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Effects of *Mysis relicta* on the Zooplankton Community and Kokanee Population of Flathead Lake, Montana

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Abstract.—Opossum shrimp *Mysis relicta* entered Flathead Lake, Montana, by dispersal from tributary systems in the late 1970s, and they reached an average density of 130/m^2 by 1986. The abundance and temporal distribution of the lake's crustacean zooplankton changed markedly as a result of mysid predation. *Daphnia longiremis* and *Leptodora kindti* were reduced to undetectable densities. The spring population increase of *Daphnia thorata* was delayed until July, and its maximum summer abundance declined from more than 4.0/L to 1.2/L. The abundance of the copepod *Diaptomus ashlandi* also declined, from more than 20/L to fewer than 5/L. Already affected by hydroelectric operations in the Flathead system, the population of kokanee *Oncorhynchus nerka* further declined after 1985. Though growth rates of young-of-the-year and yearling kokanees did not decline significantly between 1980 and 1981 and 1986 and 1987, fry-to-adult survival fell from 2.7% in 1985 to less than 0.05% in 1987. Predation by lake trout *Salvelinus namaycush* and competition with lake whitefish *Coregonus clupeaformis* may also influence survival of kokanee in Flathead Lake.

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, and the Stillwater River drain the 18,400-km^2 Flathead basin (Figure 1). The lake's mean depth is 32.5 m, and its maximum depth is 113.0 m.

The fishery for kokanee *Oncorhynchus nerka* in Flathead Lake, which until recently supported a sport harvest exceeding 200,000 fish/year (300,000 angler-hours), has declined markedly since 1985. The species was introduced into the lake in 1916 from coastal sockeye salmon stock. The scant historical data indicate that the fishery was well established and that spawning runs had developed along the Flathead Lake shore by the 1930s. Spawning runs have been composed mostly of age-3 fish, though ages 2 and 4 have composed up to 50% of some runs (Montana Department of Fish, Wildlife, and Parks, unpublished data).

The recent downturn in abundance of kokanee follows an earlier decline in reproductive success in the 1970s caused largely by hydroelectric operations that substantially reduced kokanee egg-to-fry survival. Winter power generation at Kerr Dam, built in 1937 below the outlet of Flathead Lake, annually draws the lake down 3.3 m between September and March, causing high egg mortality in exposed redds (Beattie et al. 1988). Hungry Horse Dam was constructed by the Bureau of Reclamation on the South Fork of the Flathead River in 1952. Initially, the rise in fall and winter water temperatures attributed to discharge from its reservoir attracted spawning kokanees to sites in the upper main stem and in the South Fork below the dam. But peaking power generation in the mid-1970s 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. Since 1980, much of the annual recruitment has been produced in McDonald Creek, a tributary of the Middle Fork. From 1982 to 1986, the number of kokanee fry produced annually in McDonald Creek ranged from 6.5 to 13.1 million (Clancey and Fraley 1986). Total fry production in the Flathead River ranged from 10 to 15 million. This level of production was sufficient to maintain the fishery until 1986.

The drop in sport harvest and spawning escapement in 1986 signaled an increase in kokanee mortality. This development was linked circumstantially to the establishment of opossum shrimp *Mysis relicta* in Flathead Lake. In 1968 and 1975, mysids were transplanted from Waterton Lake, Alberta, to Whitefish Lake, Ashley Lake, and

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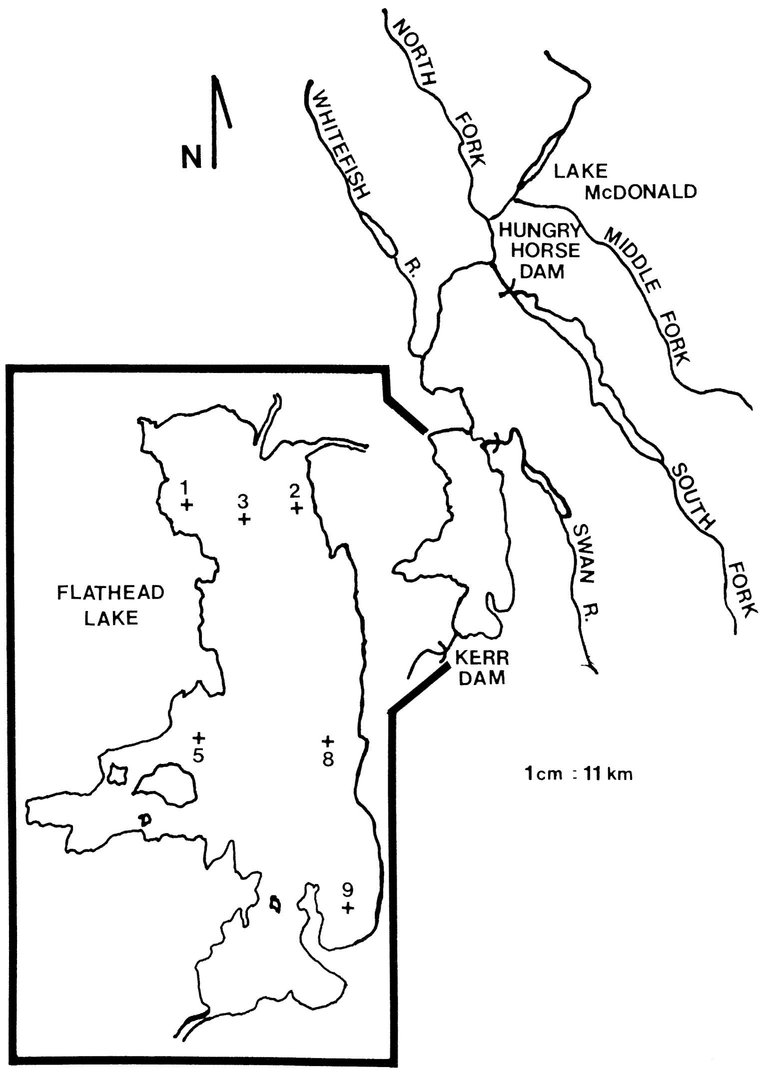

FIGURE 1.—Map of the Flathead drainage and its principal tributaries. Zooplankton sampling stations are shown on the enlarged inset.

Swan Lake—all tributaries of Flathead Lake. Populations of exotic mysids were expected to provide a superior food source for benthic-feeding fishes such as lake trout, and for pelagic planktivores such as kokanees. Downstream drift from the tributary lakes introduced mysids into Flathead Lake, where they were first collected in 1981 (Leathe and Graham 1982). The zooplankton and fish communities of other oligotrophic lakes have changed as a result of the establishment of mysids (Morgan et al. 1978; Rieman and Bowler 1979). We suspected that similar changes in the trophic ecology of Flathead Lake were influencing kokanee survival.

In 1986, the current study was begun to see if the anticipated decline in the abundance of cladoceran zooplankton, resulting from increased grazing pressure by opossum shrimp, would affect the growth and survival of kokanees in Flathead Lake. We regarded juvenile fish as particularly susceptible to food limitation, because they enter the lake from upstream spawning areas in April and May, before pulses in secondary productivity have occurred. Our hypothesis was supported by studies of other large lakes in which mysids had become established—in particular, Pend Oreille Lake, Idaho, and Lake Tahoe, California (Morgan et al. 1978; Rieman and Falter 1981). Although similar events had occurred in many lakes throughout the Pacific Northwest and Canada (Northcote 1973; Rumsey 1985), differences in the trophic status and the zooplankton and fish communities of those lakes made the outcome in Flathead Lake uncertain.

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 with a 0.5-m-diameter Wisconsin net made of 80-μm Nitex. The samples were preserved in 95% ethanol. Cladocerans and copepods were identified and counted in four 1-mL subsamples dispensed into a Sedgwick–Rafter chamber, except for species of *Epischura* and *Leptodora*, which were counted in four 30-mL subsamples. At each sampling site, temperature profiles were obtained with a calibrated thermistor thermometer.

We surveyed mysids 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: 5–40 m, 40–75 m, and deeper than 75 m. Vertical hauls were pulled from the bottom with a 1.0-m Wisconsin net made of 500-μm Nitex. The average densities in each depth stratum, expressed as the number of mysids per square meter, were weighted according to the proportion of the lake's surface area covering each stratum to calculate lakewide average density.

We surveyed the abundance of cladocerans and copepods, because of their importance in the diet of planktivorous fish. Sampling in Flathead Lake had provided a record of the spring and summer abundance of zooplankton since 1980, which we used as a basis for interpreting the results of our study in 1986 and 1987. From 1983 to 1985, zooplankton samples were taken only 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 1983–1985 density measurements were not comparable with earlier or later work. Comparisons of temporal distribution among all years were possible.

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

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

Spawning kokanees 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 ratio of 2.6 spawners/redd was used to expand the redd count (Clancey and Fraley 1986). Fry production in McDonald Creek was estimated by means of four 0.5-m^2 drift nets set from a bridge at the creek mouth. These nets were set once each week from April 1 through June 15, 1982–1986. Net catches were expanded from the volume sampled to total flow in the creek during the 24-h sample period, and extrapolated over the 7-d interval between samples.

We estimated kokanee survival by comparing fry production with abundance of age-3 adults 4 years later. Estimates of adult year-class strength were derived from sport harvest (Graham and Fredenburg 1982; Hanzel 1986) and escapement estimates, and included contributions of age-2, and -4 fish from adjacent years. Figures on spawning escapement and egg-to-fry survival indicated that McDonald Creek produced approximately 90% of the total annual recruitment from 1982 to 1984. From 1981 to 1985, the spawning escapement for McDonald Creek averaged 78% of the system total. Egg-to-fry survival in McDonald Creek exceeded that of other riverine and lakeshore spawning areas (Clancey and Fraley 1986).

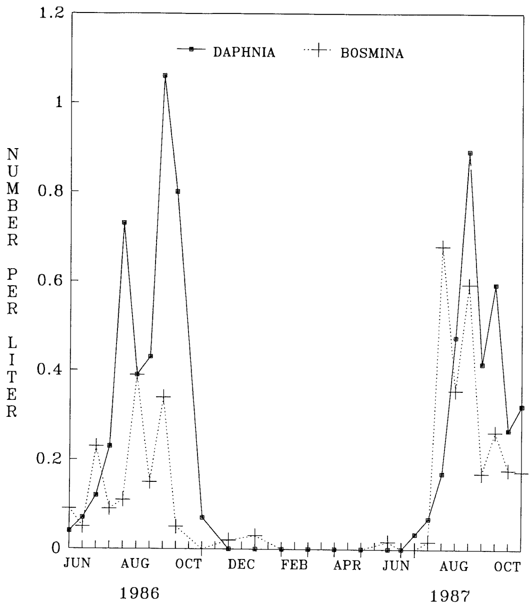

FIGURE 2.—Densities of *Daphnia thorata* and *Bosmina longirostris* at station 2 on Flathead Lake in 1986–1987.

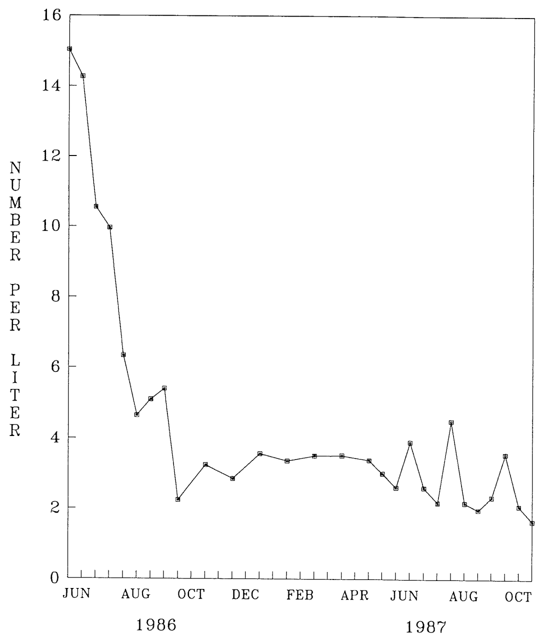

FIGURE 3.—Densities of *Diaptomus ashlandi* at station 2 on Flathead Lake in 1986–1987.

Results

Decline in Crustacean Zooplankton Abundance

The maximum summer density of *Daphnia thorata* at station 2, which varied 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, *D. thorata* reached measurable density as early as April, and increases in standing crop were evident in late May. In 1987, this species was below detectable density until late May at all stations, and the first pulse was delayed until early July.

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

Daphnia longiremis was detectable briefly in August 1986 and was not present in 1987 samples. It was present consistently from May through August in previous years, although its density fell below 0.1/L in 1982. This cold, stenothermic species was always less abundant than *D. thorata* in samples collected in the metalimnion and epilimnion in previous years (Leathe and Graham 1982). *Leptodora kindti* was present in measurable densities for successively shorter summer periods from 1983 to 1986, and it was not found in 1987 samples. Its maximum density declined from 0.04 to 0.14/L in 1980–1982 and to 0.01/L in 1986. The diel migration of *L. kindti* toward deeper water during daylight hours (Potter 1978) may have affected the accuracy of abundance measurements made by daytime 30-m vertical tows.

The abundance of the copepod *Diaptomus ashlandi* also has declined since 1985. In previous years, this species was the most abundant crustacean in Flathead Lake, with early- to midsummer peaks in density of 10–40/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 1986–1987 were not significantly different (Mann–Whitney pairs test, $P = 0.10$) within years. Subtle interstation differences in production timing were found for *Daphnia thorata*. For example, it reached measurable density

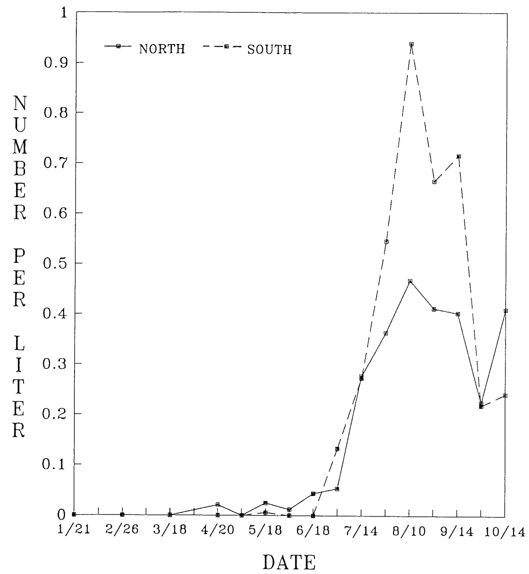

FIGURE 4.—Comparison of the mean density of *Daphnia thorata* at three northern stations with that at three southern stations on Flathead Lake in 1987.

at the three northern stations 2 weeks earlier than at the three southern stations in 1986. It was present at station 1 in late March 1987, whereas it was not found at deeper stations in the southern end of the lake until the end of June. 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 *M. relicta* was first found in Flathead Lake (Leathe 1982), its abundance increased exponentially to reach a lakewide average density of 45/m^2 in 1985 (R. Bukantis, Yellow Bay Biological Station, personal communication). The rate of increase declined slightly in 1986, when the average density was 130/m^2. Average density declined slightly, 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 10 years of introduction, as was found in many other large, oligotrophic lakes (Northcote 1973; Morgan et al. 1978; Rieman and Bowler 1980). Given the increased incidence of mysids 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 clear relationship between density and station depth was evident. Density was less than 15/m^2 at all stations shallower than 25 m. Factors that may influence the distribution of opossum shrimp include 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 mysids continue to migrate into the epilimnion (Spencer et al. 1991).

Kokanee Survival Rates

Fry-to-adult survival was approximately 2.9% in 1981 and 3.0% in 1985. It dropped sharply to 0.7% in 1986 and to less than 0.01% in 1987 (Table 1). In 1985, adult year-class strength and spawning escapement were the highest since 1979. Age-3 year-class strength fell from more than 350,000 in 1984 and 1985 to less than 8,000 in 1987. Fishing mortality frequently accounted for more than 50% of the age-3 year-class in the early 1980s, but comparatively few kokanees were

TABLE 1.—Fry production, resulting adult year-class strength, spawning escapement, and fry-to-adult survival rates for kokanees in Flathead Lake, 1981–1987. Fry estimates are for fish that produced the listed adult year-class; these fry outmigrated 4 years earlier.

Year	Outmigrant fry (millions)	Adult year-class strength	Spawning escapement	Fry-to-adult survival (%)
1981	16.6	474,400	147,200	2.9
1982		257,600	33,300	
1983		204,800	54,200	
1984		358,100	107,400	
1985	13.3	402,700	210,100	3.0
1986	13.7	99,200	21,400	0.7
1987	14.5	7,800	1,950	0.05

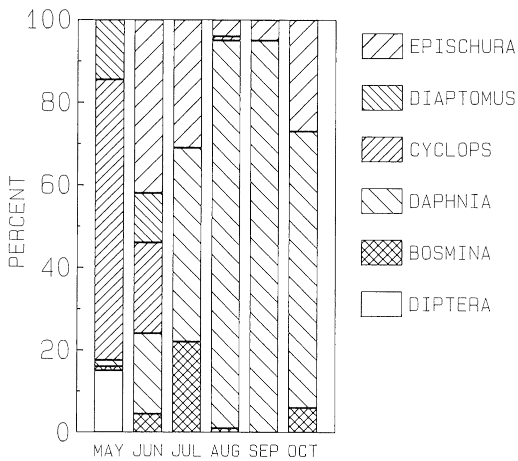

FIGURE 5.—The diet of age-0 kokanees in Flathead Lake in 1986–1987, expressed as mean monthly frequency of organisms in stomach samples.

caught in 1986 and 1987. Fry recruitment was relatively high in 1983 and 1984, numbering 13.7 and 14.5 million fish, respectively (Table 1).

Changes in the Juvenile Kokanee Diet

The diet of young-of-the-year kokanees collected in May consisted predominantly of the copepod *Cyclops bicuspidatus* (69%), plus significant numbers of *Diaptomus ashlandi* (14%) and aquatic insects (16%), mostly chironomid pupae (Figure 5). Other zooplankton species, including *Daphnia thorata*, *Bosmina longirostris*, and *Epischura nevadensis*, were found infrequently in stomach samples. June samples showed somewhat greater diversity in diet, consisting of *E. nevadensis* (42% on average), *C. bicuspidatus* (22%), *Daphnia thorata* (19%), *Diaptomus ashlandi* (12%), and *B. longirostris* (4%). For July, *D. thorata* made up almost half (46%) of the young-of-the-year kokanee diet, *B. longirostris* made up 22%, and *E. nevadensis* made up 31%. In August and September, the diet was dominated strongly by *D. thorata*; *E. nevadensis* and *B. longirostris* were somewhat better represented in October when they made up 27 and 7% of the stomach contents collected.

In a study of young-of-the-year kokanee diet in 1980–1981, Leathe and Graham (1982) showed that *D. thorata* made up at least 60% of the food biomass from June through November. *Epischura nevadensis* was the only other species that contributed significantly to their diet. Other studies have shown that kokanee and sockeye fry shift their diet in the summer from small zooplankton, such as species of *Cyclops*, *Diaptomus*, and *Bosmina*, to larger prey, such as species of *Daphnia*, *Diaphanosoma*, and *Epischura* (Goodlad et al. 1974; Doble and Eggers 1978; Lindsay and Lewis 1978). This shift, which apparently occurred before the May samples were collected in 1980 and 1981, was delayed until August in 1986–1987. That young-of-the-year kokanees selected for *D. thorata* was emphasized by the occurrence of this species in stomachs collected in May and June, when its availability was near or below detectable limits. Juvenile kokanees also selected for *E. nevadensis* in June, July, and October.

The diet of age-1 kokanees did not differ markedly from that of young-of-the-year fish, except that yearlings shifted from a diverse diet to one dominated by *Daphnia thorata* 1 month earlier, in July. We did not collect any yearling samples in May. In June 1986, *Bosmina longirostris* (23%), *Epischura nevadensis* (35%), and *D. thorata* (40%) contributed to the yearling diet. In June 1987, however, cladoceran abundance was low (<0.1/L) and *E. nevadensis* made up 72% of the yearlings' diet. In July, August, and September, diet was dominated by *D. thorata*. A strong preference for larger prey, principally *D. thorata* and *E. nevadensis*, was apparent in yearling kokanees as well. Mysids did not contribute to the diet of juvenile kokanees during the months encompassed by our sampling.

Juvenile Kokanee Growth Rate

Comparison of the lengths of young-of-the-year kokanees sampled in 1980 and 1981 with those collected in 1986 and 1987 revealed no significant differences in growth rate. Because fry hatched in McDonald Creek made up a large proportion of the annual recruitment, their size was taken as a baseline for assessing the growth rate of young of the year. 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 to 78.5 mm in mid-October (Figure 6). Apparently, juvenile kokanees continued to grow in the fall in spite of declining food availability and falling water temperature in the lake.

Yearling kokanee growth rates were similarly low in June and July of 1986 and 1987 (Figure 7). The mean length of fish did not exceed 135 mm through that period in either year. By the end of August, however, samples collected in 1986 were significantly larger than those collected in 1987. In

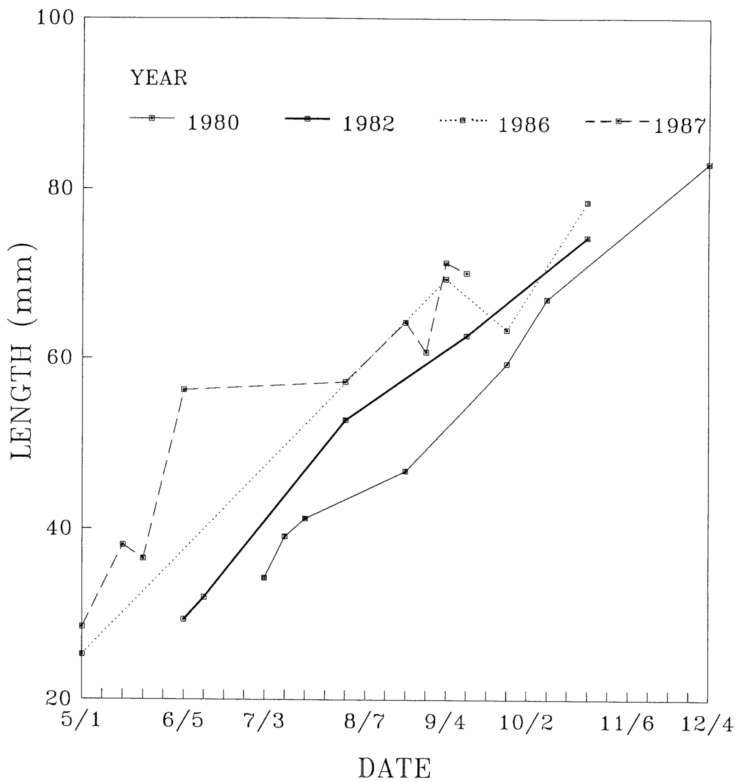

FIGURE 6.—The growth trajectory of age-0 kokanees in Flathead Lake in 1980, 1981, 1986, and 1987. Significant differences do not exist between mean lengths at each sampling date.

late August 1986, mean length approached 170 mm, whereas mean length in 1987 was about 155 mm. The summer growth trajectory in 1986 was not significantly different from that of yearling fish collected in 1980.

Discussion

Zooplankton Community

The changes observed in the zooplankton community of Flathead Lake probably were caused by increased predation by opossum shrimp. Declines in cladoceran abundance following the introduction of *M. relicta* are well documented in lakes of the western United States, Canada, and Scandinavia (Zyblut 1970; Richards et al. 1975; Langeland 1981; Rieman and Falter 1981; Grossnickle 1982). Studies of mysid diets have found a preference for cladocerans such as *Daphnia* spp. (Grossnickle 1982).

In Flathead Lake, *Daphnia thorata* and *Bosmina longirostris* occupy the water column from 30 m to the surface (Potter 1978). This upper layer becomes a refuge for cladocerans in the summer when temperatures of 15°C or more act as a barrier to most mysids. The data from Flathead Lake suggest that increases in cladoceran abundance were delayed until thermal stratification had isolated a substantial part of the population from mysid grazing (Morgan et al. 1981). Also, low mysid abundance in water less than 40 m deep allowed daphnids to multiply early in the spring in shallow parts of the lake. Interstation differences in the thermal structure of the lake appeared insufficient to cause significantly different productivity.

We attributed the decline of *Daphnia longiremis* in 1986–1987 to increased mysid grazing. This species occupies colder, deeper water (Potter 1978; Leathe and Graham 1982) and is therefore available to mysids throughout its life cycle. The decline in the abundance of *Diaptomus ashlandi* also appeared to involve mysid grazing. Feeding experiments have shown that *M. relicta* graze heavily on *Diaptomus* (Folt et al. 1982), and gravid female *D. ashlandi* may be particularly

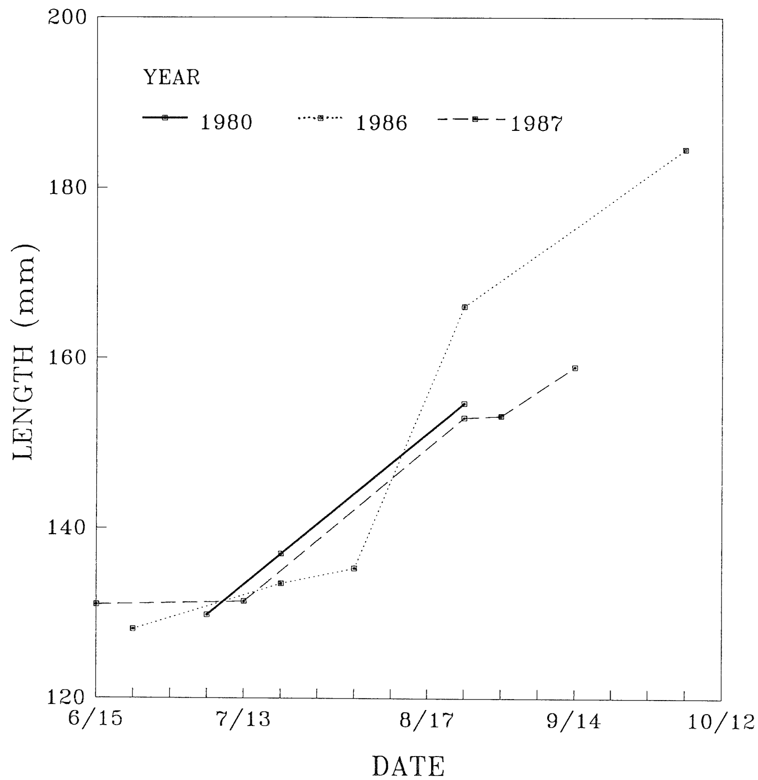

FIGURE 7.—The growth trajectory of age-1 kokanees in Flathead Lake in 1980, 1986, and 1987. Mean length in September 1987 is significantly lower than in preceding years.

vulnerable to predation because of their preference for water deeper than 30 m (Potter 1978). As cladoceran abundance declined, other predaceous species such as *Epischura nevadensis* may have shifted to the more available copepods.

Other factors that might have contributed to the observed changes in the zooplankton community were not 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, 1984–1985 and 1985–1986, but it thawed in early April in both years, and spring warming proceeded normally. Because primary productivity did not change significantly in the two succeeding spring–summer seasons relative to the preceding 5 years (B. Ellis, Flathead Lake Biological Station, personal communication), it seems unlikely that secondary productivity was limited by temperature.

Kokanee Growth and Survival

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

Intraspecific competition and food availability appeared to be the primary determinants of growth rate, given that the temperature regime was similar between years. Although correlations between food availability and juvenile sockeye salmon growth rate are not always evident, growth rate has improved in lakes where fertilization increased zooplankton availability (Hyatt and

Stockner 1985). In Flathead Lake, the growth rates of young-of-the-year and yearling kokanees have not declined significantly despite depletion of their preferred prey. If mortality occurred primarily in the first year in the lake, the density-dependence of growth rate may have exerted an equalizing effect on size.

There is no clear link between the decline in food availability and the decreased survival rate of Flathead Lake kokanees. We have not excluded the possibility that fry survival was reduced by low food availability in May and June, soon after fry enter Flathead Lake. Mortality rates exceeding 80% were shown for kokanees in their first summer in Pend Oreille Lake, Idaho (Bowles et al. 1991, this volume), where zooplankton abundance has been similarly diminished by mysid grazing.

The observed decline in abundance of adult kokanees in 1986 could not have been due to increased juvenile kokanee mortality associated with low food availability in 1983 and 1984. Mysid numbers were still low in those years, and limited sampling showed continued cladoceran abundance. 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 in conjunction with low numbers of mysids were observed in Pend Oreille Lake, Idaho, in the mid-1970s. Rieman and Bowler (1980) concluded that reduced zooplankton populations limited survival of juvenile kokanees in that system. We have not measured the survival rate of specific year-classes of kokanees in Flathead Lake.

Competition and predation also may be important factors. Juvenile lake whitefish have a diet similar to that of kokanees (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 kokanees in Flathead Lake. The growth and survival of juvenile lake trout may benefit from their use of opossum shrimp as food (Morgan et al. 1978; Rieman and Lukens 1979).

Kokanee populations have responded variously to mysid introductions. Coexistence in some systems may be related to the composition of the fish community. Abundant predators or competitive planktivores, or both, are conspicuously absent in lakes where opossum shrimp and kokanee populations coexist. Kokanees thrive in Swan Lake and Ashley Lake, where they are the only planktivorous species in the limnetic zone (Rumsey 1985). Mysid density in both these lakes exceeds that found in Flathead Lake.

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