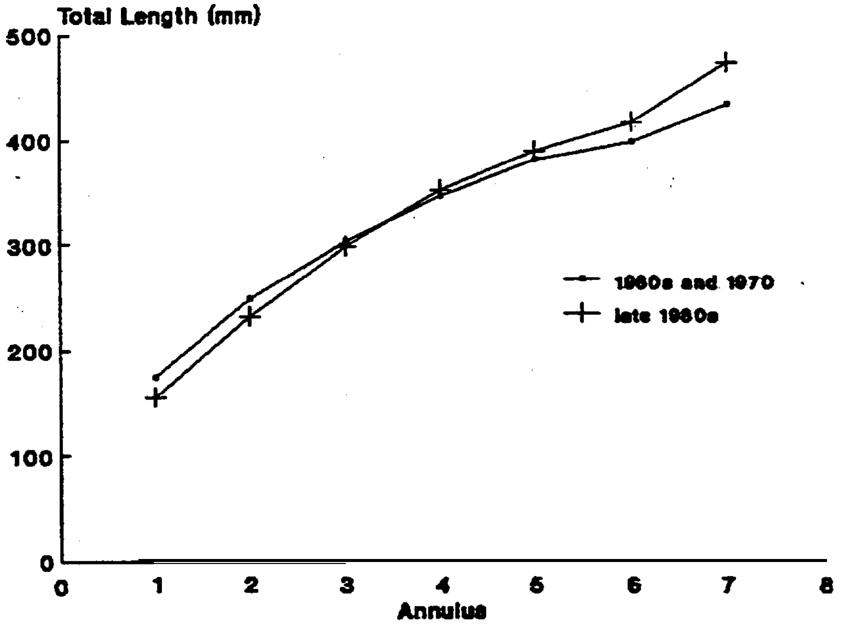

Figure 16. Mean calculated length at annulus formation for lake whitefish before and after introduction of Mysis relicta to Flathead Lake.

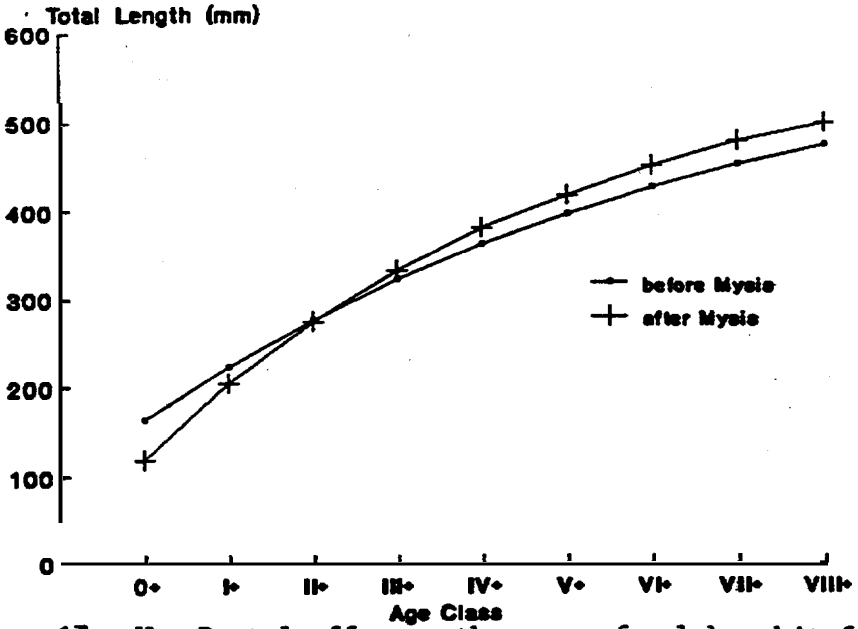

Figure 17. Von Bertalanffy growth curves for lake whitefish before and after the introduction of Mysis relicta to Flathead Lake.

youngest fish, and lower theoretical growth potential, are consistent with an increasing population. Young fish may be smaller in response to increasing numbers in the population. As developed below, von Bertalanffy growth coefficients indicate that lake whitefish growth rate is slightly higher following introduction of M. relicta. If true, the ultimate size realized as fish grow older would be expected to be less, since faster growing fish tend to attain smaller maximum sizes. Although it is still possible that factors limiting size at youngest age will detrimentally affect the lake whitefish population in coming years, at present this possibility seems unlikely. Some growth compensation is suggested for older year groups by a tendency to be larger on average ('although $p > 0.05$) than same age fish before M. relicta entered the lake. In addition, youngest fish have increased average length between 1987 and 1988.

Correlation coefficients from least squares regressions of ln(loo-Lt) on age were -0.996818 and -0.994765 respectively for pre M. relicta samples, and samples collected after introduction of the shrimp. These coefficients again suggest the appropriateness of the von Bertalanffy growth model in describing these populations. In same order, linear relationships were determined to be:

$$\ln(l_{oo}-L_t) = 6.11566 - 0.141646(\text{age } t)$$

and

$$\ln(l_{oo}-L_t) = 6.17943 - 0.194024(\text{age } t).$$

These equations provide the basis for estimating remaining von Bertalanffy parameters. Final von Bertalanffy growth modelsfor the two populations were determined to be:

$$L_t = 618.13821\,[1-e^{(-0.144404)(t+2.1959821)}]$$

for samples pooled from the 1960s and 1970, and,

$$L_t = 601.12262\,[1-e^{(-0.1955539(t+1.1293706)}]$$

for samples pooled from the late 1980s.

Lake whitefish apparently contrast with kokanee population responses to recent changes in the lake. Lake whitefish are.still abundant, and their numbers may be increasing since introduction of M. relicta. Much of this contrast is likely explained by different consequences of changing lake trophic relationships for each species. Unlike kokanee, lake whitefish have a predominantly benthic oriented life history (Van Oosten and Deason 1939, Smith 1952, Edsall 1960, Brown 1971, Scott and Crossman 1973). Lake whitefish use a variety of foods other than zooplankton, and diet changes as fish grow older. It seems reasonable that fish which are less dependent on zooplankton will respond less drastically to altered zooplankton abundance. Perhaps for these reasons, reduced zooplankton abundance, and subsequent feeding responses of all fish in the lake, do not seem to result in lower lake whitefish survival. New food items, including M. relicta, might actually benefit lake whitefish growth., This possibility is supported by slightly faster growth rates following M. relicta introduction to'the lake.

At present, the 1988 hydroacoustic survey reported here is the only data quantifying size of the lake whitefish population in Flathead bake. Although a similar survey was conducted in 1989, data from which to assess population responses are not yet available. It seems likely that changed food relationships have affected numbers of lake whitefish in the lake. Smaller average length for lake whitefish at young age may indicate an expanding population, with reduced growth a consequence of lower juvenile mortality, and individual responses to greater number of fish. Recent observations of sport anglers and other lake users support the contention that lake whitefish numbers have increased in recent years. However, it is still possible that reduced growth at young age reflects genuine growth limitations. Continued close monitoring of fish populations will be required to establish the direction of population trends.

Food Habits

KOKANEE

Fifty-seven kokanee captured in 1988 retained identifiable stomach contents. The majority of these fish (48) were age I+. Only 5 age 0+, 3 age II+, and 1 age III+ fish were available for diet analyses (Table 10).

Yearling Fish

A single fish captured in April contained only D. thorata and dipteran insects. Stomachs from fish collected in May suggest a diversifying diet in spring, including other large zooplankton species, and fewer dipteran insects. A single adult M. relicta (> 10 mm total length) was also identified in one fish caught in May. In June, stomachs predominantly contained D. thorata, although fish still incorporated a diversity of other food items,. From July through October, stomach contents were almost exclusively D. thorata.

The marked tendency towards less diverse diet entering summer, and the almost exclusive use of D. thorata from mid summer through fall, is the same pattern identified for yearling kpkanee, in 1986 and 1987 (Beattie et al. 1988). This pattern is likely explained in part by the influence and behavior of the Flathead and Swan Rivers, particularly as they affect the northwest section of Flathead Lake. Increasing diet diversity from April to May corresponds to increasing river inputs with spring run-off from the upstream drainage.?.. Flowing water carries food items directly from the rivers, and lifts items already in the lake into the upper water column. where kokanee typically feed. In addition, many food items that kokanee otherwise strongly select (e.g. D. thorata) are at very low densities, in the lake at this time (Figure 6), perhaps influencing fish to incorporate more diverse food items. Increasing incorporation of D. thorata in early summer corresponds to increasing abundance of this organism in Flathead Lake. Strong selection (Strauss L > 0.9) for D. thorata continued, however, long after abundance of this cladoceran peaked and declined.

Table 10. Food items as percent of total stomach contents for kokanee captured in 1988.

Age 0+

m[a]	n[b]	D.thorata	B.longirostris	D.bicuspidatus	E.nevadensis	L.ashlandii	Other[c]
4	1	1	3	56	0	0	40
9	I	99	1	0	0	0	0
10	3	99.5	0.2	0.1	0.3	0	0

Age I+

m	n	D.thorata	B.longirostris	D.bicuspidatus	E.nevadensis	L.ashlandii	Other
		62					
4	1	72	0	0	0	0	38
5	6		x.3	16	1	2.i	8.5
6	32	87	1.3	1.2	9.9	0.5.	0.1
7	1	100	.0	0	0	0	0
8	3	100	0	0	0	0	0
9	2	99.6	0	0.4	0	0	0
10	3	99.6	0	0.2	0	0.2	0

Age II+

m	n	D.thorata	B.longirostris	D.bicuspidatus	E.nevadensis	L.ashlandii	Other
6	1	100	0	0	0	0	0
10	1	99.2	0	0	0.6	0	0.2
I l	l	100	0	0	0	0	0

Age III+

m	n	D.thorata	B.longirostris	D.bicuspidatus	E.nevadensis	L.ashlandii	Other
5	1	96	0	3	0	0	1

---

[a] Calendar month (1 = January, 12 = December)
[b] Number of stomachs with identifiable contents
[c] Insects (Diptera, Coleoptera, Homoptera)

Other Age Classes

Sample size is small, but remaining age classes generally reflect the same diet progression observed for age I+ kokanee. Spring and early summer samples contained a greater variety of food items, with D. thorata predominant in all collections made later than June.

Although D. thorata was present in all stomachs, regardless of age class or month in which a fish was captured, age 0+ kokanee consumed relatively fewer of these cladocerans than did other age classes in the spring. This pattern appears typical of kokanee in Flathead Lake (Leathe and Graham 1982). Since age 0+ fish readily caught faster moving copepods in the spring, less incorporation of D. thorata suggests a limited ability to filter volumes of water comparable to older fish. One possibility is that smaller fish are simply weaker swimmers, which lowers encounter rates when the cladoceran is at low density. Alternatively, smaller fish may be restricted in their ability to use some areas of the lake, either by influence of older year classes, or other species in the lake.

LAKE WHITEFISH

One hundred nine stomachs from lake whitefish captured in 1988 retained identifiable contents. Most fish were age 0+ or I+ (32 and 49 respectively), a consequence of project emphasis this year to sample younger age classes. Twenty five older sub-adults (age II+ and III+), 1 age V+, and 2 age VI+ fish were also available for diet analyses (Table 11).

Younn of the Year

In July, D. thorata was by far the most common food item.in lake whitefish stomachs, totaling no less than 78 percent of all contents for any individual fish. E. nevadensis, B. loneirostris, D. bicusnidatus-thomasi and L. ashlandii were present in low numbers, and a few stomachs also contained small numbers of dipteran insects.

In August, diet was more diverse, including benthic items, although contents were still dominated by zooplankton. Stomachs predominantly contained D. thorata, with chydorids, dipteran insects, ostracods, trichopteran insects, D. bicusnidatus-thomasi and pelecypods all present in low numbers. A small proportion of stomach contents consisted of partially digested zooplankton that could not be further identified. Single B. longirostris were also identified in two stomachs.

Stomach contents from fish captured in September were primarily D. thorata, with D. bicusoidatus-thomasi and a small number of dipteran insects comprising remaining food items ingested. The large percentage of D. thorata in stomachs suggests strong selection ($L > 0.9$) for this food item despite low numbers of D. thorata in the lake. By October, a single sample indicated a diet switch to copepods, with D. bicusoidatus-thomasi agrazing influence is not as significant as the impacts of M. relicta.

Table 11. Food items as percent of total stomach contents for lake whitefish collected in 1988.

Age 0+

m[a]	n[b]	D.thorata	Other Zooplankton[c]	Pelycypoda	Ostracoda	Diptera	Other[d]
7	18	98	1.2	0	0	0.15	0.65
8	8	76	10	1.2	2.8	7.2	2.8
9	5	99	0.6	0	0	0.04	0.36
10	1	0	72	11	0	1.4	14.6

Age I+

m	n	D.thorata	Other Zooplankton	Pelecypoda	Ostracoda	Diptera	Other
4	4	1	0.8	23	29	36	10.2
6	4	69	0.4	1.9	0.4	2.5	27.8
7	1	100	0	0	0	0	0
8	14	99	0.3	0.2	0.1	0.07	0.33
9	16	99	0.34	0	0.6	0.06	0
10	9	69	0.8	I2	7	8.2	3
11	1	19	0	0	0	0	81

Age II+ and III+

m	n	D.thorata	Other Zooplankton	Pelecypoda	Ostracoda	Diptera	Other
4	2	0	0	19.5	19.5	56	5
6	12	67	0	2.2	5	5	21.8
7	2	98	0	1	0	0.6	0.33
8	4	99	0	0.3	0.1	0.07	0.53
9	3	100	0	0	0	0	0
10	1	93	0	1	1.4	0	4.6
11	1	7.7	78.3	I5	0	0	0

Age V+

m	n	D.thorata	Other Zooplankton	Felecypoda	Ostracoda	Diptera	other
11	1	40	0	0	0	0	60

Age VI+

m	n	D.thorata	Other Zooplankton	Felecypoda	Ostracoda	Diptera	Other
5	1	6	1	23	0	42	28
11	1	0	0.3	4.7	0	0	95*

---

[a] Calendar month (1 = January, 12 = December)

[b] Number of stomachs with identifiable contents

[c] _B. longirostris, D. bicuspidatus-thomasi, E. nevadensis, L. ashlandii_

[d] Insects (Hemiptera, Hymenoptera, Coleoptera), ephippia, Chydoridae, unspecified zooplankton and insect parts

* _Mysis relicta_ (81 total)

Yearling. Fish

Stomachs from lake whitefish collected in April contained large numbers of dipteran insects, ostracods, and pelecypods. Ephippia were fairly common (8 percent). About two percent of total contents was D. thorata and D. bicuspidatus-thomasi. Two adult M. relicta were also identified in one stomach.

Stomachs in June suggest increasing use of D. thorata as abundance of this cladoceran increased in the lake, but diet was still diverse. Epphippia (25 percent) were common. Dipteran insects and pelecypods were much less numerous than in April. Remaining contents were E. nevadensis, B. longirostris, D. bicusnidatus-thomasi, trichopteran insects, ostracods, and a few (<1 percent) unidentified zooplankton parts. Three adult M. relicta were identified in one stomach;

By August, D. thorata was a very common food item in fish stomachs. Trichopteran insects (0.38 percent) and pelecypods were next most common. Despite obviously strong selection for d. thorata (L >0.89), a variety of other food items were incorporated by these fish in small numbers. These last items inlcude B. longirostris, L. ashlandii, ephippia, chydorids, dipteran insects, and ostracods.

Samples from September suggest feeding patterns quite similar to those identified in August. D. thorata dominated contents, with ostracods and dipteran insects next most common. B. longirostris, 1. ashlandii, D. bicuspidatus-thomasi, trichopteran insects, and pelecypods were all present at very low numbers.

October samples suggest less incorporation of D. thorata, and increasing incorporation of benthic food items, including pelecypods and ostracods. Dipteran insects were also common. Ephippia (1.3 percent)) and D. bicuspidatus-thomasi were present in small numbers. All other food items each totaled less than one percent of all food item sin stomachs. These rarer items included B. loneirostris, L ashlandii, and a variety of different insects (coleopterans, hemipterans).

The single November sample contained numerous ephippia (81 percent), suggesting that cladocerans continued to constitute an important part of the diet although lake whitefish were shifting to a more bottom-oriented feeding behavior.

Older Sub-adults

Stomach samples from age II+ and III+ lake whitefish were pooled to increase total number of observations for diet analyses. Incorporation was assessed both by age, and size class, with no meaningful difference in the amount ingested or season of use detected for most food items. A single exception was the presence of adult M. relicta (2 and 10 respectively) in two stomachs from age III+ fish caught in April and November. One of these two age III+ fish caught in April and November. One of these two age III+ fish exceeded maximum lengths observed 'for age II+ fish. No M. relicta were identified in stomachs from age II+ fish in 1988 samples.

Stomachs from fish in April predominantly contained dipteran insects, with ostracods and pelecypods also common. About four percent of contents were ephippia. Stomachs also contained a small number of unspecified insect parts.

By June, samples indicate increasing use of zooplankton in place of foods more commonly associated with the lake bottom. Most contents were no D. thorata and ephippia (22 percent). Dipteran insects, ostracods, and pelecypods were less frequent than in April, with remaining contents comprised of trichopteran insects (2.5 percent), and unidentified zooplankton parts.

In July, contents were almost exclusively D. thorata, with dipteran insects, pelecypods, and unspecified zooplankton and insect parts also present in small numbers.

Samples collected in August indicate continued strong selection (L- >0.9) for D. thorata. Diet included small numbers of pelecypods, ostracods, dipteran insects, trichopteran insects, and ephippia.

Very few samples from age II+ and III+ fish captured in the fall were available for diet analyses. Fish collected in September contained only D. thorata. A single stomach from October contained about five percent ephippia, in addition to entire D. thorata, ostracods, and a few pelecypods and unidentified zooplankton parts. By November, a single stomach suggests that older sub-adults were shifting diet emphasis as D. thorata abundance declined. D. bicusnidatus was most common (77 percent of contents). Pelecypods were relatively numerous, with remaining contents comprised of D. thorata and unspecified zooplankton parts.

Adults

Sample size is small, but diet of older lake whitefish differs from younger fish in at least one significant respect: M. relicta was incorporated in large numbers by adult fish in the fall. M. relicta would seem an important food supplement for adult'fish as they enter spawning season; a supplement for adult fish as they enter spawning season; a supplement for which no equivalent food item existed prior to introduction of the shrimp. an enhanced food base at this critical time would likely contribute to a more successful reproductive effort, and may partly explain why lake whitefish numbers seem to be increasing in recent years.

Zooplankton Diet

KOKANEE

Five large zooplankton species comprised over 99 percent of all food items identified in kokanee stomachs: D. thorata, B. loneirostris, D. bicuspidatus-thomasi, L. ashlandii, and E. nevadensis. Among these five species, D. thorata was by far most common, comprising 89 percent of total diet, and no less than 87 percent of zooplankton ingested for any age or size class examined (Table 12). This result is consistent-with well-documented strong selection for D. thorata by kokanee in Flathead Lake (Leathe and Graham 1982,

Table 12. Percent contribution of five large zooplankton species to the zooplankton diet of kokanee captured in 1988.

Zooplankton Species	Age Class			
	O+	I+	II+	III+
D.thorata	93.65	87.93	99.73	96.63
B.longirostris	0.43	2.19	0.0	0.0
E.nevadensis	0.05	5.90	0.27	0.0
D.ashlandii	5.82	3.31	0.0	3.37
L.bicuspidatus-thomasi	0.05,	0.69	0.0	0.0

Beattie et al. 1988), although influenced by the fact that most samples were collected only in months when D. thorata was available. Only seven stomachs contained less than 50 percent D. thorata; all of these samples were from fish captured in spring or early summer.

The winter. diet of kokanee in Flathead Lake has historically been dominated by copepods (Leathe and Graham 1982, Beattie et al. 1988), shifting to D. thorata as abundance of this cladoceran increases in the spring and early summer. although sample size is'small, contents suggesst a simiiar 'diet progression occurred in 1988. However, the characteristic switch to almost exclusive"incorporation fo D. thorata occurred earlier in 1988 than reported in 1986 or 1987 (Beattie et, al. 1988). In May, 76 percent of all food items ingested were D. thorata comprising more than 99 percent of stomach contents in all months that followed. Earlier selection for D. thorata may be related to timing of peak abundance of the cladoceran, since peak densities also cocurred earlier in 1988 than in previous years (Figure 6). It is possible too, that lower total densities of other zooplankton species influenced timing of selection for d. thorata, although at this time we do not know the mechanism by which zoopalnkton densities might determine feeding behavior. The switch to D. thorata occurred earlier in 1988, for example, despite a lower total D. thorata abundance.

E. nevadensis, D. bicusnidatus-thomasi, B. longirostris, and 1. ashlandii contributed respectively 5.2 percent, 3.2 percent, 2 percent, and 0.6 percent of remaining large zooplankton stomach contents for combined age classes. Stomachs contained greatest variety of these rarer food items in spring, with each on average identified in over 50 percent of all stomachs examined. Frequency of occurrence decreased in summer, and increased again as fish entered fall and winter months (Figure 18). All four species contributed less to total diet that was reported in 1986 or 1987 (Beattie et al. 1988). This last result may again be due to lower total densities of most of these food items in 1988.

LAKE WHITEFISH

At young age, lake whitefish incorporated large numbers of the same dominant zooplankton species as kokanee. D. thorata, B. longirostris, E. nevadensis, D. bicusnidatus-thomasi, and 1. ashlandii, collectively comprised 98.7 percent of total food items ingested by age)+ fish, and about 93 percent of total numbers for age I+ fish. Among these five species, D. thorata was incorporated by both young-of-the-year and yearlings (Table 13). Like kokanee, younger lake whitefish also displayed a shift in diet to D. thorata as abundance of this cladocrean increased in the lake.

B. longirostris, E. nevadensis, D. bicusnidatus-thomasi, and L. ashlandii occurred most frequently in stomachs in spring and fall. Excluding samples comprised of single fish, frequency of occurrence was always less than 0.5 in any sample month (Figure 19). Low overall frequency of occurrence suggests that these zooplankton species are less important in the diet of young lake whitefish than was true for kokanee. But, unlike kokanee, young lake whitefish incorporate these food items persistently in summer months. It is possible that less commonly incorporated zooplankton species are an important part of the young lake whitefish diet at this time. Young lake whitefish also

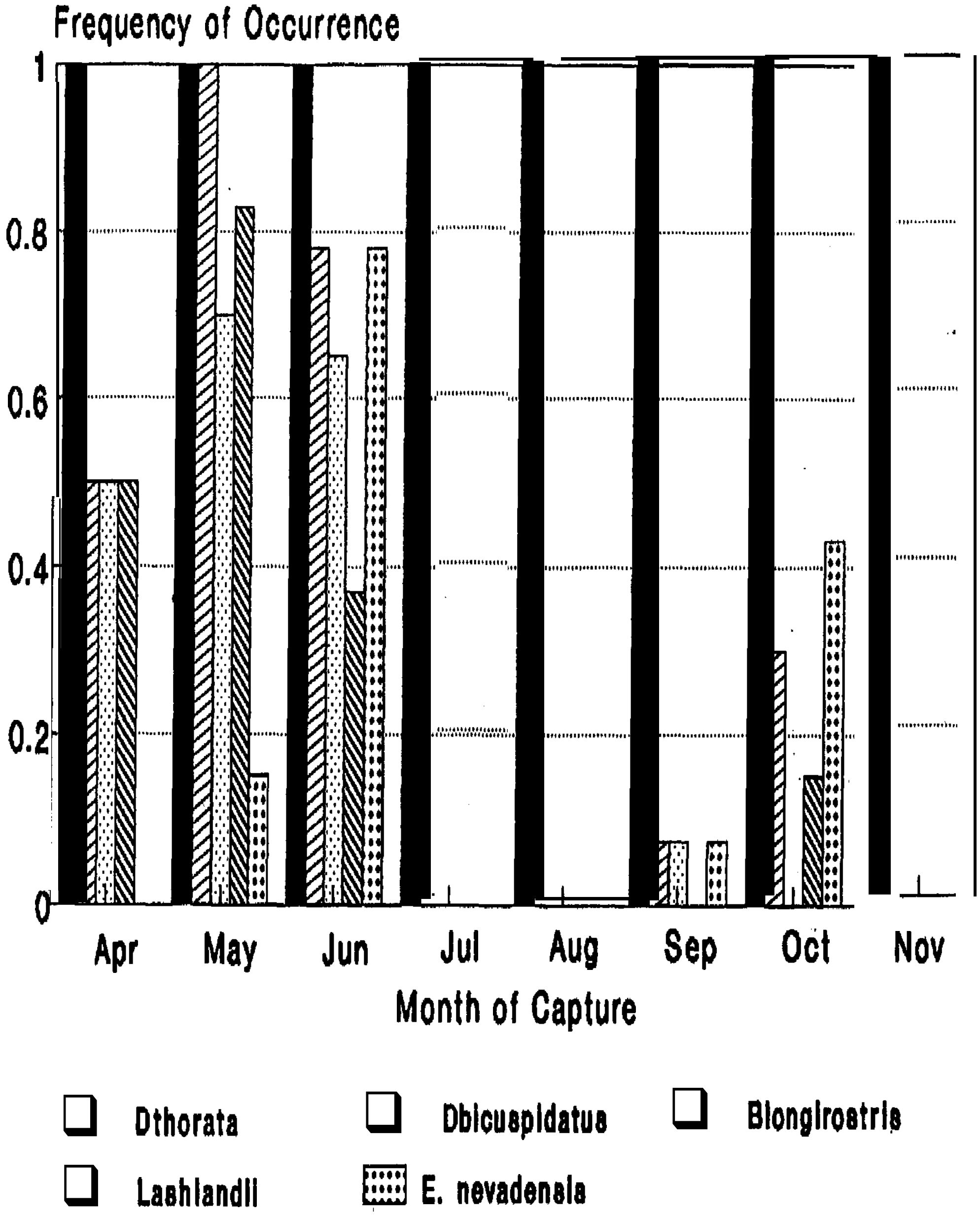

Figure 18. Proportion of kokanee incorporating five large zooplankton species by month in which fish were collected.

Table 13. Percent contribution of five large zooplankton species to the zooplankton diet of lake whitefish captured in 1988.

Zooplankton Species	Age Class					
	0+	I+	II+	III+	V+	VI+
D.thorata	98.62	99.83	100	100	100	100
B.longirostris	0.39	0.03	0	0	0	0
E.nevadensis	0.36	0.02	0	0	0	0
D.ashlandii	0.44	0.07	0	0	0	0
L.bicuspidatus-thomasi	0.19	0.05	0	0	0	0

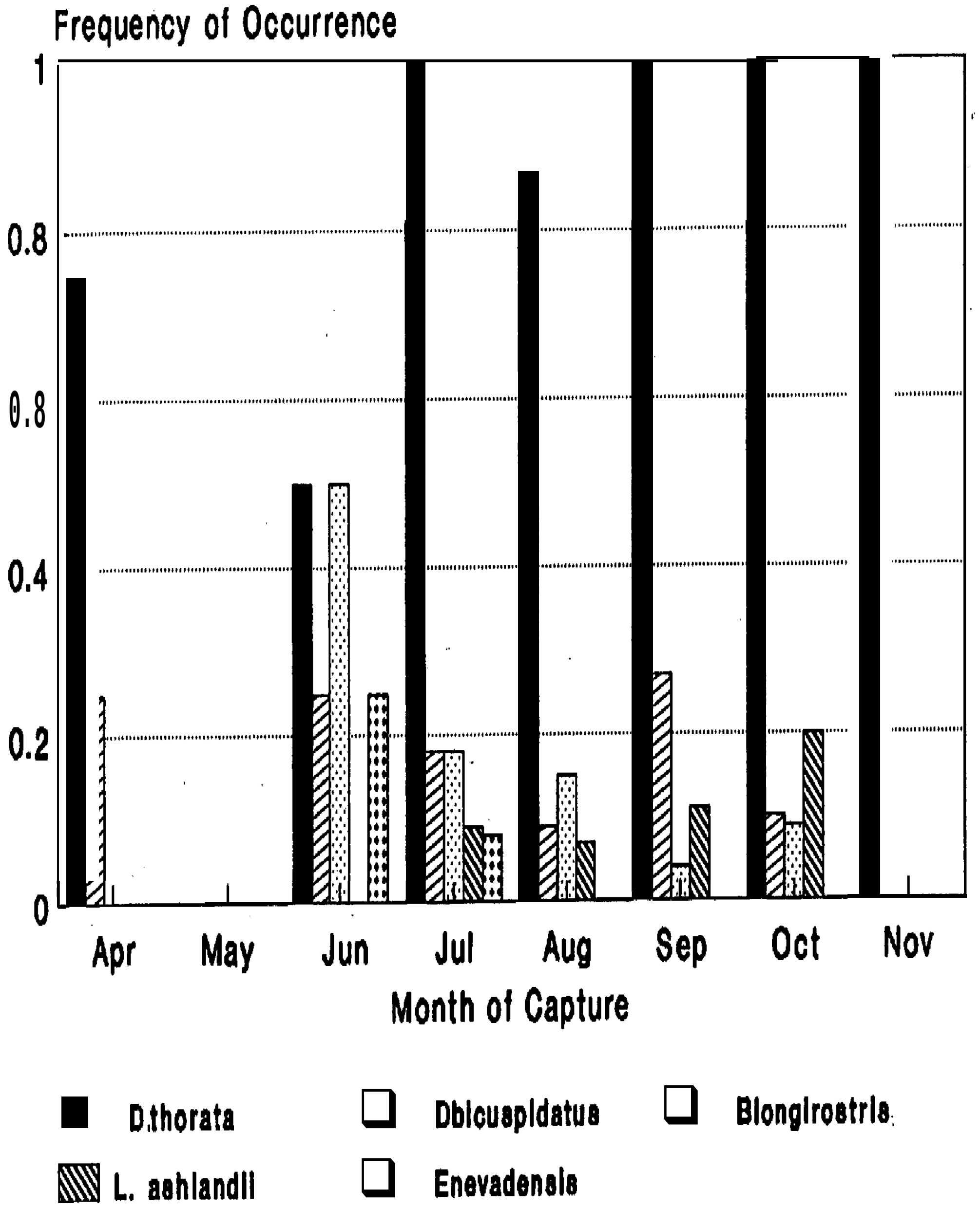

Figure 19. Proportion of age 0+ and I+ lake whitefish incorporating five large zooplankton species by month in which fish were collected.

might not feed as selectively on zoopalnkton as kokanee, although very strong selection for D. thorata from mid-summer through fall suggests similar feeding behavior.

Older Sub-adults

'The only large zooplankton species identified in stomach from age II+ and III+ fish was D. thorata. Although frequency of occurrence in all samples was only 0.64, D. thorata still accounted for 92 percent of total numbers of food items ingested. Patterns of seasonal use were similar to younger lake whitefish and kokanee, with incorporation greatest as the abundance of D. thorata increased in spring and summer.

Adults

Two of three fish older than IV+ years contained low numbers of D. thorata. No other large zooplankton species were identified in these stomachs, suggesting that zooplankton species in general no longer constituted a significant part of the diet. D. thorata accounted for less than one percent of total numbers of food items ingested by adult fish.

Zooplankton Size Selectivity

Average total lengths of D. thorata were larger ($p < 0.05$) in lake samples in August than in June, but size selection by fish was only weakly indicated in either month (Table 14).

In June, all age classes of kokanee and lake whitefish incorporated larger D. thorata in proportions slightly higher ($L < 0.16$) than their corresponding frequency in the lake. Since many of these larger cladocreans are adults, it is possible that fish grazing served to delay peak D. thorata numbers, at least until younger individuals reached reproductive maturity. In August, this pattern reversed, with smaller D. thorata positively selected, although again in proportions only slightly higher than their frequency in the lake ($L < 0.12$). Removing cladocerans at immature stages would likely contribute to rapid declines of D. thorata observed in August: losses from direct incorporation would be more significant because these individuals also fail to reproduce.

Because size selection was essentially random, our results suggest that kokanee and lake whitefish had limited influence on age structure of D. thorata population in 1988. Althouhg fish grazing has probably always been a factor in zooplankton dynamics in the lake, other lake conditions (temperature regime, nutrient availability, primary productivity) seem likely to exert greatest influence. Still, fish may now have a relatively larger role determining zooplankton numbers. We know that zooplankton abundance has decreased in recent years, and that this decrease is almost certainly the result of predation by M. relicta. However, despite lower M. relicta abundance in 1988 (Figure 7), total zooplankton densities also decreased (Figure 3). It is possible that this apparent anomaly is expalined in part by feeding behavior of fish. No data confirm this possibility, however, and at present, we

Table 14. Size 'selection for *Daphnia thorata* by kokanee and lake whitefish in 1988.

Lake zooplankton samples:

Sample month	Proportion (p_i) *D.thorata* less than 0.8 mm	Number of samples examined	Number of *D.thorata* measured
June	0.50	1	201
August	0.33	1	201

Fish stomach samples:

Species (age)	Sample month	Proportion (r_i) *D.thorata* < 0.8 mm	Number of stomachs examined	Number of *D.thorata* measured	Strauss Index (L)	SD
Kokanee						
(I+)	June	'0.45	5	733	-0.05	0.03975
(II+)	June	0.40	1	200	-0.10	0.04940
(I+)	August	0.44	3	421	0.11	0.04111
Lake whitefish						
(I+)	June	0.44	2	307	-0.07	0.04522
(II+)	June	0.35	2	400	-0.15	0.04259
(III+)	June	0.46	4	622	-0.04	0.04053
(0+)	August	0.41	5	480	0.08	0.04012
(I+)	August	0.37	4	800	0.03	0.03735
(II+)	August	0.38	2	131	0.05	0.05391
(III+)	August	0.41	1	200	0.08	0.04810

suspect that fish grazing influence is not as significant as the impacts of M. relicta.

Revised Kokanee Spawning Escapement and Harvest Estimates

. In previous reports (Beattie and Clancey 1987, Beattie et al. 1988) kokanee escapement and sport harvest in the Flathead drainage was estimated for all years that escapement data were available from this project. These data are records of kokanee performance during critical years when impacts of hydroelectric operations on spawning success were first documented (Fraley and Graham 1982, Decker-Hess and Graham 1982, Decker-Hess and McMullin 1983, Decker-Hess and Clancey 1984, Beattie et al. 1985, Clancey and Fraley 1986, Fraley et al. 1987, Fraley and Decker-Hess 1987), and when large scale ecological changes limiting kokanee survival were occurring in Flathead Lake (Bukantis and Bukantis 1987, Beattie et al. 1988). Because this information is central to understanding the fate of kokanee in Flathead Lake and its tributaries still open to fish passage, we have reexamined earlier assessments and made slight modifications. Our intention is to provide best estimates possible from available data (Tables 15, 16, 17).

We restricted harvest estimates to 1981 and 1985, the two years for which complete creel census data compliment spawner escapement surveys. We also added fish estimates for the Swan River below Bigfork Dam, and the Flathead lakeshore escapement.

Previously, McDonald Creek estimates used the largest number of fish counted in a survey as a minimum estimate of total escapement. Our revised estimates differ because we used different analyses for this data. For 1985, we summed the area under the escapement curve from 7 spawner counts that had been made at two week intervals. Fish numbers were estimated assuming a 30 day residence time (Fraley and McMullin 1984). In 1981, two spawner counts were made 28 days apart. We added these numbers assuming that all fish in the first survey had been replaced by the time the second survey was conducted. In both years the effect of these changes is to increase escapement estimates slightly, and reduce percent harvest figures, also by a small amount. Revised estimates should supersede all others, and are appropriately restricted to the two years in which complete harvest data were obtained.

Harvest estimates are large, particularly in 1981. It is possible that overfishing contributed to kokanee declines during these years. However, many fish are not counted in escapement surveys, which tends to maximize the apparent impact of sport fishing. Also, total escapement in McDonald Creek, where most recruitment to the Flathead fishery originated, was still excellent. Based on estimates of egg survival in McDonald Creek (Beattie and Clancey 1987), escapement in both years exceeded the number of fish that can make use of available gravels without conflict with other fish for spawning sites. Fry emigration to Flathead Lake was estimated to be 12.0 million in 1982 (Clancey and Fraley 1986), and 9.9 million in 1986 (Beattie and Clancey 1987) from McDonald Creek alone. -Even if maximum harvest estimates are assumed to reflect a complete loss of reproduction from harvested fish in 1981 and 1985; remaining recruitment was obviously high. The 12.0 million fry recruited in 1982 produced a record high spawning escapement in 1985 (Beattie et al. 1988), despite significant sport harvest indicated for the 1981 adult year class.

Table 15. Spawning escapement estimates for Flathead system kokanee in 1981 and 1985.

	1981	1985
McDonald Creek[a]	117,634	181,943
Main Stem Flathead River[b]	19,073	20,000
Whitefish River[b]	998	--
South Fork Flathead River[b]	720	2,071
Beaver-Deerlick Creeks[b]	1,723	1,826
Middle Fork Flathead River[b]	5,520	100
Flathead Lake[b]	1,565	2,775
Swan River[c]	--	1,350
TOTAL	147,233	210,065

Estimate Criteria:

[a] Spawner counts adjusted by 30 day residence time
[b] Redd counts (multiplied by 2.4)
[c] Survey in which greatest number of spawners were counted

Table 16. Harvest estimates for Flathead system kokanee in 1981 and 1985.

	Harvest Season			Harvest Total	Total III+ Year Class	Percent Harvest
	Winter	Summer	Fall			
1981	53,530	118,600	155,032	327,162	474,395	69
1985	50,810	126,293	15,575	192,678	402,743	48

Table 17 Trend counts of post harvest kokanee spawners in the Flathead River system, 1979-1989. Dashed lines indicate no count. Counts from 1986-1989 are not complete counts, so are not comparable to previous years.

	Estimated number of spawners										
	1979	1980	1981	1982	1983	1984	1985[c]	1986	1987	1988	1989
McDonald Creek[a]	65,000	49,500	105,500	30,965	34,306	86,729	122,875	21,450	320	120	60
Main stem[b] Flathead River	6,785	1,121	19,073	3,720	16,279	17,839	20,000	855	45	413[d]	---
Whitefish River[b]	---	1,022	998	1,836	1,272	2,359	---	---	---	---	---
South Fork[b] Flathead River	---	---	720	480	4,493	7,510	2,071	---	---	---	---
Beaver-Deerlick[b] Creeks	0	---	1,723	101	1	0	1,826	---	---	---	---
Middle Fork[b] Flathead River	---	---	5,520	1,802	1,330	400	100	---	---	---	---
Flathead Lakeshore	---	---	1,565	2,494	1,795	2,722	2,775	815	25	10	---
Swan River[a]	---	---	---	---	750	1,250	1,350	190	30	30	---
Total Trend Counts	71,785	51,643	131,534	41,398	60,226	118,809	150,997	23,310	426	603	60

[a] Live peak snorkel count plus dead fish.

[b] Estimated by multiplying redd counts by 2.4.

[c] Redd counting was difficult to accomplish due to fall flows 300 percent above normal and nearly complete ice formation in most areas before the completion of spawning. The count for the main stem is the estimated minimum number of spawners.

[d] Aerial count.

DISCUSSION

Lake whitefish are 'included in this summary at this time because-they seem to contrast with kokanee in response to M. relicta induced changes in the lake. We feel that this contrast provides useful insights into subsequent impacts on fish populations that could be anticipated when large scale reductions in pelagic food resources occur. In addition, young lake whitefish eat many large zooplankton that comprise the majority of kokanee diet. Reduced zooplankton numbers following the introduction of M. relicta suggest that lake whitefish--may now be a significant competitor for food affecting juvenile kokanee success (Beattie et al. 1988). As this project progressed; a large portion of our effort was redirected to understanding the extent to which kokanee-lake whitefish interactions might explain loss of kokanee in Flathead Lake.

Food Limitations and Competition

The effects of M. relicta introductions are well described in many lakes (e.g. Richards et al. 1978, Cooper and Goldman 1980, Rieman and Bowler 1980, Kinsten and Olsen 1981, Langeland 1981, Lasenby and Furst 1981, Grossnickle 1982, Nero and Sprules 1986, Bukantis and Bukantis 1987), and appear similar at least in a general pattern of reduced total zooplankton abundance, cladoceran losses, and shifts in timing of peak abundance for many zooplankton species. It seems reasonable that these impacts could be detrimental to planktivorous fish, and especially kokanee that primarily eat plankton throughout their life history. Several investigators have already suggested that loss of zooplankton to M. relicta has adversely affected kokanee populations in lakes they have examined (Richards et al. 1975, Morgan et al. 1978, Reiman and Falter 1981, Morgan et al. 1981, Bowles et al. 1988). In Montana, the same has been suggested in at least three lakes where M. relicta were recently established (Anderson and Domrose 1982, Rumsey 1986, Anderson 1987), including Flathead Lake (Beattie et al. 1988). In Lake Pend Oreille, Idaho, researchers also suggest that success in reestablishing kokanee by hatchery plants has been enhanced by waiting until cladoceran populations are at seasonal high numbers in the lake (Bowles et al. 1988). These results indicate that food abundance can be critical to kokanee success, and that impacts of M. relicta on zooplankton communities are sufficient to compromise kokanee survival and reproduction.

Lower zooplankton abundance caused by M. relicta predation suggests that competition among plankton feeding fish may intensify as food is less available. But whether or not this competition is a significant factor in kokanee declines remains uncertain. Many fish are planktivorous at some point in their life histories (Carlander 1969, Scott and Crossman 1973) including lake whitefish, lake trout, northern squawfish, peamouth minnows (Mylocheilus caurinus), and yellow perch in Flathead Lake (Leathe and Graham 1982). Lake, whitefish are implicated especially as competitors with kokanee because young fish occur in large numbers where kokanee were historically common, But similar distribution may simply be more apparent now that kokanee numbers are less. Also, mountain whitefish (Prosopium williamsoni) and pygmy whitefish in Flathead Lake have diets more similar to kokanee than lake whitefish (Leathe and Graham 1982).

We feel that lake whitefish numbers probably increased significantly in recent years, and if so, their feeding could contribute more to zooplankton losses caused by general feeding behavior of all plankton feeding fish. But even in this case, we have not determined that current zooplankton abundance is actually limiting for fish. No data establish that feeding by one species harms another. Swan Lake kokanee numbers remain stable despite.introducfion of M. relicta, and total zooplankton densities similar to Flathead Lake (Rumsey 1986).

Growth results suggest that food limitations do not exist for fish 'that attain the minimum size in our samples (60 mm), but our samples would include only fish that successfully overcome food "bottlenecks" if they occur. It is still possible that very young fish (perhaps larval forms) might have difficulty finding food at current zooplankton densities in Flathead Lake. A number of laboratory investigations 'demonstrate that larval survival for many fish is influenced by food density (e.g. Riley 1966, O'Connell and Raymond 1970, Wyatt 1972, Saksena and Houde 1972), and the related efficiency with which young fish locate and capture prey (e.g. Braum 1967 cited in May 1974). Feeding efficiency is often influenced by characteristics of prey organisms, including size, distribution, and motility in avoiding capture (Rosenthal and Hempel 1970, Confer and Blades 1974, Drenner et al. 1978, O'Brien 1979, Drenner et al. 1981). Since slow moving species of the genus Daohnia are particularly susceptible to M. relicta predation (Richards et al. 1975, Langeland 1981, Kinsten and Olsen 1981, Grossnickle 1982), and since peak abundance of these cladocerans has been delayed into summer since introduction of M. relicta in Flathead Lake (Bukantis and Bukantis 1987, Beattie et al. 1988), we suspect that food limitations, if they exist, would have greatest influence on kokanee survival during first feeding and early larval stages. We have not been able to test this idea by quantifying young kokanee survival. Apparently, too few fish remain in the lake to be consistently captured for this type of assessment.

Predation

Capturing kokanee has become progressively more difficult following the introduction of M relicta. This difficulty may be a consequence of smaller numbers of fish in the lake each year, kokanee dispersing to low overall densities, or fish occupying a relatively smaller area of the lake. It is likely that all of these factors affect kokanee distribution at this time.

The persistently high mortality rate among kokanee, and the precipitous recent decline in escapement, suggest that kokanee losses result from factors either lacking or not operating as detrimentally for kokanee before the introduction of M. relicta. Part of the explanation seems likely to be reduced zooplankton abundance and feeding stress on young fish. But significantly, introducing M. relicta does not always lead to loss of the kokanee fishery, even when similar reductions in the zooplankton assemblage occur (Rumsey 1988, Domrose 1989). At present, increased mortality from predation by other fish, perhaps in conjunction with lowered food abundance, seems most likely to explain all patterns observed. If true, predation may have a much larger role explaining kokanee losses than previously acknowledged.

Lower zooplankton densities in *M. relicta* impacted lakes suggest that kokanee must search more water to obtain the same food ration than was true before the shrimp was introduced. One consequence reasonably anticipated is higher mortality from predation. That predation risks can increase if schooling behavior changes is well established from many lines of research. Several mathematical models (e.g. Breder 1959, Brock and Riffenburgh 1960, Olson 1960) suggest that fish should run higher risks of predation when solitary than when living in groups. And theoretical results are corroborated by careful investigations that show that predators capture prey more efficiently as prey groups are less highly organized (Neil and Cullen 1974, Major 1978, Milinski 1977 cited in Morse 1980). Recent observations, although not yet confirmed, suggest that some kokanee predators (e.g. lake trout) are more numerous in Flathead Lake (Hanzel et al. 1988). It seems reasonable that more predators would kill more kokanee. And even if predator numbers do not change, increasing predator efficiency might account for limited distribution and fewer kokanee in the lake.

If increased predation explains the sudden kokanee losses in Flathead Lake, similar population collapses might be expected in systems with analogous predator populations. By same reasoning, dramatic loss would not be predicted in systems that lack these fish. In lakes we have examined, we now believe that lake trout have a central role in determining fate of kokanee populations after *M. relicta* introductions.

Twelve lakes in northwestern Montana with established kokanee populations were planted with *M. relicta* in 1968, 1975 and 1976 (Domrose 1982, Rumsey 1988). Introductions were made to supplement the food base, with particular interest in augmenting kokanee production. Later investigations confirmed *M. relicta* successfully established in five of these lakes (Rumsey 1988, Figure 20), and also an unintended occurrence in Flathead Lake (Leathe and Graham 1982). After shrimp populations were established, three lakes (including Flathead) experienced dramatic declines in kokanee numbers. Common to all lakes where kokanee populations collapsed was the presence of lake trout in the system; this same fish was absent from lakes in which kokanee persisted in significant numbers;.:' Interestingly, this pattern seems the same in lakes outside Montana (e.g. Morgan et al. 1978). One exception might be Lake Pend Oreille, Idaho, where kokanee numbers apparently collapsed after *M. relicta* was introduced (Bowler' et al. 1979) even though lake trout are present at very low numbers in that system. Significantly, however, this is also one of the few lakes we know where attempts to reestablish kokanee by hatchery supplementation have met with any success (Bowles et al. 1988).

Other predators would certainly contribute to kokanee losses following *M. relicta* introduction in Flathead Lake. In general, we expect that total predation pressure would increase as kokanee numbers decline. With continuing loss of youngest fish, perhaps exacerbated by limited food, smaller year classes would soon support all kokanee predators in the lake. However, lake trout seem especially likely to have had major impacts on kokanee numbers. Lake trout are known to strongly select kokanee as food (Leathe and Graham 1982), they are lake spawners with all but youngest age classes contributing to kokanee losses each year, and they are known to feed heavily on *M. relicta* (MDFWP unpublished data).

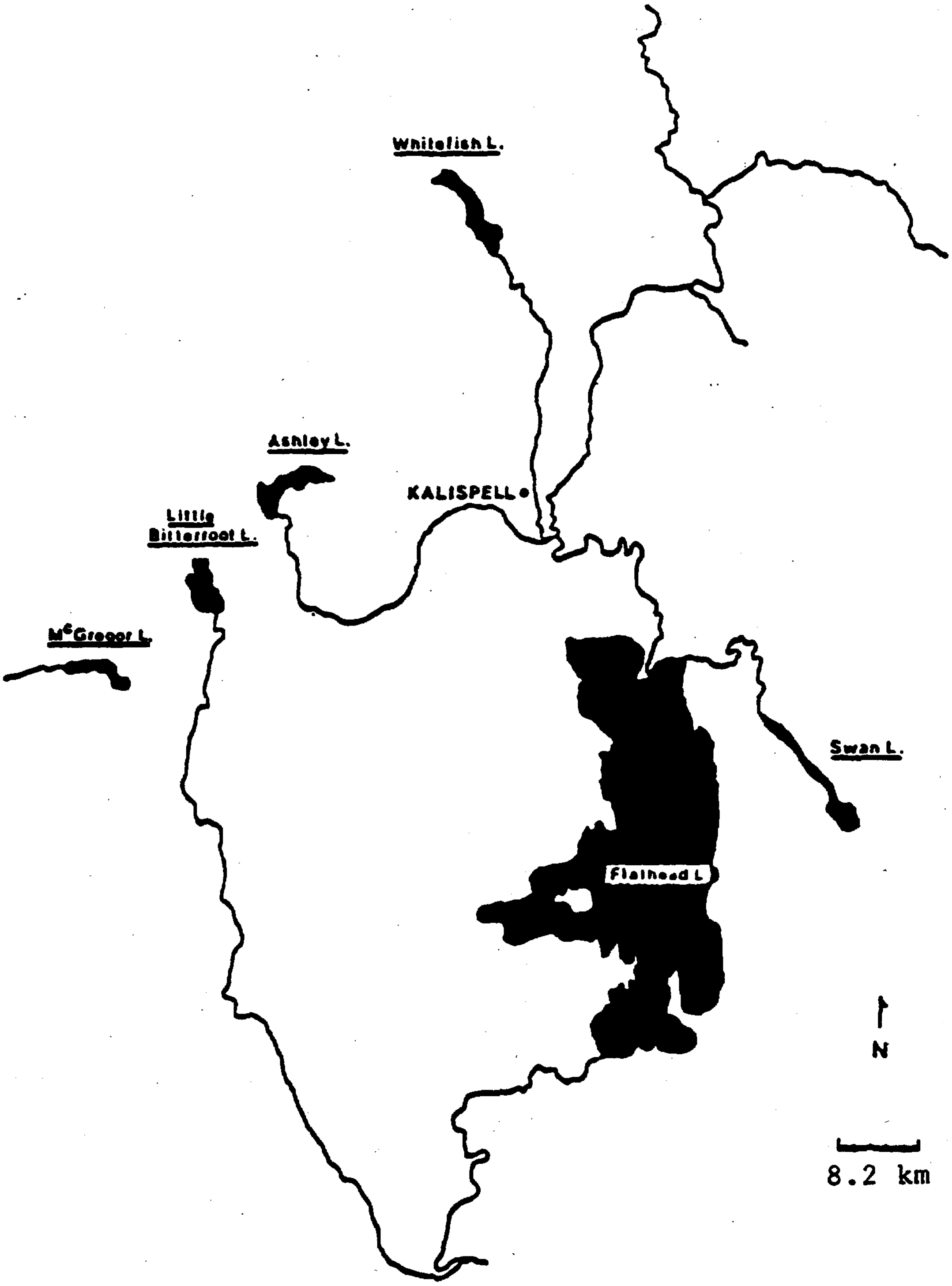

Figure 20. Locations of lakes in northwestern Montana with established *Mysis* populations.

Lake trout are bottom oriented fish, and like lake whitefish, seem to have benefited from M. relicta as a new food item. Both species incorporate many M. relicta despite dramatic diel migrations documented for the shrimp (Beeton 1960, Beeton and Bowers 1982, Bukantis and Bukantis 1987). In at least one lake comparable to Flathead Lake, total fish production was found to be dominated by fish using benthic foods (Eggars et al. 1978). We suspect a similar situation is developing in Flathead Lake. Reductions of pelagic foods caused by M. relicta, coupled with M. relicta being eaten in turn by bottom oriented fish, has shifted fish production in favor of benthic species. Unfortunately, -if true, the consequences of this shift have been devastating for the kokanee fishery.

Increased survival of young lake trout, perhaps due to the availability of M. relicta, would add more predators to the lake each year, accelerating loss of kokanee. If we are correct that predation is the dominant factor explaining the kokanee collapse, we would expect kokanee mortality to increase rapidly until kokanee seem suddenly lost from the system. In Flathead Lake, loss of kokanee certainly fits this pattern.

Very recently, kokanee fry stocking at levels of about 1 million fish each year appear effective in reestablishing kokanee in Lake Tahoe, California (Ginger Thomas, Confederated Salish and Kootenai Tribes, personal communication, 1989, from Russ Wickwire, California Fish and Game). Escapement as high as 50,000 fish in 1988 is attributed to supplementation efforts begun in 1980. Hatchery enhancement had been stopped in the 1970s because stocking efforts in the late 1960s showed no apparent improvement in the kokanee fishery. Although lake trout live in this lake, their numbers were decreasing before the most recent hatchery plants were successful. As kokanee escapement improves, lake trout numbers apparently are increasing again, while M. relicta remain abundant. It is possible that the pattern of kokanee collapse experienced after initial M. relicta introductions will repeat. On the other hand, Lake Tahoe may represent a valuable test case from which to identify successful kokanee rehabilitation strategies for Flathead Lake, even if lake trout predation is as significant in explaining kokanee losses as we have proposed.

IMPLICATIONS FOR FISHERIES MITIGATION AND MANAGEMENT IN THE FLATHEAD SYSTEM

The final report for which this document is an addendum (Beattie et al. 1988) proposed three recovery alternatives for enhancing the Flathead System fishery. These alternatives form part of mitigation planning described by Fraley et al. (1989). Two of these alternatives were premised on successful rehabilitation of the kokanee fishery. The third assumed that kokanee could not be reestablished in the lake. Because we are uncertain whether or not kokanee will recover, flexibility in management alternatives remains necessary to compensate fishery losses in the Flathead system. One major benefit of the Flathead Lake Kokanee Study, however, is that productive potential management directions have been identified in context with the changed ecology of Flathead Lake.

Kokanee Fry Planting Efforts in Flathead Lake

Our current understanding is that reduced food and increased predation in Flathead Lake have resulted in very high mortality of kokanee. If we are correct, as long as these factors impact kokanee as they have in recent years, reestablishing kokanee will be difficult. Large scale hatchery plants (not presently feasible) might help, although food limitations could be compounded by many more fish. Also, without continued and increasing hatchery supplementation, predators might eventually reduce new recruitment below levels of an acceptable fishery.

We recognize that our current understanding of factors adversely affecting kokanee is not complete. We are only now beginning to test the role of predation in explaining kokanee losses. Even if the predation hypothesis is supported in basic form, refinements may suggest ways in which complete loss of kokanee could be avoided. One test of the predation hypothesis is already underway. Fry supplementation begun in 1987 should first significantly contribute to kokanee spawning escapement in 1990. At a minimum, escapement monitoring should continue the next three years to determine if hatchery plants have had any success increasing kokanee numbers. For similar reasons, fry planting should continue at least two more years. Continued plants would preserve benefits of previous efforts, if they exist.

Hydroacoustic Surveys and Lake Trout Monitoring in Flathead Lake

The central role of lake trout we suggest in explaining kokanee losses places priority on describing its current status in Flathead Lake more thoroughly. If we are correct, lake trout numbers should be increasing at the same that kokanee have been all but eliminated. Dual-beam surveys begun in 1988 will be critical to ascertaining population responses over the next several years. For this reason, acoustic surveys should be continued. Now that the technology has been demonstrated effective, surveys should be standardized'to predetermined transects with several surveys made during the year. At a minimum, lakewide surveys should be conducted prior to and following lake stratification, and major spawning seasons. These surveys will also provide data to disprove the predation hypothesis if it is incorrect. Ascertaining whether or not predators are responding as we predict will be a significant contribution to continuing efforts to understand the full implications of _M. relicta_ introduction to Flathead Lake.

Although we believe that younger year classes of lake trout have increased numbers in recent years, loss of kokanee may lower condition and survival of older fish. Anglers on Flathead Lake suggest -that larger lake trout (20 to 30 lbs) are now less abundant. If a trophy lake trout fishery is a priority, food habits' of lake trout will require close monitoring to determine if other species, such as yellow perch or lake whitefish, are incorporated in adequate numbers to compensate loss of kokanee.

Species of Special Concern and Protecting Tributaries to Flathead Lake

Westslope cutthroat and bull trout are designated species of special concern in Montana. A policy to protect and enhance natural reproduction of these native salmonids is already adopted in fisheries mitigation guidelines by the Montana Department of Fish, Wildlife and Parks. Both species spawn in rivers tributary to Flathead Lake.which are impacted by hydroelectric operations. At a minimum, management efforts should continue to promote welfare of these populations. If kokanee can not be reestablished in Flathead Lake, these species will have increased importance replacing this formerly significant fishery.

Very little is known about the current stat& of westslope cutthroat in Flathead Lake, although the fishery was apparently more productive in previous years (Beattie et al. 1988). Hatchery supplementation is difficult with this species (Beattie et al. 1988), but provides one means of enhancement. We recommend that priority also be placed on improving spawning and rearing habitat to enhance natural reproduction. Bull trout numbers apparently are stable in the Flathead system, based on spawner surveys from the last ten years (Fraley and Shepard 1989). Again, emphasis should be placed on protecting and enhancing spawning and rearing areas. Hatchery enhancement of bull trout in the Flathead system should be explored as an alternative for augmenting the fishery.

Minimum flows in the Flathead River recommended by Fraley et al. (1989) should be maintained, with research directed to ascertaining optimum flow schedules for fish. These schedules must also provide for efficient operation of hydroelectric facilities in the drainage. Considerable work is already completed with this objective in mind (Fraley et al. 1989).

Attempts to improve fish passage at Bigfork Dam into the Swan drainage may benefit westslope cutthroat and bull trout fisheries. However, if our current understanding of kokanee declines in Flathead Lake is correct, a significant risk to the kokanee fishery in Swan Lake exists if lake whitefish and lake trout become established. For this reason, at a minimum, a comprehensive baseline assessment of the status of the Swan Lake fishery is necessary before a new fish ladder is operational. These data will provide a basis from which to assess subsequent effects of greater'numbers of fish moving between the now relatively isolated systems. When the improved fish ladder is functioning, fish passage should be monitored for at least two years to ensure that significant numbers of westslope cutthroat and bull trout are moving between drainages, and that lake whitefish and lake trout are not being introduced to Swan Lake. Future work in the Flathead system may establish that these concerns for the Swan Lake fishery were unwarranted. At present, however, we urge a conservative approach in opening new drainages to potentially devastating consequences for kokanee.

If kokanee are no longer viable in Flathead Lake, management efforts will necessarily emphasize other species. Native species are a logical choice and recommended emphasis. Many species already in the drainage have adfluvial life histories, including westslope cutthroat and bull trout. We recommend a general policy to protect tributaries from harmful development impacting fish in the Flathead system, while accommodating other water uses. The protected areas concept (Fraley et al. 1989) provides a reasonable framework to begin implementing this policy. Protecting river spawning and rearing habitat may be one of the best mitigation alternatives for the Flathead Lake fishery in years to come. Protecting rivers not only supports important sport fish that spend some part of their lives in Flathead Lake, but also maintains the integrity of the-broader drainage, upon which the quality of the Flathead Lake fishery depends.

From the mid 1970s through the early 1980s, approximately 100,000 kokanee spawners in the Flathead drainage were lost annually due to the operation of Hungry Horse Dam (Fraley et al. 1989). Because changes in the trophic structure of Flathead Lake now limit kokanee survival, offsite enhancement of kokanee may be another effective way to mitigate kokanee losses. Kokanee populations could be enhanced in other lakes in the drainage where detrimental interactions with *M. relicta* do not occur. Efficient implementation of this mitigation approach would require that appropriate lakes be identified based on their ability to support kokanee populations, and prioritized to maximize benefits to lake users.

Introductions of New Species

The ecology of Flathead Lake is still changing as fish respond to altered conditions in the lake. New population equilibria are being established, and the full implications of *M. relicta* induced changes in this process are not well understood. Although we recommend that the option to introduce new species be maintained as a management alternative, results of introductions are never entirely predictable, and could seriously compromise efforts to enhance natural reproduction of established fish. For these reasons, introductions of new species must be made only after complete and thorough consideration of all potential consequences, including worst case scenarios. An exhaustive review process is already man&ted for proposed introductions of new species to Flathead Lake.

Finally, we emphasize that whatever form fisheries mitigation may take in coming years, all efforts must be accompanied by a strong monitoring and evaluation program. Effective evaluation of responses of fish in the Flathead system is necessary to allow for adaptive fisheries management, as outlined in the recent Flathead system co-management plan (MDFWP-CSKT 1989).

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APPENDIX A

Average densities of selected large zooplankton species at three sampling stations on Flathead Lake in 1988.

Table A1. Average densities (no./l) of selected large zooplankton species at three sampling stations on Flathead Lake in1988.

Genus	Sample station	Sample Month May	Jun	Jul	Aug	Sep	Oct	Nov
<u>Bosmina</u>	l-l (E)[a]	0.06	0.52	0.12	0.28	0.12	0.08	0.12
	1-1 (H)[b]	----	0.04	0.32	0.08	0.03	co.01	----
	l-5 (E)	----	0.52	0.36	0.08	0.10	0.80	0.08
	l-5 (H)	----	co.01	0.28	0.08	0.04	----	----
	6-4 (E)	----	0.52	0.28	0.24	0.10	0.08	- -
	6-4 (H)	----	0.24	0.80	0.20	0.06	----	- -
<u>Daphnia</u>	l-l (E)	0.60	2.50	4.20	2.70	0.40	0.20	0.20
	1-1 (H)	----	1.00	2.00	1.40	0.50	0.20	----
	l-5 (E)	----	1.60	1.80	1.50	0.30	0.20	0.10
	l-5 (H)	----	1.10	1.40	0.50	0.20	----	----
	6-4 (E)	----	1.90	2.10	1.30	0.30	0.20	----
	6-4 (H)	----	0.90	1.20	1.00	0.50	0.40	- - -
<u>Diacyclops</u>	l-l (E)	0.21	0.42	0.50	0.26	0.34	0.24	0.38
	l-l (H)	----	0.22	0.35	0.23	0.21	0.25	- - -
	l-5 (E)	----	0.39	0.18	0.24	0.24	0.25	0.33
	l-5 (H)	----	0.15	0.36	0.25	0.41	----	----
	64 (E)	----	0.39	0.18	0.27	0.20	0.35	- -
	6-4 (H)	----	0.35	0.47	0.29	0.27	0.25	- - -
<u>Epishura</u>	l-l.(E)	0.001	0.004	0.008	0.046	0.006	0.006	0.004
	l-l (H)	----	0.002	0.004	0.002	----	----	----
	l-5 (E)	----	0.120	0.120	0.006	0.004	0.002	0.001
	l-5 (H)	----	0.002	0.002	0.003	----	----	- - -
	6-4 (E)	----	0.006	0.007	0.004	0.004	0.006	----
	6-4 (H)	----	0.004	0.100	0.006	0.004	0.002	----
<u>Leptodiaptomus</u>								
	l-l (E)	0.60	2.50	4.20	2.70	0.40	0.20	0.20
	l-l (H)	----	1.00	2.00	1.40	0.50	0.20	I - -
	l-5 (E)	----	1.60	1.80	1.50	0.30	0.20	0.10
	l-5 (H)	----	1.10	1.40	0.50	0.20	----	- -
	64 (E)	----	1.90	2.10	1.30	0.30	0.20	----
	64 (H)	----	0.90	1.20	1.00	0.50	0.40	- -
<u>Leptodora</u>	l-l (E)	----	----	----	----	0.00016	0.00008	- -
	1-1 (H)	----	----	----	----	0.00048	0.00024	- -
	l-5 (E)	----	----	----	0.0004	----	0.00008	----
	l-5 (H)	----	----	----	----	----	I_-	- - - -
	6-4 (E)	----	----	----	-	0.00032	0.00028	- - - -
	6-4 (H)	----	----	0.00068	0.00064	0.00036	0.00044	

[a] Epilimnion
[b] Hypolimnion

APPENDIX B

Data supplement for the 1988 dual-beam hydracoustic'survey of Flathead Lake.

Table B1. Midwater, near-bottom, and total fish density (fish.000 m^2) along 26 transects sampled in the 1988 hydroacoustic survey of Flathead Lake.

Transect	Midwater Density	(percent)	Near-bottom Density	(percent)	Total Density.
1 A1	0.3450	(100)	—	(0)	0.3450
1 A2	4.5960	(86.8)	0.7008	(13.2)	5.2968
1 B1	1.6830	(62.1)	1.0293	(37.9)	2.7123
1 B2	0.0680	(100)	—	(0)	0.0680
1 C	0.2579	(70.2)	0.1095	(29.8)	0.3674
1 D	0.1373	(51.1)	0.1314	(48.9)	0.2687
1 E	0.0779	(17.3)	0.3723	(82.7)	0.4502
2 B	1.5930	(63.4)	0.9198	(36.6)	2.5128
2 c	0.7075	(76.4)	0.2190	(23.6)	0.9265
3 A	0.5080	(55.0)	0.4161	(45.0)	0.9241
4 A	0.8530	(84.8)	0.1533	(15.2)	1.0063
4 B	1.6260	(91.4)	0.1533	(8.6)	1.7793
4 c	1.4585	(93.0)	0.1095	(7.0)	1.5680
5 A	0.8775	(85.1)	0.1533	(14.9)	1.0308
5 B	2.5215	(95.8)	0.1095	(4.2)	2.6310
5 c	1.1300	(82.4)	0.2409	(17.6)	1.3709
5 D	0.5895	(81.8)	0.1314	(18.2)	0.7209
6 A	0.8879	(74.3)	0.3066	(25.7)	1.1945
7	0.3155	(59.0)	0.2190	(41.0)	0.5354
8	0.2660	(60.3)	0.1752	(39.7)	0.4412
9 A	1.4655	(43.5)	0.2190	(56.5)	3.3690
9 B	0.8640	(61.2)	0.5475	(38.8)	1.4115
10	0.3100	(25.3)	0.9171	(74.7)	1.2271
11	1.2080	(74.4)	0.4161	(25.6)	1.6241
12	3.1045	(84.5)	0.5694	(15.5)	3.6739
13 A	2.8450	(87.2)	0.4161	(12.8)	3.2611
13 B	3.9129	(94.7)	0.2190	(5.3)	4.1319
14	1.3860	(76.9)	0.4161	(23.1)	1.8021
15	0.9960	(85.0)	0.1752	(15.0)	1.1712
16	1.1185	(83.6)	0.2190	(16.4)	1.3375

TableB2. Hydroacoustic target strength distributions for strata 1 through 5.

			Frequency by Stratum									
			1		2		3		4		5	
Class	Lower Limit (dB)	Upper Limit (dB)	nb[a]	mw[b]	nb	mw	nb	mw	nb	mw	nb	mw
At or below		-59.0	0	10	1	2	2	0	0	1	0	0
1	-59.0	-58.0	0	1	1	0	1	0	0	1	0	0
2	-58.0	-57.0	0	1	1	4	0	0	2	0	4	0
3	-57.0	-56.0	0	6	0	4	6	1	"6	4	3	1
4	-56.0	'-55.0	0	2	0	1	1	0	2	1	-0	0
5	-55.0	-54.0	0	5	0	5	5.	1	4	3	13	8
6	-54.0	-53.0	0	7	1	3	6	2	2.	2	5	0
7	-53.0	-52.0	0	7	0	6	8	0	6	1	6	2
8	-52.0	-51.0	1	18	1	6	11	7	16.	3	10	0
9	-51.0	-50.0	0	22	3	12	21	1	13	10	24	13
10	-50.0	-49.0	0	13	2	10	9	2	9	6	8	1
11	-49.0	-48.0	0	23	2	2	13	1	10	5	12	3
12	-48.0	-47.0	1	16	1	14	16	6	13	18	28	9
13	-47.0	-46.0	0	8	1	3	11	0	4	5	11	4
14	-46.0	-45.0	0'	19	2	12	16.	2	14	13	31	7
15	-45.0	-44.0	0	20	0	6	18	5	17	7	19	8
16	-44.0	-43.0	0	21	3	7	17	4	23	7	-20	16
17	-43.0	-42.0	1	23	2	3	15	3	19	9	14	7
18	-42.0	-41.0	0	16	1	13	13	5	20	13	31	20
19	41.0	-40.0	0	18	3	4	10	7	22	7	18	8
20	-40.0	-39.0	0	8	3	7	5.	2	14	9	18	7
21	739.0	-38.0	3	25	2	4	15	3	21	7	l-3	4
22	-38.0	-37.6'	0	17	3	6	19	6	19	9	14	3
23	-37.0	-36.0	1	10	0	1	10:	3	13	2	8	3
24	-36.0	-35.0	0	10	5	4	lo	4	6	1	3	1
25	-35.0	-34.0	0	5	3	2	8:	1	3.	4	7	3
26	-34.0	-33.0	0	1	4	2	3	0	2	2	8	0
27	-33.0	-32.0	0	1	0	2	2,	0	6	4	3	3
28	-32.0	-31.0	0	4.	1	2	5	1	1	0	3	0
29	-31.0	-30.0	0	0	1	1	0	0	2	2	1	0
30	-30.0	-29.0	0	0	1	0	0	1	1	2	2	1
31	-29.0	-28.0	0	1	1	0	2.	0	0	0	0	0
32	-28.0	-27.0	0	0	1	0	0	0	0;	1	0	0
33	-27.0	-26.0	0	0	1	2	0	0	1	1	0	0
34	-26.0	-25.0	0	0	0	1	1	0	0	0	1	0
35	-25.0	-24.0	0	0	0	0	0;	0	:o.	0	0	0
36	-24.0	-23.0	0	0	1	0	0.	0	0	0	.o	0
37	-23.0	-22.0	0	0	0	0	0	0	0	0	0	0
38	-22.0	-21.0	0	0	0	0	0.	0	0	0	0	0
above	-21.0		0	0	0	0	0	2	0	0	0	0

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[a] Near-bottom targets

[b] Midwater targets

Table B3. Hydroacoustic target strength distributions for strata 6 through 9.

			Frequency by Stratum							
			6		7		8		9	
Class	Lower Limit. (dB)	Upper Limit (dB)	nb[a]	mw[b]	nb	mw	nb	mw	nb	mw
At or below		-59.0	1	1	0	0	0	1	0	0
1	-59.0	-58.0	0	0	0	0	0	0	0	0
2	-58.0	-57.0	0	0	0	0	0	0	0	1
3	-57,0	-56.0	4	1	1	0	2	1	0	0
4	-56.0	-55.0	1	0	0	3	0	2	0	0
5	-55.0	-54.0	6	3	3	0	3	0	2	3
6	'54.0	-53.0	4	0	3	6	5	2	0	5
7	-53.0	-52.0	4	0	2	1	4	6	1	8
8	-52.0	-51.0	7	2	4	3	1	4	2	9
9	-51.0	-50.0	25	1	12	5	12	5	7	17
10	-50.0	49.0	8	1	4	15	6	26	5	4
11	-49.0	-48.0	10	2	10	2	9	12	5'	20
12	-48.0	-47.0	38	1	17	0	30	I.5	10	26
13	-47.0	-46.0	16	0	I.2	16	18	50	10	17
14	-46.0	45.0	23	5	21	10	24	36	11	24
15	-45.0	44.0	21'	1	17	15	17	46	11'	37
16	44.0	43.0	31	3	25	8	37	32	9	36
17	-43.0	42.0	28'	2	14	13	16	60	8	29
18	42.0	-41.0	16	5	23	13	18	30	3	17
19	-41.0	-46.0	14	3	15	10	15	42	4	24
20	40.0	-39.0	11	2	9	10	9	23	2	14
21	-39.0	-38.0	11	4	7	11	'4	14	1	12
22	-38.0	-37.0	4	1	4	9	4	9	0	13
23	'37.0	-36.0	5'	3	4	9	3	10	1	11
24	-36.0	-35.0	2	0	1	8	2	3	0	5
25	-35.0	-34.0	2	2	1	7	1	'1	1	4
26	-34.0	-33.0	-2	0	6	'5	0	0	3	11
2 7	-33.0	-32.0	0	1	2	7	'3	6	0	3
28	-32.0	-31.0	1	1	0	4	0	0	0	'1
2 9	-31.0	-30.0	1	0	1	1	0	0	1	1
30	-30.0	-29.0	0	1	2	3	0	0	0	'1
31	-29.0	-28.0	0	0	0	0'	0	1	0	0
32	-28.0	-27.0	1	0	0	2	0	0	1	0
33	-27.0	-26.0	0	0	1	1	0	0	0	0
34	-26.0'	-25.0	0	0	0	1'	0	0	0	1
35	-25.0	-24.0	0	0	0	0	0	0	0	0
36	-24.0	-23.0	0	0	0	0	1	0	0	1
37	-23.0	-22.0	0	0	0	1	0	0	0	0
38	-22.0	-21.0	0	0	0	0	0	0	0	0
above	-21.0		0	0	0	0	0	0	0	1

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[a] near-bottom targets
[b] midwater targets

TableB4. Mean target strengths by depth and transect for the 1988 hydroacoustic survey of Flathead Lake.

Transect	Depth Interval (m)	Number of Targets	Mean Target Strength (dB)
1 A1	10-15	6	-57.1
1 A2	2-5	8	-50.5
	5-10	-50	-52.6
	10-15	86	-55.2
	15-20	185	-55.2
	20-23	181	-54.5
	23-26	79	-52.5
	26-29	147	-52.9
	29-32	187	-51.2
	32-35	77	49.2
1 B1	2-5	3	-51.8
	5-8	9	-48.6
	8-11	19	-51.7
	11-14	9	-54.1
	14-17	29	-53.2
	17-20	18	-55.5
	20-23	70	-50.6
	23-26	127	-51.8
	26-29	200	-50.7
	29-32	157	-50.6
	32-35	8	-53.1
1 B2	10-15	2	-62.6
	15-20	4	-48.9
	20-25	22	-45.5
1 C	5-10	2	-56.5
	10-15	12	-56.3
	15-20	2	-58.1
	20-25	4	-52.0
	25-30	180	-59.0
	30-35	I.5	-60.3
1 D	15-20	4	-46.5
	25-30	109	-59.6
	30-35	32	-52.5
	35-40	4	-53.8
1 E	5-10	3	-41.9
	15-20	2	-63.3
	25-30	44	-48.3

Table B4. (continued).

Transect	Depth Interval (m)	Number of Targets	Mean Target Strength (dB)
2 B	5-10	7	-54.2
	10-15	13	-56.0
	15-20	10	-57.5
	20-25	7	-59.3
	25-30	24	-53.1
	30-35	93	-52.6
	35-40	287	-52.5
	40-45	758	-51.4
	45-50	1,154	-50.9
	50-55	550	-50.2
	55-60	26	-53.8
	60-65	33	-52.2
2 c	10-15	7	-61.4
	15-20	16	-61.5
	20-25	31	-59.8
	25-30	61	-57.1
	30-35	34	-55.6
	35-40	124	-54.3
	40-45	326	-54.0
	45-50	278	-52.6
	50-55	41	-55.1
	55-60	50	-53.1
	60-65	69	-52.4
	65-70	72	-55.0
	70-75	155	-52.3
	75-80	97	-54.5
3 A	10-15	10	-58.5
	15-20	25	-61.6
	20-25	27	-52.6
	25-30	33	-49.5
	30-35	158	-48.7
	35-40	860	-48.7
	40-45	820	-49.9
	45-50	206	-51.3
4 A	5-10	6	-48.2
	10-15	12	-60.3
	15-20	52	-61.9
	20-25	45	-60.4
	25-30	27	-56.6
	30-35	106	-49.9
	3540	266	-50.2
	40-45	4 4	-53.7
	45-50	57	-53.0
	50-55	5 3	-52.6
	55-60	55	-54.5
	60-65	99	-51.9

Table B4. (continued).

Transect	Depth Interval (m)	Number of Targets	Mean Target Strength (dB)
4 A	65-70	80	-52.5
	70-75	66	-54.5
	-75-80	72	-51.9
	80-85	56	-54.1
	85-90	92	-54.8
	90-95	85	-54.4
4 B	lo-l.5	2	-56.3
	15-20	5	-60.6
	20-25	47	-59.2
	25-30	317	-59.6
	30-35	388	-57.9
	35-40	48	-57.6
	40-45	25	-49.7
	45-50	75	-52.4
	50-55	152	-50.5
	55-60	79	-50.5
	60-65	94	-51.4
	65-70	55	-53.0
	70-75	41	-53.1
4 c	lo-l.5	2	-52.3
	15-20	I.3	-61.4
	20-25	120	-58.9
	25-30	203	-60.5
	30-35	91	-58.1
	35-40	62	-52.1
	40-45	82	-52.9
	45-50	147	-52.5
	50-55	244	-54.2
	55-60	159	-54.3
	60-65	187	-53.7
	65-70	117	-54.2
	70-75	119	-53.6
	75-80	293	-54.7
	80-85	427	-54.3
	85-90	552	-55.0
	90-95	494	-54.2
	95-100	46	-55.1
5 A	lo-I.5	1 4	-60.9
	15-20	30	-60.7
	20-25	17	-58.0
	25-30	13	-49.9
	40-45	20	-49.3
	45-50	16	-49.0
	50-55	29	-53.5
	55-60	48	-51.5
	60-65	66	-51.8

Table B4. (continued).

Transect	Depth Interval (m)	Number of Targets	Mean Target Strength (dB)
5 A	65-70	21	-51.0
	70-75	16	-50.7
5 B	10-15	20	-62.3
	15-20	114	-60.9
	20-25	238	-59.4
	25-30	52	-58.7
	30-35	5	-61.8
	35-40	17	-53.1
	40-45	13	-49.9
	45-50	46	-50.0
	50-55	36	-52.9
	55-60	114	-50.3
	60-65	156	-51.5
	65-70	137	-51.7
	70-75	23	-56.2
5 C	10-15	9	-57.7
	15-20	47	-61.6
	20-25	45	-61.0
	25-30	20	-58.1
	30-35	33	-53.7
	35-40	33	-55.9
	4045	87	-54.2
	45-50	104	-53.3
	50-55	142	-52.6
	55-60	143	-54.1
	60-65	130	-53.1
	65-70	156	-54.0
	70-75	35	-51.9
5 D	10-15	9	-62.1
	15-20	34	-60.3
	20-25	62	-58.6
	25-30	22	-55.5
	30-35	40	-50.8
	35-40	49	-46.9
	40-45	96	-48.5
	45-50	181	-52.7
	50-55	45	-53.1
	55-60	22	-50.4
6 A	5-10	5	-52.0
	10-15	8	-49.9
	20-25	12	-54.0
	25-30	28	-50.7
	30-35	103	47.9
	35-40	564	-48.8
	40-45	472	-51.4

Table B4. (continued).

Transect	Depth Interval (m)	Number of Targets	Mean Target Strength (dB)
6 A	45-50	253	-51.5
	50-55	191	49.6
	55-60	4	-39.5
7	5-10	4	-57.7
	10-15	8	-61.0
	15-20	10	-58.6
	20-25	55	-51.8
	30-35	40	46.3
	35-40	103	47.0
	30-45	126	-52.4
	45-50	74	-51.9
8	5-10	6	-49.6
	10-15	41	46.8
	15-20	66	47.2
	20-25	73	-53.0
	25-30	95	48.9
	30-35	20	-48.7
9 A	10-15	33	-56.5
	15-20	83	-60.9
	20-25	166	-59.1
	25-30	88	-57.1
	30-35	17	-53.4
9 B	15-20	68	-59.5
	20-25	36	-57.2
	25-30	23	-51.9
	30-35	59	-52.0
	35-40	179	-50.5
	40-45	212	-53.1
	45-50	281	-50.9
	50-55	258	-52.0
	55-60	227	-50.7
10	15-20	4	-62.9
	20-25	99	-59.2
	25-30	27	-60.6
	30-35	22	-52.6
	35-40	34	-48.0
	4045	73	-50.8
	45-50	103	-50.8
	50-55	103	-52.6
	55-60	40	-54.8
	60-65	58	-55.4
	65-70	86	-52.8
	70-75	99	-54.6
	75-80	70	-58.1

TableB4. (continued).

Transect	Depth Interval (m)	Number of Targets	Mean Target Strength (dB)
11	5-10	5	-52.0
	10-15	3	-59.0
	15-20	33	-61.3
	20-25	59	-56.5
	25-30	161	-57.9
	30-35	149	-55.9
	35-40	137	-55.4
	40-45	167	-54.7
	45-50	292	53.3
	50-55	323	-53.0
	55-60	207	-54.2
	60-65	70	-52.8
12	5-10	6	-49.1
	10-15	35	-57.3
	15-20	97	-57.1
	20-25	144	-56.0
	25-30	478	-57.1
	30-35	157	-52.6
	35-40	285	49.8
	40-45	403	-59.7
	45-50	396	-52.1
	50-55	502	-53.1
	55-60	577	-53.7
	60-65	444	-54.6
	65-70	489	-53.2
	70-75	548	-53.1
	75-80	222	-54.1
	80-85	299	-54.0
	85-90	104	-54.4
13 A	5-10	2	-39.0
	10-15	14	-50.5
	15-20	60	-56.1
	20-25	168	-57.8
	25-30	160	-57.3
	30-35	97	-51.9
	35-40	254	-50.5
	40-45	377	-50.3
	45-50	358	-52.3
	50-55	225	-55.0
	55-60	299	-53.7
	60-65	190	-52.9
13 B	5-10	2	-44.8
	10-15	9	-54.1
	15-20	51	52.9
	20-25	182	54.9
	25-30	265	-56.6

Table B4. (continued).

Transect	Depth Interval (m)	Number of Targets	Mean Target Strength (dB)
13 B	30-35	89	-53.0
	35-40	141	-50.9
	40-45	438	-48.9
	45-50	547	-52.4
	50-55	583	-53.7
	55-60	402	-54.5
	60-65	305	-55.0
	65-70	277	-55.0
	70-75	234	-56.5
	75-80	I . 9 8	-55.4
	SO-85	131	-54.9
	85-90	70	-57.2
	90-95	17	-49.4
14	10-15	8	-58.8
	15-20	46	-56.4
	20-25	68	-53.6
	25-30	25	-58.4
	30-35	48	-53.4
	35-40	125	-51.8
	40-45	131	-51.4
	45-50	136	-52.2
	50-55	319	-51.2
	55-60	265	-52.0
	60-65	41	-54.1
	65-70	40	-53.3
15	10-15	2	-56.2
	15-20	28	-51.1
	20-25	21	-56.1
	25-30	12	-58.7
	30-35	16	-54.8
	35-40	42	-48.0
	40-45	26	-55.6
	45-50	106	-54.2
	50-55	135	-53.7
	55-60	75	-54.4
	60-65	99	-52.5
	65-70	65	-52.6
16	10-15	6	-55.9
	15-20	17	-55.1
	20-25	112	-57.4
	25-30	27	-58.3
	30-35	28	-50.9
	35-40	52	-50.9
	40-45	133	-49.9
	45-50	237	-49.9

Table B4. (continued).

Transect	Depth Interval (m)	Number of Targets	Mean Target Strength (dB)
16	50-55	414	-51.8
	55-60	434	-52.3
	60-65	364	-54.0
	65-70	325	-54.2
	70-75	321	-55.7
	75-80	294	-55.8
	SO-85	372	-55.1
	85-90	414	-55.7
	90-95	318	-56.0
	95-100	161	-55.8

APPENDIX c

Information supplement for age determinations of kdkanee and lake whitefish.

Table C1. Agreement of ages determined by different scale readers.

Species	Number of Scales Examined	Percent of Total Sample	Number of Same Ages	Percent Agreement
Kokanee	30	52	25	83
Lake whitefish	30	45	21	70

Table C2. Comparison of empirically determined mean total lengths at age with lengths predicted from the Walford model for lake whitefish captured in Flathead Lake in 1986, 1987, and 1988.

Age	Observed mean Total length (mm)	Predicted mean Total length (mm)	Percent difference
III+	329.24	323.48	1.75
IV+	394.91	381.43	3.41
V+	426.17	426.35	0.04
VI+	435.96	465.01	6.25
VII+	478.75	498.28	3.92

Table C3. Results of least squares linear regressions of scale radius on total fish length for kokanee and lake whitefish samples.

Kokanee collected in 1988:

scale radius = 0.0070049 (total length) - 0.32442
r = 0.94
n = 68

Lake whitefish collected in 1986, 1987, and 1988:

scale radius = 0.0124947 (total length) - 0.556478
r = 0.97
n = 483

APPENDIX D

A bibliography of reports and scientific publications produced from project no. 81S-5.

Appendix D: A bibliography of reports and scientific publications produced from project no. 81S-5.

Beattie, W.D. and P. Clancey. 1989. Effects of the establishment of opossum shrimp (Mysis relicta) on the zooplankton community, and coincident decline in the survival of kokanee (Oncorhvnchus nerka) in Flathead Lake, Montana. Amer. Fish. Soc. Symposium Series (in press).

Beattie, W., P. Clancey, and R. Zubik. 1988. Effect of the operation of Kerr and Hungry Horse dams on the reproductive success of kokanee in the Flathead system, final report FY 1987. BPA contract no. DE-AI79-86BP39641, project no. 81S-5. MDFWP, Kalispell, MT.

Beattie, W. and P. Clancey. 1987. Effect of the operation of Kerr and Hungry Horse dams on the reproductive success of kokanee in the Flathead system, annual progress report FY 1986. BPA contract no. DE-AI79-83BP39641, project 81S-5. MDFWP, Kalispell, MT.

Beattie, W., P. Clancey, J. Decker-Hess, and J. Fraley. 1985. Impacts of water level fluctuations on kokanee reproduction in Flathead Lake. BPA contract no. DE-AI79-83BP39641, project no. 81S-5. MDFWP, Kalispell, MT.

Clancey, P. and J. Fraley. 1986. Effects of the operation of Kerr and Hungry Horse dams on the kokanee fishery in the Flathead River system, final research report, 1979-1985. BPA contract no. DE-AI79-83BP39641, project 81S-5. MDFWP, Kalispell, MI.

Decker-Hess, J. and P. Clancey. 1984. Impacts of water level fluctuations on kokanee reproduction in Flathead Lake. BPA contract no. DE-AI79-83BP39641, project no. 81S-5. MDFWP, Kalispell, MT.

Decker-Hess, J. and S.L. McMullin. 1983. Impacts of water level fluctuations on kokanee reproduction in Flathead Lake. BPA contract no. DE-AI79-83BP39641, project no. 81S-5. MDFWP, Kalispell, MT.

Decker-Hess, J. and P.J. Graham. 1982. Impacts of water level fluctuations on kokanee reproduction in Flathead Lake. Sponsored by Bonneville Power Administration. MDFWP, Kalispell, MT.

Fraley, J.J. and B.B. Shepard. 1982. Life history, ecology and population status of migratory bull trout (Salvelinus confluentis) in the Flathead Lake and River system, Montana. Northwest Science 63(4): 133-143.

Fraley, J.J., B. Marotz, J. Decker-Hess, W. Beattie, and R. Zubik. 1989. Mitigation, compensation, and future protection for fish populations affected by hydropower development in the upper Columbia system, Montana, U.S.A. Regulated Rivers 3:3-18.

Fraley, J. and P. Clancey. 1988. Downstream migration of stained kokanee fry in the Flathead River system, Montana. Northwest Science 62(4):111-117.

Fraley, J.J. and J. Decker-Hess. 1987. Effects of stream and lake regulation on reproductive success of kokanee salmon in the Flathead system, MT. Regulated Rivers 1: 257-265.

Fraley, J.J., S. McMullin, and P.J. Graham. 1986. Effect of hydroelectric development on the kokanee salmon in the Flathead system, Montana. No. Amer. J. Fish. Manage. 6(4):560-568.

Fraley, J. and S. McMullin. 1984. Monitoring kokanee salmon escapement and spawning in the Flathead River system. Fisheries research and special projects bureau, MDFWP, Kalispell, MT.

Fraley, J.J. and S. McMullin. 1983. Effects of operations of Hungry Horse dam on the kokanee fishery in the Flathead River system. Annual Report to BPA. MDFWP, Kalispell, MT.

APPENDIX E

Journal article: "The effect of the establishment of *Mysis relicta* on the zooplankton community of Flathead Lake, and coincident decline in the survival of kokanee".

EFFECTS OF THE ESTABLISHMENT OF OPOSSUM SHRIMP (Mysis relicta) ON THE ZOOPLANKTON COMMUNITY, AND COINCIDENT DECLINE IN THE SURVIVAL OF KOKANEE (Oncorhynchus nerka) IN FLATHEAD LAKE, MONTANA.

. William D. Beattie and Patrick T. Clancey
Montana Department of Fish, Wildlife, and Parks
P.O. Box 67, Kalispell, Montana, 59903

ABSTRACT

Opossum shrimp (Mysis relicta) were introduced into Flathead Lake by dispersal from tributary lakes, and reached average density of 130/m^2 by 1986. The abundance and temporal distribution of crustacean zooplanktonchanged markedly as a result of increased mysid predation. Daphnia longiremis and Leptodora kindtii were reduced to below detectable- density. The spring' population increase of Daphnia thorata was delayed until July, and it's maximum summer abundance declined from over 4.0/l to 1.2/l. The abundance of the copepod Diaptomus ashlandi also declined from over 20/l to less than 5/l. Already impacted by hydroelectric operations in the Flathead system, the kokanee (Oncorhyncus nerka) population has also declined since 1985. Though the growth rates of young-of-the-year kokanee did not decline significantly between 1980-81 and 1986-87, fry-to-adult survival fell from 2.7% in 1985 to less than 0.05% in 1987. Predationby lake trout (Salvelinus namaycush) and competition with lake whitefish (Coregonus clupeaformis) may also influence kokanee survival in Flathead Lake.

INTRODUCTION

Flathead Lake is a 510 km^2, oligomesotrophic lake in northwestern Montana. The North, Middle, and South Forks of the Flathead River, the Whitefish River, the Swan River, and the Stillwater River drain the 18,400 km^2 Flathead basin (Figure 1). The lake's mean depth is 32.5 m, and it's maximum depth is 113.0 m.

The kokanee (Oncorhynchus nerka) fishery in Flathead Lake, which until recently supported a sport harvest. exceeding 200,000 fish per year (300,000 angler-hours), has declined rapidly since 1985. The species was introduced into the system in 1916, from coastal sockeye salmon stock. The scant historical data that exists indicates that the fishery was well established, and that spawning runs had developed along the Flathead Lake shore and into the Flathead River system by the 1930's. Spawning runs have been primarily composed of age III+ fish, though age II+ and IV+ have comprised up to 50% of some runs (Hanzel 1985).

The recent downtrend in kokanee abundance follows an earlier decline in reproductive success in the 1970% that was due largely to the impacts of hydroelectric operations in the system. Hydroelectric operations in the system have substantially reduced kokanee egg-to-fry survival, Winter power generation at Kerr Dam, built in 1937 below the outlet of Flathead Lake, cause the lake level to fall 3.3 m between September and March. High egg mortality has resulted as drawdown exposed redds built in shallow water in October and November (Decker-Hess and McMullin 1983). Hungry Horse Dam was constructed by the Bureau of Reclamation on the South Fork of the Flathead River in 1952. Initially, the increase in fall and winter water temperature associated with discharge from Hungry Horse reservoir attracted spawning kokanee to sites in the upper main stem and in the South Fork' below the dam. But peaking power generation in the mid-1970's caused flow in these areas to fluctuate widely, and reproductive success fell as eggs were exposed in shallow redds along the river margin (Fraley and Decker-Hess 1987).

In spite of the decline in reproductive success, the kokanee fishery persisted until 1985. But a large proportion of the annual recruitment has, since 1980, been produced in McDonald Creek, a tributary of the Middle Fork. From 1982 to 3.986 the number of kokanee fry produced in McDonald Creek has ranged from 6.5 to 13.1 million (Clancey and Fraley 1986). Total fry production in the Flathead system is thought to have ranged from 10 to 15 million (Fraley and McMullin 1983). This level of recruitment was sufficient to maintain the fishery until 1986.

The drop in sport harvest and spawning escapement in 1986 evidenced an increase in kokanee mortality. This development was circumstantially linked to the establishment of opossum shrimp (Mysis relicta) in Flathead Lake. In 1968 and 1975 shrimp were transplanted from Waterton Lake, Alberta into Whitefish Lake, Ashley Lake, and Swan Lake - all tributaries of the Flathead system. Transplanted mysid populations were expected to provide a superior food source for benthic-feeding fishes such as lake trout, and for pelagic planktivores such as kokanee. Downstream drift from the tributary lakes introduced mysids into Flathead Lake, where they were collected first in 1981 (Leathe and Graham 1982). Changes in the zooplankton and fish communities of other oligotrophic labs occurred as a result of the establishment of mysid shrimp (Rieman and Bowler 1980, Morgan et al 1978). We suspected that similar changes in the trophic ecology of Flathead Lake were influencing kokanee survival.

The present study was begun in 1986 to see if the anticipated decline in the abundance of cladoceran zooplankton, resulting from increased grazing pressure by mysid shrimp, would affect the growth and survival of kokanee in Flathead Lake. Juvenile fish were thought to be particularly susceptible to food limitation, because they enter the lake from upstream spawning areas in April and May - before pulses in secondary productivity occurred. This scenario was supported by studies of other large lake systems in which mysid shrimp had become established - in particular Lake Pend Oreille, Idaho and Lake Tahoe, California (Rieman and Falter 1981, Morgan et al 1979). Similar events had occurred in many lakes throughout the northwestern us. and Canada (Northcote 1973, Rumsey 1985) . But differences in the trophic status and the zooplankton and fish communities of the lakes in question gave rise to uncertainty over the outcome in Flathead Lake.

METHODS

The abundance of crustacean zooplankton in Flathead Lake was measured biweekly, from May 1 to October 15 of 1986 and 1987, at six stations (Figure 1). Replicate vertical tows were hauled from a depth of 30 m using a 0.5 m diameter Wisconsin net made of 88 micron Nitex. The samples were preserved in 95% ethyl alcohol. Cladocerans and copepods were identified and counted in four 1 ml subsamples dispensed into a Sedgwick-Rafter chamber, except for Epischura and Leptodora, which were counted in four 30 ml subsamples. At each sampling site temperature profiles were obtained with a calibrated thermistor (Hydrolab Model T4).

Mysid shrimp were censused in Flathead Lake in early September by sampling 6 stations in 1986 and 25 stations in 1987. We sampled at night during the new moon. Staff from the University of Montana's Yellow Bay Biological Station cooperated in this effort. Sampling was stratified among three depth zones, 5 to 40 m, 40 to 75 m, and greater than 75 m. Vertical hauls were pulled from the bottom with a 1.0 m Wisconsin net made of 500 micron Nitex. The average densities in each depth stratum, expressed as the number of mysids/m^2, were weighted according to proportion of the lake's surface area in each stratum to calculate lakewide average density.

We sampled cladocerans and copepods, because of their importance in the diet of planktivorous fish. Sampling in Flathead Lake has provided a record of the spring and summer abundance of these species since 1980, and a basis for comparing the results of our study in 1986 and 1987. From 1983 to.1985 zooplankton samples were only taken at Station 2, and were drawn from a depth of 15 m. Because the vertical distribution of cladocerans and copepods extends deeper than 15 m, the 1983-85 density measurements were not comparable with earlier and later work. But comparisons of temporal distribution between all years were possible.

Young-of-the-year kokanee were collected primarily in the northwest quadrant of Flathead Lake with a mid-water trawl. The mouth of the trawl was 3.5 m x 4.0 m. Trawling was conducted at night, sampling depths between 15 and 20 m. Yearling and older kokanee were also collected by trawling and in overnite midwater gill-net sets. The gill-nets were constructed of 30 m x 3 m panels of 1.25 cm and 2.5 cm monofilament nylon mesh.

Stomach contents were dissected, preserved in 95% ethyl alcohol, and analyzed by the same techniques used to estimate zooplankton abundance. Diet was characterized by counting zooplankton and other organisms in individual stomachs. The average numerical composition of samples collected within each month was calculated. Total length and weight of each fish were measured, and scale samples taken to age the fish by standard techniques.

Spawning kokanee were counted by two snorkelers in McDonald Creek at 2 week intervals in October and November. Redds were counted during boat surveys of the principal riverine and lakeshore spawning areas. A "fish per redd" ratio of 2.6 (Fraley and McMullin 1983) wasusedto expand redd counts. Fry production in McDonald Creek was estimated by setting four 0.5 m^2 drift nets from a bridge at the creek mouth. These nets were set once each week from April 1 through June 15 from 1982 to 1986. Net catches were expanded from the volume sampled to total flow in the creek during the 24 hour sample period, and extrapolated over the 7-day interval between samples.

Kokanee survival was estimated by comparing fry production to age III+ adult abundance four years later. Adult year class strength estimates are derived from sport harvest (Fredenberg and Graham 1982, Hanzel 1986) and escapement estimates, and include contributions of age II+ and IV+ fish from adjacent years. Based on spawning escapement and egg-to-fry survival, McDonald Creek produced approximately 90% of total annual recruitment from 1982 to 1984. From 1981 to 1985 the spawning escapement to McDonald Creek averaged 78% of the system total. Egg-to-fry survival in McDonald Creek exceeded that in other riverine and lakeshore spawning areas (Clancey and Fraley 1986).

RESULTS

Decline in crustacean zooplankton abundance

The maximum summer density of Daphnia thorata at station2, whichvaried from 3.0 to 4.5 organisms/l between 1980 and 1982, declined to less than 1.0/l in 1987 (Figure 2). Until 1985 it attain4 measurable density as early as

April and increases in standing crop were evident in late May. In 1987 it was below detectable density until late May at all stations, and the first pulse was delayed until early July.

Previous studies (Leathe and Graham 1982, Potter 1978) found *Bosmina longirostris* to be present throughout the year in Flathead Lake, and showing spring and fall density maxima. The samples we collected in 1983, 1984, and 1985 did not indicate a decline in maximum density or a shift in temporal distribution. But it was absent from January until mid-May in 1987. The maximum summer abundance of *B.longirostris*, which ranged from 1.3/l to 4.2/l in 1980-82, fell to 0.4/l to 0.6/l in 1986-87 (Figure 2). No spring pulse was evident in 1987. Fall density also declined from about 1.0/l in 1980-82 to less than 0.2/l in 1986-87.

Daphnia longiremis was detectable for only a brief period in August of 1986, and was not present in 1987 samples. It was consistently present from May through August in previous years, though at density less than 0.1/l in 1982. This cold stenothermic species was less abundant than *D. thorata* in samples collected in the metalimnion and epilimnion in previous years (Leathe and Graham 1982). *Leptodora kindtii* was present in measurable density for successively shorter summer periods from 1983 to 1986, and was not found in 1987 samples. It's maximum density declined from 0.04 to 0.14/l in 1980-82 to 0.01/l in 1986. The diel migration of *L. kindtii*, toward deeper water during daylight hours (potter 1978), may have affected the accuracy of daytime 30 m vertical tows in measuring abundance.

The abundance of the copepod Diaptomus ashlandi has also declined since 1985. In previous years this species was the most abundant crustacean in Flathead Lake, with early- to mid-summer peak density of 20 to 40/l. It attained a spring density of 15/l in 1986 at station 2, but from then through the fall of 1987 did not exceed 5/l (Figure 3).

Average cladoceran densities at the six sampling stations in 1986-87 were not significantly different (Mann-Whitney pairs test, p = .10) within years. Subtle interstation differences in production timing were found. D. thorata, for example; reached measureable density at the three northern stations two weeks earlier than at the three southern stations in 1986. It was present at station 1 in late March of 1987, whereas it was not found at deeper stations in the southern end of the lake until the end of June. Maximum density in 1987 was higher at the southern stations than at stations 1 and 3. The maximum density of D. thorata was higher at southern stations in 1987 (Figure 4). Consistent differences in maximum density or production timing were not evident for other species.

Mysid Shrimp Abundance

From 1981, when Mysis relicta was first found in Flathead Lake, until 1985 mysid abundance increased exponentially, reaching a lakewide average density of $45/m^2$ (Bukantis and Bukantis 1987). Their rate of increase declined slightly in 1986, when the average density was

130/m^2. Average density declined, but not significantly, in 1987 to 108/m^2, though single samples ranged up to 575/m^2. It appears that mysids have approached the carrying capacity of Flathead Lake within ten years of introduction, as has been found in many other large, oligotrophic lakes (Rieman and Bowler 1980, Northcote 1973, Morgan et al 1981). Given the increased incidence of mysid shrimp in the diet of lake whitefish and lake trout, fish predation may also be a limiting factor.

The Flathead mysid population showed high spatial variability. In general, density at stations in the deeper (> 75 m), southern part of the lake exceeded that at northern stations. Density exceeded 100/m^2 only at stations deeper than 40 m, but no simple relationship between density and station depth was evident. Density was less than 15/m^2 at all stations shallower than 25 m. Various factors are thought to influence the distribution of mysid shrimp, including dissolved oxygen, light intensity, temperature, turbidity, and prey availability (Beeton and Bowers 1982). In Flathead Lake their vertical migration into the epilimnion at night is inhibited when surface water temperature reaches 15°C, though some juvenile Mvsis continue to migrate into the epilimnion (Craig Spencer, Univ. of Montana Flathead Biological Station, pers. comm).

Kokanee Survival Rates

Fry-to-adult survival was approximately 2.9% in 1981 and 2.5% in 1985. It dropped sharply to 0.6% in 1986, and to less than 0.01% in 1987 (Table 1). In1985 adultyearclass strength and spawning escapement was the highest since 1979. Age III+ year class strength fell from over 350,000 in 1984 and 1985 to less than 8,000 in 1987. Though fishing mortality had frequently exceeded 50% of the III+ year class in the early 1980's, comparatively few kokanee were caught in 1986 and 1987. Fry recruitment was relatively high in 1983 and 1984, 13.7 and 14.5 million respectively (Table 1).

Changes in Juvenile Kokanee Diet

The diet of young-of-the-year (YOY) kokanee that we collected in May was dominated by the copepod Cyclops bicuspidatus (69%), but included significant numbers of Diaptomus ashlandi (14%) and aquatic insects (16%), mostly chironomid pupae (Figure 5). Other zooplankton species, including Daphnia thorata, Bosmina longirostris and Epischuranevadensis, were found infrequently in stomach samples. June samples showed somewhat greater diversity in diet, with E. nevadensis comprising an average of 42%, C. bicuspidatus 22%, D. thorata 19%, D. ashlandi 12%, and B. longirostris 4%. D. thorata made up almost half (46%) their diet in July, B. longirostris 22%, and E. nevadensis 31%. For the remainder of the summer period, August and September, the diet of YOY kokanee was dominated strongly by D.thorata, though E. nevadensis and B. longirostris comprised 27% and 7% of the stomachs collected in October.

Study of YOY kokanee diet in 1980-81 (Leathe and Graham 1982) showed that D.thorata made up at least 60% of their food biomass from June through November. E. nevadensis was the only other species contributing significantly to their diet. Other studies have shown that kokanee and sockeye fry shift their diet in the summer from small zooplankton species, e.g. *Cyclops*, *Diaptomus*, and *Bosmina*, to larger prey such as *Daphnia*, *Diaphanosoma*, and *Epischura* (Doble and Eggers 1978, Lindsay and Lewis 1978, Goodlad et al 1974). This- shift, that had apparently occurred before the May samples were collected in 1980 and 1981, was delayed until August in 1986-87. That YOY kokanee selected for *D. thorata* was emphasized by the occurence of this species in stomachs collected in May and June, when it's availability was near or below detectable limits. Juvenile kokanee also selected for *E. nevadensis* in June, July, and October.

The diet of yearling (age I+) kokanee did not differ markedly from that of YOY fish, except yearlings shifted from a diverse diet to one dominated by *D. thorata* one month earlier, in July. We did not collect any yearling kokanee in May, but in June, 1986 *B. longirostris* (23%), *E. nevadensis* (35%), and *D. thorata* (40%) contributed to yearling diet. But in June of 1987 cladoceran abundance was low (< 0.1/l) and *E. nevadensis* made up 72% of their food. In July, August, and September diet was dominated by *D. thorata*. me characteristic high preference for larger prey species, principally *D. thorata* and *E. nevadensis*, was apparent in yearling kokanee as well, Mysid shrimp did not contribute to the diet of juvenile kokanee, at least during the months encompassed by our sampling.

Juvenile Kokanee Growth Rate

Comparison of the lengths of YOY kokanee sampled in 1980 and 1981, with those collected in I986 and 1987 did not show significant differences in size. Because fry hatched in McDonald Creek make up a large proportion of the annual recruitment, their size was taken as a baseline for assessing the growth of YOY kokanee. The mean length of outmigrant fry in 1986 was 25.3 mm. Trawl sampling in the late summer and fall showed that mean length had increased to 69.4 mm in late August, and 78.5 mm in mid-October (Figure 6). Juvenile kokanee apparently continue to grow in the fall in spite of declining food availability and falling water temperature in the lake.

Yearling kokanee growth rates were low in June and July of 1986 and 1987 (Figure 7). Their mean length did not increase beyond 135 mm through that period in both years. However, by the end of August samples collected in 1986 were significantly larger than those collected in 1987. In late August, 1986 mean length approached 170 mm, while in 1987 mean length was about 155 mm. The summer growth trajectory in 1986 was not significantly different from those of yearling fish that were collected in 1980.

DISCUSSION

Zooplankton Community

The changes we have observed in the Flathead Lake zooplankton community have probably been caused by increasing predation by mysid shrimp. Declines in cladoceran abundance in lakes where M. relicta has Been introduced are well documented in the western U.S., Canada, and Scandinavia (Rieman and Falter 1981, Richards et al 1975, Grossnickle 1982, Langeland 1981, Zyblut 1970). Studies of the food habits of M. relicta have shown, in particular, preference for cladocerans e.g. Daphnia spp. (Grossnickle 1982).

In Flathead Lake D. thorata and B. longirostris occupy the water column from 30 m to the surface (Fotter1978). Mysid shrimp are largely excluded from this surface layer in the summer by their preference for water colder than 15'C, and so a refuge for these cladocerans exists The data from Flathead Lake suggest that increase in cladoceran abundance was delayed until thermal stratification isolates a substantial part of their population from mysid grazing (Morgan et al 1981). Also, low mysid abundance in water less than 40 m deep allows dapbnids to multiply early in the spring in shallow parts of the lake. Inter-station differences in the thermal structure of the lake are likely insufficient to cause significantly higher productivity.

The decline of D. longiremis in 1986-87 is also circumstantially linked to increased mysid grazing. This species occupies colder, deeper water (Potter 3.978, Leathe and Graham 1982) and is therefore available to mysid shrimp throughout its life cycle.

The decline in the abundance of Diaptomus ashlandi is also probably linked to mysid grazing. Feeding experiments have shown that *M. relicta* graze heavily on *Diaptomus* (Folt etal1982). Gravid female *D. ashlandi* may be particularly vulnerable to predation because of their preference for water deepr than 30 m (Potter 1978). As cladoceran abundance has declined, other predaceous species e.g. *Epischura* may also have shifted to the more available copepods.

Other factors that might have contributed to the observed changes in the zooplankton community have not been identified. There have not been major differences in the spring and summer temperature regime in Flathead Lake. The lake froze completely in two consecutive winters, 1984-85 and 1985-86, but the lake thawed in early April in both years and spring warming proceeded normally. But since primary productivity did not change significantly in the two succeeding spring/summer seasons, relative to the preceeding five years (Stanford and Ellis 1988) it seems unlikely that secondary productivity was depressed.

Kokanee growth and survival

Since fry recruitment was relatively high in the years that produced the 1986 and 1987 adult year classes, we conclude that post-emergent mortality in Flathead Lake has increased. Juvenile fish experience higher mortality rates than older age classes, especially when food is limiting. (Rieman and Bowler 1980, LeBrasseur et al 1978). Mortality is thought to be size dependent, because larger fish are more adept grazers and better able to avoid predation.

Intra-specific competition and food availability are likely the primary determinants of growth rate, given that the temperature regime is more or less constant between years. Correlation of food availability and juvenile sockeye salmon growth rate has not been consistently shown. But growth rate has improved in lakes where fertilization increased zooplankton availability (Hyatt and Stockner 1985). In Flathead Lake, the growth rates of YOY and yearling kokanee have not declined significantly, despite a large reduction in the abundance of their preferred prey. If mortality occurred primarily in the first year in the lake, the density dependence of growth rate may be exerting an equalizing effect on size.

There is no clear link between decline in food availability and the decreased survival rate of Flathead Lake kokanee. We have not excluded possibility that food availability in May and June, immediately after outmigrant fry arrive in Flathead Lake, may exert a strong control over fish survival. Mortality rates exceeding 80% were shown for 0+ kokanee in their first summer In Lake Pend Oreille, Idaho (Bowles et al 1988), where zooplankton abundance has been similarly diminished by mysid grazing.

The observed decline in adult kokanee abundance in 1986 could not have been due to increased juvenile kokanee mortality associated with low food availability in 1983 and 1984. Mysid abundance was still low in those years, and limited sampling indicated that cladoceran abundance had not declined. Low food availability could have directly reduced the survival of the 1986 and 1987 adult year classes only after 1985. Similar declines in kokanee survival at low mysid abundance were observed in Lake Pend Oreille, Idaho in the mid-1970's. Rieman and Bowler (1980) concluded that reduced zooplankton abundance limited juvenile kokanee survival in that system. We have not measured the survival rate of specific year classes of kokanee in Flathead Lake.

Competition and predation may also be important factors. Juvenile lake whitefish have similar diet (Leathe and Graham 1982), grow more rapidly and may be better able to exploit the diminished plankton resource. Lake trout are the primary predator on kokanee in Flathead Lake. The growth and survival of juvenile lake trout may be enhanced by utilizing mysid shrimp as food. (Rieman and Lukens 1979, Morgan et al 1978).

Kokanee populations have been impacted to varying degrees in other lakes where mysid shrimp have been introduced. Coexistence in some systems may be related to the composition of the fish community. Abundant predators and/or competitive planktivores are conspicuously absent in lakes where mysid shrimp and kokanee populations coexist. Kokanee thrive in Swan Lake and Ashley Lake where they are the only planktivorous species in the limnetic zone (Rumsey 1985). Mysid abundance in both these lakes exceeds that found in Flathead Lake.

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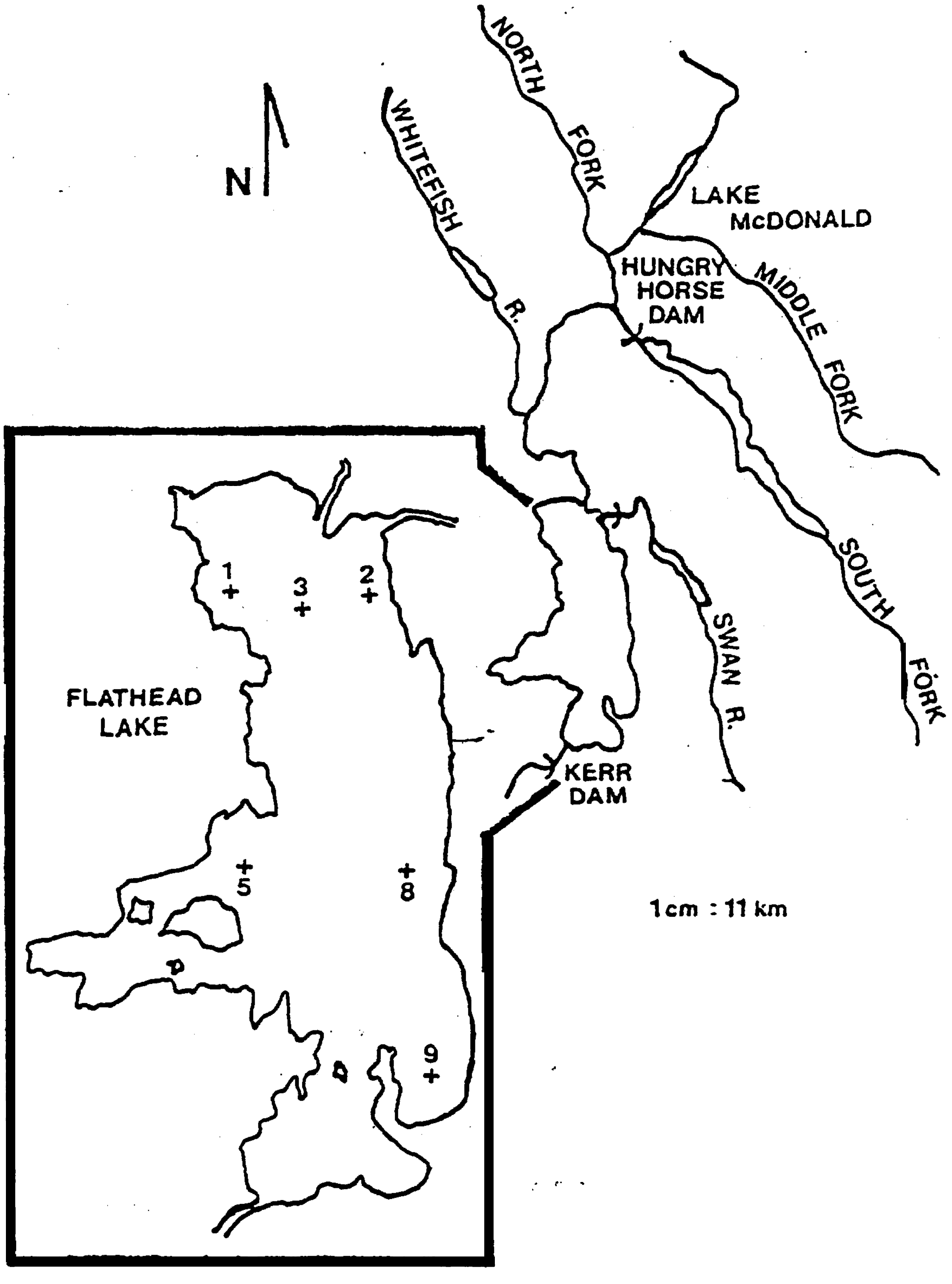
LIST OF FIGURES AND TABLES

Table 1. Fry production, resulting adult year class strength, spawning escapement, and fry-to-adult survival for kokanee in Flathead Lake, 1981 - 1987.

	Outmigrant Fry* (millions)	Adult Year Class Strength	Spawning Escapement	Fry-to-Adult Survival
1981	16.6	461,900	133,200	2.8%
1982	—	257,600	33,300	—
1983	—	204,800	54,200	—
1984	—	358,100	107,400	
1985	13.3	358,100	165,400	2.7%
1986	13.7	99,200	21,400	0.7%
1987	14.5	7,800	1,950	0.05%

*Outmigrant fry estimates are those that produced the listed adult year class, i.e. four years previous.


N
WHITEFISH R.
NORTH FORK
LAKE McDONALD
HUNGRY HORSE DAM
MIDDLE FORK
SOUTH FORK
SWAN R.
KERR DAM
FLATHEAD LAKE
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1cm : 11 km

Figure 1

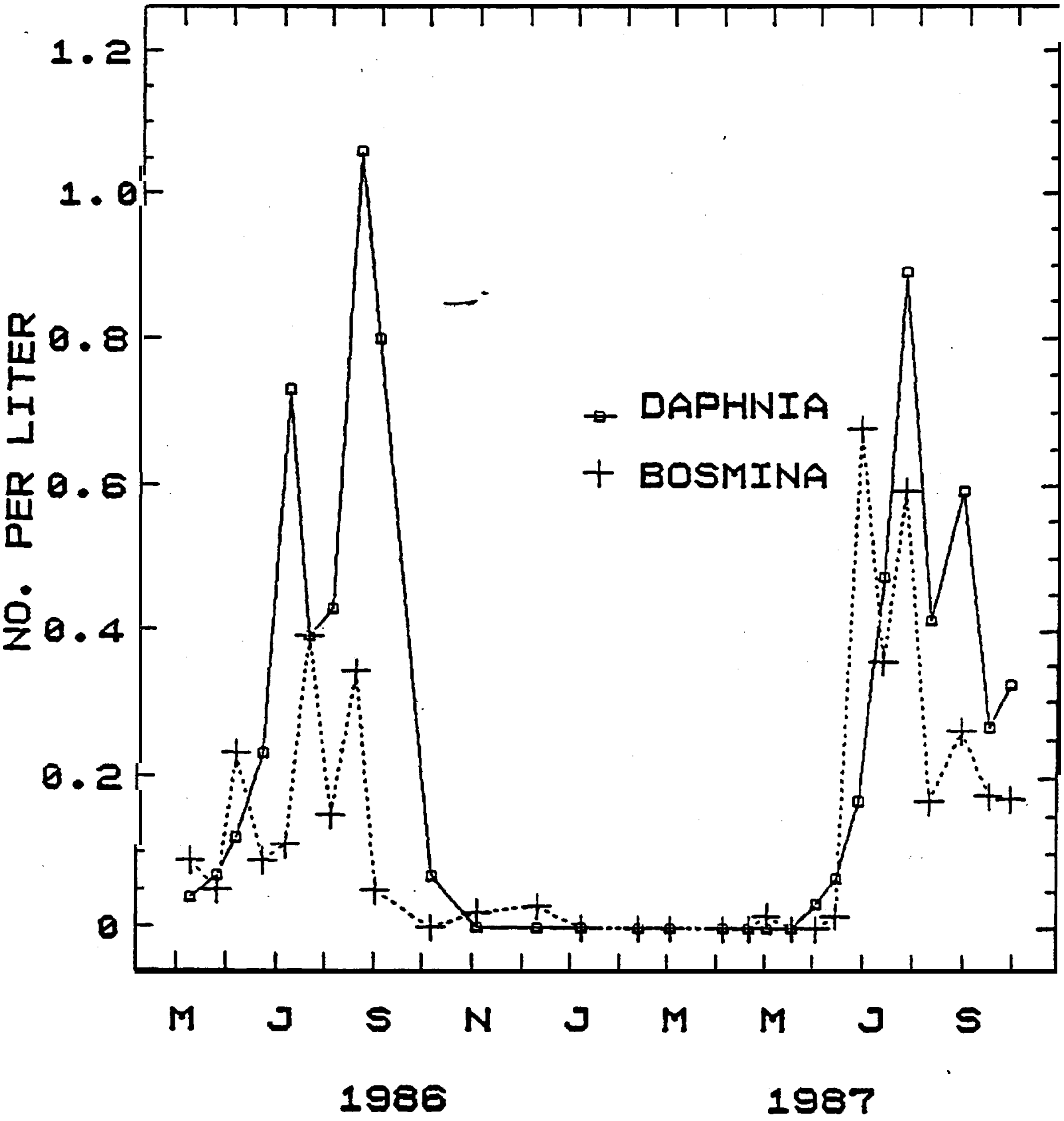

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Figure 2

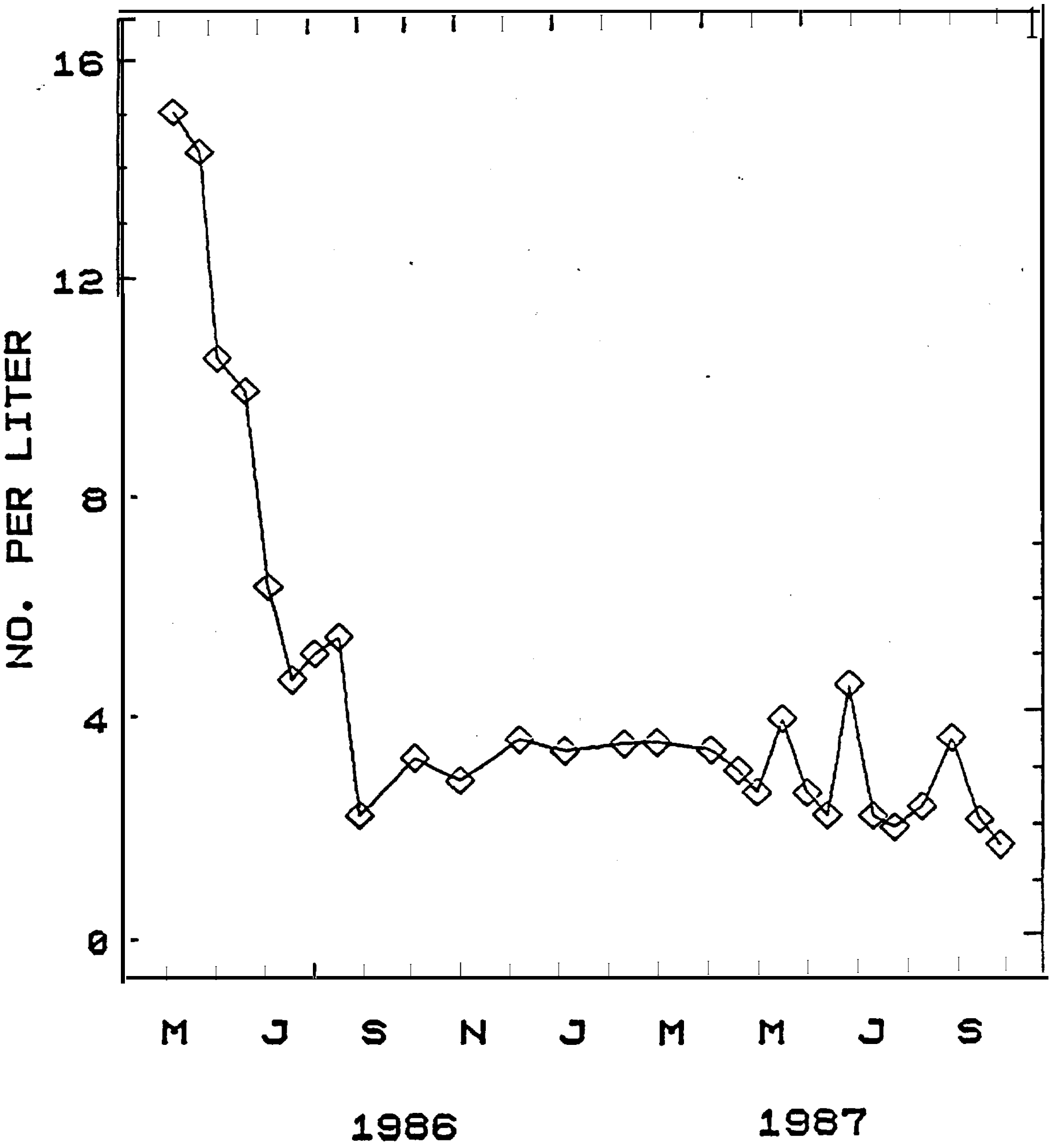


Figure 3

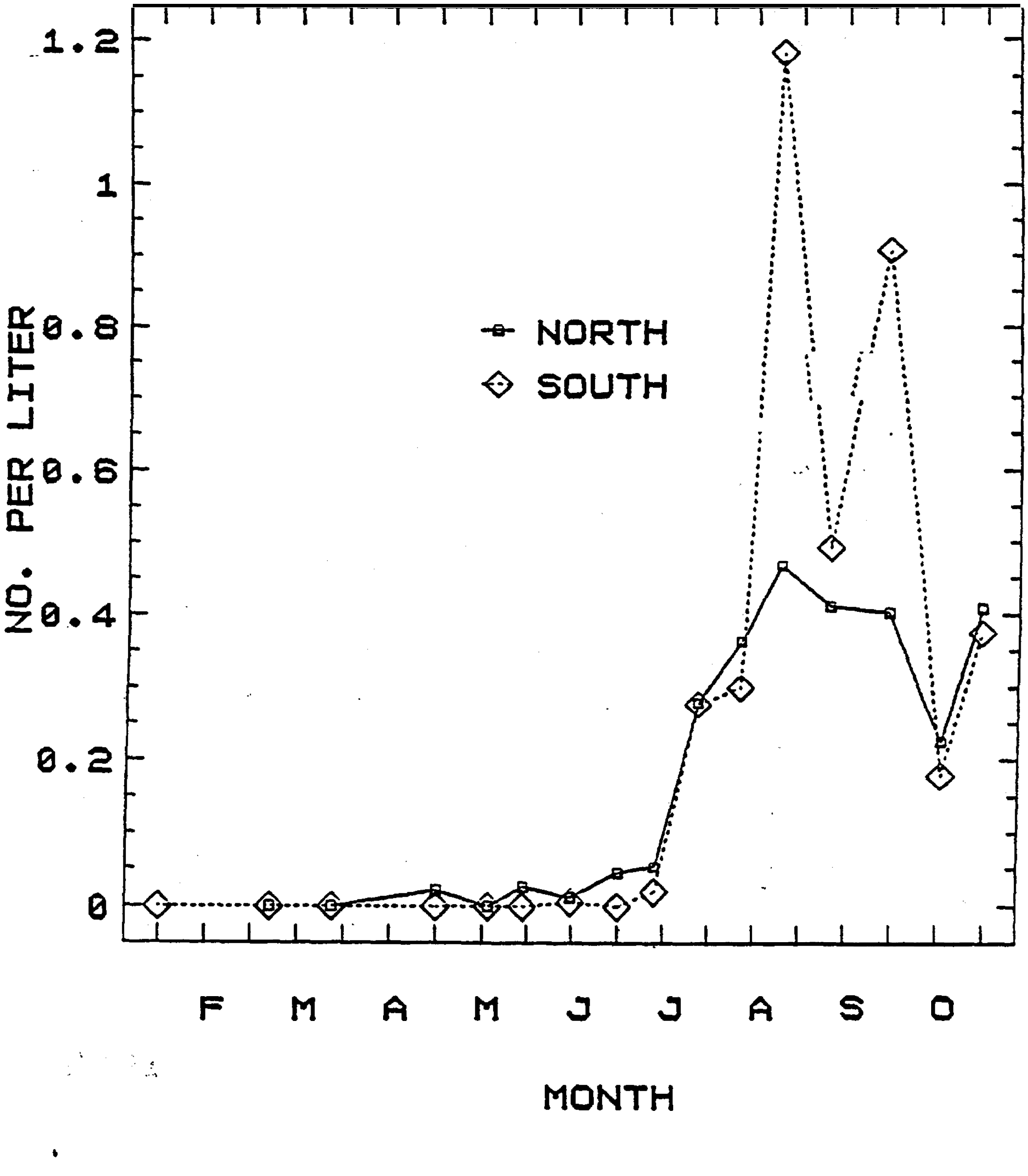


Figure 4.

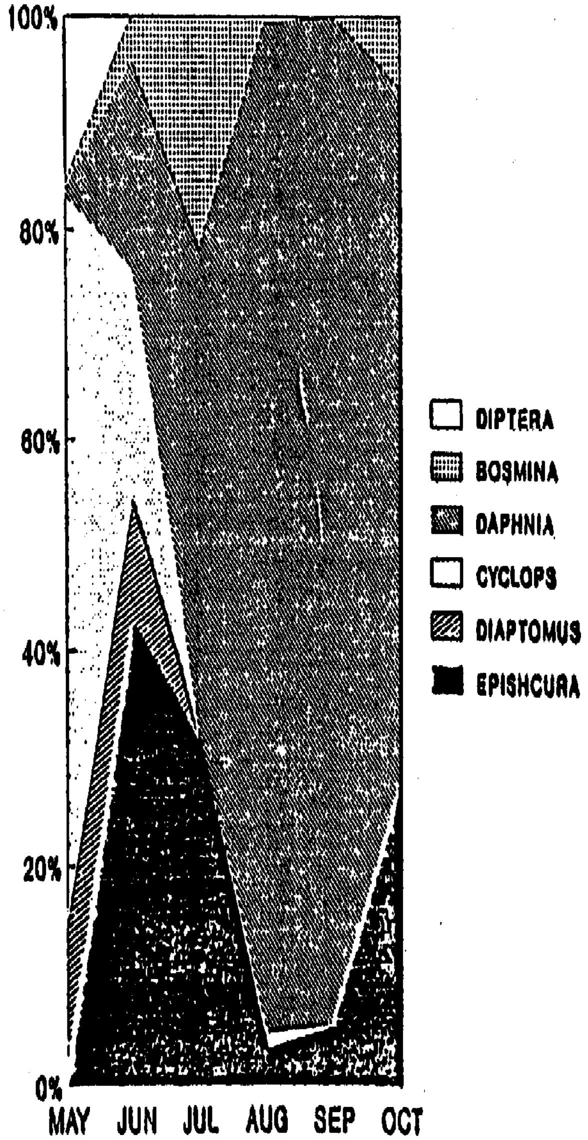
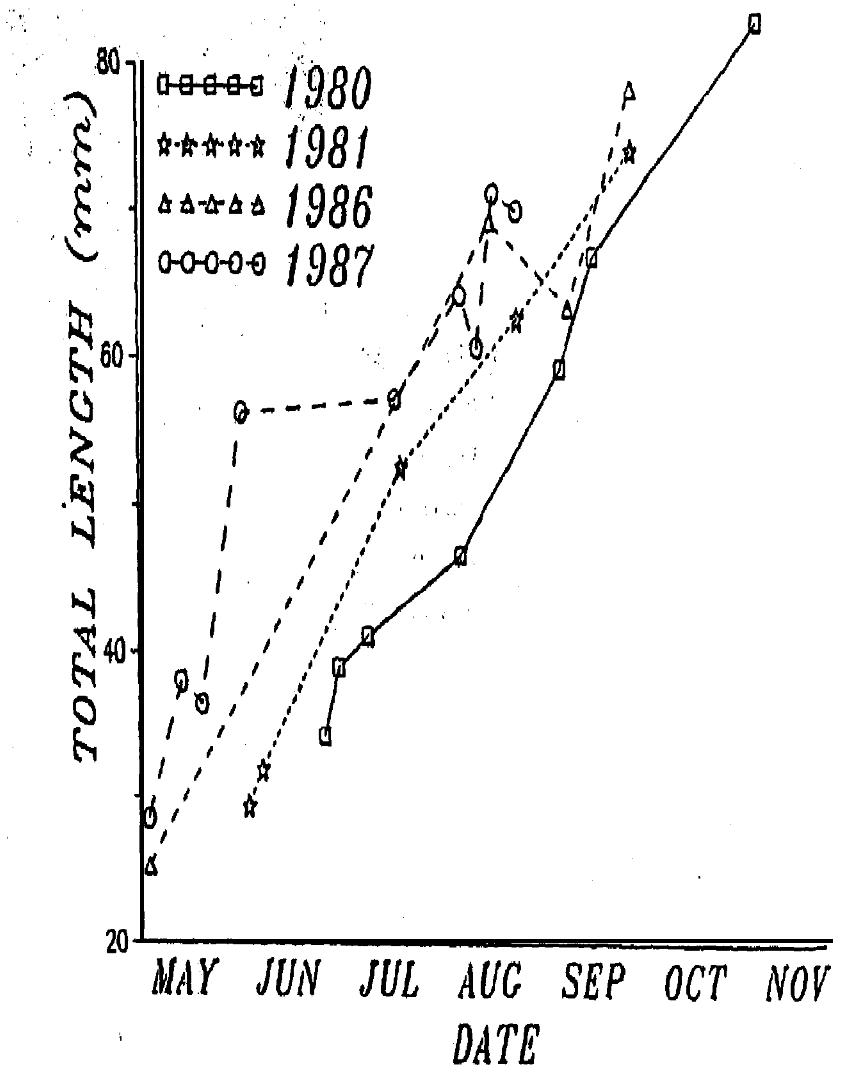
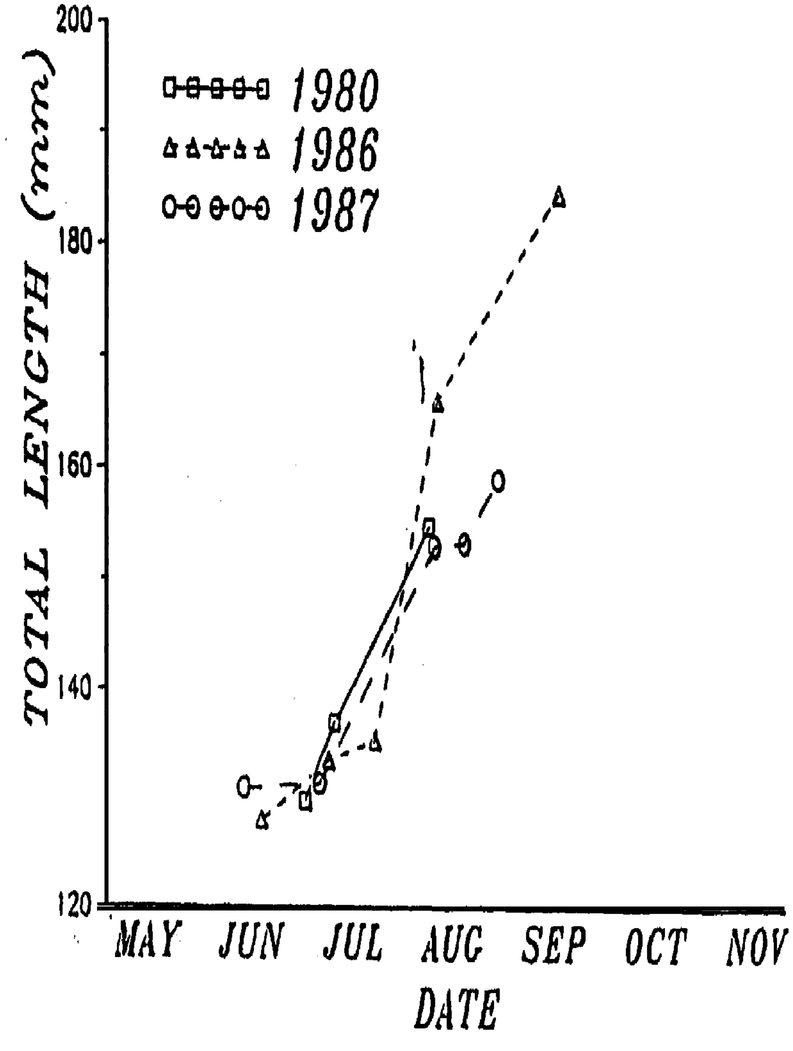

100%
80%
60%
40%
20%
0%
MAY
JUN
JUL
AUG
SEP
OCT
DIPTERA
BOSMINA
DAPHNIA
CYCLOPS
DIAPTOMUS
EPISHCURA

Figure
E-29


TOTAL LENGTH (mm)
80
60
40
20
1980
1981
1986
1987
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DATE

gure
E-30


200
180
160
140
120
TOTAL LENGTH (mm)
1980
1986
1987
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DATE

gure
E-31