

ABUNDANCE AND PRODUCTION OF ZOOPLANKTON AND KOKANEE SALMON
(*ONCORHYNCHUS NERKA*) IN KOOTENAY LAKE, BRITISH COLUMBIA DURING
ARTIFICIAL FERTILIZATION

by

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ABSTRACT

Experimental fertilization was conducted on Kootenay Lake, B.C. from 1992 to 1997 to compensate for nutrients lost behind hydroelectric dams upstream of the lake. Declining nutrient loads were correlated with lower in-lake nutrient concentrations, chlorophyll *a* concentrations, and macrozooplankton densities, and a dramatic decline in kokanee salmon (*Oncorhynchus nerka*) stocks. A simulation model of the lake suggested that increased zooplankton production resulting from fertilization might be shunted into increased abundance of *Mysis relicta*, an exotic crustacean that competes with kokanee, and that nutrient additions might actually hasten the kokanee decline. In an attempt to test this prediction, nutrients were applied at the north end of the lake, and the response of the food web was monitored along the expected longitudinal productivity gradient.

The food web structure along the lake suggests that a trophic gradient of grazeable phytoplankton abundance was established, but that *M. relicta* may have grazed down any increase in zooplankton production in the fertilized end of the lake. Kokanee distribution and size-at-age along the lake did not correlate with the nutrient gradient. Surprisingly, *M. relicta* abundance decreased during the experiment, while kokanee abundance increased four-fold, and Gerrard rainbow trout (*Oncorhynchus mykiss*), which prey mainly on kokanee, also increased in abundance. *M. relicta* is vulnerable to mortality due to export out of the lake during high flow years, whereas zooplankton replace flow-related mortality through rapid reproduction and kokanee can actively avoid export. High surface water turnover rates, due to large winter snow accumulation during the experiment, likely contributed to increased *M. relicta* mortality. This physical factor may have shifted the competitive equilibrium between kokanee and *M. relicta*, by suppressing an increase in *M. relicta* abundance, and allowed kokanee to take advantage of increased zooplankton availability.

Caution should be exercised in extrapolating the results of fertilization in Kootenay Lake to other large lakes where fish populations have been affected by hydroelectric dams or competition from exotic species introductions. Nutrient additions may not reach the desired target species unless the responses of exotic competitors are suppressed by physical factors operating independently of the dynamics of the food web.

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PREFACE

Some material included as part of this thesis has previously been published by the author in "Relationship of kokanee salmon (*Oncorhynchus nerka*) abundance to total phosphorus loading, and *Mysis relicta* density in Kootenay Lake, British Columbia", in the journal Internationale Vereinigung für Theoretische und Angewandte Limnologie (Verh. Int. Ver. Limnol.) Volume 27 (in press). The material in the article includes Figures 16, 39, and 40, and related text on Kokanee Abundance and Total Phosphorus Load in this thesis.

CHAPTER 1: HISTORICAL AND APPLIED BACKGROUND OF THE FERTILIZATION OF KOOTENAY LAKE, BRITISH COLUMBIA

Introduction

The ecosystem of Kootenay Lake, B.C., has undergone profound changes in the past fifty years as a result of human impacts, most notably the construction of large hydro-electric projects, and the introduction of exotic species. Following a period of high nutrient loading the lake became dramatically less productive during the 1970's and 1980's following the closure of an upstream fertilizer plant, and development of hydroelectric dams. The exotic freshwater crustacean *Mysis relicta* became very abundant during this period. Kokanee salmon (*Oncorhynchus nerka* (Walbaum)) populations declined, raising fears that the unique Gerrard rainbow trout (*Oncorhynchus mykiss*) that feed on these kokanee might be lost. In desperation, fisheries managers and scientists recommended in the late 1980's that lake fertilization be attempted. Computer modeling of the lake ecosystem led to contradictory predictions about fertilization. In one scenario nutrient additions moved through the food web to grazeable phytoplankton, macrozooplankton such as *Daphnia*, and to kokanee and rainbow trout. However, in another scenario (reasonable combination of parameter estimates) the benefits of nutrient additions were side-tracked to *M. relicta*, which competes with kokanee for zooplankton. Simulated *M. relicta* abundance increased, and the kokanee population crashed even more rapidly than in the absence of fertilization. A key aim of this study was to test these alternatives.

Objectives and Organization of Thesis

I studied the first six years of a nutrient addition experiment undertaken to reverse some of the adverse effects of human disturbance on the lake community. In this thesis I analyzed

rotifer, macrozooplankton, kokanee salmon, rainbow trout, and bulltrout data that were my field responsibility to collect. I focused on the changes in abundance and productivity of macrozooplankton and kokanee salmon during the fertilization experiment. I also analyzed the ecosystem as a whole, using my own field data, and water chemistry, phytoplankton, and *Mysis relicta* data collected by other researchers. In addition, I designed, developed and maintained the project database, incorporating data from all aspects of the experiment.

Chapter 1 gives a historical overview of changes in Kootenay Lake leading up to the fertilization experiment, outcomes of previous fertilization experiments on other lakes, and predictions about the effects of nutrient additions on Kootenay Lake based on a simulation model developed prior to the experiment. Chapter 2 describes the design of the experiment, and the uncertainties and potential problems involved in the experimental design that was chosen. I then describe the hypotheses I tested regarding the structure of the Kootenay Lake food web along a productivity gradient caused by nutrient additions localized in the North Arm of the lake. I discuss the possible food web scenarios that could develop, depending on the response of different phytoplankton size classes to additional nutrients, the ability of *M. relicta* to compete for zooplankton, and the ability of kokanee and trout to crop down their food sources along the length of the lake. In Chapter 3, I detail the field, laboratory, and analytical methods used. Methods are grouped according to trophic level, beginning with fertilizer distribution, and moving upward through physical and chemical limnology, phytoplankton, zooplankton, kokanee, and trout. In Chapter 4, I present the results of the experiment. Physical and chemical limnological patterns are described first, and biological results are grouped into two main categories: patterns observed in abundance and distribution, and patterns observed in production, diet, and consumption. Within these categories I report time series data where available, and then look in detail at patterns observed along the expected productivity gradient. In Chapter 5, I

return to the hypotheses proposed in Chapter 2 and assess the outcome of the fertilization experiment in terms of the food web structure of the lake, the influence of factors independent of the food web, and competition between kokanee and *M. relicta*. I finish with a consideration of the management implications of the Kootenay Lake fertilization experiment, and suggestions for improving whole-lake experiments on this and other lakes.

It is unlikely that nutrient additions alone would restore the lake to a pristine state, given the range of impacts the lake has experienced, some of which may be irreversible. However, should fertilization be shown to improve the state of the ecosystem, its continued use may help to conserve the natural biota of the lake, and nutrient additions could then be considered for several other large lakes in the Pacific Northwest that have experienced similar impacts.

Lake Description

Kootenay Lake is a large, interior lake situated in the Purcell Trench in southeastern British Columbia (49°38'N, 116°54'W; Fig. 1). The lake is 107 km long and 4 km wide, with a maximum depth of 154 m. There are two major tributaries: the Duncan River enters the North Arm, and the Kootenay River enters the South Arm (Note: this river is known as the Kootenai River where it flows in the United States). Water flows out into the West Arm at the central-west side of the lake and forms the Kootenay River, which joins the Columbia River at Castlegar. Both of the major tributaries are impounded by hydroelectric dams which were constructed as a result of the 1961 Columbia River Treaty (BPA 1989). The Duncan Dam formed the Duncan Reservoir (previously Duncan Lake) northeast of Kootenay Lake in 1967 (Northcote 1973), and the Libby Dam, on the Kootenai River in Montana, formed the Koocanusa Reservoir, which stretches back into Canada near Cranbrook, in 1973 (Daley et al. 1981). There are also five dams on the Kootenay River between Nelson and Castlegar: Corra Linn, Slocan, Upper Bonnington, Lower Bonnington and Brilliant, as well as the Kootenay Canal. The Corra

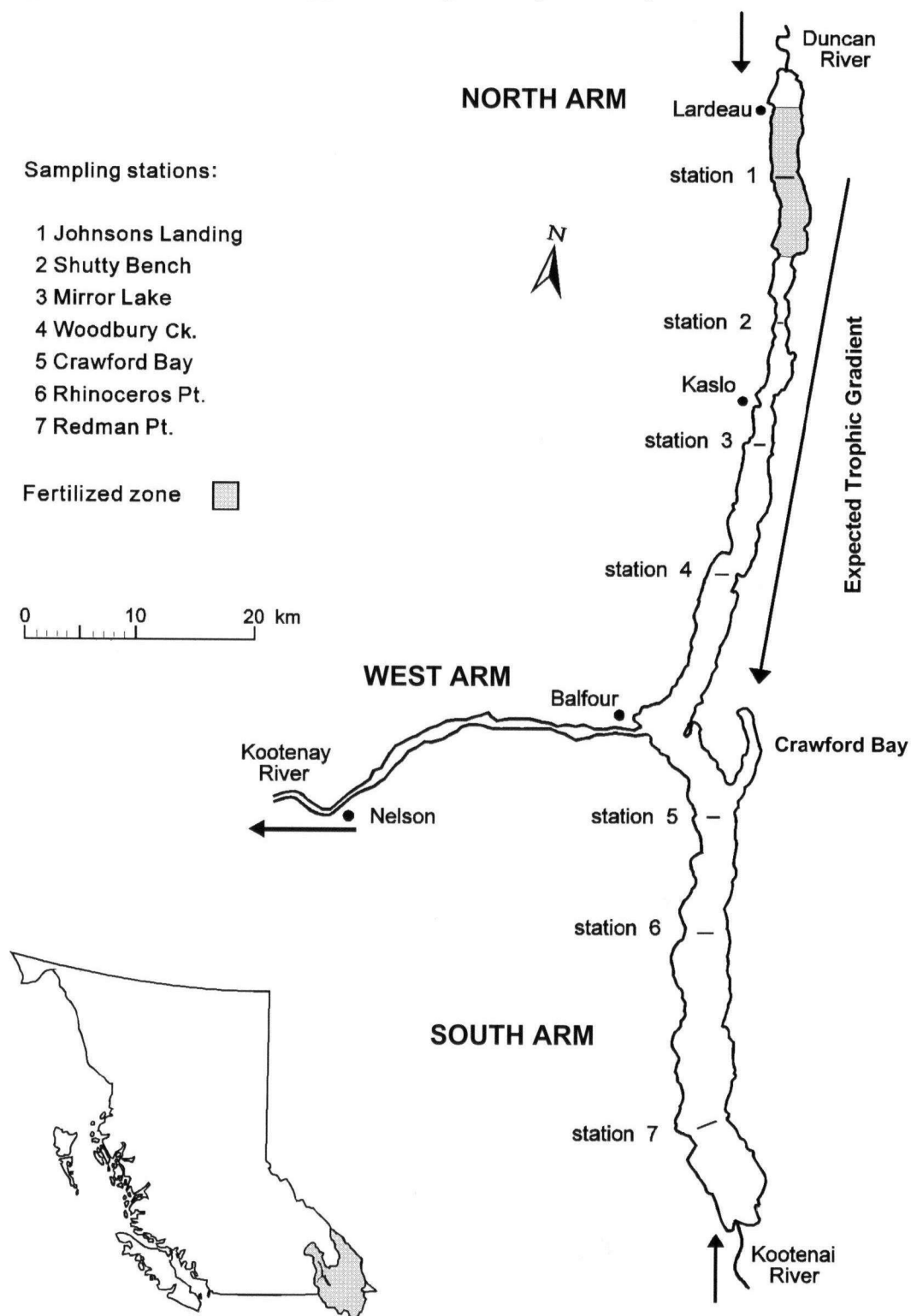


Fig. 1. Map of Kootenay Lake showing fertilization addition zone, sampling sites, and direction of expected trophic gradient.

Linn Dam was completed in 1932, but did not begin regulating lake levels until 1939 (Daley et al. 1981). The main basin of Kootenay Lake has a theoretical hydraulic residence time of 1.8 years (Daley et al. 1981), but the summer epilimnetic residence time is about 0.33 year, and the hypolimnion may take as long as six years to turn over completely.

Major Fish Species

There are several sportfish in Kootenay Lake. Kokanee salmon is the predominant pelagic planktivore (Andrusak and Parkinson 1984). There are three distinct spawning stocks of kokanee: North Arm, South Arm, and West Arm (Vernon 1957). Rainbow trout and bull trout (*Salvelinus confluentus*) are present and grow to trophy size by feeding on kokanee (Sisson 1943; Andrusak 1981; Andrusak and Parkinson 1984). The Gerrard strain of rainbow trout spawns in a small section of the Lardeau River, a tributary of the Duncan River (Cartwright 1961), and is the basis of a popular sportfishery for anglers using steelhead-type gear. A stock of smaller "resident" rainbow is present in the West Arm and is fished with artificial flies only to prevent accidental kokanee catches (Andrusak 1981). The lake also contains brook trout (*Salvelinus fontinalis* (Mitchill)), burbot (*Lota lota* (Linnaeus)), largemouth bass (*Micropterus salmoides* (Lacépède)), largescale sucker (*Catostomus macrocheilus* Girard), longnose dace (*Rhinichthys cataractae* (Valenciennes)), longnose sucker (*Catostomus catostomus* (Forster)), northern squawfish (*Ptychocheilus oregonensis* (Richardson)), peamouth chub (*Mylocheilus caurinus* (Richardson)), prickly sculpin (*Cottus asper* Richardson), pumpkinseed (*Lepomis gibbosus* (Linnaeus)), pygmy whitefish (*Prosopium coulteri* (Eigenmann and Eigenmann)), redbside shiner (*Richardsonius balteatus* (Richardson)), slimy sculpin (*Cottus cognatus* Richardson), torrent sculpin (*Cottus rhotheus* (Smith)), westslope cutthroat (*Salmo clarki* Richardson), white sturgeon (*Acipenser transmontanus* Richardson), and yellow perch (*Perca*

flavescens (Mitchill)) (pers. comm., Mr. Albert Chirico, B.C. Ministry of Environment, Lands and Parks, 333 Victoria St. Suite 401, Nelson, B.C., V1L 4K3, Canada).

Economic Value of Kootenay Lake Fisheries

The annual value of the fisheries on Kootenay Lake was estimated at \$1,136,800 (1989 dollars), based on the average angler days in 1987-88 and 1988-89 (Korman et al. 1990). This analysis assumed that most of the fishing effort was for Gerrard rainbow trout, but included angling effort for other species such as kokanee, bull trout, and whitefish.

The abundance of the kokanee stock is essential for the maintenance of trophy fishing in Kootenay Lake. Kokanee make up over half the diet volume of rainbow trout over 30 cm in length, and other fish species are seen only rarely in trout diet contents (Andrusak and Parkinson 1984). About 99% of the fish in the pelagic zone of Kootenay Lake are kokanee, so kokanee density is an indicator of the integrity of the pelagic food web and its ability to support a natural species assemblage from phytoplankton to zooplankton and up to the planktivore level. A decline in kokanee abundance would be of concern on several fronts: conservation of the wild stocks of kokanee, conservation of their predators, maintenance of recreational fishing opportunities for kokanee and piscivores, and economic benefits of recreational fishing to the local area (e.g., guide fees) and to the province (license sales).

Exotic Species Introduction: *Mysis relicta*, a Competitor, and a Prey of Kokanee

The freshwater macroinvertebrate *Mysis relicta* was introduced to Kootenay Lake in 1949 and 1950, as an additional food source for juvenile rainbow trout (Sparrow et al. 1964). The intention was to provide a food item intermediate in size between zooplankton and terrestrial insects, and young kokanee, as it had been observed that trout growth slowed down during the transition to feeding on kokanee. Approximately 25,000 individuals were transported from Waterton Lake, Alberta, and it took over ten years for numbers to increase enough that *M. relicta*

were observed near the surface in the West Arm (Sparrow et al. 1964), and for *M. relicta* to appear in the diet of West Arm kokanee (Reid 1967). This was the first successful transplant of *M. relicta*, and was followed by introductions in Sweden in 1954 (Furst 1965).

M. relicta is a glacial relict species which is native to lakes east of the Rocky Mountains, and has a 1 to 4 year life history (Lasenby et al. 1986; Lasenby 1991). Females carry eggs and then the hatched young in a brood pouch (marsupium) resulting in the common name, "opossum shrimp". *M. relicta* often displays vertical migration, probably to avoid visual predators yet allow feeding on pelagic zooplankton (Bowers 1988; Moen and Langeland 1989). During the day *M. relicta* stays in deep, dark water, and even on the bottom sediments, and migrates vertically at night to feed on zooplankton. Following introduction into Pend Oreille Lake, Idaho, *M. relicta* did not move into near-surface waters (upper 10 m) during August and September when the water was warmer, so it may have been thermally isolated from much of its zooplankton prey during this period (Rieman and Falter 1981). However, in Kootenay Lake *M. relicta* has been seen within 1 m of the surface at night, when the daytime surface water temperature was 21°C (pers. observation). *M. relicta* has large eyes on stalks, and long antennae to allow the capture of prey in very low light conditions, probably using both tactile and visual cues (Ramcharan et al. 1985; Ramcharan and Sprule 1986). In its natural environment *M. relicta* feeds on detritus, phytoplankton (Grossnickle 1979), rotifers (Nero and Sprules 1986), pelagic zooplankton, and benthic detritivores such as *Pontoporeia* (Parker 1980). Of the zooplankton, *M. relicta* prefers *Daphnia* over other cladocerans, and over copepods (Cooper and Goldman 1980). In turn, deep dwelling fish such as lake trout (*Salvelinus namaycush*), deepwater sculpins (*Myoxocephalus thompsoni*) (Lee and Hall 1993), and slimy sculpins (*Cottus cognatus*) (Owens and Weber 1995) prey on *M. relicta*. Vertically migrating fish such as alewife (*Alosa pseudoharengus*) are also able to prey on *M. relicta* when their vertical distributions overlap (Mills et al. 1991).

Rainbow trout did not benefit as expected from the introduction of *M. relicta* to Kootenay Lake (Northcote 1991). In the 1960's, kokanee in the West Arm of Kootenay Lake grew to unprecedented size by feeding on the mysids that washed out into the relatively shallow, turbulent riverine West Arm (Martin and Northcote 1991). This led to a large sport fishery on the West Arm kokanee. For example, in 1967 anglers spent 42,416 angler-days on the West Arm, out of a total 56,109 angler-days for the whole lake (Pearse and Laub 1969). Following this perceived success, *M. relicta* was introduced to many other lakes. Mysid introductions have been documented for 20 lakes in British Columbia (Lasenby et al. 1986), and lakes in most western states including Idaho (Rieman and Bowler 1980; Rieman and Myers 1992), Montana (Spencer et al. 1991), Washington (Wydoski and Bennett 1981), Nevada (Goldman et al. 1979), and California (Morgan et al. 1981). Mysids were also added to and became established in fifty Swedish lakes (Fuerst et al. 1985).

While many of these introductions resulted in viable *M. relicta* populations, *M. relicta* has not always become a successful addition to fish diets, and has often had deleterious effects on zooplankton and fishes, especially kokanee (Northcote 1991). Mysid introductions coincided with decreased zooplankton abundance, particularly of cladocerans, in Lake Stugusjoen, Sweden (Langeland 1988). In Pend Oreille Lake, Idaho there was a change in the species of *Daphnia* observed, and the species present appeared later in the season than before mysids were transplanted (Rieman and Falter 1981). Following the introduction of *M. relicta* to Lake Tahoe, all three cladoceran species disappeared from the lake (Goldman et al. 1979). High densities of *M. relicta* and of kokanee were thought to have increased cladoceran mortality rates. However, lower cladoceran birth rates were also observed, and this was thought to be linked to change in the timing of peak primary productivity which occurred over the same period.

Lasenby et al. (1986) report that for the twenty British Columbia lakes to which *M. relicta* was added, kokanee abundance decreased in nine. Kokanee abundance also decreased in Pend Oreille Lake, Idaho following mysid introductions (Rieman and Falter 1981). In Lake Tahoe, both kokanee and *M. relicta* densities decreased following decline of cladoceran densities (Morgan et al. 1978). Five years later *M. relicta* densities recovered somewhat (Goldman et al. 1979), but kokanee continued to have low abundance and weight (Morgan et al. 1978). Mysids may be largely unaffected by fish in deep lakes because they spend daylight hours at the lake bottom, rising to feed only after dusk, when the fish have finished feeding, and descending before dawn (Beeton and Gannon 1991).

In a few cases *M. relicta* introductions appear to have resulted in increased fish abundance. Northcote (1991) suggested that fish which feed on benthos rather than pelagic zooplankton, such as lake trout (*Salvelinus namaycush*) may show improved growth and survival, and Fuerst et al. (1985) reached a similar conclusion based on observations of Swedish lakes. In lakes with upwelling and mixing zones (either natural or caused by impoundment regulation) mysids may be unable to take refuge at the lake bottom and therefore may be more vulnerable to fish predation (Northcote 1991).

Lake productivity may also affect the impact of mysids on zooplankton and fish abundance. Li and Moyle (1981) used loop analysis to predict the behaviour of aquatic systems following the introduction of an exotic species. They found that oligotrophic systems are more likely to become unstable following an introduction than more productive systems, and noted that cladocerans were able to survive in the presence of mysids in a small productive bay within the otherwise ultraoligotrophic Lake Tahoe (Morgan et al. 1978). In 1983, thirteen years after it had disappeared, *Daphnia rosea* reappeared in the main body of Lake Tahoe (Byron et al. 1986). In that time cultural eutrophication had occurred in the lake, and primary productivity had increased. *D. rosea* now have

higher birth rates than in the past, which appears to balance the mortality rate caused by *M. relicta* and kokanee.

In the main body of Kootenay Lake, *M. relicta* competes with kokanee for zooplankton such as cladocerans and copepods. Because the mysids are also able to use smaller prey such as *Bosmina*, copepod nauplii (Cooper and Goldman 1980), and rotifers, they may be better able to withstand declining cladoceran densities than kokanee, which rarely eat cladocerans as small as *Bosmina*, and do not appear to eat nauplii or rotifers (see Fig. 75). Microzooplankton such as rotifers are part of the microbial loop, along with bacteria, and heterotrophic flagellates (Azam et al. 1983). Bacteria uptake nutrients that could otherwise become part of the classical food chain of phytoplankton, zooplankton, and fish. These nutrients may re-circulate within the microbial loop, or they may be returned to the classical food chain when bacteria die and their nutrients are re-mineralized, or when crustacean zooplankton prey upon flagellates or rotifers (Weisse and Stockner 1993). If the microbial loop in Kootenay Lake were to predominate over the classical food chain, *M. relicta* would have an advantage over kokanee, since kokanee do not eat rotifers. This could be especially important for juvenile stages, when *M. relicta* feeds predominantly on detritus and rotifers (Ashley et al. 1996), while young-of-the-year kokanee feed on prey the size of *Bosmina* or larger.

Some potential predators of *M. relicta* are present in Kootenay Lake. Kokanee, particularly age 2+ and 3+, are capable of eating mysids (see Fig. 76 and Fig. 77), but mysids largely avoid kokanee predation by staying in deep, dark water by day, and migrating vertically between dusk and dawn to feed (Zyblut 1967). Sculpins have been captured in bottom trawls at 70 m depth in Crawford Bay (Mr. Donald Miller, Harrop, B.C., pers. comm.), but it is not possible to do trawls deeper than this with current equipment, so it is not known if sculpins are present on the bottom of the main body of the lake, up to 140 m deep. Burbot (*Lota lota*) may

prey on *M. relicta*, but burbot abundance is currently very low (and the subject of a conservation study), so mortality due to burbot predation would be low.

At present there is no way of removing mysids from a lake once they are established, although species-specific poisons, manipulation of thermal stratification and upwelling, and changes of lake trophic status have been suggested (Northcote 1991). The evidence from Lake Tahoe suggests that with an increased nutrient base for primary productivity, a lake ecosystem may be able to support a historical zooplankton assemblage, even in the presence of introduced *M. relicta*. Similarly, cultural eutrophication of Kootenay Lake in the years following *M. relicta* introduction may have tempered the impact of mysids on zooplankton and kokanee until excess nutrient inputs ceased (Northcote 1972).

Comparison with *Bythotrephes cederstroemi* Invasion in Eastern North America

Bythotrephes cederstroemi (Schoedler), a large predatory cladoceran zooplankter native to oligotrophic waters in Europe, invaded the Laurentian Great Lakes in the late 1970's or early 1980's, probably via the ballast water of ships returning from European ports (Sprules et al. 1990). *Bythotrephes* was first seen in Lake Huron in 1984, and then Lake Erie (Lehman 1987) and Lake Ontario in 1985 (Lange and Cap 1986), Lake Michigan in 1986 (Lehman 1987), and Lake Superior in 1988 (Garton and Berg 1990). By 1989, it had also invaded smaller lakes around the Great Lakes such as Lakes Muskoka, Joseph, and Rosseau (Hutchinson et al. 1995).

Like *M. relicta*, in its native environment *Bythotrephes* preys on smaller zooplankton, and is preyed upon by planktivorous fish such as cisco smelt. The cisco are in turn prey for piscivores such as burbot, sander and salmon (Nilsson 1979). The role of *Bythotrephes* in North American lakes is uncertain. *Bythotrephes* may compete for zooplankton with planktivorous fish, particularly juveniles, but this effect may be balanced by predation of these planktivores on *Bythotrephes* (Clark et al. 1995).

The invasion of Lake Michigan by *Bythotrephes* is linked with changes in the zooplankton community between 1983 and 1992 (Makarewicz et al. 1995). Cladoceran biomass remained fairly constant, but cladoceran species diversity declined, while calanoid copepod species diversity increased. However, predation by alewives and bloater chubs (*Coregonus hoyi*) may also be affecting macrozooplankton size and biomass. In Lakes Muskoka, Joseph and Rosseau, invasion of *Bythotrephes* coincided with a decline in herbivorous zooplankton densities, increased chlorophyll concentrations, and decreased water clarity (Hutchinson et al. 1995). Conversely, in Lake Michigan, although *Daphnia* biomass declined following the introduction of *Bythotrephes*, chlorophyll concentrations did not increase significantly. The depth of water mixing, and the temperature of the epilimnion were more closely correlated with chlorophyll concentrations (Lehman and Caceres 1993). Harp Lake was invaded by *Bythotrephes* in 1992. The lake experienced no other major external perturbations following the invasion. By 1994, zooplankton biomass was similar to pre-invasion levels, but zooplankton abundance had declined, and there was a shift to predominance of zooplankton with larger body size, while smaller forms became rare (Yan et al. 1995). However, in an enclosure experiment using zooplankton that had been filtered (using 253 µm mesh) to remove macrozooplankton, (Coulas et al. 1995) found that neither total rotifer nor copepod nauplii abundance were affected by the presence of *Bythotrephes*.

Another similarity between *M. relicta* and *Bythotrephes* is that each species has a behaviour and / or physical characteristic which gives it a form of refuge from predation. Both species show diel vertical migration, which probably allows them to avoid predators (Bowers 1988; Kamman and Riessen 1994). In addition, *Bythotrephes*' mortality rate is decreased because of the zooplankter's large caudal spine, which causes avoidance by fish such as lake trout, particularly juveniles less than 10 cm long (Barnhisel 1994). The spine was found to

increase handling time by rainbow trout by 800% compared with de-spined *Bythotrephes*, and only a small proportion of fish were able to decrease the handling time with repeated exposure (Barnhisel 1991). Lake herring (*Coregonus artedii*) in Harp Lake, Ontario, are reported to feed on *Bythotrephes* once the fish are past the young-of-the-year stage, if *Bythotrephes* is present in large aggregations (Coulas et al. 1995). *Bythotrephes* is also eaten by alewives over 90 mm total length in Lake Ontario (Mills et al. 1991). The diet of yellow perch (*Perca flavescens*) in Lake Michigan contains a large proportion of *Bythotrephes* when it is available, suggesting that the introduction of *Bythotrephes* may give a competitive advantage to fish species that are able to consume it effectively (Peterson 1993).

Impacts of Hydroelectric Dam Construction and Operation

The Duncan Dam, which impounds the Duncan Lake Reservoir, was constructed as part of the Columbia River Treaty and became operational in 1967 (Daley et al. 1981). The Libby Dam, which impounds Koocanusa Reservoir in Montana and British Columbia near Cranbrook, is also a Columbia River Treaty dam, and came into operation in 1973. Prior to the completion of the Duncan Dam, Peterson and Withler (1965) anticipated that there would be severe damage to fish habitat, including loss of spawning grounds and food of fish resident in Duncan Lake, and loss of spawning grounds of kokanee salmon, bull trout, and rainbow trout stock native to Kootenay Lake. In compensation for the loss of the Duncan stock of trophy size rainbow trout, a spawning channel and hatchery for kokanee were constructed on Meadow Creek, west of the dam. Before the Libby Dam became operational, Northcote (1973) predicted that there would be changes in flow regime, temperature, and turbidity of the Kootenay River, and that this could in turn affect salmonid populations in Kootenay Lake.

Annual average discharge from the Duncan Dam is $160.40 \text{ m}^3\text{s}^{-1}$ (1964-1996 average), and the Kootenai River flow averages $449.36 \text{ m}^3\text{s}^{-1}$ (1929-1996 average). The total mean

outflow from Kootenay Lake is about $780 \text{ m}^3\text{s}^{-1}$ (Daley et al. 1981), or $2.46 \times 10^{10} \text{ m}^3\text{yr}^{-1}$.

Therefore minor tributaries contribute approximately $170 \text{ m}^3\text{s}^{-1}$ (22%) of the inflow, without correcting for evaporation from the lake surface, while the Duncan and Kootenai inflows contribute 20% and 58%, respectively. Since the volume of Kootenay Lake is $3.75 \times 10^{10} \text{ m}^3$, the lake's hydraulic retention time is about 1.52 yr, although this calculation is not corrected for summer stratification, when the hydraulic retention times of the epilimnion and hypolimnion would be shorter and longer, respectively.

The dams upstream have had a major impact on the hydrology of Kootenay Lake (Northcote 1972; Northcote 1973; Daley et al. 1981). Duncan Dam flow is regulated for water storage and flood control, while Libby Dam is used for water storage, flood control and hydroelectric power generation (Hirst 1991). To conserve water for peak energy requirements during the winter months, water that would naturally have flowed into Kootenay Lake as a spring freshet is now held back and released in the winter, which was a low flow time historically (Fig. 2).

Duncan River summer flows are now about 60 percent of those prior to impoundment (Hirst 1991). Conversely, in mid-winter flows are now 100 to 200 percent higher. Monthly average flow data, representing the inflows from the Duncan and Kootenai Rivers, have been compiled for the Duncan Dam discharge, and for the Kootenai River at Porthill, Idaho (Lekstrum et al. 1994; Larkin 1998). Prior to impoundment of Duncan Lake, outflow during the spring peak month, June or July, averaged $497 \text{ m}^3\text{s}^{-1}$ (Duncan Lake/Reservoir flow data were obtained for 1964-1990, and 1992-1995). The lowest monthly mean flow during winter averaged $29 \text{ m}^3\text{s}^{-1}$, and occurred in March from 1964 to 1966. Following impoundment, the outflow had a spring peak monthly average of only $278 \text{ m}^3\text{s}^{-1}$ which usually occurred in July, but varied from May to

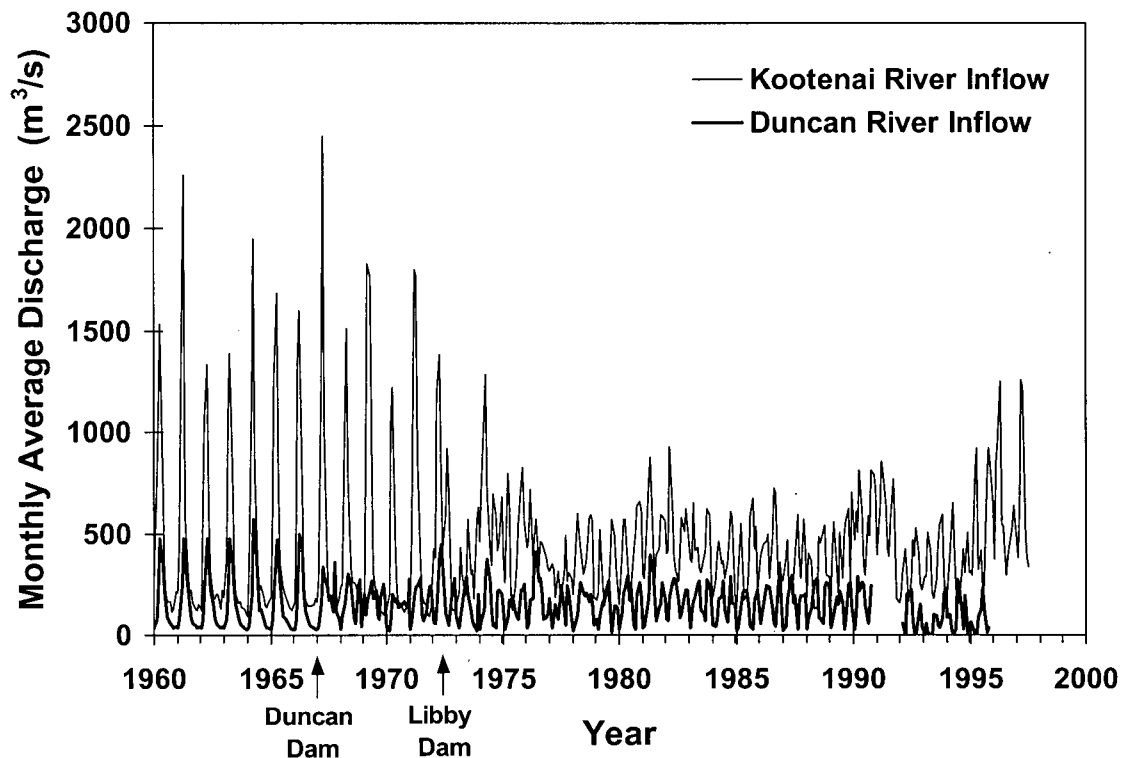


Fig. 2. Historical water flows in the Duncan River and the Kootenai River (data reproduced from Lekstrum et al. 1994, and Larkin 1998).

as late as September. However, there is now a second peak flow period that happens during winter, between December and February, with an average monthly flow of $241 \text{ m}^3\text{s}^{-1}$.

A similar pattern has been observed for the Kootenay River inflow from Libby Dam (Kootenay River/Libby Dam flow data were available for 1929 to 1996). Prior to impoundment the spring peak discharge occurred in May or June, and averaged $1575 \text{ m}^3\text{s}^{-1}$. The winter minimum monthly average was $107 \text{ m}^3\text{s}^{-1}$ and occurred between October and March, but usually in December or January. After impoundment the spring peak flow month was more variable, occurring between April and July, and flow averaged $668 \text{ m}^3\text{s}^{-1}$. For the first few years after impoundment winter flows were very erratic, but since 1974 there has also been a winter peak month, between October and February, in which flow has averaged $635 \text{ m}^3\text{s}^{-1}$.

Despite the change in timing of water flows into Kootenay Lake, midsummer lake temperatures have not changed significantly since 1949 (Daley et al. 1981). The average temperature in the top 60 m in July has been approximately 9°C in 1949, in the mid-1960's, and in 1976-77, when both upstream dams were operational. Also, estimates of the mean temperature of the entire lake have been approximately 7°C throughout these same periods. Vertical temperature structure has shown a similar pattern across years. By midsummer a thermocline forms at about 25 m. Surface water reaches 15-20°C, while temperature drops to about 5°C below 50 or 60 m (Daley et al. 1981).

Historically the Duncan River carried a high concentration of glacial silt and was very turbid in spring and summer. However, turbidity declined when the construction of the Duncan Dam caused much of the silt and its associated nutrients to be retained in the reservoir (Hirst 1991). The Kootenai River freshet inflow was historically very turbid, and caused the South Arm to be more turbid than the North Arm, which in turn decreased transparency, light penetration, and phytoplankton production in the South Arm (Northcote et al. 1998). The operation of the Libby Dam has been correlated with decreased turbidity and increased transparency in the South Arm of Kootenay Lake, particularly during the freshet peak (Cloern 1976). From 1949 to 1972, prior to the operation of the Libby Dam, the light extinction coefficient in the South Arm ranged from 0.2 to 3 m⁻¹ within a given year, with the highest values occurring during the freshet (Daley et al. 1981). From 1973 to 1977 the coefficient did not exceed 1 m⁻¹. However, light extinction coefficients in the middle of the lake were similar across the period from 1949 to 1978, and ranged between 0.2 and 1.3 m⁻¹ within a given year.

Changes in Nutrient Loading

While nitrogen inputs to Kootenay Lake have been fairly stable over time, phosphorus inputs have fluctuated dramatically in the latter half of this century (Northcote 1972; Northcote

1973; Daley et al. 1981). In 1953 a phosphate fertilizer plant began production as part of the Sullivan Mine in Kimberly, B.C., and released nutrients into the Kootenai River system, resulting in the eutrophication of Kootenay Lake (Northcote 1973). The plant doubled production in 1962, and tripled production in 1964 (Cloern 1976). However, settling ponds were installed in 1969, and an effluent recycling program began in 1975 (Crozier and Duncan 1984). Phosphorus concentrations in the Kootenai River declined sharply in conjunction with these controls (Crozier and Duncan 1984). The annual mean concentration of total phosphorus (TP) in the Kootenai River declined from over 0.2 mgL^{-1} to about 0.015 mgL^{-1} between 1966 and 1977 (Fig. 3 a, data from B.C. Ministry of Environment, Environmental Management System (EMS) database). Annual mean total dissolved phosphorus fell from about 0.15 mgL^{-1} to 0.01 mgL^{-1} from the late 1960's to 1976. Over the period from 1967 to 1977 the annual mean ortho-phosphorus concentration fell from over 0.15 mgL^{-1} to about 0.004 mgL^{-1} . Riverine phosphorus concentrations were stable from 1978 to 1988.

Nitrogen concentrations in the Kootenai River were stable from 1965 to 1988, with the exception of a spike in dissolved nitrate and nitrite in 1971 (Fig. 3 b). The long-term annual average of total Kjeldahl nitrogen was 0.12 mgL^{-1} , while the long-term averages of dissolved nitrate and nitrite, and dissolved ammonia were 0.034 mgL^{-1} and 0.092 mgL^{-1} , respectively. Patterns of nutrient loading to Kootenay Lake are similar to the patterns observed for riverine concentrations. Annual orthophosphate load increased from a historical value of 140 tyr^{-1} in 1949 to 2350 tyr^{-1} in 1966 (Daley et al. 1981). Phosphorus load declined after pollution control measures were introduced at the Kimberley fertilizer plant, but the dams likely caused a further decrease in downstream nutrient loads by trapping sediments and associated nutrients in the reservoirs upstream (Brune 1953; Vollenweider 1969; Baxter 1977). By 1977 the orthophosphate load to Kootenay Lake had declined to 51 tyr^{-1} , one-third of the historical level

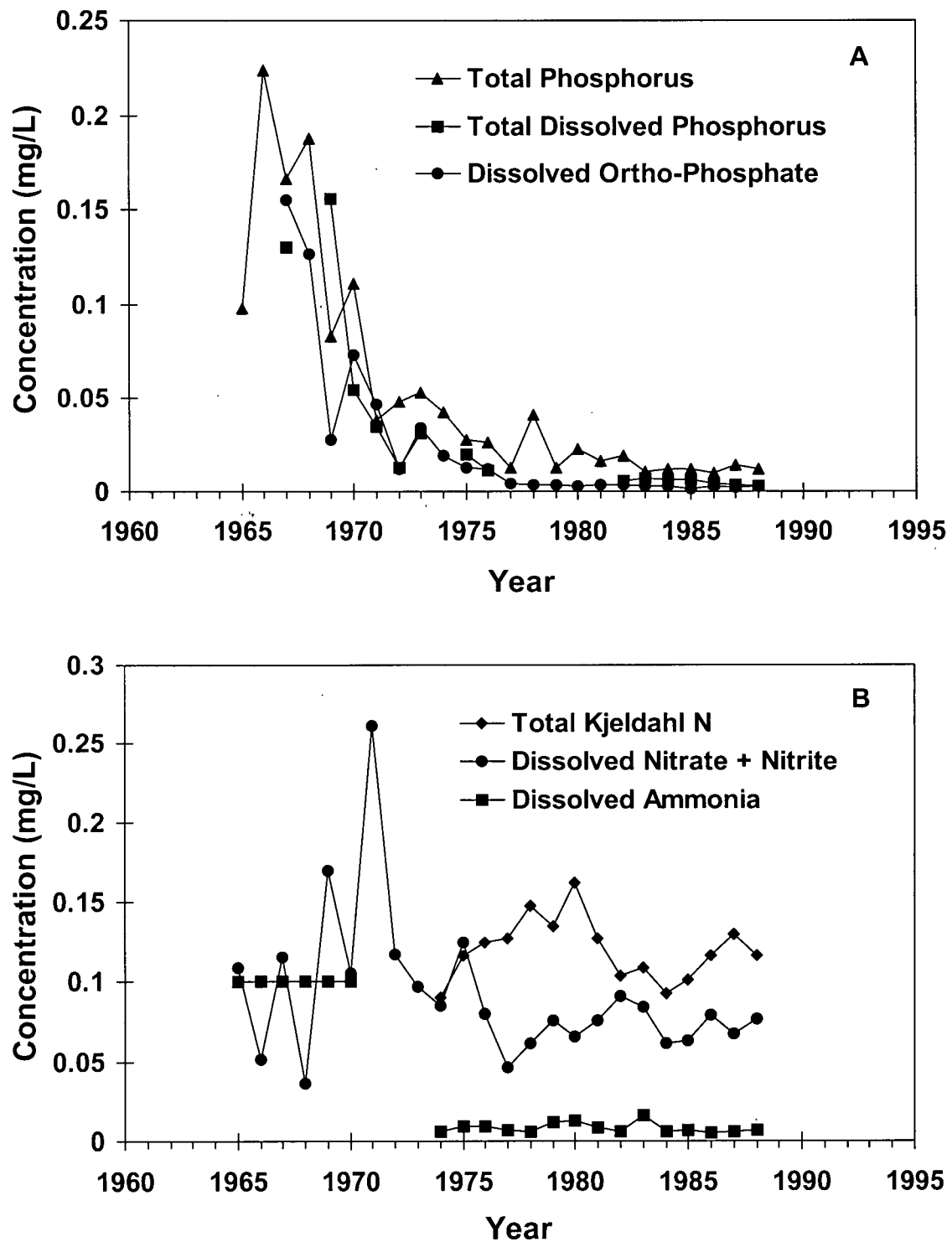


Fig. 3 (a & b). Historical annual average phosphorus and nitrogen concentrations in the Kootenai River near its inflow to Kootenay Lake (station 0200013).

(Daley et al. 1981). During the period from 1949 to 1973, nitrate-nitrogen loads were fairly constant (Daley et al. 1981), and ranged between 1400 tyr^{-1} and 1800 tyr^{-1} . Nitrate-nitrogen loads were higher in 1974 and 1976 because of high water flows (2800 tyr^{-1} and 2500 tyr^{-1} , respectively), and the load in 1977 was lower than average, at 1000 tyr^{-1} .

More recently, TP loads were calculated for the Duncan and Kootenai Rivers from 1960 to 1990 (Lekstrum et al. 1994). The annual TP load from the Duncan River did not show a strong increase (due to increase in flooded area and leaching) nor decline during the 23 years following impoundment, and ranged from about 60 to 100 tyr^{-1} . However, TP loads from the Kootenai River were high in the 1960's, peaking at about 3800 tyr^{-1} in 1968, then declined to about 200 tyr^{-1} during the 1980's, similar to the pattern seen for orthophosphate loads. Larkin (1998) re-examined TP loading from both the Duncan and Kootenai Rivers, focusing on the period from 1980 to 1996. Average annual TP load from the Duncan River during this period was 67 tyr^{-1} . Annual TP load from the Kootenai River was 216 tyr^{-1} (Note: The 1997 TP load, 546 tyr^{-1} , was the highest in the 1980-1997 data set, despite including only data from January to August at the time Larkin's report was compiled. If the partial 1997 load is included, the long-term average becomes 235 tyr^{-1}). Thus, on average, the Kootenai River contributes 76% of the TP load to Kootenay Lake, and the Duncan River contributes 24%, not including contributions from minor tributaries. However, in low flow years such as 1992, 1993, and 1994, the contribution by the Duncan River of the total TP load rose to 51%, 35%, and 43% respectively.

In addition to retention of nutrients in the upstream impoundments, the change in timing of inflows also decreases the supply of nutrients available to phytoplankton (Carmack and Gray 1982). In summer, which the authors defined as mid-June to late September, most new nutrients entering the epilimnion come from riverine inputs. The river inflows enter the lake and plunge

below the surface waters to a depth dependent on the relative densities of the inflow and the lake, generally below the epilimnion. Wind events may cause the riverine water to be entrained into the epilimnion, making new nutrients available to phytoplankton (Carmack et al. 1986). With the operation of the upstream dams, spring and summer inflow volumes are lower, because of upstream water storage. Thus, summer nutrient loading is further reduced in comparison with the pre-dam situation.

Annual mean total phosphorus and ortho-phosphorus concentrations in Kootenay Lake were reported for 1970 to 1984 (Crozier and Duncan 1984), and additional data are available from the B.C. Ministry of Environment's EMS database. As described above for riverine concentrations, and nutrient loads, phosphorus concentrations in the lake declined sharply in conjunction with the control of pollution from the Kimberley fertilizer operation (Fig. 4 a; data from B.C. Ministry of Environment, EMS database). Total phosphorus ranged from 0.018 to 0.049 mg·L⁻¹ in 1971, with lower values in surface water (1 m) than for water-column average samples (Crozier and Duncan 1984). Also, phosphorus concentrations were higher in the south end of the lake. Ortho-phosphorus showed a similar pattern in 1971. Values ranged from 0.007 to 0.038 mg·L⁻¹, with higher values in deeper water, and in the south end of the lake. By 1976 the north-south gradient in phosphorus concentrations had disappeared and by 1980 annual mean phosphorus concentrations were very similar in the epilimnion, metalimnion and hypolimnion, indicating that in-lake phosphorus concentrations were near to being in equilibrium with phosphorus inputs (Crozier and Duncan 1984). The authors noted that if there were no further changes in phosphorus loading, in-lake phosphorus concentrations would remain at the 1984 levels. Thus, it took 17 years of Duncan Dam operation, plus 11 years of Libby Dam operation for Kootenay Lake's hypolimnion to "discharge" (flush out) the excess phosphorus contributed from the fertilizer plant, the excess phosphorus contributed from the newly flooded land

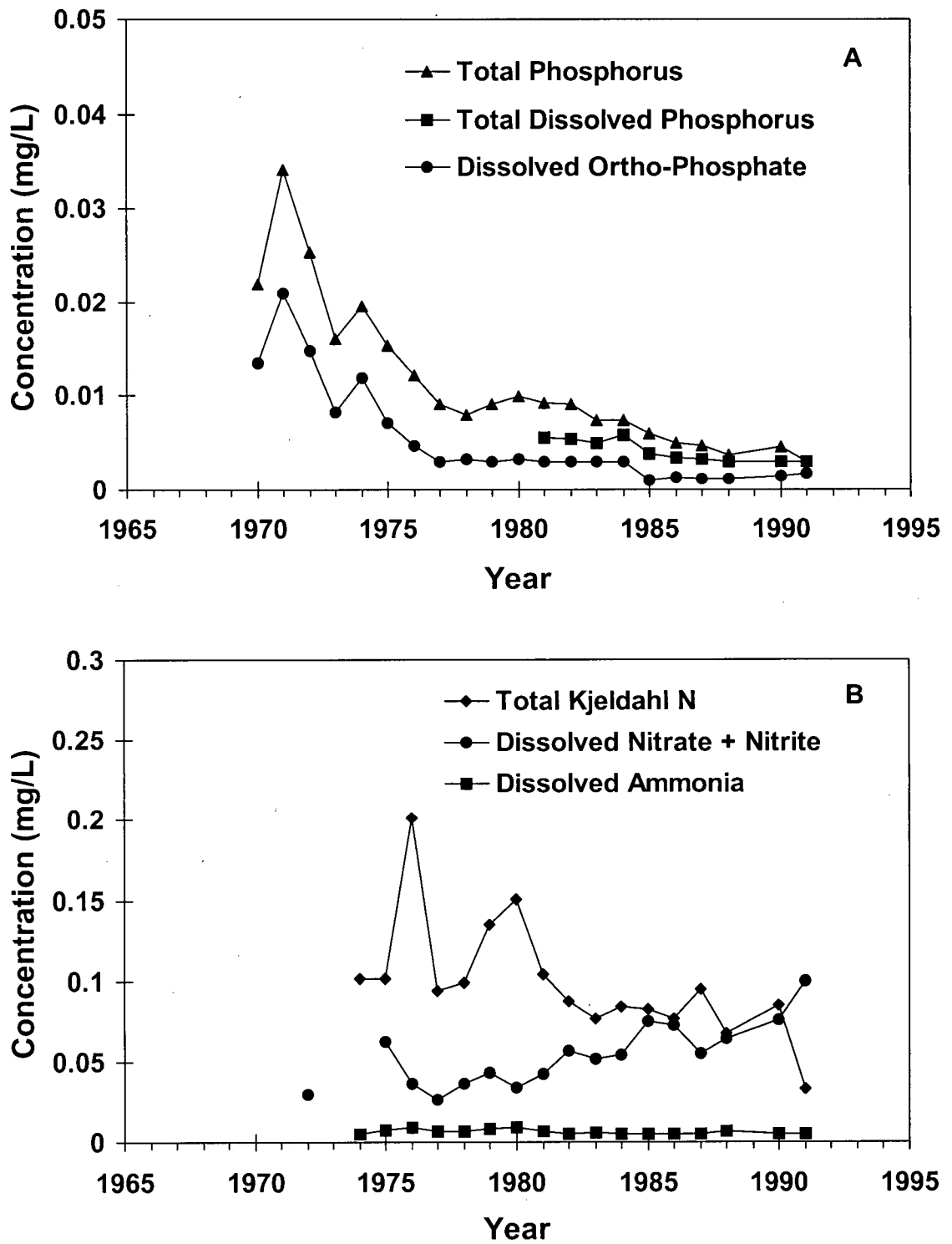


Fig. 4 (a & b). Historical phosphorus and nitrogen concentrations in Kootenay Lake (mid-lake station 0200034, near Crawford Bay, and in approximately the same location as Station 5 in the current fertilization experiment). Values are surface water annual averages.

upstream of the dams, plus the natural amount of phosphorus which was no longer replenished due to nutrient retention behind the dams. From 1985 to 1991 surface TP concentrations averaged 0.005 mgL^{-1} , while total dissolved phosphorus, and dissolved ortho-phosphate concentrations averaged 0.003 mgL^{-1} , and 0.001 mgL^{-1} , respectively, in surface waters.

Nitrogen concentrations in Kootenay Lake did not change noticeably during the period from 1970 to 1984 (Crozier and Duncan 1984). Water column annual average concentrations of total nitrogen were about 0.225 mgL^{-1} . Organic nitrogen, nitrate and nitrite nitrogen, and ammonia concentrations were about 0.080 mgL^{-1} , 0.110 mgL^{-1} , and less than 0.010 mgL^{-1} , respectively. Concentrations were similar during the period from 1985 to 1991, when surface total Kjeldahl nitrogen concentrations averaged 0.073 mgL^{-1} , while dissolved nitrate and nitrite, and dissolved ammonia concentrations averaged 0.074 mgL^{-1} , and 0.005 mgL^{-1} , respectively, in surface waters (Fig. 4 b; data from B.C. Ministry of Environment, EMS database).

Biological Changes in Kootenay Lake During Eutrophication and Oligotrophication

Phytoplankton biomass increased as the phosphorus load from the fertilizer plant increased in the 1960's, resulting in algal blooms (Northcote 1972). After the phosphorus load and in-lake phosphorus concentration declined in the 1970's, the phytoplankton standing crop (measured as chlorophyll *a*) also decreased (Cloern 1976). Chlorophyll *a* concentrations continued to decline in the early 1980's (Crozier and Duncan 1984). The annual average was between 3 mgm^{-3} and 4.5 mgm^{-3} in 1975 and 1976 (Fig. 5, data from B.C. Ministry of Environment, EMS database). In 1985 the annual average was 1.45 mgm^{-3} , and it then rebounded slightly to 2.06 mgm^{-3} in 1991.

Zooplankton densities averaged about $8 \text{ individualsL}^{-1}$ in 1949, and increased to an average of about $12 \text{ individualsL}^{-1}$ by 1964 (Zyblut 1967). Additional data were available from 1972-1988, and 1990-1991 (Crozier and Duncan 1984, and raw data sheets, R.J. Crozier, B.C.

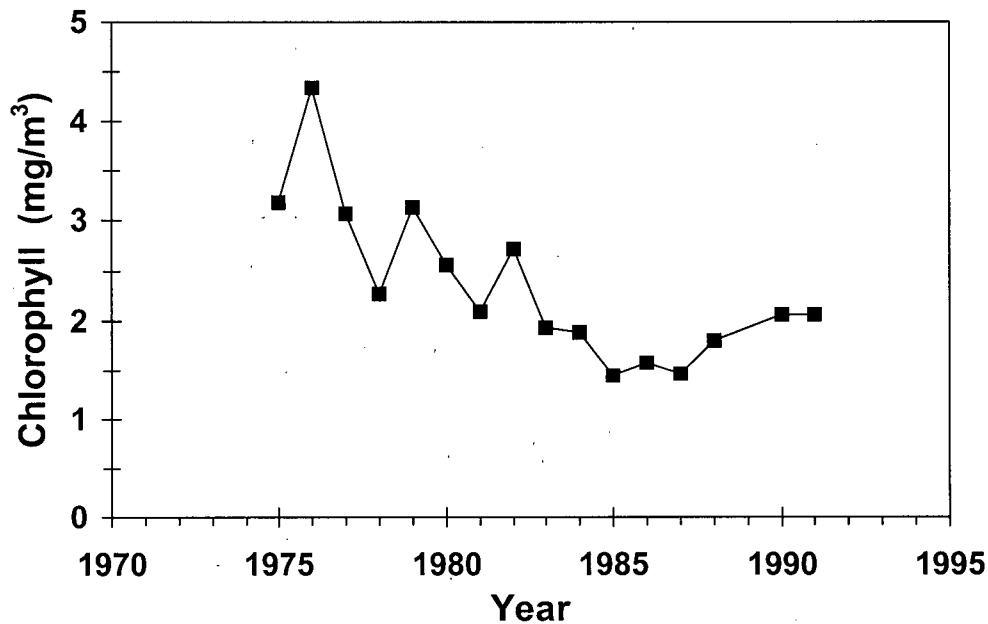


Fig. 5. Historical chlorophyll concentrations in Kootenay Lake (mid-lake station 0200034, near Crawford Bay, and in approximately the same location as Station 5 in the current fertilization experiment).

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4K3). From 1972 to 1984 annual average zooplankton densities fluctuated widely, and ranged from 5 to 35 individuals·L⁻¹ (

Fig. 6). Densities began a steady decline in 1985, and reached about 8.4 individuals·L⁻¹ by 1988.

The proportion of cladoceran zooplankton averaged about 3% in 1949, and declined to about 1% by 1964, despite overall increase in macrozooplankton densities (Fig. 7). Between 1949 and the mid-1960's there was a shift in cladoceran species from *Daphnia* spp. to *Diaphanosoma leuchtenbergianum* in the North Arm (Zyblut 1970). *Daphnia* spp. abundance was negatively correlated with both the eutrophication of the lake, and the increase in *M. relicta* abundance, particularly in the North Arm (see following section). Since adult mysids feed on macrozooplankton, and prefer *Daphnia* spp. if they are available, increase in mysid densities should have increased predation pressure on *Daphnia* spp. (see Chapter 2). Possibly the decline in cladocerans was also related to a relative increase in blue-green algae, which are larger and

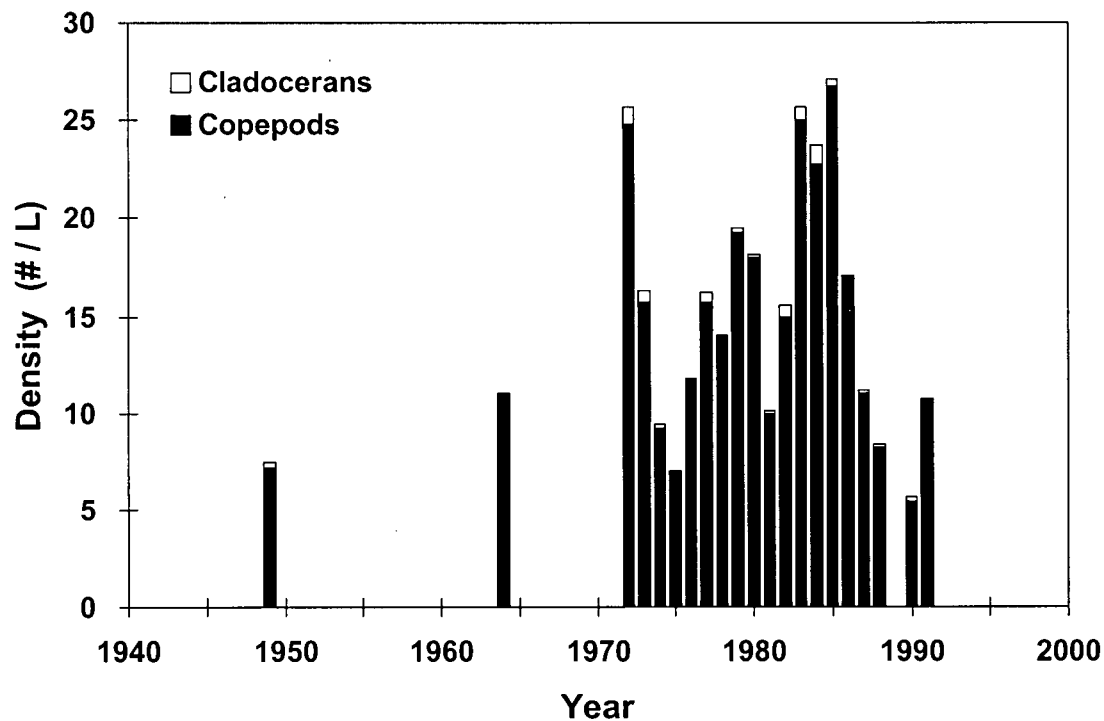


Fig. 6. Historical densities of macrozooplankton in Kootenay Lake.

more difficult to graze than zooplankton in the 2 - 20 μm size class (Ross and Munawar 1981), and may in some cases be toxic to zooplankton (Haney et al. 1994). From 1972 to 1991 the proportion of cladocerans varied but never rose above 5% (Note: Although different sampling nets were used during the zooplankton time series, the nets were cross-calibrated in Queen's Bay in 1996. No significant differences were found in the nets' selectivity for different species. See Chapter 2). A complicating factor is that the frequency of sampling decreased over this time period. Initially zooplankton were sampled across the growing season, but, due to funding cuts, in the late 1980's the number of stations sampled was decreased to only one mid-lake station, and sampling was done only in August. Since cladocerans in Kootenay Lake make up a greater proportion of the zooplankton in mid-summer and early fall than in the spring (see Chapter 2),

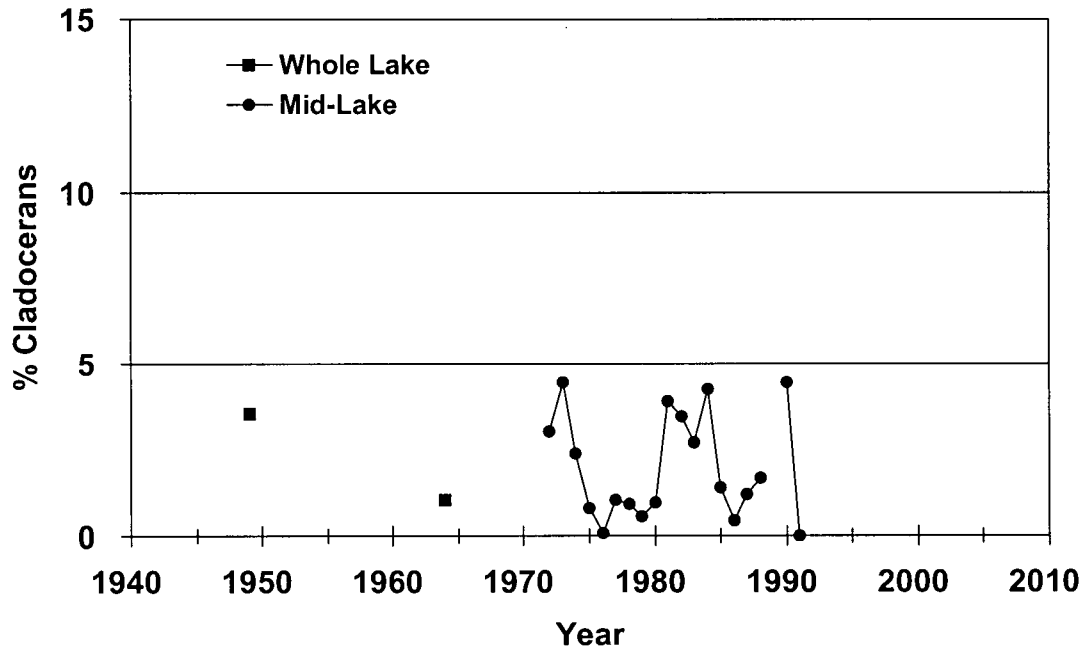


Fig. 7. Historical proportions of cladoceran zooplankton, relative to total macrozooplankton, in Kootenay Lake.

the samples taken in the late 1980's and early 1990's probably overestimate the proportion of cladocerans present.

Following the 1949 introduction, mysids were observed in the West Arm of Kootenay Lake in 1961, 1962, and 1963 but quantitative sampling was not done (Sparrow et al. 1964). Mysids were sampled in June, July, and early September of 1964, at night, in the top 17 m, using a horizontally towed Clarke-Bumpus net with No. 10 (153 μm) mesh (Zyblut 1967). By this time densities were 23 individuals:1000 L⁻¹ in the North Arm, 16 individuals:1000 L⁻¹ in the central part of the lake, 1.5 individuals:1000 L⁻¹ in the South Arm, and 10 individuals:1000 L⁻¹ in the West Arm. Although these densities are not directly comparable to more recent collections, made through the entire water column with a large Wisconsin-style net, Zyblut showed that mysids were more abundant in the North Arm and West Arm than the South Arm (Zyblut 1967). At this time the South Arm of Kootenay lake was more turbid than the rest of the lake (Northcote et al. 1998). It is possible that the survival of mysids in the South Arm was affected

by decreased transparency, as this would have forced mysids to feed in shallower, warmer water, and potentially be exposed to greater fish predation, as well as higher metabolic costs. Sampling recommenced in 1972, during the time of the decline in nutrient loading, and was done at stations in the North Arm, mid-lake and South Arm (Crozier and Duncan 1984). Samples were collected with a circular Wisconsin net, pulled from the lake bottom to the surface, during the day (from 1972 to June 1973 a 73 μm net with 12 cm diameter was used; from July 1973 to December 1974 a 153 μm net with 12 cm diameter was used, and from January 1975 to 1991 a 153 μm net with 50 cm diameter net was used). Generally the North Arm station showed the highest densities, with a peak of 1415 individuals $\cdot\text{m}^{-2}$ in 1979. However, the mid-lake station showed the highest densities from 1975 to 1978, and in 1980. Mysid densities in the South Arm were lower, with a peak of 285 individuals $\cdot\text{m}^{-2}$ in 1980. From 1982 to 1991 only the mid-lake station was sampled. Average annual lake average densities ranged from 13 individuals $\cdot\text{m}^{-2}$ to 745 individuals $\cdot\text{m}^{-2}$, with an average of 270 individuals $\cdot\text{m}^{-2}$ (Fig. 8, data from (Crozier and Duncan 1984), and raw data sheets, R.J. Crozier, B.C. Ministry of Environment, Lands and Parks). However, it is likely that these values underestimate the actual density of *M. relicta* in the lake. Nets with small mouth diameters were used for the early years of sampling, and in all years the nets had mesh finer than necessary to catch *M. relicta*, so mysids were likely able to sense the bow wave of the net and avoid it. Also, sampling was done during the day, rather than at night when mysids less able to see and avoid the net. In spite of these difficulties it appears that *M. relicta* densities are quite variable from year to year, and that densities were relatively low immediately prior to the start of the fertilization experiment in 1992.

Kokanee spawner abundance data were collected from the Lardeau River beginning in 1964, and from the Meadow Creek spawning channel from 1967 onward. Two West Arm spawning channels, Redfish Creek, and Kokanee Creek, were sampled beginning in 1972.

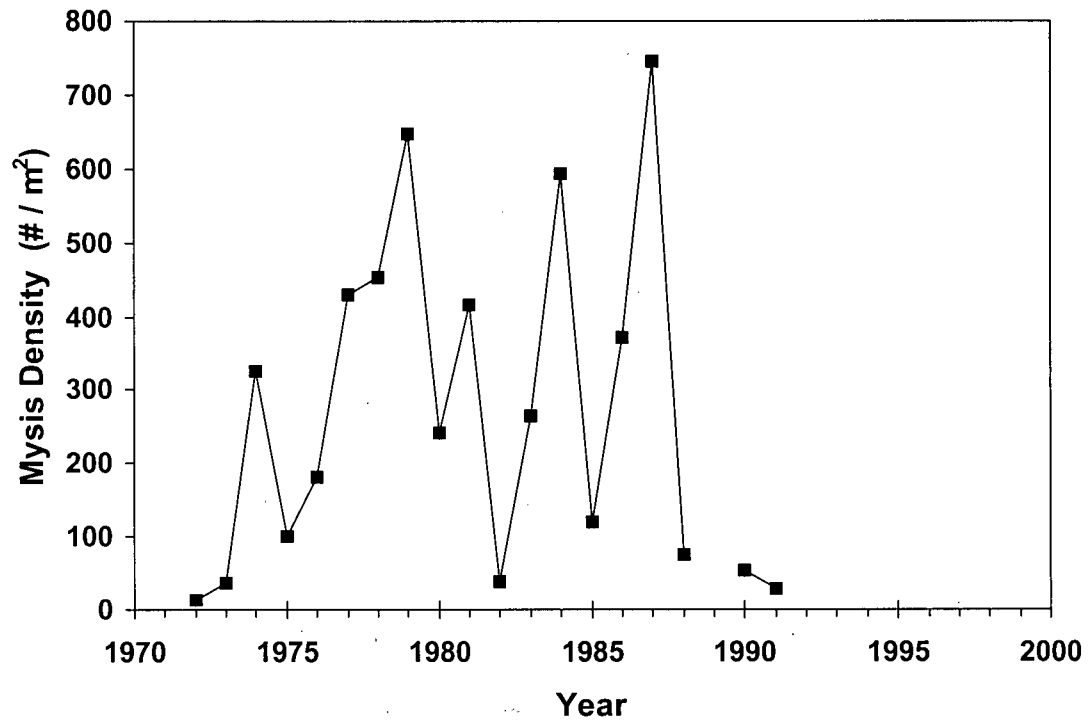


Fig. 8. Historical *Mysis relicta* abundance in Kootenay Lake, from 1972 to 1991. Values are the annual average of North Arm, central, and South Arm stations for 1972 to 1981, and the annual average from the central station for 1982 to 1991.

Kokanee spawners at South Arm, and other West Arm creeks were sampled intermittently from 1969 and 1972 onward, respectively. Autumn hydroacoustic surveys of the main lake began in 1984, and provided abundance information on all ages classes in the lake.

Kokanee spawner numbers increased in the Lardeau River, and at the Meadow Creek channel in the early 1970's (Fig. 9 a). The Meadow Creek values are complicated by the fact that the channel operators were in a learning phase in the late 1960's and early 1970's, so spawner increases may be the result of improving channel operations (e.g., increased egg-to-fry survival) rather than increases in-lake survival and growth (pers. comm., J. Hammond, B.C. Ministry of Environment, Lands and Parks, 333 Victoria St., Suite 401, Nelson, B.C., V1L 4K3). Abundance increased in the early 1970's, perhaps as a result of nutrients leaching out of newly flooded land behind the Duncan and Libby Dams, temporarily increasing production in

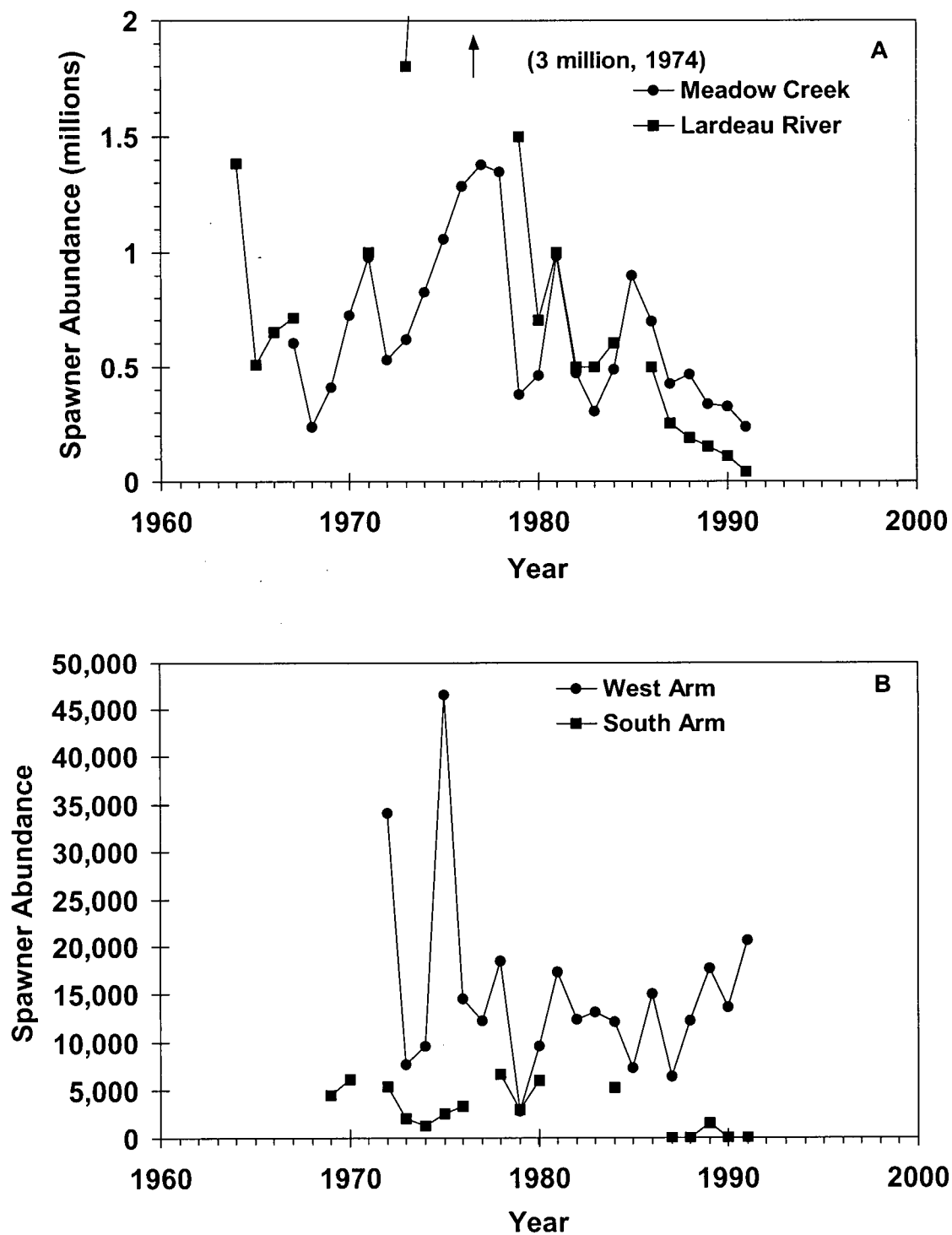


Fig. 9 (a & b). Historical kokanee spawner abundance in Meadow Creek, Lardeau River, South Arm, and West Arm of Kootenay Lake.

Kootenay Lake. However, in 1985 kokanee spawner abundance began a steady decline in both the Lardeau River and Meadow Creek. Observations of spawner abundance in the South Arm between 1987 and 1991 were the lowest on record. Kokanee spawner numbers in the West Arm remained high in the early 1970's, then decreased to about 15,000 during the 1980's (Fig. 9 b). During the decline of the main lake kokanee stocks (1985 - 1991), spawner numbers in the West Arm were variable, but appeared to increase slightly.

West Arm kokanee size increased dramatically in the late 1950's, and the change was considered to be a result of the introduction of *M. relicta*, which were exported from the main lake, over the sill at the entrance to the West Arm (Martin and Northcote 1991). However, this response was likely complicated by the increased nutrient loading which also occurred at this time. Furthermore, there was no evident change in the size of main lake kokanee at this time (Martin and Northcote 1991), although occasionally very large individuals were caught off the mouth of creeks such as Midge Creek (pers. comm., Mr. Donald Miller, Harrop, B.C.), and large kokanee spawners were observed at the upper end of the Lardeau River, near the Gerrard rainbow spawning grounds (pers. comm., Mr. Harvey Andrusak, Victoria, B.C.). Martin and Northcote (1991) concluded that the unique hydrology of the West Arm allowed kokanee there to prey very effectively on *M. relicta*, and thus grow to greater size, since the mysids were unable to sound to deep enough water to avoid kokanee predation. Ironically, Martin and Northcote also suggested that the increased productivity of Kootenay Lake during the operation of the fertilizer plant in the 1950's and 1960's may have buffered the main lake stocks from the effects of competition with mysids for zooplankton. In a review of the impacts of hydroelectric developments on fishery resources, Hirst (1991) noted that decreased nutrient loading was a major factor in the decline in sport fish densities and catches. He suggested that nutrient

replenishment to pre-impoundment levels be considered, in hopes of restoring the lake's productivity and its fisheries.

Gerrard rainbow trout spawn in the upper Lardeau River, near the outlet of Trout Lake (Cartwright 1961), and are counted each spring in April and May. The trout spawner peak count increased from 1957 to 1965, declined slightly in the late 1960's, then increased in the 1970's during the period when North Arm kokanee spawner numbers were increasing (Fig. 10). Trout numbers decreased again from 1979 to 1984, then increased slightly in the late 1980's, despite the decline in kokanee spawner numbers. The long-term average peak count is 285, and the average total spawner number is approximately 855 (total number returning is estimated to be three times the peak count; pers. comm., Mr. Les Fleck, B.C. Ministry of Environment, Lands and Parks, 333 Victoria St., Suite 401, Nelson, B.C., V1L 4K3). Limited size data are available for rainbow trout; male weights average about 9 kg, and female weights, about 7 kg.

Lake Fertilization Experiments

Determination of the effects of changing nutrient loads to Kootenay Lake is complicated by the introduction of *M. relicta*. The kokanee salmon and rainbow trout populations in Kootenay Lake did not appear to be adversely affected by the introduction of *M. relicta* between 1949 and the construction of the dams upstream. However, once nutrient loads had decreased to below historical levels, the competitive effect of *M. relicta* may have combined with low nutrient concentrations to hasten the decline in kokanee abundance. Given that there were currently no methods available to eliminate *M. relicta* from Kootenay Lake, replacement of the missing nutrient loads was considered as a management option for restoration of kokanee stocks, and conservation of the trophy rainbow trout fishery (Walters et al. 1991).

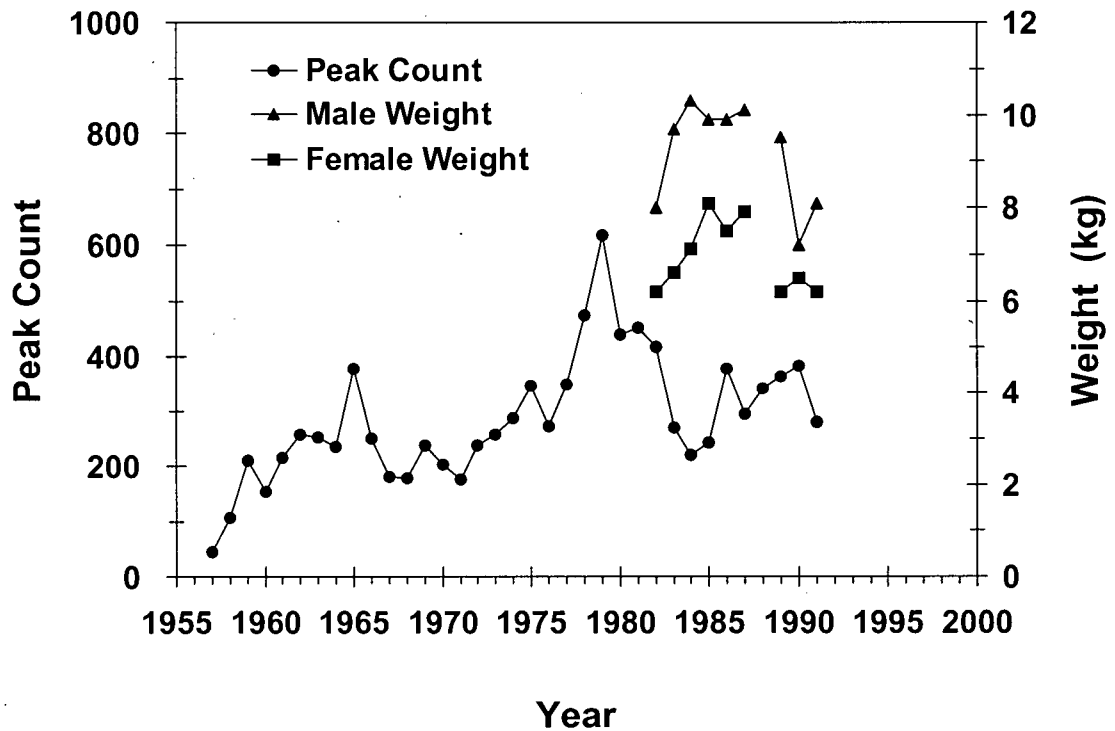


Fig. 10. Historical Gerrard rainbow trout spawner numbers and weight. The total spawning run is estimated to be three times the peak count (pers. comm. Mr. Les Fleck, B.C. Ministry of Environment, Lands and Parks, Nelson, B.C.).

Nutrient addition experiments for the restoration or enhancement of fish populations have been performed on many lakes in North America (Juday et al. 1938; Smith 1955; Hyatt and Stockner 1985; Mills 1985; Koenings et al. 1989), as well as lakes in Australia (Weatherley and Nicholls 1955), Scandinavia (Jansson 1978; Johannessen et al. 1984; Milbrink and Holmgren 1988), and Scotland (Munro 1961). Many experiments reported increased fish growth following fertilization (Juday et al. 1938; Weatherley and Nicholls 1955; Johannessen et al. 1984; Kyle 1994; Stockner and MacIsaac 1996). Several of these studies documented increased survival (Smith 1968; Robinson and Barraclough 1978; Mills 1985; Stockner and MacIsaac 1996), and Smith (1955) observed increased yield. Kyle (1994) reported increased adult production of sockeye salmon (*Oncorhynchus nerka*), but did not use control lakes for comparison.

The effectiveness of nutrient additions is still uncertain. Numbers of sockeye salmon returning to Great Central Lake, British Columbia increased following fertilization, but sockeye returning to an adjacent, unfertilized lake also increased (LeBrasseur et al. 1978). In another fertilized British Columbia lake sockeye growth decreased while the stickleback (*Gasterosteus aculeatus*) population increased (Stockner 1981). Furthermore, a review of the B.C. Salmon Enhancement Program concluded that it is very difficult to measure the production of adult salmon attributable to lake fertilization effects on juveniles, as opposed to marine environment effects (Hilborn and Winton 1993). Budy et al. (1998) found no significant difference in kokanee juvenile growth rates in response to experimental nutrient additions, despite significant positive responses in primary production, chlorophyll *a* concentrations, and zooplankton biomass.

Considering the variable and ambiguous results of previous nutrient addition experiments, it was unclear whether nutrient additions to Kootenay Lake would adequately compensate for the effects of the upstream dams, particularly given the presence of *M. relicta*. Experience suggests that nutrients added in the correct ratio of phosphorus to nitrogen should result in increased grazeable algal biomass (Elser et al. 1990), and in turn, increased macrozooplankton biomass. However, it is not certain that the increased macrozooplankton biomass will be consumed by the desired planktivorous fish, rather than a competitor such as *G. aculeatus* or *M. relicta*. If the initial condition of the lake at the time of lake fertilization were critical, and the actual conditions were unfavourable, fertilization might do more harm than good. Interestingly, nutrient additions to British Columbian lakes had been considered as far back as 1952, by W.A. Clemens, who concluded that the risks involved in enhancing lakes beyond their natural productivity outweighed the potential benefits (Clemens 1952).

Adaptive Environmental Assessment Process

Drastic decline in the kokanee salmon population in Kootenay Lake necessitated some form of management intervention, but there were many uncertainties involved in the response of the ecosystem to a large-scale manipulation such as whole or partial lake fertilization. The adaptive environmental assessment (AEA) process was used to develop an experimental management plan which took these uncertainties into account (Walters 1986). The AEA process involves a series of workshops which bring together people with a wide variety of experience and expertise relevant to the problem at hand. The theoretical and technical information they contribute is used to identify a range of possible management actions, and to screen possible outcomes of different actions using computer simulation models. A management option that appears most likely to succeed can then be chosen and tested in the field. Monitoring and re-assessment of the field experiment is essential so policy can be changed and improved as new information becomes available. This 'adaptive management' approach allows managers and scientists to 'learn as they go'. It allows a reasoned response despite limited baseline data, and improves future management decisions by gathering more data as the experiment progresses. Ideally, the experiment is designed to increase the range of data available for future management decisions. For example, increasing or decreasing nutrient loads would provide data on the response of phytoplankton, zooplankton and planktivores to a range of nutrient loads, rather than just the load occurring immediately prior to the experiment.

Kootenay Lake Fertilization Response Model

Two AEA workshops were held by the B.C. Ministry of Environment, Lands and Parks in 1991 at the University of British Columbia (Walters et al. 1991). At the second workshop the Kootenay Lake Fertilization Model was completed and used to test possible management strategies for Kootenay Lake. The model predicted that the addition of nutrients would benefit

mysids more than kokanee, and would actually hasten the kokanee stock collapse (Walters et al. 1991), probably because of *M. relicta*'s shorter life cycle and consequent ability to increase in abundance faster than kokanee. However, the participants at this workshop concluded that there were no viable methods to remove *M. relicta* from the lake, and thus eliminate the effect of its competition with kokanee for zooplankton. They also noted that kokanee numbers had not shown a marked decline as *M. relicta* abundance increased. The decrease in nutrient loading was considered to be the greater problem, and was more closely correlated with the kokanee decline. With no other options to consider, the B.C. Ministry of Environment, Lands and Parks, in conjunction with B.C. Hydro, began experimental fertilization of the North Arm of Kootenay Lake in April 1992 in an attempt to restore the kokanee salmon stock, and to protect the large piscivores which depend on it (Ashley et al. 1997a). The AEA model suggested that mixing rates along the lake should be low enough that fertilization in the North Arm only should result in a clear north-south gradient in primary production and zooplankton responses if such responses occur at all. That is, there should be a partial, in-lake control for fertilization tests.

Goals of Nutrient Additions

In accordance with the strategic objectives of the B.C. Ministry of Environment, Lands, and Parks, the primary goal of the managers involved in the fertilization experiment was the conservation of wild stocks of fish (Gunton et al. 1995). Secondly, they wanted to restore the abundance of kokanee in the lake, thereby preserving the kokanee fishery, and ensuring a food supply for the trophy rainbow trout. In contrast, the goal of the fertilization experiment was to test whether or not any changes in kokanee abundance or production were attributable to fertilization, regardless of whether kokanee abundance increased or decreased. The fertilization experiment would be successful if it were able to detect changes in the lake biota, and ascertain

whether the changes were nutrient-induced. The management policy would be successful only if changes due to fertilization resulted in improved kokanee stocks.

Summary

Kootenay Lake has experienced major impacts from hydroelectric development and exotic species introductions, that appear to have caused a major decline in kokanee salmon stocks. In addition to their natural, intrinsic value, kokanee have socioeconomic value through enhancement of local lifestyles and tourism. Also, the fish are ecologically critical to the lake food web, as kokanee are the major food of the top piscivores, trophy size bull trout and Gerrard rainbow trout.

The impacts of the introduction of the exotic freshwater macroinvertebrate *M. relicta* are uncertain and depend largely on lake morphology. Mysids are likely to be a problem in the main part of Kootenay Lake (as opposed to the outflow river) since they compete with kokanee for zooplankton, but are able to take refuge from predation by staying in deep waters during daylight.

The Duncan and Libby Dams, upstream of Kootenay Lake, have impacted the lake by destroying fish spawning habitat, altering the flow regime, and trapping nutrients. While the spawning channels constructed near Kootenay Lake have helped to replace lost spawning habitat, these measures have not addressed the problems caused by the abnormal hydrograph and decreased nutrient load.

The biota of Kootenay Lake has experienced large fluctuations over the last fifty years. Lake trophic state has shifted from oligotrophic to eutrophic and back. *Daphnia* spp. has been a dominant cladoceran in oligotrophic periods, but declined during the period of high phosphorus loads in the 1960's. The exotic *M. relicta* has increased from approximately 25,000 individuals, to on the order of 1×10^{11} individuals lake-wide, with large inter-annual fluctuations. Kokanee

salmon spawner numbers have fluctuated over an order of magnitude, with patterns that appear correlated with changes in nutrient loading, but obscured by changes in spawning channel management, altered zooplankton species composition, and competition from *M. relicta*.

Despite evidence from numerous previous fertilization experiments, it was impossible to predict accurately the outcome of nutrient additions to Kootenay Lake, particularly given the presence of *M. relicta*. Kootenay Lake was a marginal candidate for nutrient additions. The Kootenay Lake fertilization response model predicted that kokanee stocks would crash regardless of nutrient additions, and that the crash might actually be accelerated by fertilization. Because of this, the nutrient additions were done using an adaptive management approach. Ideally, a major aspect of the adaptive environmental assessment process is that the management of the lake ecosystem is done as an experiment, and monitoring of the effects of the management technique is crucial. In the case of nutrient additions to Kootenay Lake, monitoring had to be able to detect responses throughout the food web. This meant monitoring a space 400 km², and up to 140 m deep, over a period of 6 years. The observations from the monitoring program were compared with expected results, to detect the effects of the management technique, so that the policy being followed could be maintained, refined or rejected, as the data warranted.

As an adaptive management experiment continues, the implications for future management of impacts are continually reconsidered. This chapter gives a point of comparison between the Kootenay Lake scenario and that of other large interior lakes which have been adversely affected by hydroelectric dams and exotic species introductions.

CHAPTER 2: EXPERIMENTAL DESIGN, AND HYPOTHESES ABOUT THE EFFECTS OF NUTRIENT ADDITIONS

Experimental Design

Assessment of the effects of fertilization on the Kootenay Lake ecosystem required an experimental design that would allow us to determine whether the system had changed during fertilization, and whether any changes observed were actually due to fertilization. Several types of experimental design have been suggested for large-scale ecological experiments. The Before-After-Control-Impact (BACI) design involves sampling a control site, and the impact site both before and after the impact occurs (Stewart-Oaten et al. 1986). If the difference between the two sites changes once the impact occurs, this is taken as evidence that the impact caused the change at the impact site. An improvement on this design is BACI sampling with a set of control locations (Underwood 1992). This method is preferable because there could be a difference between a single control site and the impact site that was caused by a factor other than the studied impact. The use of multiple controls allows any change that occurs at the impact site to be compared with the natural range of variability at the control sites. In the case of Kootenay Lake there was no other lake similar enough in terms of morphometry, flow regime, or initial ecological conditions to have served as a control for this experiment. Furthermore, the cost of fertilization and monitoring precluded replicating this experiment on another lake. Because of the lack of replicate and control lakes, a gradient design was used on Kootenay Lake, where nutrients were added in the north end of the lake, and potential effects of nutrient additions were monitored at different points along the length of the lake (Fig. 1). Gradient designs have been used to detect differences that occur at a range of distances from a disturbance, such as effects of point source contaminant releases from ocean oil rigs (Ellis and Schneider 1997). Effects are analyzed as a function of distance from the disturbance, rather than the

difference between the impact site and a control site at a single distance from the impact.

Fertilizer was added to the North Arm of Kootenay Lake at weekly intervals during the growing season (for details see p. 52). The Kootenay Lake fertilization response model predicted that this application would result in a north-south gradient of algal productivity (Walters et al. 1991).

The effects of the fertilizer were expected to be most intense at or near the area where the fertilizer was added, and to become gradually less intense with increasing distance southward along the lake. Patterns observed in the abundance and production of the biota could then be used to determine whether the fertilization was having an effect on the lake, and whether the effect was desirable.

There were potential problems with this choice of experimental design. The South Arm of the lake is not “pristine” in the sense of being a control area for comparison with the opposite end of the lake. Water and nutrient inputs to the South Arm come from the Kootenai River via the Libby Dam, and this inflow dominates the lake hydrograph. In high flow years there can be large nutrient inputs to the South Arm, although the usefulness of these nutrients to phytoplankton are uncertain because of turbidity effects (Northcote et al. 1998). In addition, spring and summer flows to the South Arm were increased in some years of the experiment to encourage sturgeon spawning, and to facilitate the seaward migration of sockeye smolts lower in the Columbia River system. The mobility of kokanee and trout could homogenize the effects of nutrient additions along the lake (e.g., by feeding near the fertilizer application site, then recycling nutrients through defecation or mortality near the other end of the lake), making gradient effects more difficult to detect. Another complication was that the majority of kokanee fry enter the lake from tributaries at the top of the North Arm, so the initial distribution of fry in spring is skewed along the lake from north to south, in alignment with the anticipated nutrient gradient. Thus, a concentration of fry near the fertilization site cannot be attributed solely to

nutrient effects. Another concern was that since Kootenay Lake was deemed to be in a crisis situation, no time was taken to collect baseline data along the proposed gradient for several years immediately prior to fertilization. Limnological data were collected along the lake consistently starting in 1972, but sampling was reduced to one mid-lake station in the 1980's because of funding cuts (Crozier and Duncan 1984).

My basic advance plan for statistical analysis of spatial gradient data was to test for significance of gradients against the null hypothesis of independent sampling variation only among sites and times. Such tests simply involve showing by regression analysis whether or not the observations are likely to have come from a system without gradients, where a gradient statistically can also be represented by spatial autocorrelation of observations. I recognized that the treatment plan which did not have temporal untreated reference observations for gradients in the absence of fertilization could leave me unable to decide whether any measured gradients were in fact due to fertilization alone. For example, I expected fry distribution along the lake to be skewed toward the fertilized end of the lake due to fry source locations.

Several variations of the fertilization application were considered that might have made the effects of nutrient additions more clear. For example, fertilization could have been done for four years, and then stopped for one or more years to see if the system reverted to its pre-treatment state. Alternatively, fertilizer could have been added to the North Arm for four years, and then added to the South Arm for several years, to test the efficacy of the gradient design. Neither of these modifications was tested because of concerns on the part of the provincial government staff that the compensation fund money allocated for the experiment would be lost permanently if it were re-allocated during a year without fertilization, or if there seemed to be great uncertainty about whether fertilization was "working" (it should be noted that there was never a guarantee of long-term

funding for the experiment, and that government staff had to justify the funding for the experiment every year during the annual budget cycle).

It will eventually be possible to compare the outcome of nutrient additions to Kootenay Lake with similar experiments on other large lakes in southern British Columbia. Fertilization of Upper Arrow Lake, part of the Arrow Lakes Reservoir, began in April, 1999, in response to drastic declines in kokanee stocks. Fertilization is also being considered for Okanagan Lake, which has also experienced kokanee declines in recent years. The Arrow Lakes Reservoir and Okanagan Lake have food webs that closely resemble the Kootenay Lake system, including the presence of *M. relicta*. Although the water flow regimes in these lakes differ considerably from that of Kootenay Lake, there are long-term data sets on kokanee abundance for both these systems, and Okanagan Lake and the Arrow Lakes Reservoir have been monitored intensively since 1996 and 1997, respectively (Ashley et al. 1998; Pieters et al. 1998). While these experiments are not replicated, repetition of the same ecosystem manipulation in a range of lakes may broaden our knowledge of its effects (Carpenter 1990), and allow generalizations about the effects of nutrient additions to large lakes that are impacted by hydroelectric dams and exotic species. Fertilization of similar lakes, starting several years apart, offers a form of staircase design (Walters et al. 1988). If lakes respond in similar ways to nutrient additions started several years apart, there is less chance that the responses were due to a transient factor rather than the experimental treatment.

Food Web Structure, and Top-Down and Bottom-Up Processes

The abundance of a population at a given trophic level in a food web will be controlled by its resources (bottom-up effect), unless it is controlled by predation (top-down effect) (Hairston, Smith and Slobodkin 1960, HSS). The HSS model was developed for three-level terrestrial food webs, in which herbivores are limited by predators, while the plants they feed upon are limited by resources such as space, light, and nutrients for which they compete

intraspecifically, and with other species. The expansion of these ideas to food webs with more than three trophic levels was suggested by Smith (1967), and further expanded by Oksanen et al. (1981) as the OFAN model. This model predicts that as primary productivity increases in a four-level food chain, new production will be transferred up through the food web, resulting in accumulation of new biomass at the top level, and at alternating levels below (e.g., piscivores, and zooplankton), provided that the links in the food chain are tight (this implies that prey have few refuges from predators, so that new prey production is quickly transferred to predator biomass). Carpenter et al. (1985) showed that increases in the abundance of top predators in aquatic systems can have cascading effects down the food web, decreasing the abundances of planktivores, increasing zooplankton abundance, and in turn causing phytoplankton abundance to decrease.

Several factors may affect the strength of top-down versus bottom-up linkages, and the relative changes in biomass at each trophic level if nutrients are added to a system. Top-down forces tend to act most strongly near the top of the food web, while bottom-up forces act most strongly on lower trophic levels (McQueen et al. 1986). McQueen et al. suggest that lake fertilization may have little effect on planktivore standing stock biomass, if new planktivore production is readily cropped by piscivores. Time lags may occur because organisms at different trophic levels reproduce on different time scales (Persson et al. 1992). Larger organisms near the top of the food web move on different spatial scales than smaller organisms at the bottom of the food web, and may spread the impact of a localized effect at the bottom of the food web over a wider area. The distribution of predators and prey in space may also affect their interactions. If predators and prey are heterogeneously distributed then the functional response of predators may be dependent on the ratio of prey and predator densities, not the density of prey (Arditi and Saiah 1992). As productivity of a ratio-dependent food web increases, there will be increases in

biomass at all trophic levels (Arditi and Ginzburg 1989). This is similar to what would be expected from a pure bottom-up food web model, and contrasts with the increases at alternating levels predicted by top-down models (Power 1992). Heterogeneity in the form of prey refuges may act to stabilize food webs in the presence of enrichment. Rosenzweig (1971) predicted that nutrient additions to a two-level food web could cause the predator species to increase enough that prey abundance crashed, resulting in extinction of the system. However, Abrams and Walters (1996) suggested that if prey have states in which they are invulnerable to predation, for example when they are in spatial refuges, or in invulnerable life history stages, the system may remain stable when enriched. Increasing the numbers of species at each trophic level, another form of heterogeneity, complicates predictions about the effects of enrichment (Abrams 1993). Increasing nutrient inputs may favour one primary producer (e.g., nanoplankton) over another (e.g., netplankton). In turn, one consumer (e.g., *Daphnia*) may be better able to use the new primary production than a competing consumer (e.g., copepods). At the next level, one predator (e.g., *M. relicta*) may obtain more or less consumer production than its competitor (e.g., kokanee).

Of particular interest for Kootenay Lake is Abrams' (1993) prediction regarding enrichment of a system where one species at a trophic level is predator-free, as may largely be the case for *M. relicta*, while its competitor has a predator, as is the case for kokanee. If increased nutrient inputs alter the competitive advantage in favour of the predator-free species (*M. relicta*), the population of the other species (kokanee) will decline, resulting in a decrease in the top predator population (in this case, trout).

Potential Effects of Nutrient Additions on Food Web Structure in Kootenay Lake

The decision to add nutrients to Kootenay Lake rested on the assumption that decreased nutrient loading was the primary cause of the decline in algal production and kokanee

abundance. However, even if this assumption were correct, there was a further assumption that the added nutrients would move up through the food web (Fig. 11) to reach the kokanee and subsequently the trout. There were two major uncertainties in this assumption. First, the nutrients would have to encourage the growth of phytoplankton in size classes which are edible by macrozooplankton such as *Daphnia*. Second, the additional macrozooplankton production would have to be consumed mainly by kokanee, and not by mysids.

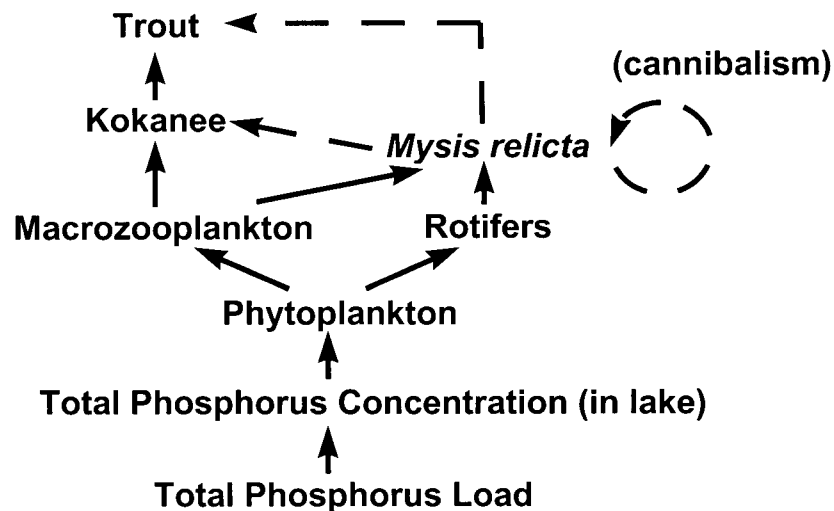


Fig. 11. Kootenay Lake food web. Dashed lines indicate links which are relatively uncertain.

Time Lags in Top-Down Bottom-Up Interactions

During nutrient additions to Kootenay Lake, biomass should move up through the food web, according to top-down theory, such that alternating trophic levels show increased standing stock biomass (Fig. 12). There are time lags in numerical responses toward the top of the food web, because of the progressively longer reproductive times of phytoplankton, zooplankton, *M. relicta*, kokanee and trout. While individuals would exhibit increased growth or survival rates, or both, numbers would not increase until the organisms affected were old enough to reproduce. Because no new organisms (i.e., entirely new trophic levels) such as trout were introduced at the

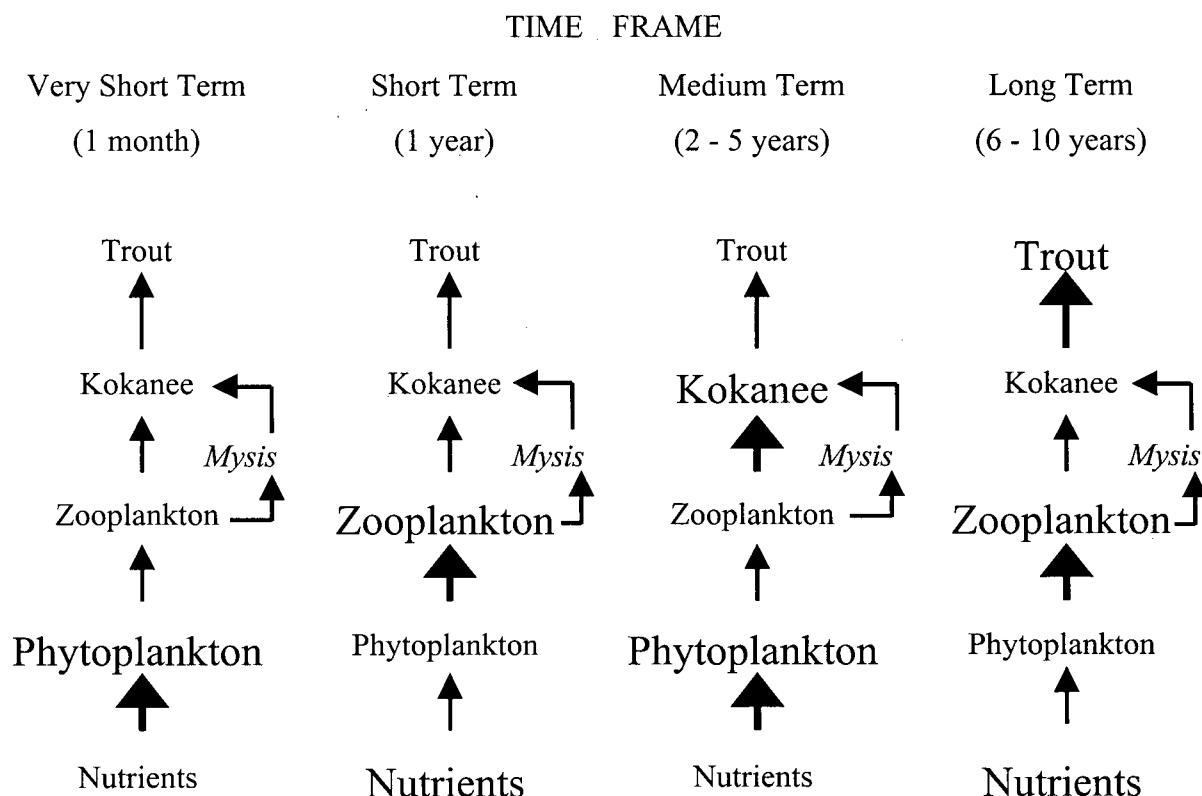


Fig. 12. Expected changes in food web interactions as a result of nutrient additions, with respect to top-down bottom-up theory. The thickness of each arrow indicates the amount of nutrients or biomass transferred through the food web relative to the unfertilized situation. Font size shows relative biomass at each trophic level over time.

top of the food web, increased predation pressure from one trophic level on the level below would occur first near the bottom of the food web. For example, in the very short-term there could be increased uptake of nutrients by phytoplankton, which would cause lower in-lake nutrient concentrations than expected from the nutrient additions. In the very short term phytoplankton biomass would increase. In the short-term, zooplankton would increase consumption of phytoplankton, zooplankton biomass would increase, phytoplankton biomass would decrease, and in-lake nutrient concentrations could rise. In the medium-term, kokanee would increase predation on the increased zooplankton biomass. Kokanee biomass would increase as the zooplankton biomass was cropped down, phytoplankton concentrations would

rise, and in-lake nutrient concentrations would decline again. Finally, in the long term, trout would consume the additional kokanee biomass, zooplankton biomass would increase, phytoplankton biomass would decrease, and in-lake nutrient concentrations would increase. The predictions in Fig. 12 assume that mysids are less able than kokanee to eat zooplankton, particularly *Daphnia*, or that *Daphnia* out-compete microzooplankton (rotifers) which are eaten by mysids, but not by kokanee.

Alternate Food Web Scenarios Along the Nutrient Gradient

The top-down bottom-up interactions described in Fig. 12 are an example of what might be seen if nutrients were added to a whole lake, so that additional nutrients were equally available throughout the habitat. The experimental design used in Kootenay Lake was more complex because nutrients were added at one end of the habitat, so a gradient of top-down bottom-up responses was expected in the food web along the lake. Ideally, in terms of kokanee restoration, the response near the fertilizer application site would be very similar to that shown in Fig. 12, while there would be little or no change in the food web structure at the unfertilized end of the lake. However, there were numerous uncertainties about the response of different trophic levels to fertilization, and about how clear and strong the food web response would be at different points along the nutrient gradient. The outcomes of these uncertainties lead to several very different potential food web scenarios along the length of Kootenay Lake (Fig. 13). In the following section I outline four potential food web scenarios in terms of both abundance and production of different trophic levels, and describe the mechanisms that would lead to each scenario.

Bottom-Up, No Top-Down Response

The simplest scenario for the Kootenay lake food web during nutrient additions to the North Arm is a bottom-up response with no top-down control at any trophic levels. The case I

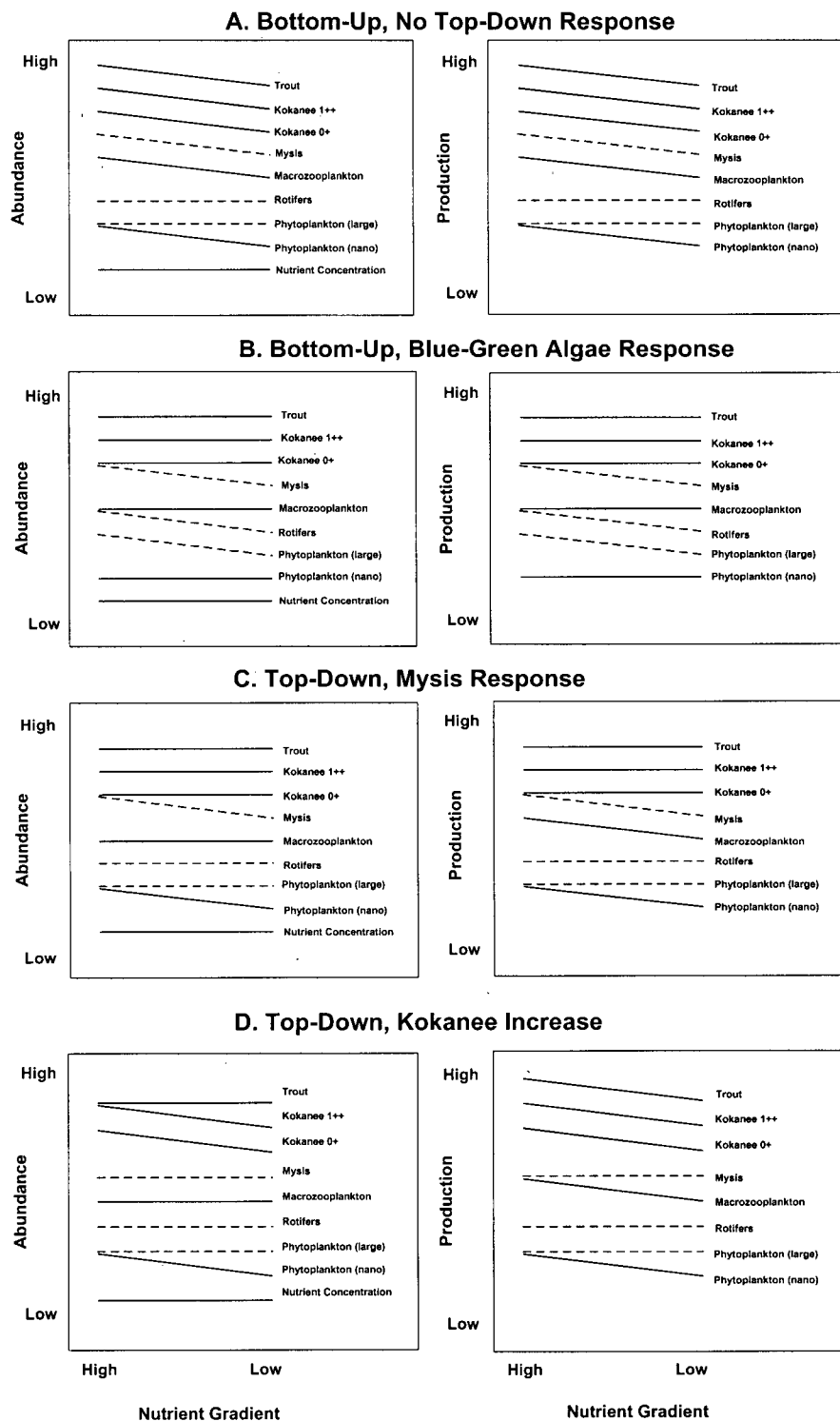


Fig. 13. Potential patterns of abundance (biomass of phytoplankton, rotifers and macrozooplankton, and density of *M. relicta*, kokanee and trout) and production (growth) along the length of Kootenay Lake, for different trophic levels. The left panels show the expected patterns of abundance at each trophic level, along the productivity gradient. Right panels show expected patterns of production associated with changes in abundance. Dashed lines indicate organisms whose increase in abundance, production or both in the fertilized end of the lake, could indicate that fertilization was not beneficial to kokanee.

have illustrated assumes that there will be positive effects on production of all the components of the classical food chain, starting with grazeable algae, and moving up to macrozooplankton, kokanee, and trout. At each trophic level the organisms would show a positive correlation between their production and biomass, and the production of their prey species one trophic level below. Alternate trophic levels would not show flat abundance patterns long the lake, due to prey “refuges” such as vertical migration to darker depths (zooplankton, *M. relicta*, kokanee fry), or schooling behaviour (kokanee). If there were a high N:P ratio the production of large phytoplankton would not be stimulated, and there would be no difference in large phytoplankton production or abundance along the nutrient gradient. In this example I have assumed that macrozooplankton such as *Daphnia* would out-compete rotifers for nanoplankton (Neill 1984; Gilbert 1988), through exploitative competition for food, and mechanical interference. Thus rotifer production and abundance would also show no trends along the gradient.

Bottom-Up, Blue-Green Algae Response

The second scenario is a bottom-up response by cyanobacteria (blue-green algae). If the N:P ratio in the North Arm were too low, through a swamping of the fertilizer ratio by natural loading, or late summer nitrogen depletion, large, ungrazeable nitrogen-fixing cyanobacteria would have a competitive advantage over nanoplankton. As ungrazed cyanobacteria died, production of microbial loop components such as bacteria would be stimulated, leading to increased food resources for rotifers. This would stimulate *M. relicta* production, particularly by juveniles, which feed preferentially on small zooplankton. Biomasses of cyanobacteria, rotifers, and *M. relicta* would be higher in the fertilized end of the lake. Since kokanee do not feed on rotifers, kokanee production and abundance would be the same along the gradient. Likewise, trout production and biomass would show no trends along the lake because kokanee were not affected.

A similar scenario would result if nutrient additions stimulated the production of autotrophic picoplankton (0.2-2.0 μm), since rotifers are the main grazers of these phytoplankton in oligotrophic lakes (Stockner 1988). Movement of the added nutrients into autotrophic picoplankton and rotifers, which are part of the microbial loop, would “misdirect” nutrients away from the classical food chain that includes macrozooplankton, kokanee, and trout.

Top-down Response, *M. relicta* Increase

In the third scenario nanoplankton production in the North Arm is stimulated by increased nutrient loads. Macrozooplankton production would then increase, and *M. relicta* production would increase as mysids outcompeted kokanee for the increased food resource. But macrozooplankton would be unable to escape heavy predation by *M. relicta*, so macrozooplankton abundance would be similar along the gradient, although macrozooplankton production would be higher in the North Arm. *M. relicta* would be able to escape predation by kokanee and trout by vertically migrating to deep water by day, so *M. relicta* abundance would increase in the North Arm. Production and abundance of rotifers, kokanee, and trout would not change throughout the lake.

Top-Down, Response, Kokanee Increase

In the final scenario nanoplankton production is stimulated by increased nutrient loads to the North Arm, and macrozooplankton production would increase in response to increased food supply. Kokanee would be able to outcompete *M. relicta* for zooplankton, and kokanee production would increase in the fertilized end of the lake. In turn, trout production would increase in response to increased kokanee production. In the medium term (e.g., less than 6 years), trout numbers would not have increased fast enough to crop down kokanee biomass, so kokanee abundance would be higher in the North Arm. Kokanee would crop down macrozooplankton biomass so that it would be similar along the gradient. Nanoplankton

biomass would be released from intensive predation, so nanoplankton abundance would be higher in the North Arm, and dissolved nutrient concentrations would be similar throughout the lake.

It is possible that within a few years this scenario could shift, provided that trophic links at the top of the food web are tight (that is, kokanee are fairly vulnerable to trout predation). Once trout numbers increase, trout could crop down kokanee abundance in the North Arm. This would allow macrozooplankton abundance to increase, and cause nanoplankton abundance to be cropped down, and dissolved nutrient concentrations to increase. However, it is also possible that increased growth rates may make kokanee less vulnerable to trout predation. Kokanee may eat more and grow faster through the size range where they are most vulnerable to trout predation, thereby lowering kokanee mortality rates.

Another possibility is that fry may opt to obtain the same amount of food at all points along the gradient, in order to reach a threshold size for over-winter survival (Walters and Juanes 1993), but would have to spend less time doing so in the North Arm. Since time spent feeding is also time spent vulnerable to predation fry in the North Arm should have higher survival rates than fry in the unfertilized end of the lake. Fry could accomplish this by spending less time near the surface feeding at dawn and dusk, and more time in deeper, darker water where they are less vulnerable to predation. Kokanee fry in Okanagan Lake, B.C. are known to migrate vertically to feed near the surface at dawn and dusk, and move to deeper water in midday (Levy 1991). Juvenile sockeye make a trade-off between time spent feeding, and vulnerable to predation, versus time spent in deeper, darker water where there is less food but less chance of predation (Clark and Levy 1988). Alternatively, fry could spend more time in schools, where they are safer from predation, but probably cannot forage as effectively as if they were alone. Fry could do this by forming schools earlier in the dawn period, and leaving schools later at dusk. The end

result of these strategies would be more small-sized kokanee, rather than the same number of kokanee as before fertilization, but with larger average size.

As I noted in the section on experimental design, there were a number of factors which could complicate the interpretation of the experiment's results. Active movement of organisms around the lake would tend to "smear" the effects of nutrient additions along the lake. Since kokanee and *M. relicta* have a greater ability to move around the lake than plankton do, their growth response would be expected to homogenize the effects of the fertilization throughout the lake. Kokanee fry are naturally concentrated in the fertilized end of the lake in spring because most fry in the lake originate from North Arm tributaries. Fry may opt to stay in the fertilized zone, and older kokanee may move from the unfertilized end of the lake to the fertilized end in response to increased zooplankton production, hence preventing any strong zooplankton abundance response in areas of increased zooplankton productivity due to fertilization. Individual kokanee growth rates would be similar along the lake, but greater total kokanee production would occur near the fertilization site. In turn, if trout moved toward the fertilized end of the lake to take advantage of the concentration of kokanee, kokanee mortality would increase unless kokanee decreased the time they spent feeding and vulnerable to predation.

Environmental factors further complicate the detection of responses to nutrient additions. There is a net movement of water from the inflow rivers toward the West Arm, and a resulting passive movement of plankton toward the outflow. Zooplankton that ate increased amounts of phytoplankton near the fertilized zone (north end of lake) might be carried half way down the North Arm before they reproduced, so their increased growth or abundance would be observed at a different location than the consumption that caused it. Water flow may also affect *M. relicta*, by increasing mortality rates due to export from the lake. The Kootenay Lake Fertilization Response Model showed that the outcome of fertilization was very sensitive to *M. relicta*

mortality rates, and *M. relictus* would experience increased mortality due to export from the lake in high snow pack years. This effect would be particularly strong if there were a large spring freshet which would coincide with the release of juveniles from females' brood pouches. Mortality from a physical factor such as flow, as opposed to trophic factors such as starvation, cannibalism, or predation, could suppress *M. relictus* abundance, and affect the interactions of *M. relictus* with other species along the nutrient gradient. Kokanee distribution could be affected by environmental factors such as temperature or oxygen gradients associated with the Duncan or Kootenai River inflows. The skewed kokanee distribution could then affect zooplankton in ways not predicted in the fertilization food web scenarios.

CHAPTER 3: METHODS

Temporal and Spatial Scales of Observations

The fertilization experiment was conducted for six years, from 1992 to 1997. Data were collected biweekly or monthly, so comparisons were possible on temporal scales from two weeks to six years. This allowed for detection of time-lags in relationships between organisms at different levels of the food web. Between-year comparisons of within-season patterns and lake-wide distributions were necessary to look for medium-term trends related to nutrient additions. The availability of historical data, some dating as far back as 1949, allowed comparison with current data for detection of longer-term trends.

To assess the effects of nutrient additions it was considered worthwhile to collect data on the whole lake ecosystem, from water flow, physical limnology, and water chemistry, to abundances of organisms at all levels of the food web. Where possible, information on consumption, production (growth and reproduction), and mortality rates were also collected. For spatial comparisons along the gradient, most types of data were collected at a set of 7 fixed stations, from “upstream” of the north end fertilization site to the south end of the main lake (Fig. 1).

Fertilizer Additions

Fertilizer was added to the surface waters near Station 2, and was distributed from two 40,000 L tanks on a barge pushed by a tugboat (Ashley et al. 1997a). The fertilizer was a blend of 10-34-0 (ammonium polyphosphate) and 28-0-0 (urea-ammonium nitrate). From 1992 to 1996, 47.1 t of phosphorus (approximately the load missing from the North Arm due to dam operations) and 206.7 t of nitrogen were added per year, while the total amount of fertilizer added per year was 942 t. The amount of fertilizer added per week increased early in the season, then decreased toward

the end of the growing season, and was timed to mimic a natural nutrient loading regime (Fig. 14 a). The N:P ratio increased from 0.67:1 to 7.5:1 (weight:weight) as the season progressed (Fig. 14 b), in order to compensate for the uptake of dissolved inorganic nitrogen (Ashley et al. 1997a). The N:P ratio of the fertilizer was low compared with N:P weight:weight ratios considered to be high enough to discourage the growth of nitrogen-fixing cyanobacteria (blue-green algae). Cyanobacteria do not contribute significantly to algal biomass when TN:TP ratios exceed 30:1 (Smith 1983) (Note: an N:P atomic weight ratio of 6:1 corresponds to an N:P ratio of 13:1 by atoms). However, cyanobacteria do not necessarily predominate at lower TN:TP ratios, and thresholds of 10 - 12:1 are often used (Pick and Lean 1987). Background concentrations of nitrogen in Kootenay Lake were relatively high, with values of about 0.12 mg L^{-1} nitrate + ammonia - N at spring overturn from 1968 to 1978 (Daley et al. 1981). Thus, it was anticipated that the natural nitrogen plus the fertilizer nitrogen would result in an N:P ratio that would encourage the growth of grazeable algae, as opposed to cyanobacteria (pers. comm., Mr. Kenneth I. Ashley, Fisheries Research and Development Section, B.C. Ministry of Environment, Lands and Parks, 2204 Main Mall, Vancouver, B.C. V6T 1Z4). In 1997 the spring algae bloom, as observed by field staff during water sampling, was greater than expected or esthetically desirable. In response the fertilizer loading in the spring (20 April - 22 June) was reduced to 80% of the 1992-96 levels, and the load in the summer (29 June - 31 August) was reduced to 40% of previous levels (pers. comm., K.I. Ashley). In total, 29.5 t of phosphorus and 111.6 t of nitrogen were added in 1997, and the total amount of fertilizer added was 526 t.

Field Sampling Procedures

Data were collected along the length of the lake at 7 sampling stations, either semi-weekly or monthly during the summer months (May - October), or monthly, year-round in the case of *M. relicta*. (Note: Station 7 was added in the spring of 1993 because of concerns about kokanee being

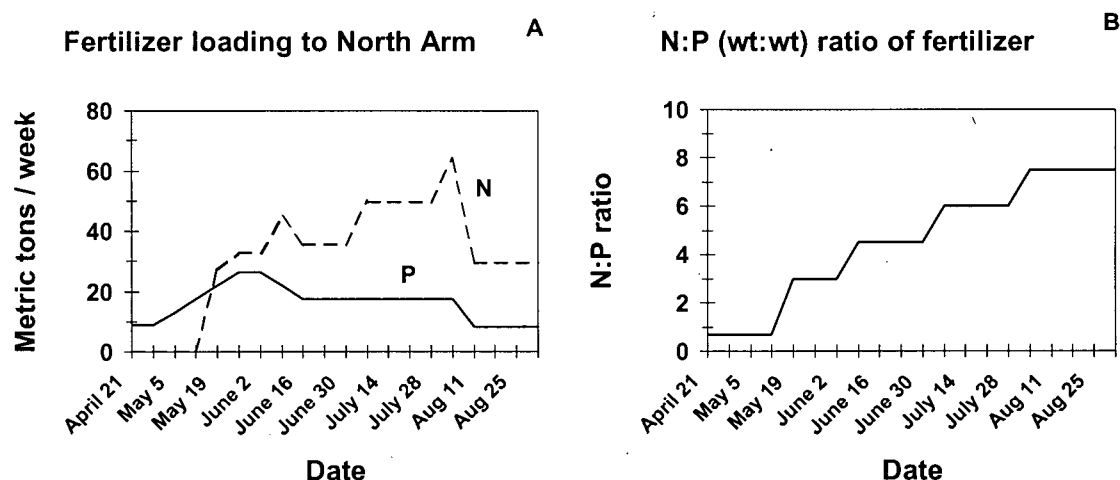


Fig. 14 (a & b). Pattern of phosphorus and nitrogen loading to Kootenay Lake used annually from 1992 to 1996, and N:P ratio (weight:weight) of fertilizer.

entrained in the Libby Dam outflow and surviving to enter the south end of Kootenay Lake). The stations were numbered from north to south, with Stations 1-4 in the North Arm, and Stations 5-7 in the South Arm. There were no sampling stations in the West Arm. A summary of the sampling program for physical limnology, water chemistry, phytoplankton, rotifers, zooplankton, *M. relicta*, kokanee, and trout is shown in Table 1.

The sampling protocols and analytical procedures for physical limnology, water chemistry, phytoplankton, and *M. relicta* are outlined in the following section. Detailed descriptions of methods for rotifers, macrozooplankton, *M. relicta* relationship with water flow, kokanee, and trout are given in subsequent sections.

Physical Limnology, Water Chemistry, Phytoplankton, Chlorophyll *a*, and *M. relicta*

Physical limnology data were collected bi-weekly from April to October with a Hydrolab (Surveyor II) within the top 50 m of the water column, at 1 m intervals at each of the seven stations. Temperature, dissolved oxygen, pH, oxidation-reduction potential, specific conductance and turbidity were measured. In addition Secchi disk transparency was measured bi-weekly at all

Table 1. Sampling program for physical, chemical, phytoplankton, zooplankton, *M. relicta*, kokanee, and Gerrard rainbow trout data. Parameters in bold were my responsibility in the overall data collection and analysis program.

Parameter sampled	Sampling frequency ^a	Sampling technique
Temperature, dissolved oxygen, pH, oxygen reduction potential, specific conductance, salinity	Bi-weekly, April - October	Hydrolab from 0 to 50 m (at 1 m intervals) at 7 sampling stations
Transparency	Bi-weekly, April - October	Secchi disk depth (without viewing chamber) at 7 sampling stations
Water chemistry: general ions, nutrients, metals, turbidity, alkalinity	Bi-weekly, April - October	Integrated sampling tube from 0 - 30 m at 7 sampling stations
Chlorophyll <i>a</i>	Bi-weekly, April - October	Integrated sampling tube from 0 - 20 m at 7 sampling stations
Phytoplankton	Bi-weekly, April - October	Integrated sampling tube from 0 - 20 m at 7 sampling stations
Rotifers (microzooplankton)	Monthly, April - October, 1994 - 1996	3 vertical Birge net hauls from 40 to 0 m at 7 sampling stations (35 μm net), vertical net speed = 1 m s^{-1}
Macrozooplankton	Bi-weekly, April - October	3 oblique Clarke-Bumpus net hauls (3-minutes each) from 40 to 0 m at 7 sampling stations (150 μm net), boat speed = 1 m s^{-1}
<i>M. relicta</i>	Monthly, year-round	3 vertical hauls from lake bottom to surface, with a 1 m^2 square-mouthed net (1,000 μm primary mesh, 210 μm terminal mesh, 100 μm bucket mesh), at 7 sampling stations, vertical net speed = 0.3 m s^{-1}
Kokanee (growth and diet)	Monthly, April - October	Up to six straight or oblique trawls with a 5 m by 5 m beam trawl net towed at 1 m s^{-1} , at 7 stations (6 standard 40-minute oblique trawls from 45 - 0 m at each station in September or October)
Kokanee (hydroacoustic abundance)	Monthly, April - October	One transect across the lake at 7 stations; 18 transects (including usual 7 stations) done in September or October.
Kokanee (spawner abundance)	Annual, August - September	Spawners enumerated, size and fecundity sampled at Meadow Creek channel, and two West Arm channels (Redfish Creek & Kokanee Creek)
Rainbow Trout	Annual, April - May	Spawners at Gerrard spawning site counted, and weight measured
Trout (size and diet of angled fish)	Ongoing	Size and stomach contents of angled rainbow trout and bulltrout analyzed as samples turned in at marinas

^a Station 7 was introduced in April 1993. All bi-weekly sampling was reduced to monthly in 1997, and was done at Stations 2, 4, 6, and 7 only. In 1997 kokanee trawls and hydroacoustics were done in July and September only.

stations with a standard 20 cm disk. Water chemistry was sampled with a 2.54 cm (inside diameter) tube sampler to obtain an integrated water column sample from 0 to 30 m at each station bi-weekly from April to October. Water samples were placed on ice and shipped to Zenon Environmental Laboratories (Burnaby, B.C.) for analysis of major nutrients, general ions and total metals.

Phytoplankton were sampled bi-weekly from April to October using a 2.54 cm (inside diameter) tube sampler to obtain an integrated water column sample from 0 to 20 m for chlorophyll *a* and phytoplankton species composition. Chlorophyll *a* samples were placed on ice and sent to Zenon Environmental Laboratories for analysis. Phytoplankton samples were preserved with Lugol's solution and shipped to the laboratory of Dr. Frances Pick (University of Ottawa) for analysis. Samples were enumerated using the Utermöhl method on a Wild M40 inverted microscope (Utermöhl 1938; Lund et al. 1958). Taxa were placed in size classes according to the mean of their longest dimension: picoplankton (0.2-2 μm), μ -ultraplankton (2.1-5 μm), ultraplankton (5.1-10 μm), nanoplankton (10.1-22 μm), microplankton (22.1-64 μm) and netplankton (>64 μm). Algal biomass was determined from estimates of the volume of each algal taxon multiplied by its density. Phytoplankton were also identified to species, and algal biomass was separated into seven main divisions: Cyanobacteria, Chlorophyta, Euglenophyta, Chrysophyta, Chryptophyta, Pyrrophyta and diatoms.

M. relictus samples were collected monthly on nights on or about the new moon from January to December. Three vertical hauls were collected (with the boat stationary) along each of the seven hydroacoustic transects (Fig. 1), using a 1 m² square-mouthed net with 1,000 μm primary mesh net, 210 μm terminal mesh and 100 μm bucket mesh. Two hauls were made from the deepest part of each transect (i.e., > 100 m) and one haul was collected from a shallow (i.e., < 60 m) near-shore zone. The net was raised with a hydraulic winch at 0.3 m s⁻¹. Samples were back-washed into a

cylindrical filter to remove most of the water, then preserved in 95% ethanol and shipped to the laboratory of Dr. David Lasenby (Trent University, Ontario) for analysis. Mysids were counted, aged and sexed using a low power dissecting microscope. Gut content analysis was performed on a sub-sample of 10 adult mysids per station using a compound microscope at 100X magnification. Rotifers, and zooplankton mandibles and postabdominal claws were counted, and the average number of food items per mysid was determined. Juvenile mysids were also sampled to determine the time at which juveniles are able to consume larger prey items such as macrozooplankton. Further details of sampling and analyses of physical limnology, water chemistry, phytoplankton, and *M. relicta* are covered in Ashley et al. (1997b).

Rotifers (Microzooplankton)

Rotifers (35 - 150 μm) were sampled to check whether they were responding to fertilizer additions, potentially at the expense of macrozooplankton such as *Daphnia*. Rotifers were collected monthly at the seven sampling stations, from June to October in 1994 and 1995, and from May to October in 1996. Triplicate samples were collected at each station in June and September of 1994, and in all months in 1995, at other times one sample was taken at each station. Rotifers were sampled with a 35 μm mesh Birge closing net (a Wisconsin-style net with a conical mesh and a nylon reducing cone at the front to increase efficiency) with a 35 μm mesh on the bucket. A 4.5 kg (10 lb.) cannonball was attached to the bottom of the net (with supporting string tied to the middle metal ring of the net) to help keep the net from drifting sideways and upward (as would have occurred if there were a current, or the boat drifted in the wind). If the net was still not sinking straight down it was necessary to operate the boat during the haul to keep the boat above the net. Vertical hauls were done from 40 to 0 m, to give a filtered volume of approximately 1,140 L. The net was raised at a speed of 1 m s^{-1} . A 35 μm mesh back-filter was used when rinsing the dolphin bucket, to reduce the amount of water to a volume that would fit in the sample bottle. Samples

were preserved in Lugol's solution, using 1 mL Lugol's per approximately 100 mL lake sample water.

In the lab, the contents of each sample bottle was re-suspended in a beaker and topped up with filtered tap water (filtered through a 74 μm mesh filter, to remove any large particulate matter) to a known volume (e.g., 200 ml). The beaker was gently swirled to suspend the rotifers uniformly in the mixture, and a 1 ml sub-sample was taken with a digital pipette (Eppendorf Varipette, model 4710). The end of the plastic pipette tip was cut off to give an opening of 2 mm diameter, to prevent blockage. The sub-sample was placed in a Sedgewick-Rafter cell and examined with a compound microscope at 100 X magnification. Rotifers were identified to genus (Pennak 1989) and lengths were measured using the same camera system as for macrozooplankton (see below). All the individuals in the sub-sample were counted. If less than a minimum of 200 individuals (all genera combined) were counted in one sub-sample, a second sub-sample was analyzed. The lengths of the first 10 individuals of each genus were measured. Individual volumes and biomasses (wet weight) were estimated from empirical length-weight regressions (McCauley 1984) and averaged for use in genus biomass calculations.

Data on the rotifer species present in the 1980's were obtained from Crozier and Duncan (Crozier and Duncan 1984), and from raw data sheets (R.J. Crozier, B.C. Ministry of Environment , Lands and Parks).

For the Ecopath model I estimated rotifer wet weight biomass on an areal basis (t km^{-2}), by multiplying the biomass of rotifers in 1994 (Table 4) per cubic metre by the sample depth of 40 m, and converting to t km^{-2} . Production was estimated as one of the literature values for temperate lakes shown in Table 7 (Makarewicz and Likens 1979). Rotifers eat a wide variety of food types, including phytoplankton, protozoa, other rotifers, and other small metazoans (Barnes 1980). For this model the diet composition included rotifers, phytoplankton, and detritus.

Consumption was arbitrarily set at 10 times production, assuming the rotifers have relatively high metabolic rates because of their small body size.

Macrozooplankton

Macrozooplankton (length $>150\ \mu\text{m}$) were sampled every two weeks mid-April to mid-October in 1992 - 1996, and monthly in 1997. At each of the seven stations, three replicate oblique tows were made using a Clarke-Bumpus net. The net had $153\ \mu\text{m}$ mesh and was raised from a depth of 40 to 0 m, at a boat speed of $1\ \text{m s}^{-1}$. Tow duration was usually 3 min, with approximately 2500 L of water filtered per tow. During periods of higher algal biomass, zooplankton tow times were reduced to 1.5 min, to minimize algal clogging of the mesh. The volume sampled was estimated from the revolutions counted by the Clarke-Bumpus flow-meter. A historical calibration value was available for the net (pers. comm., Dr. T. Johnson, B.C. Ministry of Fisheries, Research and Development Section, 2204 Main Mall, Vancouver, B.C. V6T 1Z4) and the net and flow-meter were calibrated after each sampling season (April 1993 and 1994, February 1995, March 1996, January 1997, and April 1998). From 1993 onward all the calibrations were done in a flume at the Civil Engineering Department at the University of British Columbia.

Zooplankton samples were preserved in 70% ethanol and analyzed for species density, biomass (estimated from empirical length-weight regressions (McCauley 1984)), and fecundity. Samples were re-suspended in tap water filtered through a $74\ \mu\text{m}$ mesh and sub-sampled into "splits" using a four chambered Folsom-type plankton splitter. Sample splits were placed in gridded plastic petri dishes and stained with Rose Bengal to facilitate viewing with a Wild M3B dissecting microscope. A black and white video camera was attached to the microscope with a side tube. Images were sent to a 486 PC computer via an Aver 2000 Pro video card plugged into the computer's motherboard. This allowed the computer monitor to display a live television image of the zooplankton. A customized counting window (Visual Basic 2.0) was opened on top of the video

window. The counting window had a transparent picture box which allowed the video image to be seen and measured, and additional text boxes where information identifying the sample, and species counts were recorded. Information entered in the window was dumped to a raw text file and an Excel spreadsheet.

For each replicate, organisms were identified to species and mature individuals were sexed. Most of the zooplankton species were identified with reference to Pennak's taxonomic keys (Pennak 1989), but Wilson's key was also used for the identification of calanoid copepods (Wilson 1959). Chydorid zooplankton were rarely seen and were not identified to genus or species level. Sample splits were counted until a minimum of 200 individuals of the predominant species were recorded. All organisms in a given split were always counted. If 150 organisms were counted by the end of a split, a new split was not started. The lengths of 30 organisms of each species were measured, for use in biomass calculations, using a mouse cursor on the television image of the organism. The number of eggs carried by gravid females and the lengths of these individuals were recorded for use in fecundity calculations.

Historical zooplankton abundance data were obtained for 1949 and 1964 (Zyblut 1967), 1972 to 1984 (Crozier and Duncan 1984), 1985 to 1988, and 1990 to 1992 (raw data sheets, R.J. Crozier, B.C. Ministry of Environment, Lands and Parks).

For comparison of current zooplankton species with species observed in the past, archived 1949 samples were obtained from the Royal British Columbia Museum, Victoria, B.C. in 1994. A sub-sample of zooplankton was identified to species to see if there had been any changes in the species present since 1949. In addition, the species observed from 1992 to 1997 were compared with the list of species observed by Zyblut (1970) in the 1960's, during the period of high nutrient loading from the fertilizer plant upstream. Zooplankton observed in the 1980's were reported to genus by Crozier and Duncan (1984). Raw data sheets from this period were obtained to check the

species identifications made by the contractors who analyzed the samples (R.J. Crozier, B.C. Ministry of Environment, Lands and Parks).

Calculation of Macrozooplankton Production

Zooplankton production was calculated at each station along the lake for the summer season (April to October or early November) from 1992 to 1997. The raw data used were: species density (individuals·L⁻¹), species biomass (µg·L⁻¹, dry weight), the numbers of eggs per water volume (eggs·L⁻¹, calculated from the total number of eggs attached to gravid females in the sample, divided by the water volume represented by the sample), and water temperature. Water temperature was sampled on a different day from zooplankton during each round of sampling because it was more efficient to sample all stations on the lake for zooplankton on one day, and to do all the Hydrolab sampling on another day. Over the six year period, 65% of temperature samples were taken within 1 day of zooplankton sampling, and 91% of temperature samples were taken within 3 days of zooplankton sampling. The most extreme cases were one temperature sample that was done 9 days before the zooplankton, and another that was done 8 days after the zooplankton. The temperature used in production calculations was the average temperature in the top 40 m of the water column at a particular station on the date closest to the day of zooplankton sampling.

First I calculated the instantaneous rate of increase, r , during each time interval (between sampling trips) using the formula of Paloheimo (1974), where N is density, and t_1 and t_2 are the dates at the beginning and end of the interval respectively:

$$r = \left(\ln N_{t_2} - \ln N_{t_1} \right) \cdot (t_2 - t_1)^{-1} \quad (\text{units are days}^{-1}) \quad (1)$$

Next I calculated the development time, K , from Bělehrádek's (1935) equation where T is temperature (°C), and a , α and β are constants fitted to experimental egg development curves:

$$K = a \cdot (T - \alpha)^\beta \quad (\text{units are hours}) \quad (2)$$

I used the constants developed by Cooley et al. (1986) for *Daphnia retrocurva* as estimates for *Daphnia* spp. in Kootenay Lake, and the constants for *Diaphanosoma birgei* for *Diaphanosoma brachyurum* (Liéven) (Table 2). For *Leptodiaptomus ashlandi* and *Diacyclops bicuspidatus thomasi* I used the constants for calanoid and cyclopoid copepods, respectively.

Table 2. Curve parameters used in estimating egg development time, K, from Cooley et al. (1986).

Species or Group	Constants used in Bělehrádek's equation		
	a	α	β
<i>Daphnia retrocurva</i>	65,912	-6.1	-2.12
<i>Diaphanosoma birgei</i>	1,767	-1.9	-1.08
Calanoid copepods	38,474	-3.7	-2.00
Cyclopoid copepods	7,590	-3.4	-1.40

I then used K to calculate instantaneous birth rate, b, using the formula of Paloheimo (1974), (see Borgmann et al. (1984) and Cooley et al. (1986) for adaptations of this) where E is the number of eggs per water volume (eggs·L⁻¹), and N is density (individuals·L⁻¹):

$$b = \ln \left\{ \left[\left(E_{t_1} / N_{t_1} + E_{t_2} / N_{t_2} \right) / 2 \right] + 1 \right\} / (K / 24) \quad (\text{days}^{-1}) \quad (3)$$

The number of new individuals produced during each time interval, N_{new} , was calculated following formulae in Borgmann et al. (1984), adapted from Paloheimo (1974):

$$N_{\text{new}} = (b / r) \cdot N_{t_1} \cdot (e^r - 1) \quad (\text{individuals} \cdot \text{L}^{-1}) \quad (4)$$

which is equivalent to:

$$N_{\text{new}} = b / r \cdot (N_{t_2} - N_{t_1}) \quad (5)$$

If r was equal to 0 then N_{new} was calculated using the alternate formula:

$$N_{new} = b \cdot N_t \cdot (t_2 - t_1) \quad (6)$$

The average biomass of an individual of a species during a given interval was estimated from empirical net haul data as:

$$M_{mean} = (B_{t_1}/N_{t_1} + B_{t_2}/N_{t_2})/2 \quad (\mu\text{g individual}^{-1}) \quad (7)$$

where B_t is the total biomass of a species at time t , and N_t is the species density.

The production of new biomass during each time interval ($\mu\text{g L}^{-1}$) was:

$$P_{new} = N_{new} \cdot M_{mean} \quad (\mu\text{g L}^{-1}) \quad (8)$$

as in Borgmann et al. (1984).

The mean biomass of the species during the sampling interval ($\mu\text{g L}^{-1}$) was obtained from Cooley et al. (1986):

$$B_{mean} = [(N_{t_1} + N_{t_2})/2] \cdot M_{mean} \quad (\mu\text{g L}^{-1}) \quad (9)$$

The average biomass produced per day (seasonal average, $\mu\text{g L}^{-1} \text{ day}^{-1}$) was calculated as:

$$\bar{P}_{new} = (\sum_{t_0}^{t_n} B_{new}) / (t_n - t_0) \quad (10)$$

where t_0 is the first sample date of the season, and t_n is the final sample date (Cooley et al. 1986).

The average standing stock biomass during the season ($\mu\text{g L}^{-1}$) was (Cooley et al. 1986):

$$\bar{B}_{mean} = \left\{ \sum_{t_0}^{t_n} [B_{mean} \cdot (t_2 - t_1)] \right\} / (t_n - t_0) \quad (11)$$

Next I computed a daily P/B ratio using the average biomass produced per day and the average standing stock biomass during the season (Cooley et al. 1986):

$$P/B_{DailyAverage} = \bar{P}_{new} / \bar{B}_{mean} \quad (\text{day}^{-1}) \quad (12)$$

and the mean daily turnover time (days), which is the inverse of the daily average P/B.

Finally, I calculated the seasonal average P/B:

$$P/B_{SeasonalAverage} = \left(\sum_{t_0}^{t_n} P_{new} \right) / \bar{B}_{mean} \quad (13)$$

Assumptions and Potential Biases of Production Calculations

These calculations assume that the population had constant birth rate, constant death rate, and fixed development time within each time interval (Paloheimo 1974). It is assumed that population growth is approximately exponential, which in turn requires a stable age distribution if birth or death rates vary with the age of the organisms (Gabriel et al. 1987). Error will be introduced into estimates of b if the population structure is unstable. In addition the time interval between sampling relative to the duration of the egg stage is important. If these times are similar, Paloheimo's formula for b is the most accurate of the six formulae tested by Gabriel et al. (1987). Since the sampling interval of two weeks or one month was usually shorter than the calculated egg development times (Note: these were long compared with the times in Gabriel et al.'s (1987) lab experiments, done at 18 °C), the use of Paloheimo's formula was appropriate.

The use of water temperature averaged over the top 40 m may have resulted in a temperature estimate that was too low, if zooplankton stay within, for example, 20 m of the surface for most of the time. Vertically migrating zooplankters usually feed near the surface, but may gain increased fecundity by spending time in deeper, colder water, although this may lead to slower egg development times (McLaren 1963). Clarification of the temperature actually experienced by zooplankton was not possible since I did not have detailed data on zooplankton diel migration during each time interval, which was beyond the logistics and budget of this project. A low temperature estimate would cause overestimation of development time, K , and underestimation of instantaneous birth rate, b . This would in turn cause the estimates of N_{new} , B_{new} , \bar{B}_{new} , and the P/B ratios to be low. Since copepod nauplii were not identified to species, but it was of interest to consider the

production of *L. ashlandi* and *D. bicuspidatus thomasi* separately, nauplii numbers and biomass were omitted from production calculations. This contributed to an overestimate of b , since N_t would be lower than the true value, and consequent overestimation of N_{new} , B_{new} , \bar{B}_{new} , and the P/B ratios. Copepod production calculations also overestimate M_{mean} , since only larger individuals of copepod or adult size were used to calculate average individual biomass. Thus there was both an upward bias on B_{mean} , and the seasonal average, \bar{B}_{mean} , because of the overestimate of M_{mean} , and a downward bias because of the underestimate of N_t . The upward biases in B_{mean} and \bar{B}_{mean} would result in a downward bias in the P/B ratios, while the downward biases would cause an overestimate of the P/B ratios.

There was almost certainly some loss of eggs from females during field sampling because a Clarke-Bumpus net was used, which would cause more jarring of the zooplankton than a Schindler sampler. The Clarke-Bumpus net was chosen for its ability to sample larger volumes of water, at multiple depths and along a horizontal area, thus improving the density estimates, which were the first priority of the zooplankton sampling program. Further loss of eggs probably happened during preservation as zooplankton were washed out of the dolphin bucket, despite the use of sodium bicarbonate as an anaesthetic in the rinse water. There was definitely loss of eggs during sample splitting (loose eggs were often seen in the bottom of the counting dish). Therefore values of E_t used in calculations were low, which would have contributed to underestimates of b , N_{new} , B_{new} , \bar{B}_{new} , and the P/B ratios. This method also assumes that all eggs counted would have survived to hatching. However, any mortality of gravid females during an interval would also result in the mortality of her eggs prior to hatching (Threlkeld 1979), and would cause overestimates of E_t , b , N_{new} , B_{new} , \bar{B}_{new} , and the P/B ratios.

The biases mentioned above were likely similar between stations and between years, so they probably do not have much effect on the comparison of relative production values along the

phytoplankton productivity gradient in Kootenay Lake. However, if there is size selective predation on a zooplankton species, and if this predation differs along the length of the lake, there would be a differential bias in the production values calculated for the fertilized and unfertilized ends of the lake.

The egg ratio method of calculating zooplankton production assumes that the production of biomass equals the average weight observed in the population times the birth rate of new individuals, b . As I show below, this will only be true if the mortality rate of numbers (Z_{num}) equals the mortality rate of biomass (Z_{biom}). If predators selectively remove large individuals from the population then Z_{biom} will be greater than Z_{num} , and production of biomass will be underestimated.

Change in biomass over time is

$$\frac{dB}{dt} = \left(\frac{P}{B}\right)B - Z_{biom}B \quad (14)$$

where B is biomass, and P/B is production. Biomass can be defined as

$$B = Nw \quad (15)$$

where N equals numbers and w equals average individual weight. Therefore change in biomass is also:

$$\frac{dB}{dt} = \frac{wdN}{dt} + \frac{Nd w}{dt} \quad (16)$$

Combining these two definitions we get

$$\frac{dB}{dt} = \frac{wdN}{dt} + \frac{Nd w}{dt} = \left(\frac{P}{B}\right)B - Z_{biom}B \quad (17)$$

Since change in numbers over time is

$$\frac{dN}{dt} = bN - Z_{num}N = (b - Z_{num})N \quad (18)$$

we can substitute to get

$$w(b - Z_{num})N + \frac{Nd w}{dt} = \left(\frac{P}{B}\right)B - Z_{biom} B \quad (19)$$

then substitute B for wN to get

$$B(b - Z_{num}) + \frac{Nd w}{dt} = \left(\frac{P}{B}\right)B - Z_{biom} B \quad (20)$$

We then solve for P/B

$$\frac{P}{B} = \left(bB - Z_{num} B + N \frac{d w}{dt} + Z_{biom} B \right) / B \quad (21)$$

$$\frac{P}{B} = b - Z_{num} + \frac{N}{B} \frac{d w}{dt} + Z_{biom} \quad (22)$$

$$\frac{P}{B} = b - (Z_{num} - Z_{biom}) + \frac{d w}{w dt} \quad (23)$$

Therefore

$$\frac{P}{B} = b \quad (24)$$

only if $\frac{d w}{w dt}$ and $(Z_{num} - Z_{biom})$ equal 0, or if

$$Z_{num} - Z_{biom} = \frac{d w}{w dt}$$

Zooplankton size in the diet of *M. relicta* was not measured in this experiment (Smokorowski 1998), and it has been suggested that *M. relicta* in Kootenay Lake are not size selective in their consumption of macrozooplankton (pers. comm., Dr. David Lasenby Trent University, Peterborough, Ontario, Canada). However, in a laboratory experiment young *M. relicta* from Lake Tahoe were observed to prefer smaller macrozooplankton, and adults preferred larger size classes (Cooper and Goldman 1980). Likewise, juvenile *Neomysis mercedis* feed preferentially on smaller zooplankton, while adult *N. mercedis* select larger prey (Murtaugh

1981). Depending on the relative densities and feeding rates of different size classes of *M. relicta* the predation effect of the *M. relicta* population as a whole may alter the size distribution of macrozooplankton observed in net hauls. However, because of the lack of data on diet size selectivity of Kootenay Lake mysids I did not attempt to include mysid effects in a correction factor for bias in zooplankton production.

Kokanee do prey selectively on larger individual macrozooplankton (see Fig. 44 and Fig. 78). The average weight of copepods in fry stomachs was 1.5 to 2 times that observed in net haul samples. Fry contained cladocerans (mainly *Diaphanosoma*) 4 to 10 times the average weight seen in the lake. *Daphnia* spp. in fry stomachs averaged 1.2 to 2 times the average weight in net hauls.

I used kokanee diet data to estimate the potential bias that size selective predation by kokanee may have caused in the estimate of zooplankton production. Kokanee removed a very small proportion of the standing stock biomass of zooplankton, but removed relatively more of the standing stock of cladocerans, especially *Daphnia* spp. (see Table 19). Kokanee aged 1+ and older were evenly distributed along the lake (see Fig. 41) so any bias they may have caused would have occurred at all stations, and should not have obscured a comparison of zooplankton production along the lake. Kokanee fry were distributed unevenly for much of each year, so their higher abundance in the North Arm may have caused a downward bias in the estimate of *Daphnia* spp. Z_{biom} in the North Arm versus the South Arm.

I focused on kokanee fry, and calculated the potential bias in *Daphnia* spp. Z_{biom} that may have been caused at Stations 2 (fertilized, high fry density) and 6 (unfertilized, low fry density) in August 1995 by the combination of size selective predation and skewed kokanee fry distribution. Z_{num} was calculated as

$$Z_{\text{num}} = N_{\text{con}} / N. \quad (25)$$

where N_{con} is the numbers consumed per hectare, and N is *Daphnia* spp. density per hectare.

N_{con} was calculated as

$$N_{\text{con}} = B_{\text{con}}/B_{\text{indiv}} \quad (26)$$

where B_{con} is the *Daphnia* spp. biomass consumed by fry per hectare, and B_{indiv} is the average biomass of individual *Daphnia* in fry stomachs.

Macrozooplankton Production Enclosure Experiment

An enclosure experiment was conducted from July to September 1994 to obtain estimates of *Daphnia* and *Diaphanosoma* production in the absence of predation. Nine enclosures were placed near the boathouses at the Kaslo Marina in Kaslo Bay (between Stations 2 and 3) in the North Arm (Fig. 15). Three sets of three enclosures were stocked with natural zooplankton assemblages. The second and third sets of enclosures were installed and stocked about one and two weeks, respectively, after the first, to control for potential effects of seasonal and lunar changes. Each enclosure was cylindrical, with 1 m diameter and 4 m depth, and constructed of 200 μm mesh. This mesh size was chosen to keep the majority of macrozooplankton inside, and to exclude *M. relicta* and fish, yet allow phytoplankton to drift in to maintain food supplies for the zooplankton. Zooplankton from the main lake (between Stations 2 and 3) were collected with a Birge closing net with mouth diameter of 0.14 m, 100 μm net mesh and 35 μm mesh on the bucket, at a vertical haul speed of 1 m s^{-1} . Thirteen vertical hauls from 20 to 0 m were made to collect organisms from a volume equal to the volume of each enclosure. Zooplankton were held in a large plastic garbage can under the boat canopy until transfer to the enclosure. Water temperature was monitored to be sure that the transfer occurred without overheating. During collection of zooplankton for the second and third set of enclosures, three extra vertical hauls were made and the zooplankton were preserved in 70% ethanol, to provide an estimate of the zooplankton species present and the concentrations which were stocked.



Fig. 15. Layout of enclosures for zooplankton production experiment.

Each set of enclosures was run for at least four weeks, but growth of algae on the sides of the enclosures was apparent within two weeks of the start of each run, and could have affected the type of phytoplankton available to the zooplankton. The enclosures were sampled every third day, beginning on the third day after the enclosures were filled (not including the day of filling), using the same net as was used for stocking. One vertical haul was made from 3 to 0 m. The sample volume of one vertical haul represented 1.46 % of the enclosure volume. The zooplankton were anaesthetized and rinsed out of the net using an aqueous solution of 4% sodium bicarbonate (to help prevent them from releasing their eggs), and were preserved in 70% ethanol. Samples were analyzed using the same microscope system and counting protocol as for the routine lake zooplankton samples. Production rates, including the average daily P/B ratio and the mean daily turnover time, were calculated using the same method as described above for the regular lake zooplankton samples.

Macrozooplankton Biomass, Production and Consumption for Ecopath Model

In the Ecopath model macrozooplankton biomass was taken from Table 4, with proportions of copepods, cladocerans, and *Daphnia* spp. estimated from Fig. 30 (May-October proportions) and converted to t km^{-2} assuming all zooplankton were in the top 40 m of the lake. Production per unit biomass (P/B) values for 1994 were taken from Table 11, Table 12, and Table 13. Copepods were assumed to feed primarily on phytoplankton, but to also eat small amount of other copepods, cladocerans, *Daphnia* spp., and rotifers. Cladocerans ate mainly phytoplankton, but also small amounts of other cladocerans, rotifers, and *Daphnia* spp., since this group included *L. kindti*. *Daphnia* spp. were assumed to eat only phytoplankton. Consumption was estimated to be 7 times production, adapted from a study of Lake Turkana, Kenya (Kolding 1993).

Potential Phytoplankton Production

I estimated potential phytoplankton biomass production, and potential zooplankton grazing, to see if they were consistent with the hypothesis that zooplankton standing stock biomass was too low to control phytoplankton biomass. Phytoplankton biomass increased in the fertilized end of the lake during the first five years of the experiment. If there had been a top-down response by zooplankton then phytoplankton biomass would have been the same along the length of the lake, and zooplankton biomass would have increased, unless it in turn was cropped down by *M. relictus* and kokanee. The presence of a phytoplankton biomass gradient indicates that zooplankton were unable to increase enough to control phytoplankton biomass. Primary productivity was not measured throughout the fertilization experiment, so I used 170 g C m^{-2} , the annual average value obtained in Kootenay Lake in 1977 (Jasper et al. 1983). Chlorophyll *a* averaged approximately 1.5 mg m^{-3} in mid-July 1977, while chlorophyll *a* in July during the fertilization experiment averaged about 3 mg m^{-3} (Fig. 20). Jasper et al. (1983) found that primary production and chlorophyll *a* concentrations were well correlated ($r=0.79$), so the use of

this primary production value may result in a low estimate of production. However, I did not attempt to correct for this bias, since the use of a primary productivity value from a different period in the lake's history will already result in only a rough estimate of potential production. I multiplied primary productivity by 2 to get total dry weight biomass production (Wetzel 1983), and multiplied by 10 to get wet weight biomass production. I assumed that this areal production took place in the top 20 m of the lake. Jasper et al. (1983) sampled primary production in the euphotic zone which averaged approximately 20 m during the growing season that their experiments were done, and phytoplankton were sampled in the top 20 m in this experiment.

***M. relicta* Abundance and Water Flow Rates**

I examined the relationship between *M. relicta* abundance in Kootenay Lake, and water flow rates, to test whether interannual differences in flows may have affected the *M. relicta* population prior to and during fertilization. The Kootenay Lake Fertilization Response model suggested that *M. relicta* population dynamics are very sensitive to changes in mortality rate (Walters et al. 1991). Mortality was modelled as a fixed baseline monthly mortality, which included losses to predation, and export over the West Arm sill. If the volume of surface water passing over the sill increases (e.g., during the spring freshet), the number of *M. relicta* exported should also increase, provided that the water export occurs during night hours when *M. relicta* will be feeding in surface waters. During high flow years the export and mortality of *M. relicta* should increase. In addition, if spring peak flows are high (similar to a natural freshet) the mortality of *M. relicta* juveniles should be particularly high, since most juveniles are released from the brood pouch in early spring. Since *M. relicta* reproduce only once, and must survive to be about 2 years old to do so, losses to export could have a large impact on *M. relicta* population dynamics, and on the competition between *M. relicta* and kokanee for zooplankton. The removal of large numbers of *M. relicta* in spring could relieve competitive pressure on kokanee salmon for the remainder of the growing season, and benefits of

fertilization would be more likely to accrue to kokanee than to *M. relict*. When policy scenarios were tested with the Kootenay Lake Fertilization Response Model, the monthly *M. relict* mortalities were the same from year to year, so the modelled *M. relict* densities were not fit to the actual interannual flow variations during model testing (pers. comm., C.J. Walters, Fisheries Centre, University of British Columbia). Thus, the potential effects of high or low flow years on the outcome of the fertilization experiment were not explicitly considered prior to the experiment.

I plotted *M. relict* annual average density with the annual average flows from the Kootenai River and Duncan River to check for any general trends between *M. relict* density and flow. If flow is a factor in *M. relict* mortality, it should be most closely related to the rate that surface waters leave the lake near Balfour. I fit exponential curves to average annual *M. relict* density versus surface water turnover rates for different months of the year, and found that the period from May to August produced the strongest negative relationship with *M. relict* density.

I then fit a Beverton-Holt style recruitment model to the time series for annual average *M. relict* density (Beverton and Holt 1957). The model includes both density dependent and density independent mortality rates, where mortality related to intraspecific competition for resources is density dependent, but mortality related to environmental factors such as flow is density independent (Walters and Parma 1996). The model predicts *M. relict* density in the current year, N_{t+1} , as:

$$N_{t+1} = \frac{f N_t e^{(-m_{base} - m_{flow} W_{t+1})}}{1 + m_{cap} N_t (1 - e^{(-m_{base} - m_{flow} W_{t+1})})} \quad (27)$$

where f is fecundity, N_t is *M. relict* density in the previous year, m_{base} represents density independent baseline mortality (e.g., due to disease), m_{flow} represents mortality due to export out of the lake, W_{t+1} is the surface water turnover rate in the current year, and m_{cap} represents mortality due to intraspecific competition. Surface water turnover rate was calculated using Corra Linn Dam

discharge, since this is the first dam downstream of Kootenay Lake, and its discharge should most closely reflect outflow from the lake (flows from 1989 to 1997 was approximated as 10% of discharges from Brilliant Dam, which includes flow from Kootenay Lake, plus flow from Slocan Lake). Depth at the outflow sill was set at 5 m, and used to calculate the volume of water involved in turnover. The time *M. relicta* spends at the surface, and therefore vulnerable to export, was set at 6 hours per night. This was factored in to the surface water turnover rate so that the rate reflected turnover of water actually containing mysids. Fecundity was set at 18 eggs per capita. Female mysids in Kootenay Lake carry approximately 18 eggs (Smokorowski 1998), so the fecundity per capita should be approximately 9 eggs per capita of the mature year class. Mysids in Kootenay Lake have a two-year life cycle, so fecundity should be approximately 4 eggs per capita of the two year classes combined (historical data for mysid life history stages were insufficient for development of a recruitment model with separate juvenile and adult age classes). However, when fecundity values less than 18 were used in the model, m_{base} became negative (i.e., the baseline mortality rate was positive). The Excel Solver (Excel 97, Microsoft Corporation 1997) function was used to find values for m_{base} , m_{flow} , and m_{cap} that gave a “best fit” of the model density to the observed density time series (by minimizing the sum of squared differences between the observed and predicted densities).

M. relicta Consumption of Zooplankton

I calculated the proportion of zooplankton standing stock cropped per day by *M. relicta* along the length of the lake in 1992, 1993 and 1994. I used *M. relicta* density at deep stations along the lake in 1992 to 1994, *M. relicta* diet data analyzed by month and station (Kootenay Lake Fertilization Database, unpublished data), and standing stock biomasses of copepods, cladocerans, and *Daphnia* spp. to calculate consumption rates of different classes of zooplankton by *M. relicta*. Mysid consumption may be biased upward because *M. relicta* tends to be more

abundant at deep stations, and diet data I was able to obtain were for adult mysids and thus may be biased toward consumption of larger zooplankton.

M. relicta Biomass, Production and Consumption for Ecopath Model

I also calculated seasonal average biomass, production, and consumption values for *M. relicta* for use in an Ecopath model. Biomass was estimated from average mid-season lengths of juveniles, and mature mysids, which I converted to wet weight using regressions in Smokorowski (1998). I used the 1994 total annual average density for 1994 (Smokorowski 1998), (assuming juveniles made up 0.66 of the density, and mature individuals 0.33), and converted to t km^{-2} . *M. relicta* P/B was adapted from values for macrobenthos in Lake Victoria (Moreau et al. 1993), and consumption per unit biomass (Q/B) was estimated to be two times P/B, based on the value for prawns used by Aravindan (1993). Both age classes were assumed to eat macrozooplankton with a preference for *Daphnia* spp., and to eat rotifers (Smokorowski 1998).

Kokanee

Hydroacoustic Abundance and Distribution

Hydroacoustic surveys were conducted monthly in conjunction with kokanee trawls from 1992 to 1996, and in July and September of 1997. In September of each year an extended series of 18 transects was sampled to allow whole-lake abundance estimates. Surveys and data analyses were done by Ministry of Environment staff, and details of techniques used are presented in Ashley et al. (1997b). In summary, hydroacoustic surveys were conducted monthly on or about the new moon, in the limnetic habitat, at six stations in 1992, and at 7 stations in 1993 - 1997. Continuous recording of acoustic signals were made along radar navigated transects at a boat speed of 2 m sec^{-1} . A Simrad model EY200P (70 kHz) and a Biosonics model 105 (420 kHz) were used simultaneously. Transducers were mounted on the bottom of planars and towed alongside the boat at a depth of 1.5 m. Data were recorded on Sony Digital Audio Tape (DAT)

and echosounders were calibrated on site and the start of each survey session at a depth of 20 m using a standard -39.5dB copper calibration sphere. Simrad data were digitized, then analyzed using the Hydroacoustic Data Acquisition System (HADAS) program 3.98 (Lindem 1991). This program determines the number of targets per unit area by depth stratum, and estimates the fish size distribution using a statistical deconvolution procedure based on Craig and Forbes (1969). The procedure gave a bimodal acoustic size distribution which was used to divide the kokanee target strengths into two size classes, age 0+ fish, and age 1+ - 3+ fish. The size cut-off between fry and older fish was adjusted during the growing season to account for changed in size-at age. Size cut-offs were verified using size frequency distributions from the montly trawl surveys, where measured fork lengths were converted to acoustic target strengths using Love's (1977) equation. The data collected using the Biosonics 105 system were archived for later comparison with historical periods when data that were collected using only the Biosonics equipment.

North Arm Spawner Escapement, Size and Fecundity

Adult kokanee returning to spawn in the Meadow Creek spawning channel were observed from late August to late September, 1992 - 1997 (pers. comm., Mr. John Bell, B.C. Ministry of Environment, Lands and Parks, 333 Victoria St. Suite 401, Nelson, B.C., V1L 4K3, Canada). The channel was considered full when the theoretical capacity of 250,000 fish was reached. If there was a build-up of fish at the lower fence, the upper fence was opened to allow some fish to move above the channel through the settling basin and into John Creek or upper Meadow Creek. Once these fish had been counted out of the channel additional fish were allowed to enter the channel from downstream. The number of adults entering the spawning channel was counted at the lower fence, and visual shoreline counts were made of kokanee spawning in Meadow Creek between the channel and Kootenay Lake. A standardized visual estimate of the number of adults returning to the Lardeau

River was made by helicopter. Kokanee in Meadow Creek were sampled for length, sex ratio, fecundity and egg retention, and otoliths were taken for ageing.

South and West Arm Spawner Escapement

Spawners in the West Arm spawning channels (Kokanee Creek and Redfish Creek) were enumerated using methods similar to those for kokanee at the Meadow Creek channel. Numbers of kokanee spawners in other creeks in the West Arm, and creeks in the South Arm were estimated from visual counts from the bank.

Kokanee Abundance and Total Phosphorus Load

Fish yield and standing crop were positively related to total phosphorus (TP) concentration for north-temperate lakes (Hanson and Leggett 1982). Salmonid production was correlated with TP concentration in a global lake data set (Plante and Downing 1993). Lee and Jones (1991) extended the approach by showing a strong positive relationship between fish yield and phosphorus load.

I tested the relationship between the abundance of kokanee salmon returning to spawn and total phosphorus (TP) loads to Kootenay Lake prior to and during the fertilization experiment. Phosphorus loading and water inflow for the two major inflows to Kootenay Lake, the Kootenai River and the Duncan River, were obtained from Lekstrum et al. (1994) and Larkin (1998). These authors calculated TP loads from inflow water chemistry and river discharge data. A complete set of data for both inflows was available from 1960 to 1996.

Lardeau River kokanee spawner numbers were regressed against TP load to Kootenay Lake between 1964 and 1996. Data from this site were used because the Lardeau River was sampled over a greater time span than Meadow Creek, and during the period of very high nutrient loading during the 1960's. The phosphorus load values used were the mean of the four years of the lifetime of the kokanee which spawned in a given year, to reflect the average nutrient

conditions which may have affected a fish cohort's growth and survival. For example, the number of kokanee which spawned in 1996 was regressed against the average phosphorus load from 1993 to 1996. A regression of the relationship between kokanee spawner abundance and TP loading was calculated using kokanee data from years where the 4-year annual TP load was less than 500 t, and between 0 t and 1000 t. These values correspond to areal loads less than 1.25 and 2.13 gP/m²/yr, respectively. These cut-off points were chosen based on the predicted trophic state of Kootenay Lake over the four year period, according to theoretical loading limits (Vollenweider and Dillon 1974). I plotted phosphorus load to Kootenay Lake against areal water load, with loading limit lines adapted from Vollenweider and Dillon's Figure 3 (Fig. 16). Areal phosphorus loads in the range of 1.37 to 1.94 gP·m⁻²·yr⁻¹ (550 - 780 t) cover the range of the "dangerous" limit for eutrophication in Kootenay Lake. At or above this limit ungrazeable algal blooms, and depressed macrozooplankton abundance are likely, which would have negative effects on a planktivorous species such as kokanee. Regressions and Durbin-Watson tests for autocorrelation were done with SYSTAT Version 7.0 for Windows (1997) and test bounds tables in Neter et al. (1990).

Kokanee Abundance and *M. relicta* Density

I tested the relationship between the abundance of kokanee salmon returning to spawn and the density of *M. relicta*. Meadow Creek kokanee spawner numbers were regressed against *M. relicta* numbers. Meadow Creek data were used because this site had a greater overlap of years in which both kokanee and *M. relicta* were sampled than the Lardeau River. Summer average (May - October) *M. relicta* densities were obtained for 1972 to 1988, and 1990 to 1996 (Crozier and Duncan 1984; Richard J. Crozier, unpublished data, B.C. Ministry of Environment, Lands and Parks; Smokorowski et al. 1997).

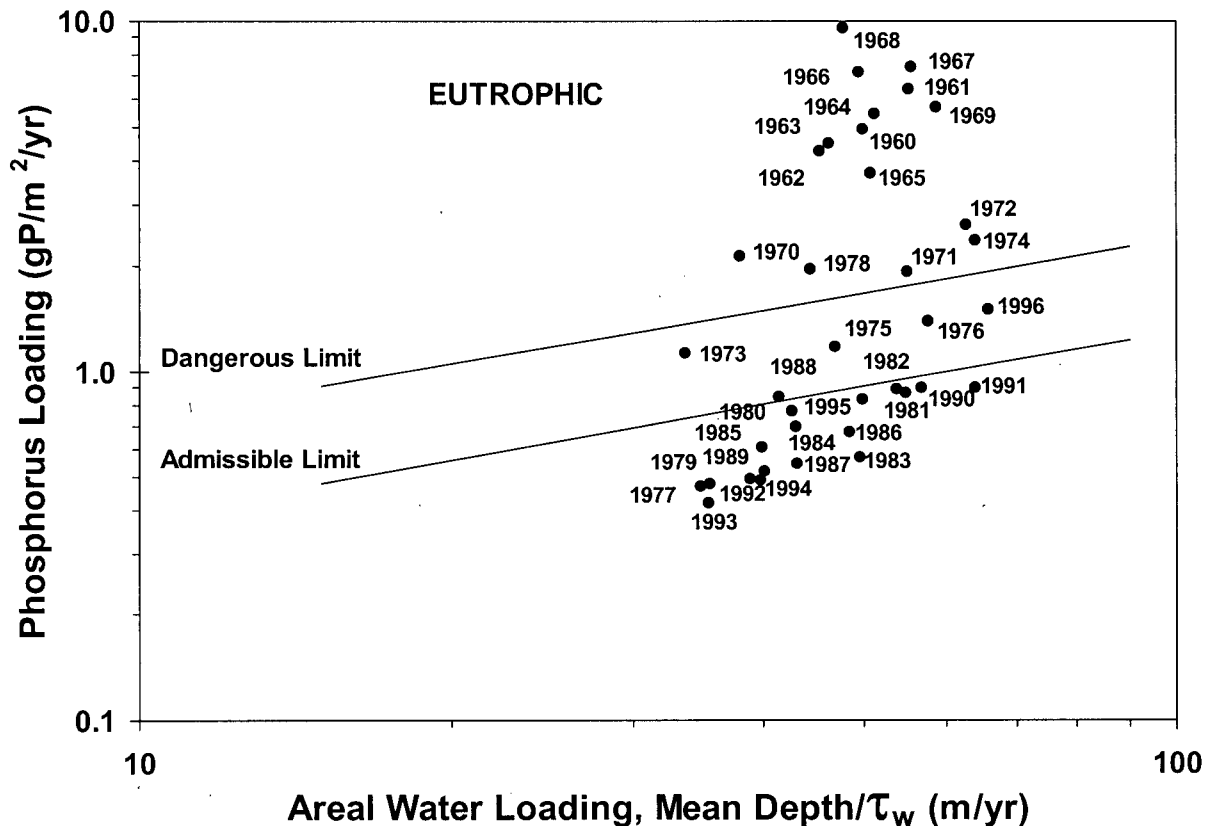


Fig. 16. Annual areal total phosphorus loading plotted against areal water loading, to predict trophic condition of Kootenay Lake from 1960 to 1996. τ_w is annual hydraulic retention time. Lines are upper and lower critical loading limits from (Vollenweider and Dillon 1974, Fig. 3). Note log scales for both variables.

North Arm (Meadow Creek) Fry Outmigration

Juvenile kokanee migrating out of the Meadow Creek spawning channel were monitored mid-April to mid-June (pers. comm., J. Bell, B.C. Ministry of Environment, Lands and Parks). Stop nets were used at the lower end of the channel to estimate numbers of kokanee fry emigrating from the channel. Sampling was conducted on about 35 nights each year, mainly from 2100 h to 0200 h. No daytime sampling was performed. Appropriate expansion factors were used to estimate total emigration from the spawning channel. Calculations accounted for the width of the channel compared with the width sub-sampled by the stop nets, the time available for migration relative to

the length of time the stop nets were in the water, and the variability of numbers of fry migrating at different times of the night.

Kokanee Growth

Kokanee were sampled monthly from May to October of 1992 - 1996, and in July and September of 1997. Trawling was done during the new moon, when the fish are found nearest to the surface and are least able to avoid the sampling gear. Trawls were done at Stations 1-6 in 1992, and at Stations 1-7 from 1993 onward. Trawling for kokanee began at dusk using a 4 m by 4 m beam trawl net attached to a bridle and single tow line cable. The net mesh is small enough to allow the capture of fry early in the season. This net was lost on August 16, 1993 during trawling at Station 3 (Mirror Lake) and was replaced with a 5 m by 5 m net with the same pattern of mesh sizes. The net was towed at a speed of 0.9 m s^{-1} . A depth sounder was used to determine efficient trawling depths. Up to six hauls were made at each station in order to capture at least fifty fry. These hauls were of varying duration, oblique or straight, and made at depths chosen to maximize the capture of fry for diet samples. At each station, twenty fry caught within two hours of dusk were preserved in 70% ethanol for diet analysis (ethanol was replaced within three days for long term storage). A further thirty fry were preserved temporarily on ice and their fresh lengths and weights measured. These fish were then frozen for subsequent otolith analysis and back-calculation of growth histories of surviving fish. Any older fish caught within two hours of dusk were also preserved for diet analysis, and those caught later were measured, weighed and had scales removed for ageing.

In September of each year the standard annual trawl series (dating back to 1984) was done to monitor annual variation in kokanee density, and length and weight-at-age. A different 5 m by 5 m net with wider mesh was used, since it had been used for fall trawls in previous years. Six 40-min hauls were made at each of Stations 2, 4, 5, 6 (and Station 7 from 1993 onward). Oblique hauls were made by towing the net for 8 min at each 5 m depth stratum, from 40 m to 20 m. The top of

the net was at 40 m at the start of the trawl, so the actual depth range sampled was 20 to 45 m. A sample area of 0.216 ha was covered by each haul. Trawls at Stations 1 and 3 were done as in other months, with the finer mesh 4 m by 4 m net (5 m by 5 m net from August 17, 1993 onward).

Kokanee Fry Size-at-Age Along Nutrient Gradient - Otolith Analysis

I analyzed kokanee fry size relative to daily age along the length of the lake by counting daily otolith rings in samples of fry from Stations 2 and 6. These results allowed a test of whether size differences in fry along the lake were due to different growth rates, or due to fry being different ages. Kokanee fry size in the South Arm was often larger than fry size in the North Arm for a particular month (Fig. 54). This may have been due to higher growth rates in the South Arm, or due to gradual movement of fry southward from the North Arm. Since most fry in Kootenay Lake emerge from Meadow Creek or the Lardeau River, then gradually disperse throughout the lake between April and September, I expected that on average fry in the South Arm would be older than fry in the North Arm. Thus fry in the South Arm could be larger than those in the North Arm because South Arm fry are older, and have had more days in the lake to grow, not because they have experienced higher growth rates.

Fish otolith microstructure is often used in aging fish, by counting annual or daily ring increments (Pannella 1971; Campana and Neilson 1985; Stevenson 1992). Kokanee fry produce daily rings on their otoliths which can be used to back-calculate days from a known mark (Paragamian et al. 1992). To compare growth rates of fry along the nutrient gradient I back-calculated the number of days that fry had been in the lake (days since emergence) at Stations 2 and 6 by counting the number of daily growth rings on sagittal otoliths. The use of the emergence ring as a starting point for counting daily rings makes the experiment like a tagging study. It is as though we marked fry on the day they entered the lake (therefore known emergence date), and then went out along the lake over the season and re-captured the marked fish to see how much

they had grown. However, an important difference between this method and a tagging study is that we have no way of knowing where an individual fish entered the lake, so we cannot distinguish a fry that emerged from a North Arm tributary and swam to the South Arm, from a fry that emerged from a South Arm tributary and stayed in the South Arm.

Both sagittal otoliths were obtained from each frozen fish used (see trawl methods above) by excising the top of the head, lifting out the brain, and removing the otoliths with dissection tweezers. A dissection microscope with incident light was used to aid in seeing the otoliths. Otoliths were immediately placed in pre-labelled micro-centrifuge tubes, without glycerine, or other staining agent. Because otoliths were not washed, they stuck easily to the side of the tube, so they were placed with the left and right otolith on the left and right side of the tube, respectively, for future reference. Both otoliths of up to the first 30 fry caught at each station in all months sampled from 1993 to 1996 were removed. Fry from 1992 were accidentally destroyed (thawed, spoiled, and mixed up in freezer bag) during transit from Kootenay Lake to Vancouver, so it was not possible to obtain otoliths from these fish. At the time of collection of kokanee in 1997 I did not anticipate using these data for my thesis, so these fish were not preserved after length and weight measurements were taken, and otoliths were not removed.

A random sub-sample of 10 fry was chosen from each of Stations 2 and 6, from September of 1993 to 1996, for a total of 79 otoliths (only 9 fry were caught at Station 6 in September, 1993). Otoliths were prepared for viewing as follows: A microscope slide was placed on a hot plate set at 60 °C, and an approximately 3 mm diameter piece of thermoplastic glue (CrystalBond, Aremco Products, Inc.) was melted on the slide (Stevenson 1992). The right sagittal otolith was removed from the microcentrifuge tube, placed on another slide with a drop of water and cleaned under a dissecting microscope. The cleaned otolith was placed on the glue droplet with its sulcus facing up, pushed down into the glue, then the slide was removed from the hotplate and cooled. The otolith

was ground down almost to the primordia, without removing any outer rings, by moving the slide in a circular motion over wet 600 grit sandpaper, then rinsed with water. The slide was again placed on the hotplate until the CrystalBond melted, then the otolith was flipped over, cooled, and ground down almost to the primordia on the distal side, and polished with wet lapping paper. The otolith was repeatedly examined under the dissecting scope during the grinding process to avoid grinding past the primordia, or removing any outer rings.

When all otoliths had been prepared the identification label on each slide was covered with an opaque sticker, then the slides were shuffled and given a code number. The otoliths were read in the coded sequence, then reshuffled and read a second time. Otolith rings were counted using a compound microscope at 1000 X magnification, using immersion oil to stain the rings. Immersion oil was also used between the condenser lens and the bottom of the slide, to increase the numerical aperture, and in turn the resolution (Campana 1992). A black and white video camera was connected to one eyepiece, and fed an image to a computer screen, via an AVER 2000 Pro video card. The AVER window's contrast was set to maximum to increase grey-scale contrast and enhance ring identification; all other settings were left on default. The identification of the emergence ring and daily rings were checked by comparison with photos of *O. nerka* otoliths in Marshall and Parker (1982), and West and Larkin (1987), and of chinook (*O. tshawytscha*) in Zhang et al. (1995). Since many previous studies involving *O. nerka* otolith daily rings used hatchery reared fry, while my study used wild fry, reference was made to Zhang et al. (1995) for differences in structure between hatchery-reared and wild salmon. Emergent fry from Meadow Creek were collected on three dates in the spring of 1996, and the size and appearance of otoliths at this life stage were examined to determine the likely minimum diameter of otoliths within the emergence ring. Daily rings were counted from the emergence ring outward, on the computer screen, by clicking each ring with the mouse. Data were downloaded to a text file, and included the total

number of rings counted, the ring widths, and comments on magnification, and ring quality.

Generally rings were counted along a dorsal-posterior radius. However, if rings were easier to see along different radii at different distances from the emergence ring the counting path was adjusted by moving laterally along a given ring and counted along several radii. After the first two readings, otoliths were read a third time (coded and re-shuffled) if the first two readings differed by more than 5%. In general the second readings were higher than the first set, probably due increased reader experience at identifying rings and at moving along a given ring to be able to count rings in a clearer section of the otolith.

Lengths and back-calculated ages (ring counts) of fry at Station 2 and 6 were compared for September of 1993 to 1996. Length, and ring count distributions of fry at each station in each year were tested for normality with a Kolmogorov-Smirnov goodness of fit procedure (Zar 1984). The distributions of length, and of ring count for each pair of stations were tested for equality of variance, then the appropriate t-test was used to test for differences in mean length and ring count (Excel 97, Microsoft Corporation 1997).

Kokanee Diet

Stomach samples were analyzed for zooplankton counts and biomass by species (weights estimated from published empirical length-weight regressions, (McCauley 1984), mysid counts and biomass (weights estimated from empirical length-weight regression, D.C. Lasenby, unpublished data), and counts of other organisms such as terrestrial insects. Samples were examined with the same apparatus as the macrozooplankton samples. Zooplankton were identified to species where possible, and were otherwise identified as either cladocerans or copepods. For small fry the entire stomach contents were analyzed; for larger fish one quarter of the petri dish was counted so that at least two hundred organisms were recorded. In either case, up to thirty organisms of each zooplankton species were measured. Mysids were usually fragmented so total length was calculated

from regressions relating total length to length of the antennal scale, carapace, exopod or endopod (L.C. Thompson, unpublished data).

It was necessary to know the weight of each fish, to be able to calculate how much food it had eaten, relative to its own size. Since the fish were preserved in ethanol or formalin, their fresh weights could not be obtained. Therefore, their weights were predicted from length-weight regressions. For each month-station combination a length-weight regression was calculated from the fresh lengths and weights of fish caught at the same time as the diet fish. Preservation in formalin caused the fish to shrink slightly in length, so lengths were corrected before calculating weight. The correction factor used was obtained from a shrinkage experiment done on Kootenay Lake kokanee in 1992 (L.C. Thompson, unpublished data). Preservation in ethanol did not cause a consistent change in fish length, so the lengths of fish preserved in ethanol were not corrected.

The consumption of each fish was calculated as the biomass of zooplankton present in the gut at dusk, as a percentage of the fish's own biomass. This was calculated from the wet weight biomass of zooplankton eaten by a fish, divided by the wet weight biomass of the fish, multiplied by 100. This method assumes the fish have only one major feeding period per day, at dusk. The validity of this assumption was tested as part of the Ecopath model balancing (p. 197).

Kokanee diet analyses focused mainly on the diet of the fry. The growth of fry in their first summer in the lake is thought to be critical for their survival through their first winter. For most month-station combinations, stomachs were analyzed for 10 fish. In some cases less than 10 fry were caught at a station, so fewer fish were examined. Following the analysis of the 1994 data for all months, we decided to focus on the August and September samples from 1992, 1993 and 1995. Where available, 10 fry from each station were analyzed. For 1993, a smaller number of fish were also analyzed for other months, as a check that the seasonal pattern of zooplankton consumption was consistent from year to year.

Prior to the current experiment, kokanee fry samples were collected near the present Station 3 (near Kaslo), in July and September 1975, and July 1985. Ten fry from each of the samples were analyzed using the same methods as above. This allowed a comparison of fish diet before and during the fertilization experiment.

Kokanee Biomass, Production and Consumption for Ecopath Model

For the Ecopath model kokanee were placed in three groups, fry, 1+, and 2+ and 3+ kokanee combined (because of the difficulty of separating older kokanee age classes in the hydroacoustic data, and the infrequent catches of older kokanee in trawls). Biomass of each group was estimated from 1994 hydroacoustic data (Fig. 41) and the frequency and individual weight of each age group in trawls (Fig. 42). Production was estimated using the method of Kline (1998) for production of salmon fry in Price William Sound, which assumes linear growth and mortality over short time periods.

$$\frac{P}{B} = \frac{\Delta B + (\Delta N \bar{W})}{\bar{B}} \quad (28)$$

where $\Delta N = N_1 - N_2$, the change in number of individuals, $\bar{W} = (W_1 + W_2) / 2$, mean weight of an individual during the time interval, $B = N \bar{W}$, biomass, $\Delta B = B_2 - B_1$, the change in biomass over the time interval, and $\bar{B} = (B_1 + B_2) / 2$, mean biomass. Numbers were estimated from spring and fall trawl data, and weights were obtained from trawl data. Consumption was estimated from kokanee diet data, where consumption was expressed as the weight of stomach contents as a proportion of total fish weight, multiplied by 180 days of feeding (see previous section). It was expected that kokanee consumption estimated in this way would be low because this method doesn't account for food eaten at other times of day, nor for differences in diet composition at different feeding times. Kokanee fry were assumed to eat macrozooplankton, with a preference for *Daphnia* spp., and to eat

a small amount of juvenile *M. relicta*. Older kokanee ate the same food types as fry, with the addition of adult mysids.

Kokanee Vertical Migration

Hydroacoustic transects were made at Stations 1 and 4, over a period of 12 days, from 21 July to 2 August 1994. A staircase design was used where sampling alternated between the two stations to control for possible progressive change in environment or behaviour during the sampling period (e.g., water cooling or heating, lunar effects on behaviour). Data were collected for three consecutive days at Station 4, then three days at Station 1, and again for three days each at Station 4 and Station 1, to control for the effects of the lunar cycle and weather on fish behaviour. Transects were made back and forth across the lake for 1.5 h on either side of dawn and dusk; a total of 72 h of target strength and depth data were collected.

Hydroacoustic data were collected using a dual beam echosounder (BioSonics Model 105 @ 420 kHz, 6 degree beam angle) and recorded on Digital Audio Tape (DAT). The transducer was mounted on a fin and towed from a 140 m cable at a depth of 40 m so that upward-looking data could be collected (Enzenhofer and Hume 1992). Upward-looking stationary transducers have been used to examine fish movement and size (Thorne 1980; Stables and Thomas 1992; Nost and Langeland 1998). I have not been able to find any references to towable, inverted systems such as that developed by (Enzenhofer and Hume 1992), and I have not been able to find any studies prior to the one I describe here that have made use of a towed, upward looking sounder for examination of fish behaviour. This technique allows a clear “view” of fish targets near the surface, unlike downward-looking methods. The transducer cannot receive signals from targets less than 1 m away, and the cone of sound is very narrow near the transducer, so placing the transducer well below the fish allows the collection of data on their vertical positions near the surface. A dual beam sounder was used to allow the calculation of fish target strength. Since fish target strength is related to

fish size (Love 1977), the length of fish targets can be calculated. Fish age can then be predicted from length-frequency distributions observed in trawl catches. Dual-beam sounding and data analysis were necessary to allow the separation of fry from older kokanee age classes, since older kokanee may not migrate to deeper water during the day. The major drawback of the dual beam method is that only targets that the echosounding data analysis program can distinguish as individual fish will be kept in the data set. Targets that do not meet the criteria (e.g., sound echo wave width too wide compared with height) are probably from more than one fish, and will be discarded. Fish in schools cannot be distinguished as individual targets, so any schools of fish will be “invisible” when doing dual beam sounding. As fish begin to form schools at dawn they can no longer be observed by dual beam sampling.

The echosounder was operated at a ping rate of 2 pings \cdot s⁻¹, a pulse width of 0.4 ms, and gain of 0 dB. The echosounder was set for use in freshwater (speed of sound = 1457 m \cdot s⁻¹), with a total variable gain (TVG) of 40 log R.

Incident light intensities were monitored at 1 m above the water surface (on the boat) using a LiCor lightmeter (Lambda Instruments LI-185 Quantum/Radiometer) at 10 minute intervals. The vision of juvenile salmonids is sensitive to ultraviolet light (Beaudet et al. 1993) and young salmonids may feed more effectively at dusk and dawn, when the proportion of ultraviolet light is greatest (Novales-Flamarique et al. 1992). To correct for possible differences in ultraviolet light absorbance at the two stations, we collected triplicate 50 ml water samples each dawn, and filtered them through a 0.45 μ m Sartorius 11103 cellulose acetate filter. Later the samples were analyzed for ultraviolet absorbance at 310 nm using an LKB Biochrom Ultrospec II 4050 UV/Visible spectrophotometer. These absorbances can be converted into UV-B₃₁₀ downwelling attenuation coefficients (K_{d310}) to predict the depth of penetration of ultraviolet light (Scully and Lean 1994) at

the two stations. This may help in explaining any differences in time spent feeding at the two stations that is not attributable to differences in zooplankton and/or fish abundance.

Secchi depth was measured during daylight, either before or after echosounding was done. Vertical profiles for temperature and light were done at 1-metre intervals to check for differences between stations that might affect the timing and duration of vertical migration.

Data were analyzed with echosignal processing hardware (ESP Model 281 Dual-Beam Processor, BioSonics, Inc., Seattle, Washington) and software (ESP_v30, BioSonics, Inc., Seattle, Washington). On playback the noise threshold was set to 0.12 V. The 1/2 amplitude pulse width was 0.4 – 0.6 ms, 1/4 amplitude pulse width was 0.4 – 0.72 ms, and the 1/8 amplitude pulse width was 0.4 – 0.8 ms. I designed an algorithm to identify targets of sizes that could be kokanee, and to group multiple “hits” of the same fish into single observations (Table 3).

I used length frequency distribution software (MIX, Release 2.3, January 1988, Ichthus Data Systems) to divide the targets into two size classes, fry and older kokanee. It was not possible to separate the older age classes because the difference in length was insufficient to form clear frequency peaks. For subsequent analyses the cut-off between fry and older kokanee was set at –55 dB, and the minimum target strength for a target to be a fish was set at –70 dB (smaller targets were probably *M. relicta*).

I then calculated the average depth of the two age groups of kokanee, averaged over 5-minute intervals, for dawn and dusk sampling days. Time-depth plots were compared for the two stations to see if there were differences in time spent near the surface (and presumably feeding) that could be related to differences in zooplankton abundance or production.

Table 3. Components of echosignal processing algorithm used to identify individual kokanee targets from vertical migration study.

Criterion	Value
Fish tracking maximum ping gap	3 pings
Fish tracking window	2.0 m
Fish tracking range	1.0 – 50.0 m
Fish filter reference range	10.0 m
Fish filter beam pattern threshold	- 20.0 dB
Fish filter equation	A + B + C
A	- 2.0 m <= average slope <= 2.0 m
B	1 <= absolute echoes in fish <= 10
C	- 90.0 dB <= average target strength <= - 15.0 dB

Gerrard Rainbow Trout

Escapement and Size

Visual counts of Gerrard rainbow trout spawners have been made each spring from 1957 to 1997, in April and May, at the spawning ground in the Lardeau River near Gerrard. Annual peak counts are recorded, and total escapement is estimated to be three times the peak count (pers. comm., Les Fleck, B.C. Ministry of Environment, Lands and Parks, Nelson, B.C.). Samples of fish were trapped over the period from 1982 to 1992. Fish weight and length were measured, and fish were examined for fecundity. Additional size data were obtained from fishing derby records from 1982 to 1996, maintained at the Birch Grove Campground, Balfour, B.C. (pers. comm., Marilyn and Walter Erikson, RR#3, Nelson, B.C.).

Trout Diet

Historical trout diet data were available for Kootenay Lake rainbow trout (Clemens 1951; Andrusak and Parkinson 1984; Parkinson et al. 1989; Bell 1990). Additional trout stomach samples were collected from anglers by marina operators from 1988-1992, and from 1993-1994, by B.C. Ministry of Environment, Lands and Parks staff (pers. comm., J. Bell, B.C. Ministry of Environment, Lands and Parks). The location and date of capture, species, length, weight, sex and maturity of fish were recorded by the anglers on waterproof data sheets. After the stomach was removed from a fish it was frozen for subsequent analysis at the Balfour Fish and Wildlife field station. The type and number of prey items were noted, and the fork lengths of prey fish were measured if the fish were not too digested to measure.

Trout Biomass, Production, and Consumption for Ecopath Model

Rainbow trout biomass was calculated from a population model that assumed trout start from a maximum of 60,000 eggs (spawning channel capacity) and that 10,000 trout recruit to the fishery at age 3 (Walters et al 1991). Trout were assumed to live to a maximum of age 9, to have a natural mortality of 0.8 at age 0+, and 0.05 in subsequent years. Fishing mortality starts at 0.05 when fish are age 4, and increases to 0.6 by age 9 (Andrusak 1981). The total weight of Gerrard rainbow trout in the main lake was calculated in t, then converted to t km^{-2} . Trout P/B was estimated as 0.4, a common value for predatory fish such as Nile perch (Moreau et al. 1993). Trout were considered to eat all ages of kokanee, as well as smaller amount of adult and juvenile mysids, and a very small proportion of terrestrial insects, modeled as an import to the system. Trout consumption was estimated from empirical diet data (see Fig. 80 and Fig. 81) as the number of kokanee eaten per day per trout, times the average weight of kokanee, times the number of days in the interval, divided by average trout weight (6 kg, from Birchgrove derby data).

Bull trout calculations were done in the same way, except that bull trout numbers were estimated to be 2 times that of rainbow trout, and bull trout average weight was 4 kg, based on Birchgrove derby records.

Ecopath Model Check on Calculated Biomass, Production, Diet and Consumption

I balanced an Ecopath model (Version 4.0 alpha) of the Kootenay lake pelagic food web in the growing season of 1994 (May-October). For several organisms I had data on stomach contents, and on growth, but no direct data on the total amount of food consumed. The Ecopath model was used to check that the values I calculated for biomass, production, diet composition, and consumption for use in my food web analysis of the fertilization experiment were reasonable. Ecopath software solves simultaneous linear equations to balance the biomass and energy flows within a food web over an arbitrary time period (Christensen and Pauly 1993). The procedure assumes that the system being modeled is at equilibrium. However, since the Kootenay Lake system was currently undergoing a large-scale manipulation it did not fit this requirement. Thus, the model was used only as a check on values I calculated for use in my analysis of the food web patterns along the lake.

Wherever possible I input empirically derived values into the Ecopath model, but if the model was unbalanced this was an indication that the empirical values were inaccurate. For example, kokanee consumption derived from evening stomach contents alone probably does not give an accurate picture of the total amount of food consumed per day. Also, diet composition samples taken at only one time of day, as is the case for kokanee (because they are very difficult to catch in daylight trawls) may be biased toward prey types that are available only part of the day. Kokanee may feed more on *M. relicta* at dawn than at night. This would not be reflected in our samples, but might appear as an imbalance in an Ecopath model.

I used the Ecopath output to calculate the proportion of biomass mortality (Z) of each prey type that was caused by each predator type,

$$Z_{prey_i} = \frac{Q_{of\ Prey_i\ by\ Predator\ j}}{B_{prey_i}} = \frac{B_{predator\ j} \left(\frac{Q_{predator\ j\ on\ Prey_i}}{B_{predator\ j}} \right)}{B_{prey_i}} \quad (29)$$

where Q is consumption, and B is biomass. These partitioned Z values were summed to give the ratio of biomass mortality to standing stock biomass for a growing season, for comparison with each prey's seasonal P/B ratio.

CHAPTER 4: RESULTS

Water Chemistry

Time Series Data

Whole-lake total phosphorus concentrations showed measurable increase by 1995, and increased more dramatically in 1996 and 1997 (Fig. 17 a; pre-treatment data from B.C. Ministry of Environment Environmental Management (EMS) database). In contrast, total dissolved phosphorus and dissolved ortho-phosphate increased in 1995 and 1996, then decreased in 1997. The natural total phosphorus load from the Kootenai River was lower than average from 1992 to 1994, but was high in 1996 and 1997 (approximately twice the average from 1980 to 1991) when flows were very high (Larkin 1998). The total phosphorus load from the Duncan River did not show any clear trends from 1992 to 1996.

Nitrogen concentrations in Kootenay Lake did not change markedly during nutrient additions, relative to the pre-fertilization period (Fig. 17 b; pre-treatment data from B.C. Ministry of Environment EMS database). Total Kjeldahl nitrogen and ammonia concentrations were similar to levels seen since the mid-1980's. The concentration of dissolved nitrate + nitrite has shown a gradual increase since 1977, which continued during the fertilization period.

Total nitrogen (TN) was measured in 1992 and 1993 only. In these years the TN:TP ratio averaged 38:1, with a range of 10:1 - 70:1, which should have been sufficient to encourage the growth of algae in grazeable size classes, as opposed to cyanobacteria.

Gradient Data

Total dissolved phosphorus (TDP) concentrations in Kootenay Lake were generally less than $0.005 \text{ mg}\cdot\text{L}^{-1}$ at all stations from 1992 to 1994 (Fig. 18). Concentrations were slightly

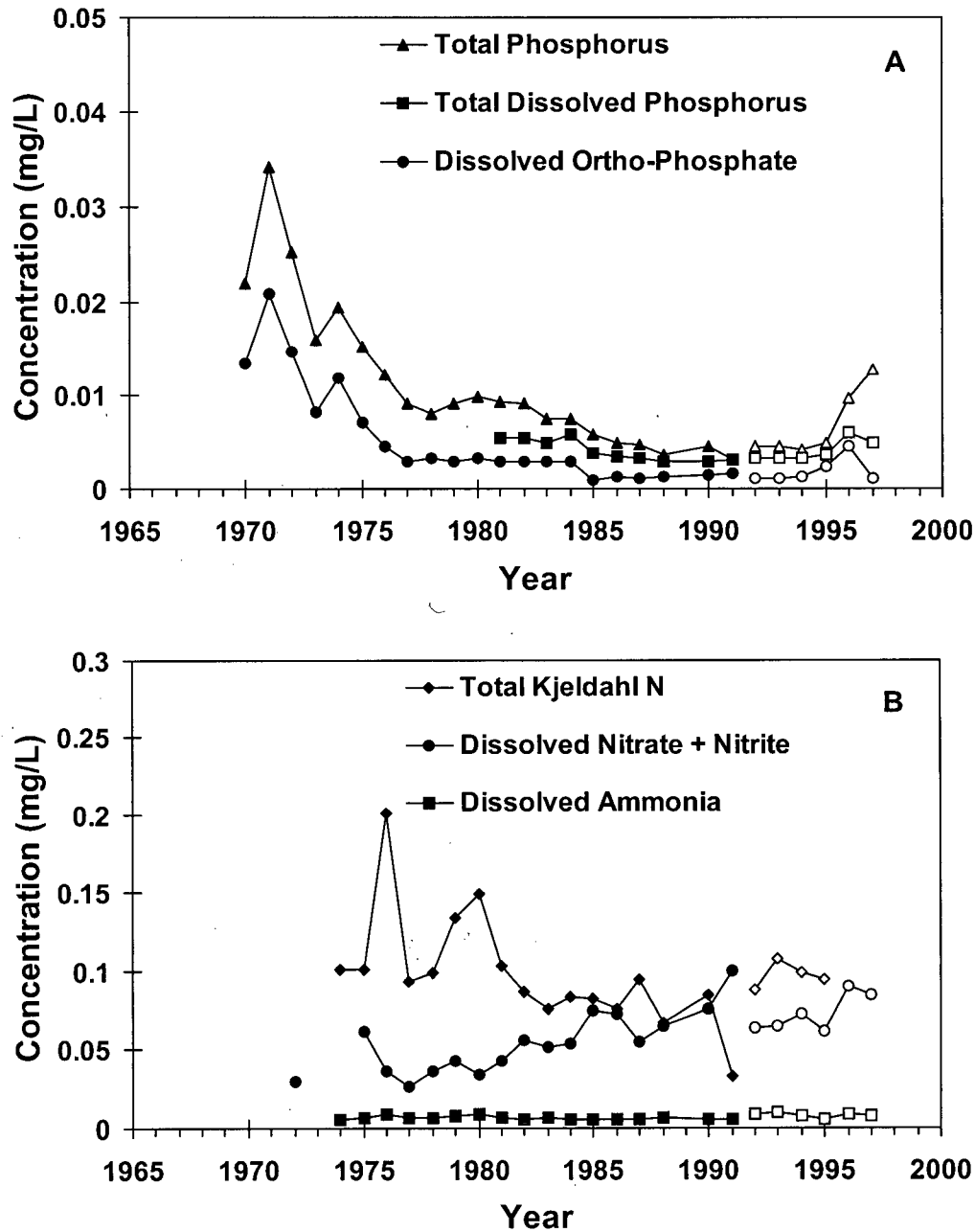


Fig. 17. Growing season average phosphorus (A) and nitrogen (B) concentrations in Kootenay Lake before and during experimental fertilization. Black symbols show data prior to fertilizer additions (mid-lake station 0200034, near Crawford Bay, and in approximately the same location as Station 5 in the current fertilization experiment), white symbols show data during fertilization (whole-lake average of Stations 1-6 in 1992, Stations 1-7 in 1993 to 1997). Total Kjeldahl nitrogen was not analyzed in 1996 and 1997.

higher in 1995, but there were no trends along the length of the lake. However, in 1996 there was a trend toward higher TDP concentrations in the South Arm (unfertilized) of the lake from April to July. This trend disappeared from August onward. In 1997 the same trend was seen, but TDP concentrations were lower than in 1996. The 1996 and 1997 concentration gradients, when loadings from the Kootenai River (South Arm) were high, are consistent with along-lake mixing rates of the magnitude estimated during AEA modeling and experimental design studies.

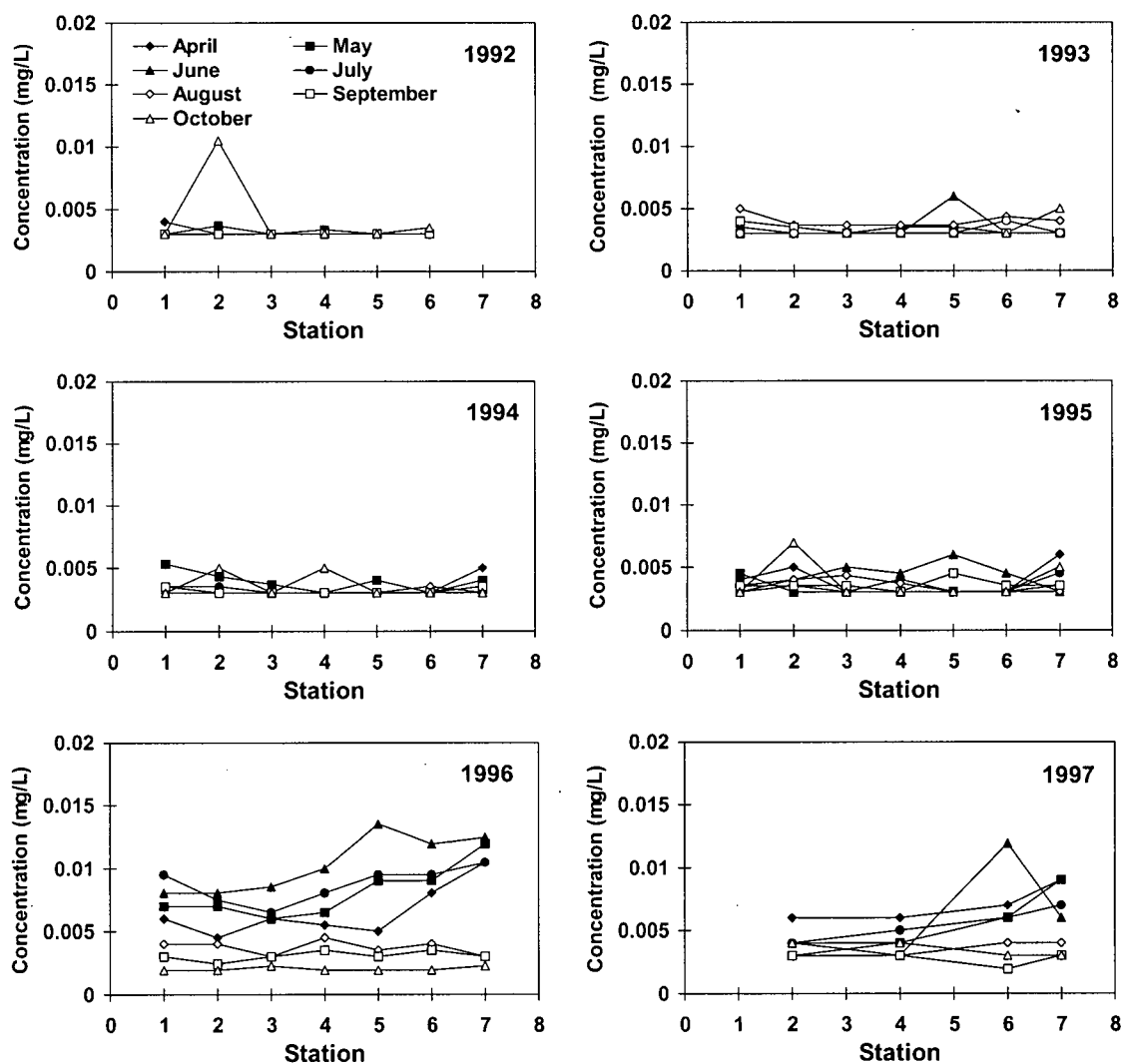


Fig. 18. Monthly average total dissolved phosphorus concentrations along the length of Kootenay Lake from 1992 to 1997.

Abundance

Chlorophyll *a*

The growing season chlorophyll *a* concentration at Station 5 averaged 2.4 mgm^{-3} from 1992 to 1996, and was higher than in the eight years (1983-1991) preceding the fertilization experiment, when concentrations averaged 1.8 mgm^{-3} (Fig. 19; pre-treatment data from B.C. Ministry of Environment EMS database). From 1992 to 1997 growing season whole- lake average chlorophyll *a* concentrations were slightly higher than at Station 5, and averaged 2.7 mgm^{-3} .

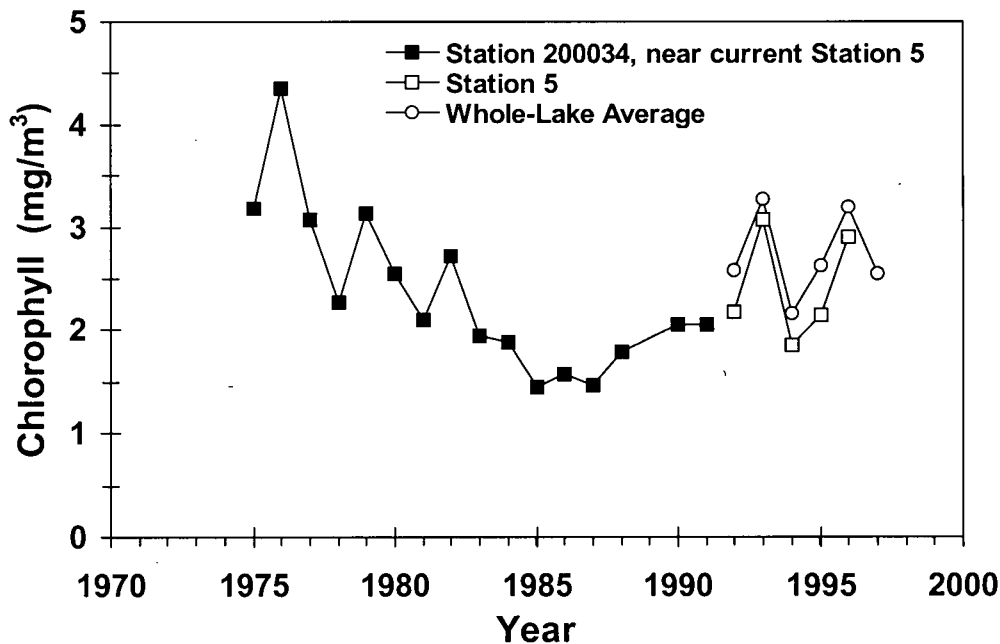


Fig. 19. Growing season average chlorophyll *a* concentrations in Kootenay Lake before and during experimental fertilization. Black symbols show data prior to fertilizer additions, white symbols show data during fertilization (circles are whole-lake average of Stations 1-6 in 1992, Stations 1-7 in 1993 to 1996, and Stations 2, 4, 6, and 7 in 1997).

Within season chlorophyll *a* concentrations tended to be higher in the fertilized end of the lake during the phytoplankton bloom periods of June and July-August (Fig. 20). At other

times of the year concentrations were similar throughout the lake. In 1996 and 1997 there appeared to be effects of high inflows from the Kootenai River. The differences along the lake were more accentuated in April - June, 1996, and in June, 1997. Despite the high total phosphorus inputs from the Kootenai River (Larkin 1998), chlorophyll *a* values in the south Arm were depressed. Turbidity levels were also higher in the South Arm during these periods. (Fig. 21).

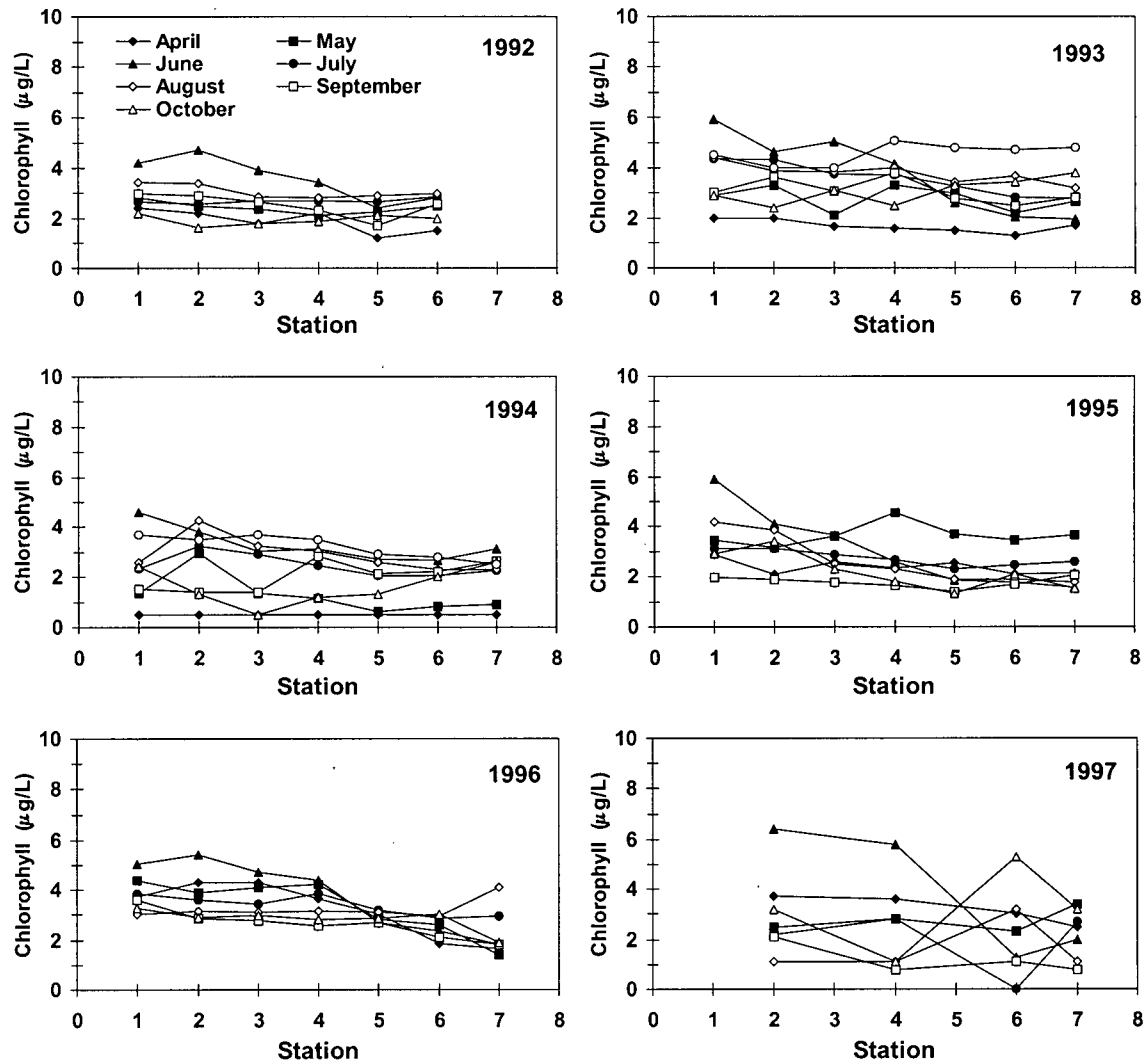


Fig. 20. Monthly average chlorophyll *a* concentrations along the length of Kootenay Lake from 1992 to 1997.

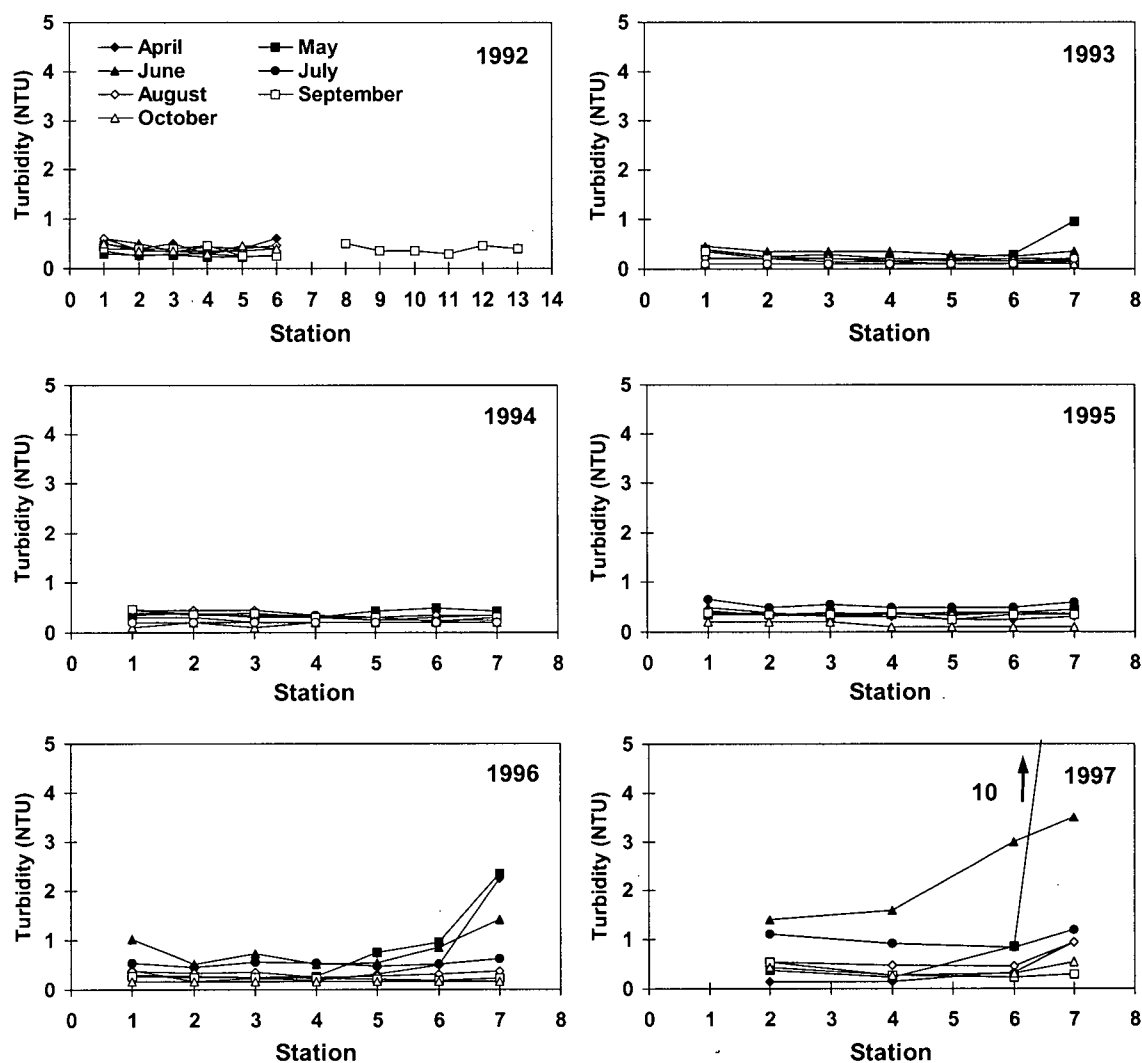


Fig. 21. Monthly average turbidity values along the length of Kootenay Lake from 1992 to 1997.

Annual average Secchi depth transparencies show a pattern of increase in the 1970's and early 1980's, then a decline during fertilization. Secchi depths generally became deeper from 1970 to 1984, increasing from about 4 m to 8 m (Fig. 22). There was no trend along the lake in the annual data during this period. From 1992 to 1997 Secchi depths became shallower, declining from about 7 m to 4 m (Station 7 was not sampled in 1992, and Stations 3 and 5 were dropped from the sampling program in 1997). During this period the Secchi depth was about 1 m shallower at Station 7 than at the other 2 stations, which were closer to the fertilization site.

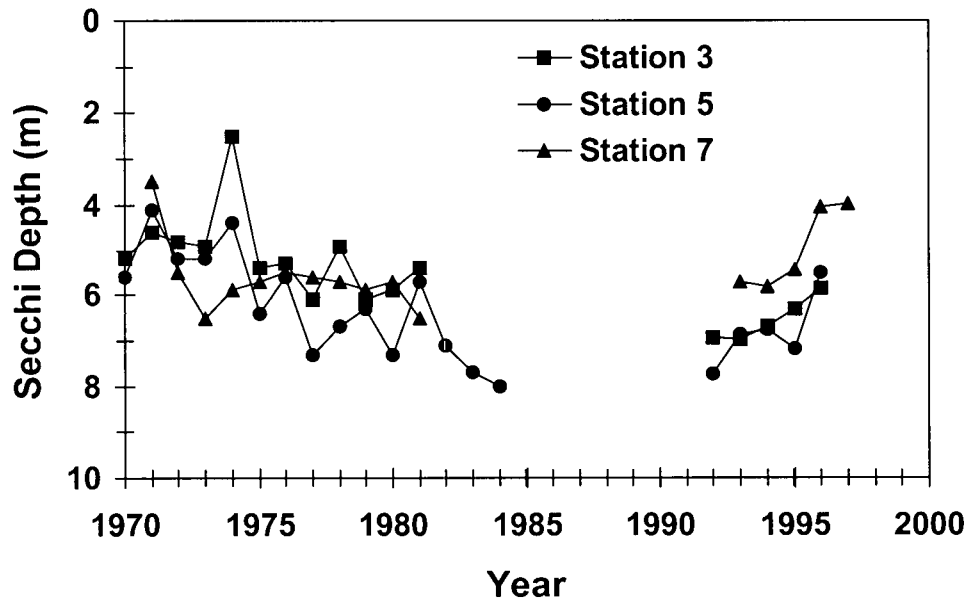


Fig. 22. Annual average Secchi depth in Kootenay Lake at Stations 3, 5, and 7, from 1970 to 1997. At Station 7 in 1970 and 1971, and at Station 5 in 1970, two values or less were used to calculate the means. From 1992 onward values from April to October were used to calculate the means. Data from 1970 to 1984 are from Crozier and Duncan (1985).

Monthly Secchi depths along the lake for 1992 to 1997 show that the greatest transparencies likely occur in winter, since the April and October Secchi depths were the deepest observed in all years (Fig. 23). Secchi depths were shallower from May to August, then began to deepen in September. In 1992 there was a trend toward deeper Secchi depths in the South Arm in most months, but in 1993 Secchi depths were similar at the ends of the lake, and deeper in the middle. In 1994 Secchi depths were similar along the lake in most months, with the exception of April, when the Secchi reading at Station 7 was much shallower than in the rest of the lake. The patterns in 1995, 1996, and 1997 were similar to 1993, with shallow Secchi readings at the ends of the lake, and deeper readings in the middle.

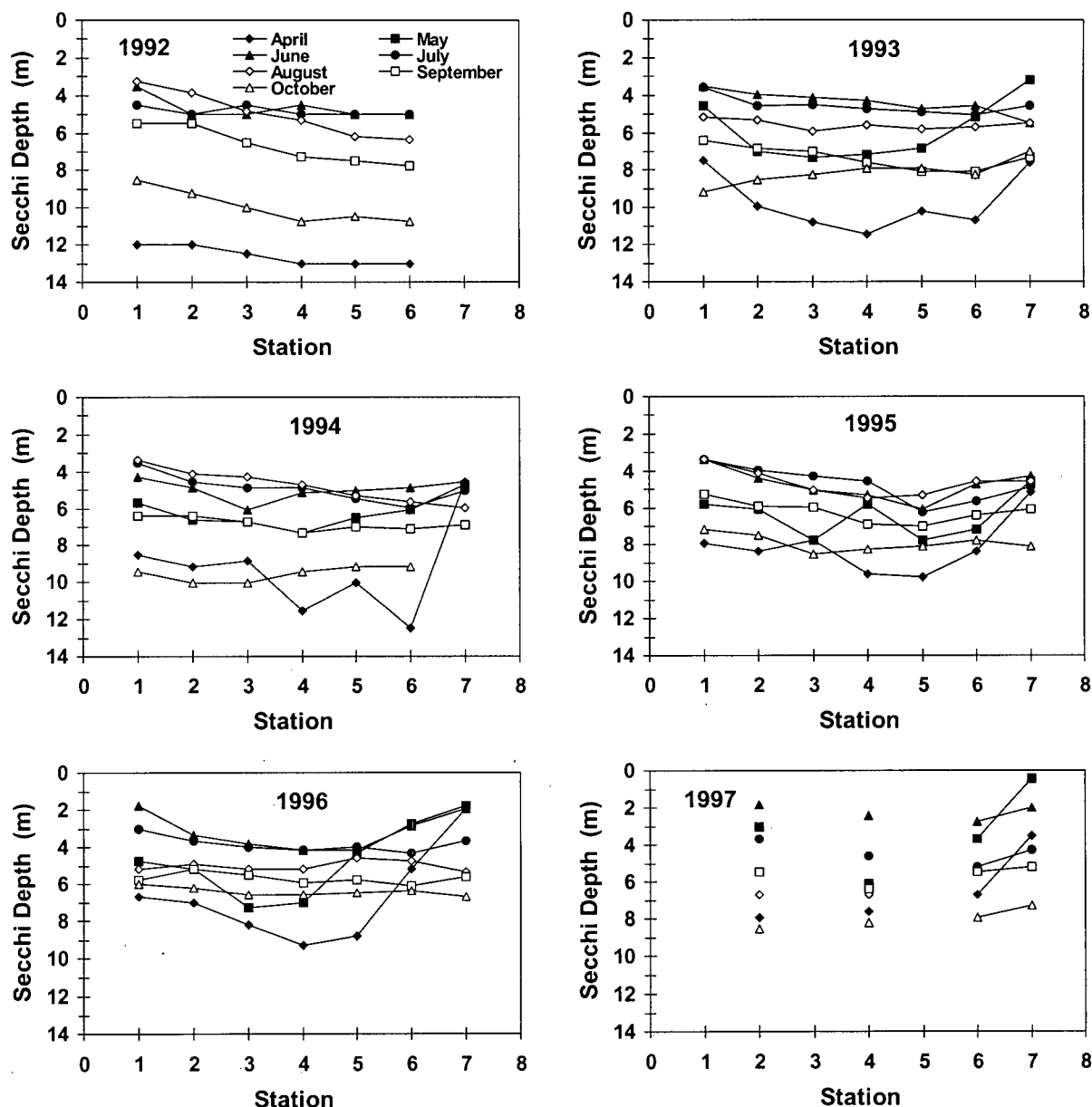


Fig. 23. Monthly average Secchi depth values along the length of Kootenay Lake from 1992 to 1997.

Phytoplankton Biomass

Phytoplankton biomass in Kootenay Lake increased during the first five years of fertilization (Yang et al. 1995; Yang et al. 1996a; Rae et al. 1997; Yang et al. 1997). Growing season average biomass was higher in the fertilized end of the lake, although the entire lake showed higher biomass from year to year (Fig. 24; electronic data were unavailable, so I hand-

entered phytoplankton size-class data from 1992 to 1997 for Stations 2 and 6 to produce the figure). However, in 1997 algal biomass declined throughout the lake. Biomass of smaller, grazeable algae (nanoplankton, 2-22 μm ; (Ross and Munawar 1981; Pick et al. 1998) was higher in the fertilized end of the lake from 1992 to 1996 (Fig. 24). In 1997 there was no difference in grazeable algal biomass along the length of the lake, and the grazeable algal biomass was the lowest observed during the fertilization experiment.

In 1992 and 1993 the difference in total algal abundance between the North and South Arms was most apparent during the spring bloom, while during summer stratification the two ends of the lake had similar algal abundance (Yang et al. 1996b). In the North Arm the 1992 and 1993 spring diatom assemblages were dominated by *Synedra delicatissima* W. Smith, and *Asterionella formosa* Hassal, respectively, both of which are usually found under mesotrophic conditions. Yang et al. (1996b) stated that the North Arm had a higher abundance of diatoms in 1993 than in 1992, but no difference was seen between years in the South Arm, and concluded that the nutrient additions had enhanced diatoms.

Microzooplankton (Rotifers)

Composition

In this study the following rotifer genera and species were commonly observed: *Kellicottia*, *K. cochlearis*, and *Polyarthra*. Rotifers which were moderately common and abundant were: *Asplanchna*, *Chromogaster*, *Keratella hiemalis*, and *Trichocerca*. The following genera were seen only rarely and in low abundance: *Gastropus*, *Lecane*, *Notommata*, *Ploesoma*, and *Synchaeta*. In comparison, from 1972 - 1984 Asplanchnidae, *Kellicottia* sp., and *Keratella* sp. were observed (rotifers were identified to family or genus level only). From 1985-1992 Asplanchnidae, *Asplanchna* sp., *Filinia* sp., *Gastropus* sp., *Kellicottia* sp., *Kellicottia longispina*,

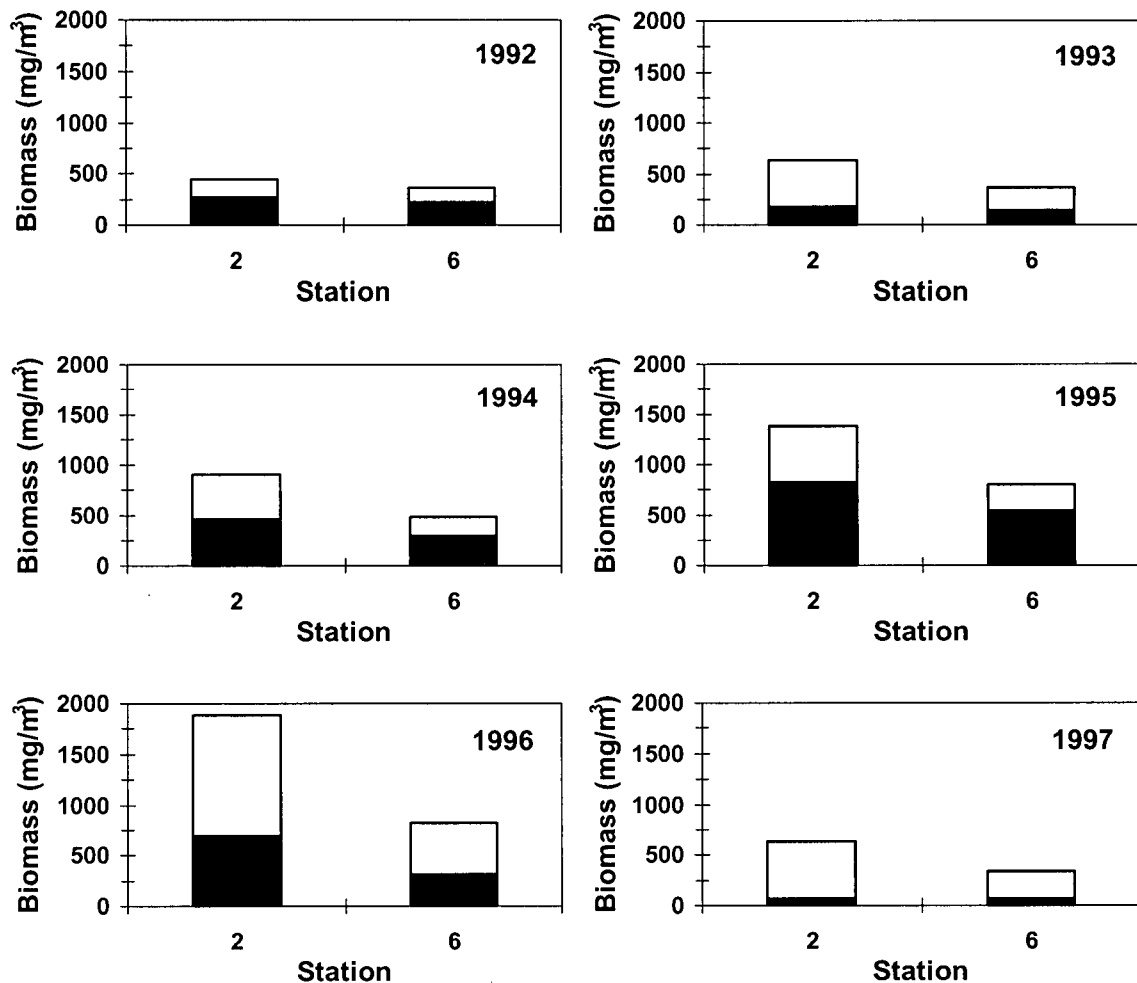


Fig. 24. Growing season average phytoplankton biomass at Station 2 (fertilized North Arm) and Station 6 (unfertilized South Arm) from 1992 to 1997. Black bars are grazeable algae (nanoplankton, 2-22 µm); white bars are ungrazeable algae (< 2 µm, and > 22 µm). Data adapted from (Pick et al. 1994; Rae et al. 1994; Yang et al. 1995; Yang et al. 1996a; Yang et al. 1997; Pick et al. 1998).

Keratella sp., *Keratella cochlearis*, *Keratella quadrata*, *Polyarthra* sp., and *Testudinella* sp. were noted (data from raw data sheets).

Rotifer Density and Biomass

Rotifer data presented are from this study only, since the historical zooplankton collection was done with a 150 µm mesh net (Crozier and Duncan 1984), too large to sample rotifers accurately. Growing season average densities and biomasses were similar from 1994 to

1996 (Fig. 25). Densities ranged from 156 to 172 individuals·L⁻¹, and biomasses (wet weight) ranged from 22 to 35 mg·m⁻³. Rotifer densities were about six times higher than macrozooplankton densities (Fig. 25 and Fig. 27), and comprised 88%, 90%, and 89% of the total zooplankton density in 1994, 1995, and 1996, respectively (total zooplankton = rotifers + macrozooplankton). However, macrozooplankton growing season average biomass was ten to twenty times higher than rotifer biomass in all years, even though macrozooplankton averages were calculated including data from spring and fall months, when standing stocks were lower than in summer (Table 4). On average rotifers made up only 4% to 8% of the total zooplankton biomass.

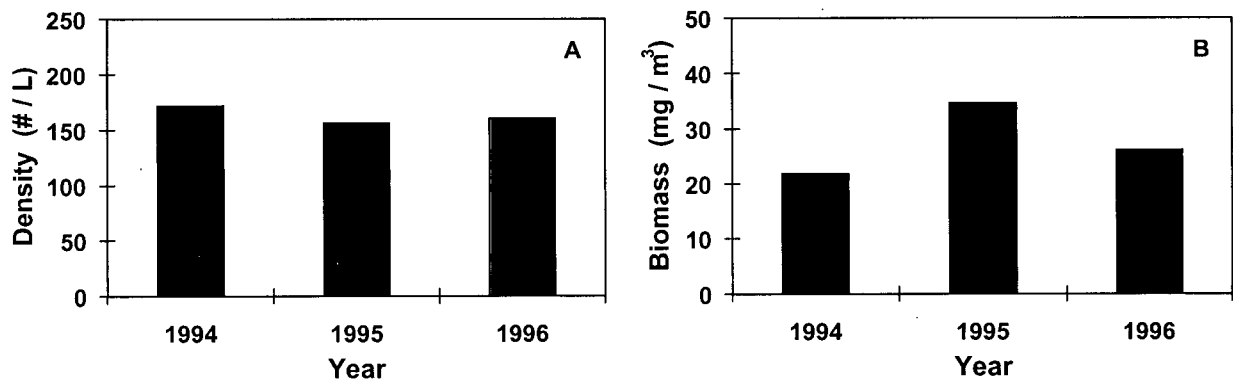


Fig. 25. Rotifer growing season average density (A) and biomass (wet weight) (B) in Kootenay Lake from 1994 - 1996. Values are the average of stations 2, 4, and 6, sampled on 4 dates across the season from June to September.

Temporal and Spatial Patterns During Experiment

There was no consistent trend in rotifer density or biomass along the lake in 1994, 1995, or 1996 (Fig. 26.) In 1994 and 1996 the highest densities and biomasses occurred in August. In 1995 the highest densities were seen in July, while biomasses were more variable than in other years. Although annual average density and biomass were lower in 1996 than in 1995, the highest monthly values of the three years were seen in August 1996. Phytoplankton biomass in

Table 4. Rotifer average biomass (June - September; Stations 2, 4, and 6; wet weight), and macrozooplankton growing season average wet weight biomass (April - October, converted from dry weight assuming wet weight = 10 X dry weight). Macrozooplankton values are the average for 6 stations in 1996, and 7 stations in subsequent years.

Year	Rotifer Biomass (mgm ⁻³)	Macrozooplankton Biomass (mgm ⁻³)	% Rotifers
1992	---	481	---
1993	---	444	---
1994	22	475	4
1995	35	378	8
1996	26	407	6
1997	---	424	---

1996 was the highest observed during the fertilization experiment, but the increases over 1995 were in the form of large, less grazeable algae.

Macrozooplankton

Species Composition

From 1992 to 1997 two calanoid copepod species were observed, *Leptodiaptomus ashlandi* (Marsh), and *Epischura nevadensis* Lillj.. One cyclopoid copepod species was identified, *Diacyclops bicuspidatus thomasi* (Forbes). Seven species of cladoceran zooplankton were commonly observed from 1992 to 1997: *Daphnia galeata mendotae* Birge, *Daphnia schoedleri* Sars, *Diaphanosoma brachyurum* (Liéven), *Eubosmina longispina* (Leydig), *Scapholeberis mucronata* (O.F.M.), *Leptodora kindti* (Focke) and *Ceriodaphnia* sp. Chydorid zooplankton were seen very rarely, and were not identified to genus level. In 1997 one

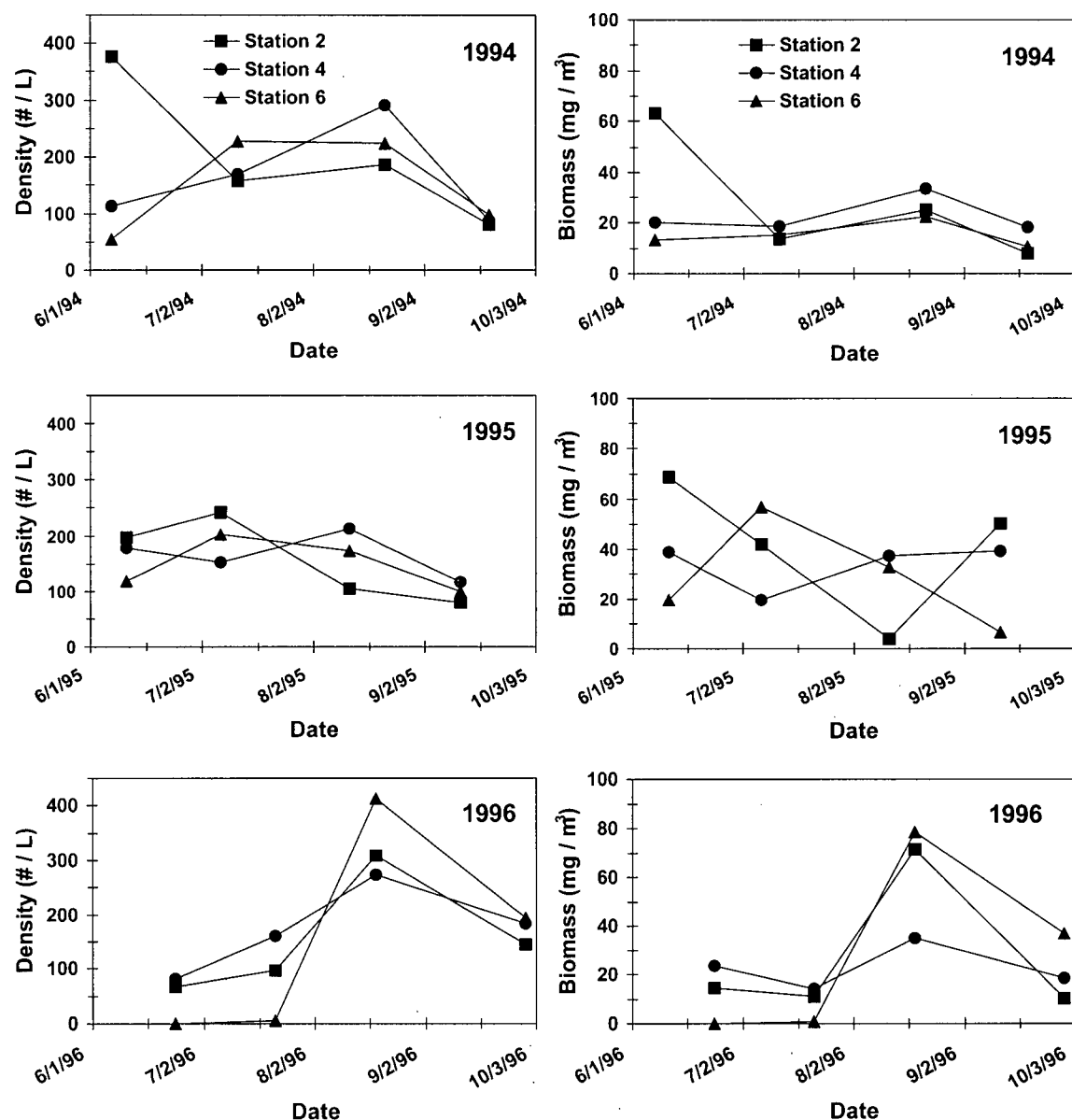


Fig. 26. Rotifer density and biomass (wet weight) at three stations along the lake productivity gradient in 1994, 1995, and 1996.

individual of *Polyphemus pediculus* (L.) was observed in a sample from Station 7 (Redman Point) collected on June 20, 1997.

Historical Macrozooplankton Species Observations

Zyblut (1970) compared the macrozooplankton species present in Kootenay Lake in 1949 and 1964. He found that all the copepod species seen in 1949 were also seen in 1964, but were more abundant in 1964, during the period of cultural eutrophication. He observed *Epischura*

nevadensis Lilljeborg, and also identified *Diaptomus kenai* M.S. Wilson, which has not been seen during the fertilization experiment. Both these species were rare in the mid-1960's, and *E. nevadensis* was also rare from 1992 to 1997. Adult *D. kenai* are very large in comparison with *E. nevadensis* and *L. ashlandi*, so it is highly unlikely that *D. kenai* individuals were present but misidentified in samples taken during the fertilization experiment. Zyblut also saw *Diaptomus ashlandi* Marsh (now called *Leptodiaptomus ashlandi* (Marsh)), and *Cyclops bicuspidatus thomasi* S.A. Forbes (now called *Diacyclops bicuspidatus thomasi* (Forbes)) which were the most abundant forms of copepods in the mid-1960's. These two species have been consistently present and abundant from 1992 to 1997.

From 1972 to 1984 the copepod species observed were identified as *Diaptomus ashlandi* and *Cyclops bicuspidatus* (Crozier and Duncan 1984). *Epischura nevadensis* Lilljeborg and *Diaptomus kenai* M.S. Wilson were not reported. From 1985 to 1992 (raw data sheets) copepods were not consistently identified to species, and were variously recorded as: *Cyclops* sp., *Cyclops bicuspidatus*, *Cyclops bicuspidatus thomasi*, *Cyclops scutifer*, *Cyclops varicans*, *Diaptomus* sp., *Diaptomus ashlandi*, *Diaptomus franciscanus*, and *Diaptomus tyrelli*. However, the identification of *Cyclops varicans* was noted as being in error on some data sheets, and a letter accompanying the sheets states that these were actually *Cyclops bicuspidatus* copepodites. Also, counts, and presumably, identifications, were done by a variety of people which may have lead to the range of species reported being wider than seen before or after this period. Due to the inconsistencies in these data it is unclear whether the copepod species currently observed in Kootenay Lake have changed since the period immediately before fertilization.

The same species of cladocerans were seen in 1949 and 1964, and all species except *D. galeata mendotae* and *Bosmina coregoni* were more abundant in 1964, during the period of eutrophication (Zyblut 1970). The zooplankton samples collected in 1949 (and borrowed from

the Royal B.C. Museum in 1994) contained the same two species of *Daphnia* as have been seen from 1992 to 1997. This suggests that there has not been a shift in *Daphnia* species as a result of the introduction of *M. relicta*, the increased nutrient load in the 1960's, or the current nutrient addition experiment. Zyblut (1970) identified only one species of *Daphnia* in samples collected from 1964 to 1966, *Daphnia galeata mendotae* Birge. However, *D. galeata mendotae* and *D. schoedleri* look very similar under low magnification (i.e., 80 X), so it is possible that both species were actually present in Zyblut's samples. Physical samples from Zyblut's collection have not been located (inquiries were made to the B.C. Ministry of Environment, Nelson, B.C., and to the Royal B.C. Museum, and the Balfour Fish and Wildlife Station on Kootenay Lake was thoroughly searched). Samples from this period probably no longer exist, so it has not been possible to compare the species identifications made in 1964 with identifications made in the current study. Zyblut frequently observed *Diaphanosoma leuchtenbergianum* Fischer; this species has not been seen in the current study, but *Diaphanosoma brachyurum* (Liéven) has been common. Zyblut identified *Bosmina coregoni* Baird, which was rare, while *Eubosmina longispina* (Leydig) has been common from 1992-1997. Other cladoceran species seen rarely by Zyblut were *Scapholebris kingi* Sars, *Leptodora kindtii*, and *Ceriodaphnia* sp. The current study has noted a different species of *Scapholeberis*, *S. mucronata* (O.F.M.), as well as *Leptodora kindti* (Focke) and *Ceriodaphnia* sp. These species have also been rare from 1992 to 1997. Zyblut did not mention chydorid zooplankton or *Polyphemus pediculus* (L.), which have been seen very rarely from 1992-1997.

From 1985 to 1984 cladocerans were not reported to species, but the genera observed were *Daphnia* sp., *Diaphanosoma* sp., *Bosmina* sp., and *Ceriodaphnia* sp. (Crozier and Duncan 1984). From 1985 to 1992 (raw data sheets) cladocerans, like copepods, were not consistently identified to species, and were variously reported as: *Diaphanosoma* sp., *Diaphanosoma*

brachyurum, *Bosmina* sp., *Bosmina longirostris*, *Ceriodaphnia* sp., *Daphnia* sp., and *Daphnia rosea*. As in the case of the copepod data, due to the inconsistency of these analyses, and the lack of physical samples to check the identifications, it is uncertain whether the cladoceran species currently observed in Kootenay Lake have changed since the period immediately before fertilization.

Density and Biomass Time Series

Historically, the annual mean abundance of zooplankton has ranged from 5.6 individuals L^{-1} in 1990, to a high of 27.1 individuals L^{-1} in 1985 (Fig. 27). In 1949 and 1964 the averages were relatively low, at 7.5 and 11.1 individuals L^{-1} , respectively (Zyblut 1967). From 1992 to 1997 the mean abundance ranged between 17.4 and 22.8 individuals L^{-1} . The six-year average was 19.5 individuals L^{-1} , higher than the long term average abundance of 15.5 individuals L^{-1} . In the late 1980's the length of the season sampled changed as a result of funding cuts. From 1985 to 1987 sampling was done from February or March until November. In 1988 sampling began in April and ran until November. In 1989 no sampling was done. In 1990 samples were collected in March, April, July, and August. Sampling was only done in May and July of 1991, and in June and July of 1992 (the old sampling program was still in operation, doing vertical haul sampling, during the first few months of the fertilization experiment). *Daphnia* were rarely seen during this period, and usually did not appear until August or later, although they were found in May and June 1986. Some *Daphnia* were seen in the August sampling done in 1990, and the 1990 average is probably still a reasonable estimate of zooplankton abundance since it should have encompassed the summer abundance peak. However, no *Daphnia* or *Diaphanosoma* were seen in any of the 1991 samples, nor in the 1992 samples taken by the old sampling program. The 1992 "average" from the old sampling program is not shown in Fig. 27, but was 18.55 individuals L^{-1} (copepods = 18.38 individuals L^{-1} ,

cladocerans = 0.172 individuals·L⁻¹), similar to the average obtained by the new sampling program. The 1991 and 1992 averages from the old sampling program likely underestimate the density of cladocerans, particularly *Daphnia*, since sampling did not continue through the summer peak. However, the decline and increase of zooplankton immediately prior to the beginning of fertilization are probably reasonably well tracked by the old sampling program.

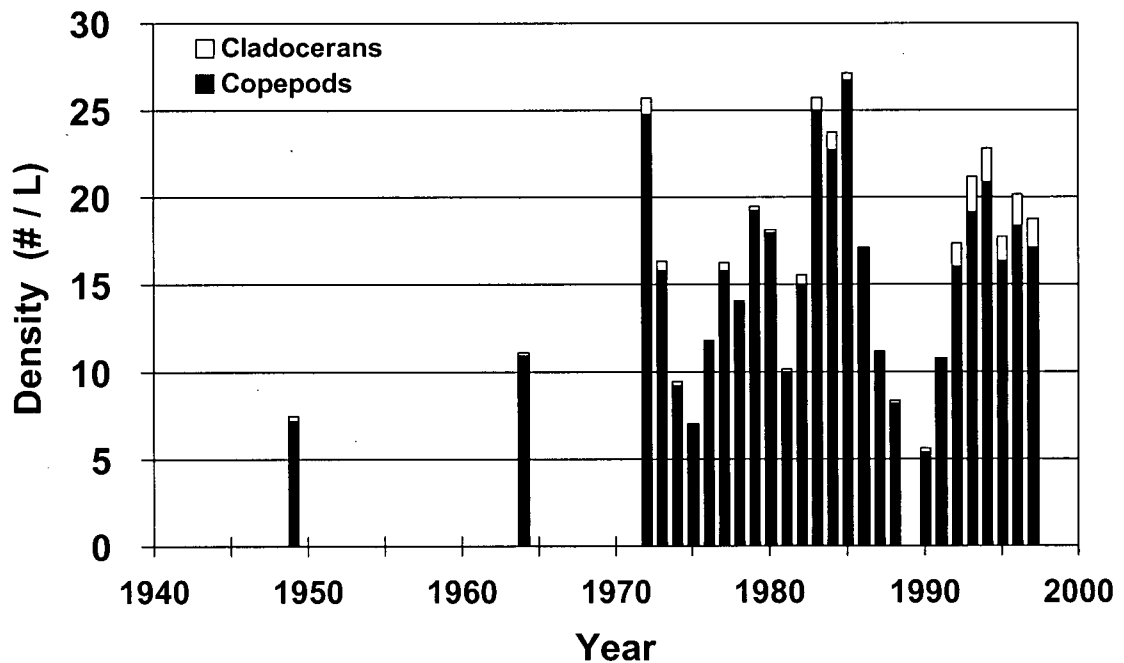


Fig. 27. Cladoceran and copepod zooplankton density in 1949, 1964, and 1972 - 1991 for mid-lake station (at or near current Station 5, Crawford Bay), and 1992 to 1997 (whole-lake average). Note: no data were collected in 1989, and data were collected only early in the season in 1991.

Proportion of Cladocerans

Prior to the fertilization experiment the proportion of cladocerans in the North Arm of Kootenay Lake was below 5% of the total zooplankton abundance (Fig. 28). From 1992 to 1996 the proportion increased to between 7.4 and 12.6%, with an average of 9% cladocerans. However, in 1997 the proportion of cladocerans in the North Arm decreased to 4.6%. This

decline was more severe in the North Arm than in the lake as a whole, so the change does not show on the whole lake annual average graph (Fig. 27).

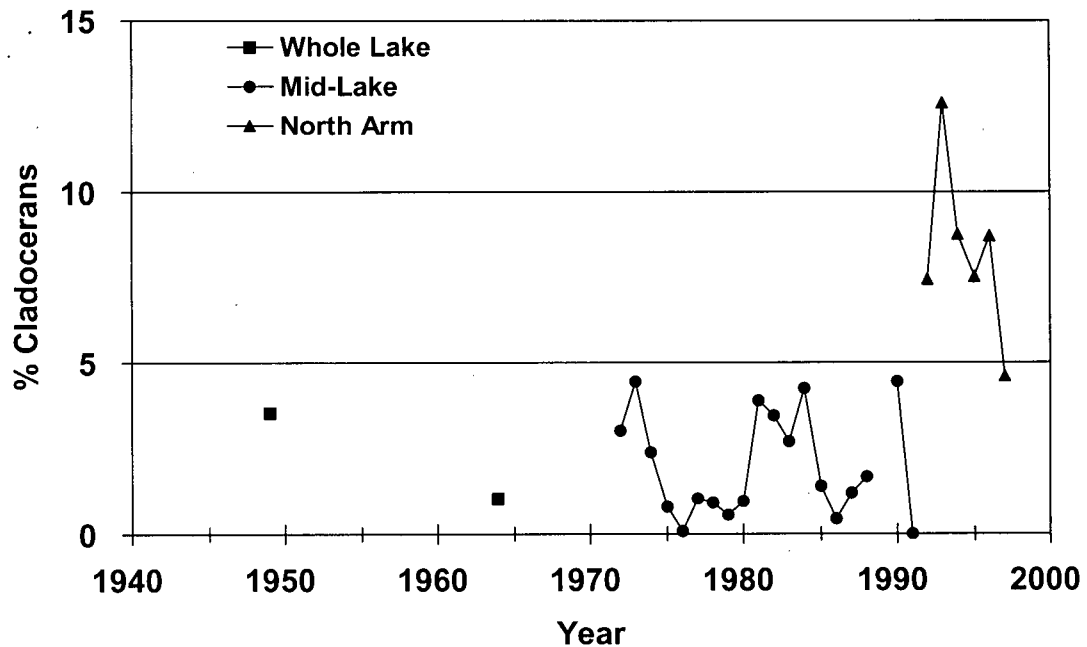


Fig. 28. Proportion of cladocerans, relative to annual average total macrozooplankton density, in Kootenay Lake, in 1949, 1964, and 1972 - 1990 . Values for 1949 to 1991 are whole-lake or mid-lake averages. Values from 1992 to 1997 are North Arm averages for May to October). Note: no data were collected in 1989, and data were collected only early in the season in 1991.

Seasonal Development of Density and Biomass

The zooplankton community showed the same general pattern of seasonal development from 1992 to 1997 (Fig. 29). Copepods were present throughout the sampling season (mid-April to Late October or early November) with peak densities occurring in late June in 1992 to 1995. However, in 1996 and 1997 copepod densities peaked in mid-July. In all years *L. ashlandi* was the predominant copepod in the first half of the season, while *D. bicuspidatus thomasi* predominated in the second half. Cladocerans were also present throughout the sampling season,

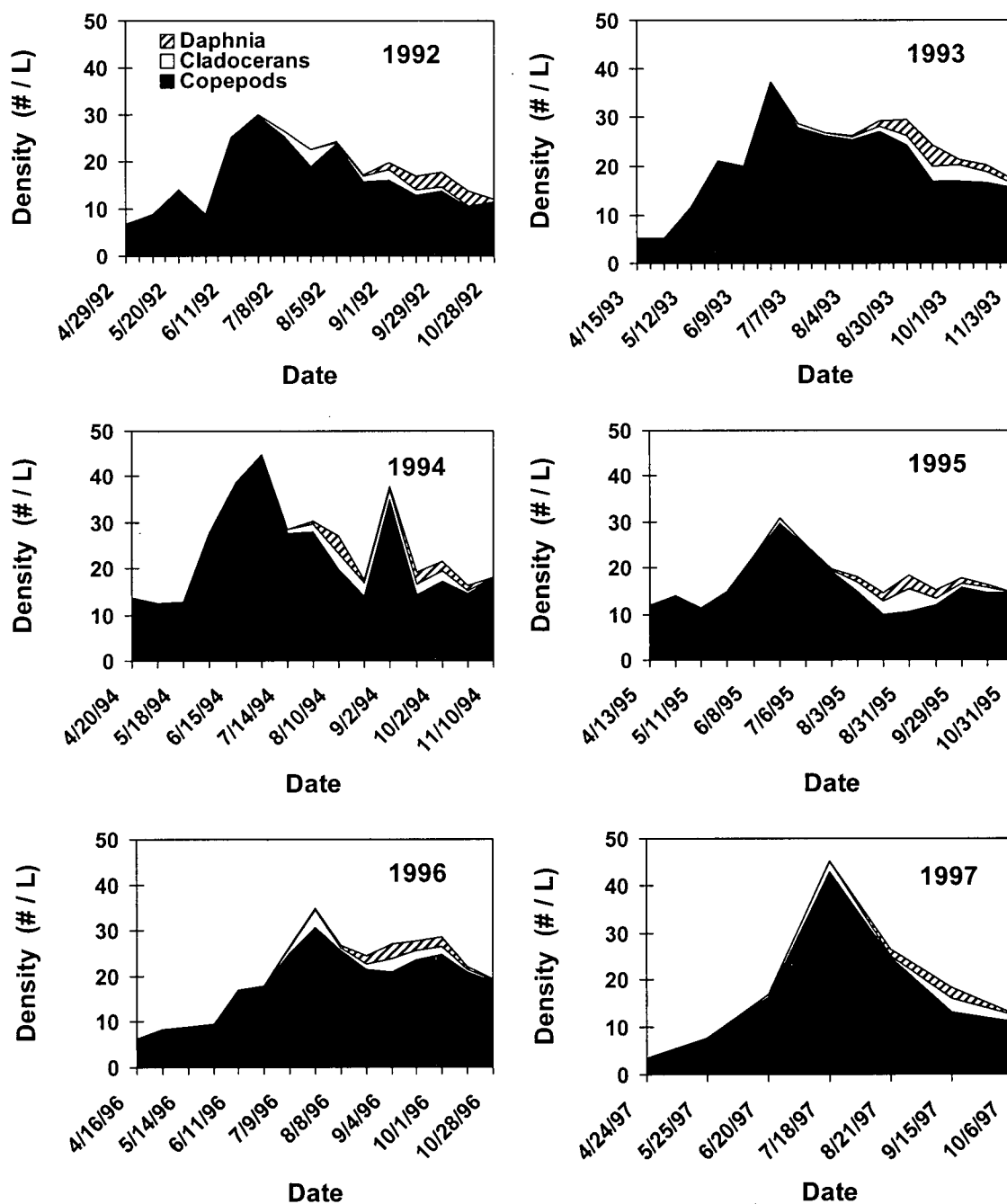


Fig. 29. Seasonal patterns of zooplankton density in Kootenay Lake from 1992 to 1997. Values for each date are the average of 6 stations in 1992 and of 7 stations in subsequent years. The cladoceran category includes all cladoceran species except *Daphnia*.

but in extremely low numbers until late June or mid-July. The first occurrence of *Daphnia* in samples ranged from May 6 (1992) to June 15 (1994), but densities did not reach 1 individual L⁻¹ or greater until mid-August to early September in all years.

The peak total zooplankton biomass (all macrozooplankton biomasses are dry weight unless specified otherwise) ranged from a high of 127 mg m⁻³ in 1992 to a low of 53 mg m⁻³ in 1997 (Fig. 30). *Daphnia* biomass was highest in 1992, with a peak of 112 mg m⁻³. The peak *Daphnia* biomass was steady from 1993 to 1996, at 56, 52, 52 and 50 mg m⁻³ respectively. *Daphnia* peak biomass was lower in 1997, at 25 mg m⁻³. In all years except 1997 the date of the peak total zooplankton biomass coincided with the *Daphnia* biomass peak, which occurred between late August and early October. Each year at the time of the *Daphnia* biomass peak, *Daphnia* comprised more than half the total zooplankton biomass, despite never making up more than 12 - 22% of the total zooplankton density.

Density and Biomass Along the Productivity Gradient

Zooplankton abundance did not display a consistent pattern along the length of the lake, in response to the clear gradient in phytoplankton biomass (Fig. 31). Densities were higher in the North Arm than in the South Arm in only a few months of the six year study (July 1994, June 1995 and 1996, and June and August 1997). In other months densities were variable along the length of the lake, or higher in the South Arm (May - July 1993, April 1994, July and September 1997). In July 1997 the total zooplankton biomasses in the South Arm (Stations 6 and 7) were the highest seen in the six year study. If there had been a time lag in the numerical response of zooplankton to increased phytoplankton biomass in the North Arm, an increase in zooplankton abundance would have occurred downstream of the phytoplankton peak area, for example at Station 3 or 4. However, zooplankton densities were not consistently higher in the middle of the lake either.

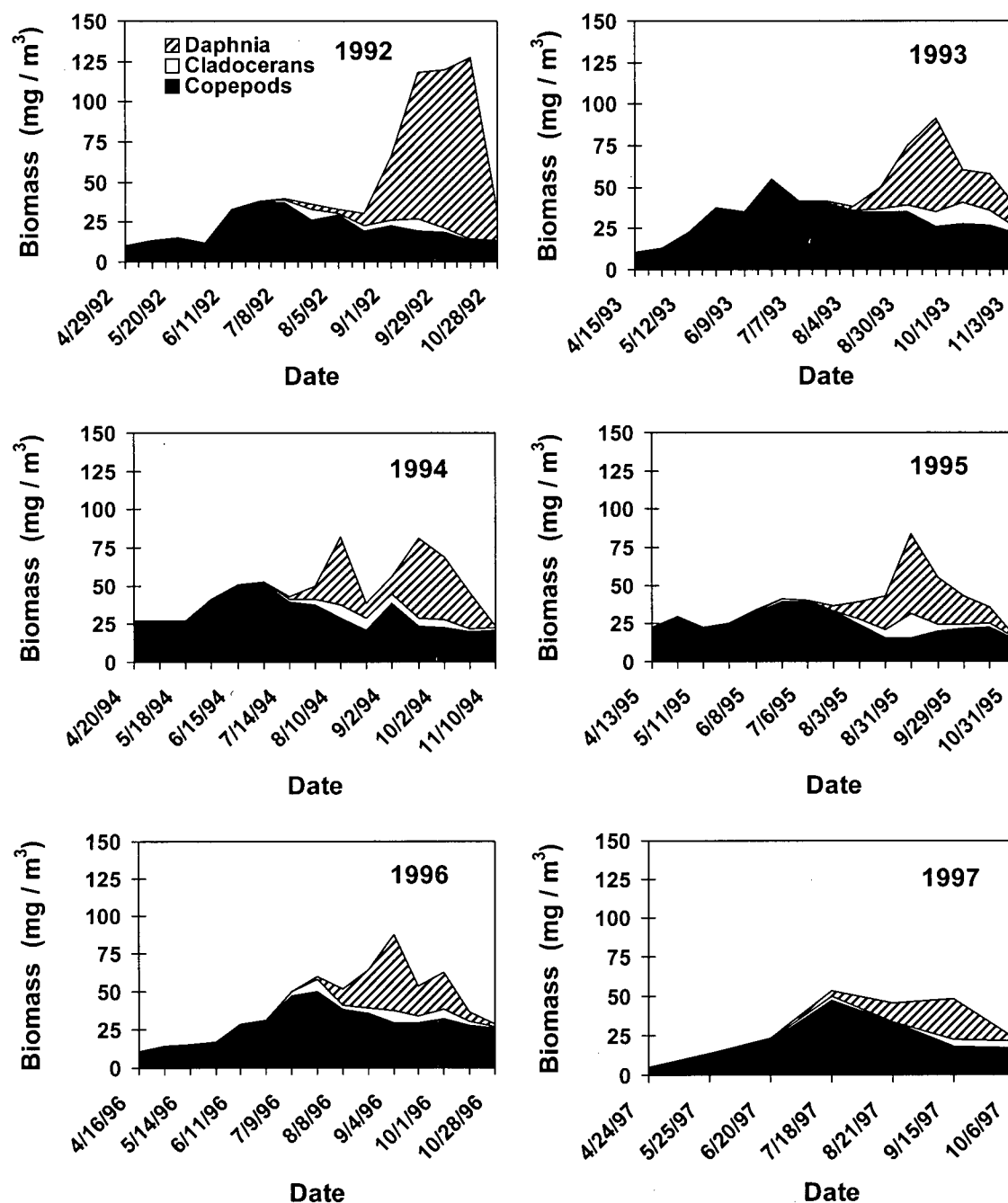


Fig. 30. Seasonal patterns of zooplankton biomass (dry weight) in Kootenay Lake from 1992 to 1997. Values for each date are the average of 6 stations in 1992 and of 7 stations in subsequent years. The cladoceran category includes all cladoceran species except *Daphnia*.

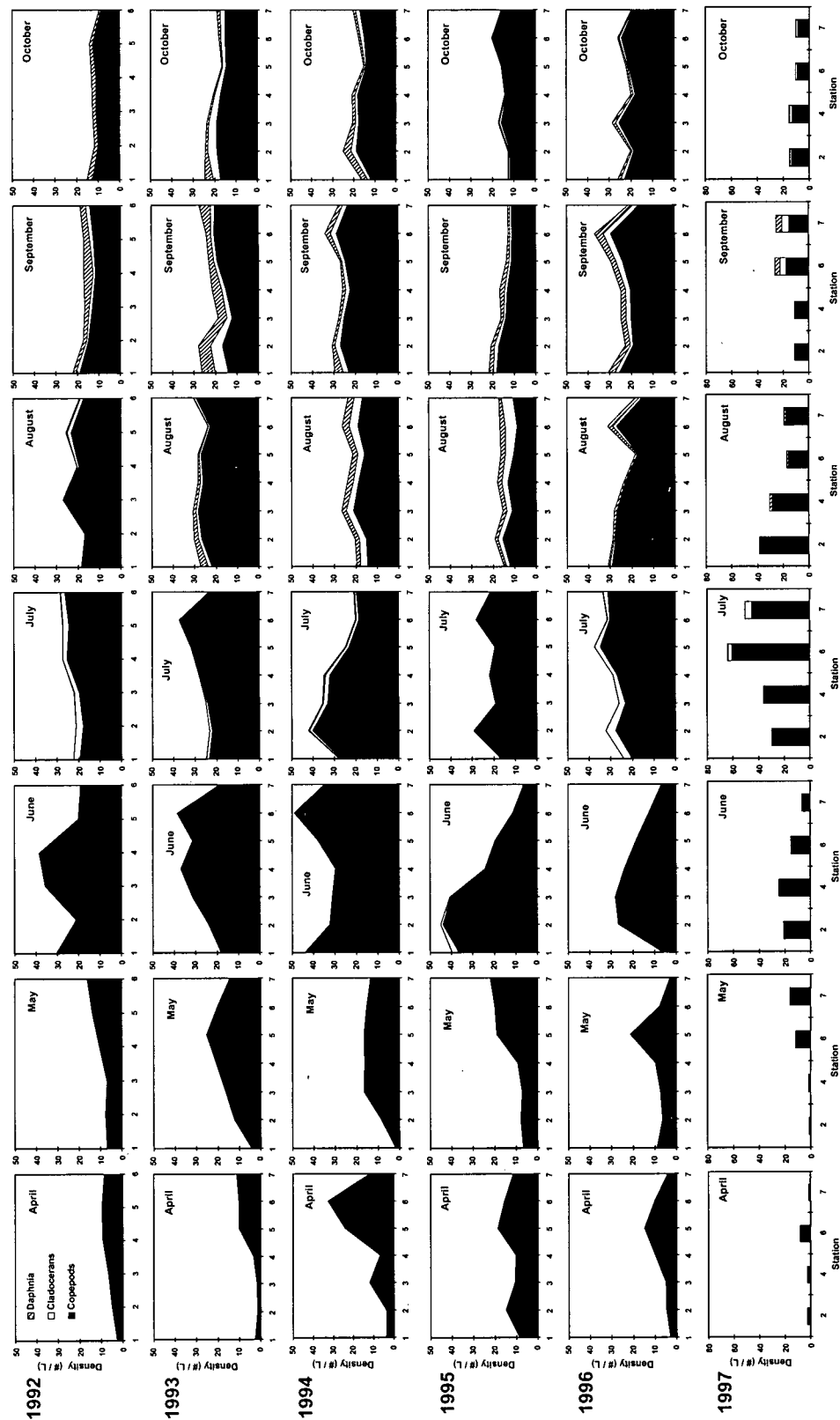


Fig. 31. Zooplankton density by month and station for 1992 - 1997. The cladoceran category includes all cladoceran species except *Daphnia*. Note that scale for 1997 is increased to 80 individuals·L⁻¹.

I also examined zooplankton biomass along the length of the lake, since *Daphnia* make up a relatively large proportion of the biomass when they are present, and because *Daphnia* are the preferred food of kokanee and *M. relicta* (Fig. 32). Again there were no consistent patterns along the phytoplankton gradient in any of the years.

Macrozooplankton Species Density Along Lake

I plotted the densities of individual zooplankton species by month and station, in case the merging of data into copepod and cladoceran categories had obscured any species patterns along the gradient (Fig. 33). This was particularly important in the case of *E. nevadensis*, and *L. kindti*, which prey upon smaller macrozooplankton species. If predatory zooplankton were more abundant in the fertilized end of the lake this could contribute to increased mortality of herbivorous species such as *Daphnia* spp., and suppression of *Daphnia* spp. density and biomass. As was the case for the merged data, most species did not show consistent trends along the lake. *L. kindti* densities were very low along the lake in all months and years. *E. nevadensis* was sometimes more abundant in the North Arm, such as June 1993, June and October 1994, June to September 1995, and May to September 1996. From 1993 to 1996 the skew in the *E. nevadensis* distribution increased, and occurred over a greater portion of the growing season. However, in 1997 *E. nevadensis* was much less abundant, and its distribution was not skewed. The pattern of *E. nevadensis* distribution across years is similar to that seen for phytoplankton biomass (especially netplankton), which increased from 1992 to 1996, then declined in 1997.

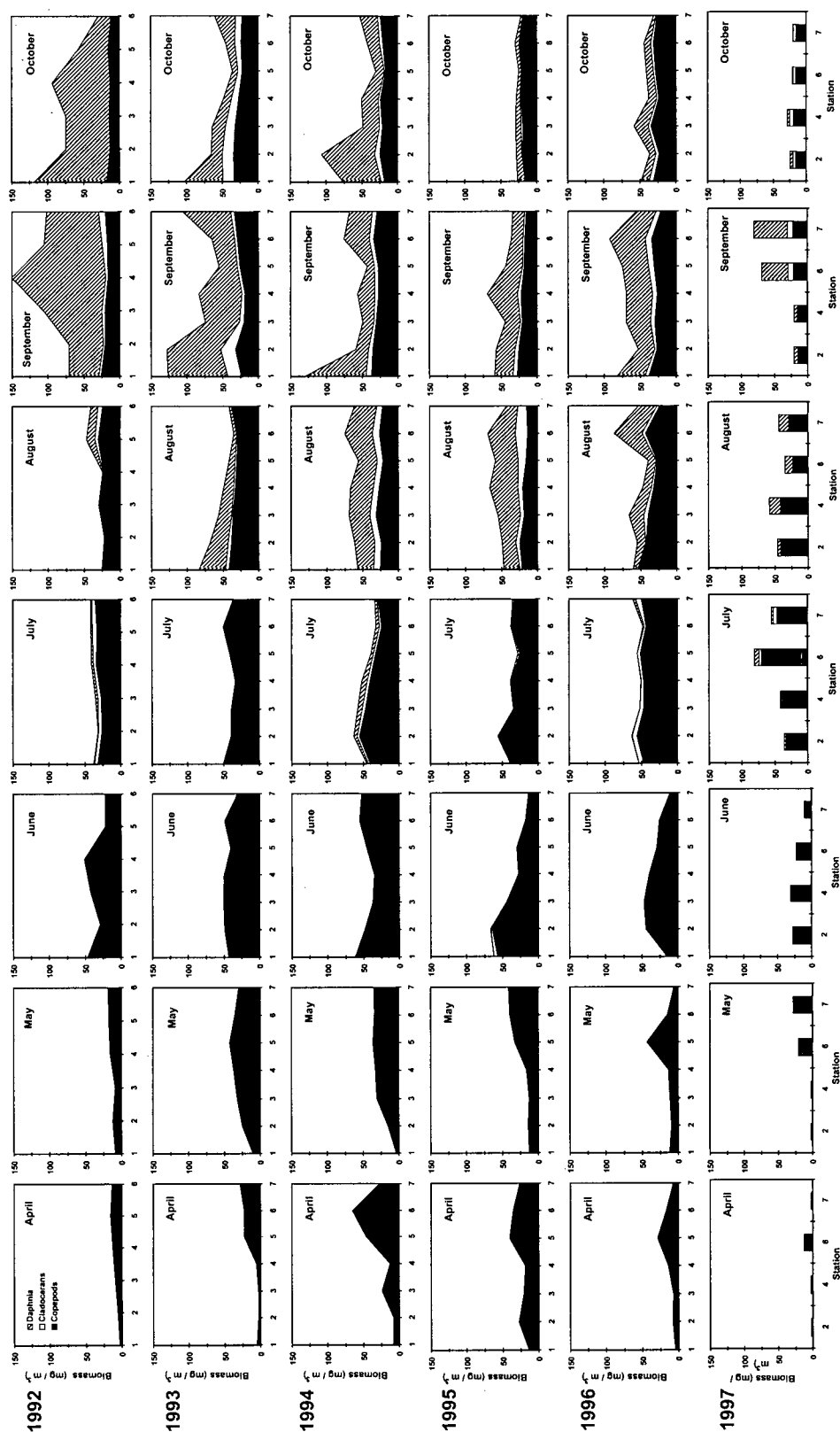


Fig. 32. Zooplankton biomass (dry weight) by month and station for 1992 - 1997. The cladoceran category includes all cladoceran species except *Daphnia*.

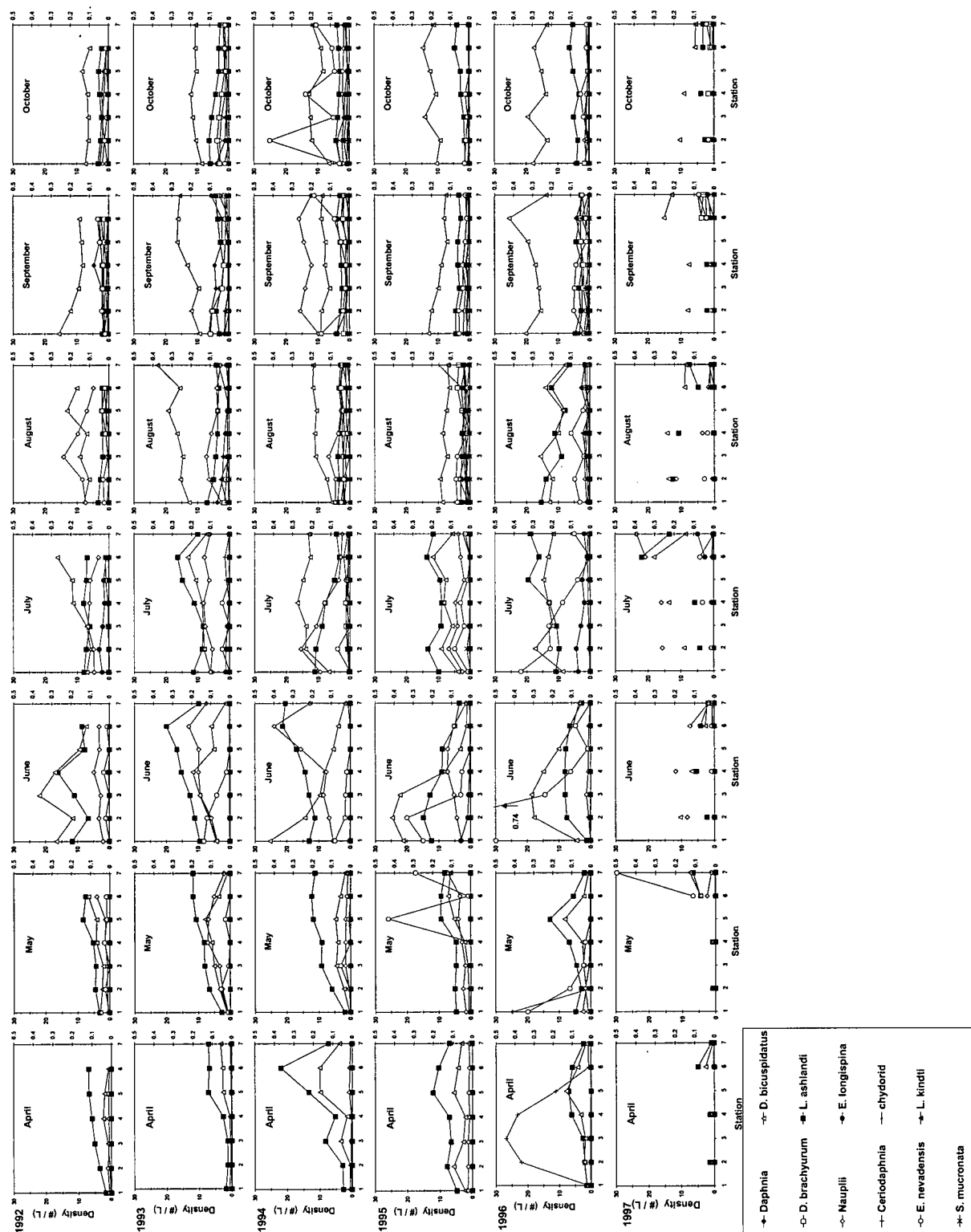


Fig. 33. Zooplankton species density by month and station for 1992 - 1997. *Daphnia* spp., *D. bicuspidatus thomasi*, *D. brachyurum*, *L. ashlandi*, nauplii, and *E. longispina* are plotted on the left Y-axis (up to 30 individuals L^{-1}). Less abundant species, *Ceriodaphnia*, chydorids, *E. nevadensis*, *L. kindti*, and *S. mucronata*, are plotted on the right Y-axis (up to 0.5 individuals L^{-1}).

Mysis relicta Abundance

Annual average *M. relicta* density increased during the period from 1971 to 1979, from 13 individuals·m⁻² to 647 individuals·m⁻² (Fig. 34). Densities then showed large inter-annual fluctuations during the 1980's, peaking at 745 individuals·m⁻². Densities were low immediately prior to the start of fertilization, increased to 405 individuals·m⁻² in 1992, then steadily declined from 1993 to reach 126 individuals·m⁻² in 1996. Densities rose slightly in 1997, to 195 individuals·m⁻². Much of the interannual variability in density prior to the fertilization project may be the result of inconsistent and infrequent sampling (due to lack of funding). The 3-year running average is also shown since it may give a better estimate of the interannual range in *M. relicta* density.

Lasenby et al. (1998) compared densities for 1992 to 1997 (May-October averages) in the North Arm, mid-lake, and South Arm, from shallow, deep, and combined samples. In shallow samples, densities were highest in the North Arm in 1995, at mid-lake in 1992, and 1997, and in the South Arm in 1993, and 1996. Shallow sample densities were higher in the North and South Arms than at mid-lake in 1994. In deep samples, densities were highest in the North Arm in 1992, 1995, and 1996, at mid-lake in 1997, and in the South Arm in 1993, and 1994. In the combined samples, densities were highest in the North Arm in 1992, 1995, and 1996, at mid-lake in 1997, and in the South Arm in 1993, and 1994. The report of Lasenby et al. (1998) may include samples that were not yet analyzed at the time that data were entered into the Kootenay Lake Fertilization Database. *M. relicta* density along the fertilization gradient has not shown a consistent pattern over the six years of fertilization.

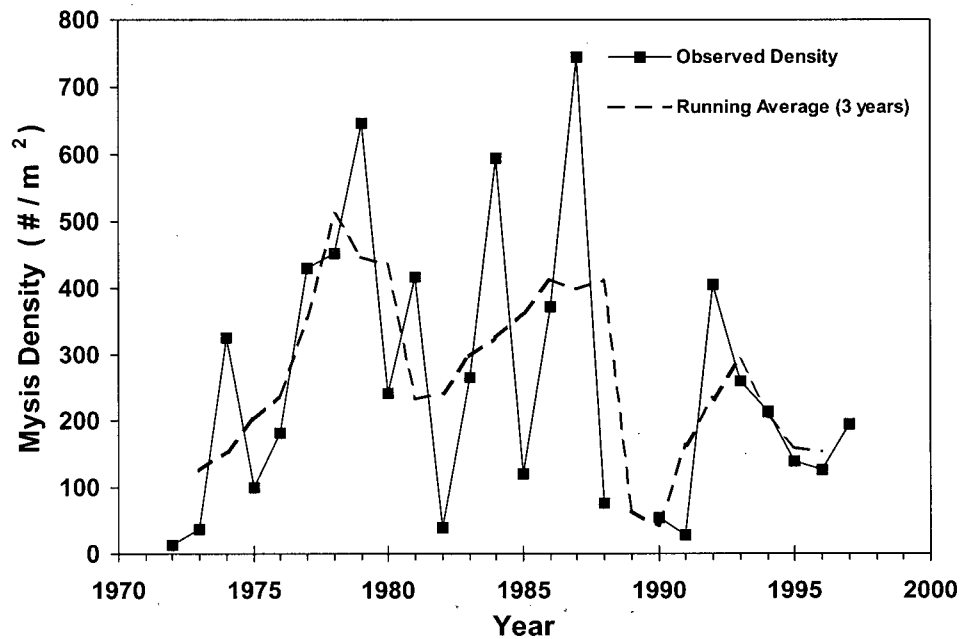


Fig. 34. Density of *M. relicta* in Kootenay Lake from 1972 to 1997. Values are the annual average of North Arm, central, and South Arm stations for 1972 to 1981, and the annual average from the central station for 1982 to 1996. Dashed line is 3-year running average of density. Values from 1972 to 1988 from Crozier and Duncan (1984), 1990 to 1991 from Richard J. Crozier, unpublished data, B.C. Ministry of Environment, Lands and Parks, 1992 to 1996 from Smokorowski et al. (1997), 1997 from Lasenby et al. (1998).

Relationship Between *M. relicta* and Water Flow Rates

M. relicta density was negatively related to water flow through Kootenay Lake. Time series data show that *M. relicta* density tended to be higher in low flow years, but there was a great deal of variability in this pattern (Fig. 35). *M. relicta* density was negatively related to surface water turnover rate (May-August) in Kootenay Lake, calculated from discharge at Corra Linn Dam (Fig. 36). This pattern suggests that in high flow years *M. relicta* are more likely to be exported out of the main lake into the West Arm, so *M. relicta* mortality rates are higher in high flow years.

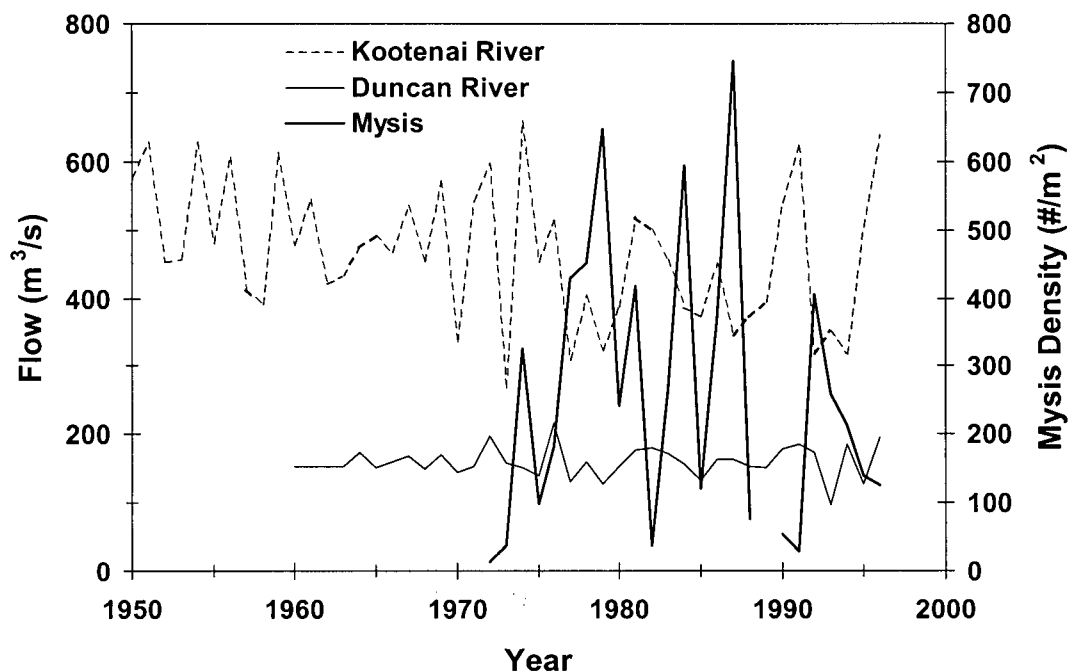


Fig. 35. *M. relicta* annual average density, plotted with annual average flows in the Kootenai and Duncan Rivers.

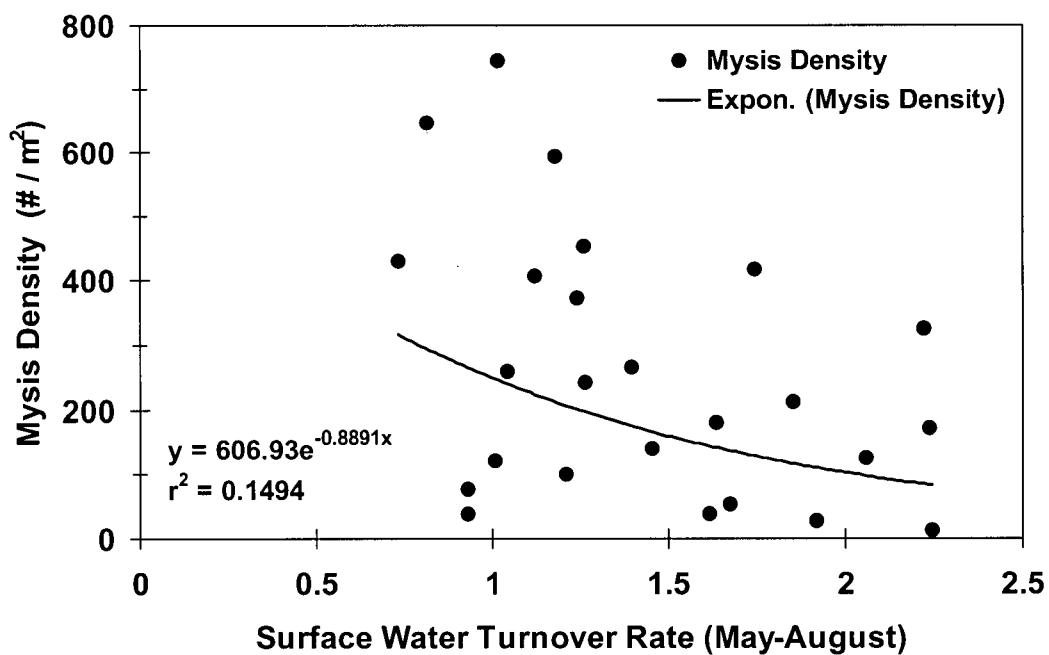


Fig. 36. *M. relicta* annual average density plotted against Kootenay Lake surface water turnover rate, calculated from Corra Linn Dam discharge. Trend line is an exponential fit, shown with its equation, and coefficient of determination (r^2).

The Beverton-Holt model gives a fairly good approximation of *M. relicta* density over time (Fig. 37). The model predictions coincide closely with observed densities in the 1970's, and during the fertilization experiment. However, the model does not capture the variability in *M. relicta* densities in the mid-1980's. This may be because flow effects were less influential during that period, or because limited sampling of *M. relicta* produced overly variable population estimates, biased by a few very high or low samples. The optimized mortality parameters were: baseline mortality, $m_{\text{base}} = 0.04$, flow mortality, $m_{\text{flow}} = 0.35$, and density dependent mortality, $m_{\text{cap}} = 0.09$.

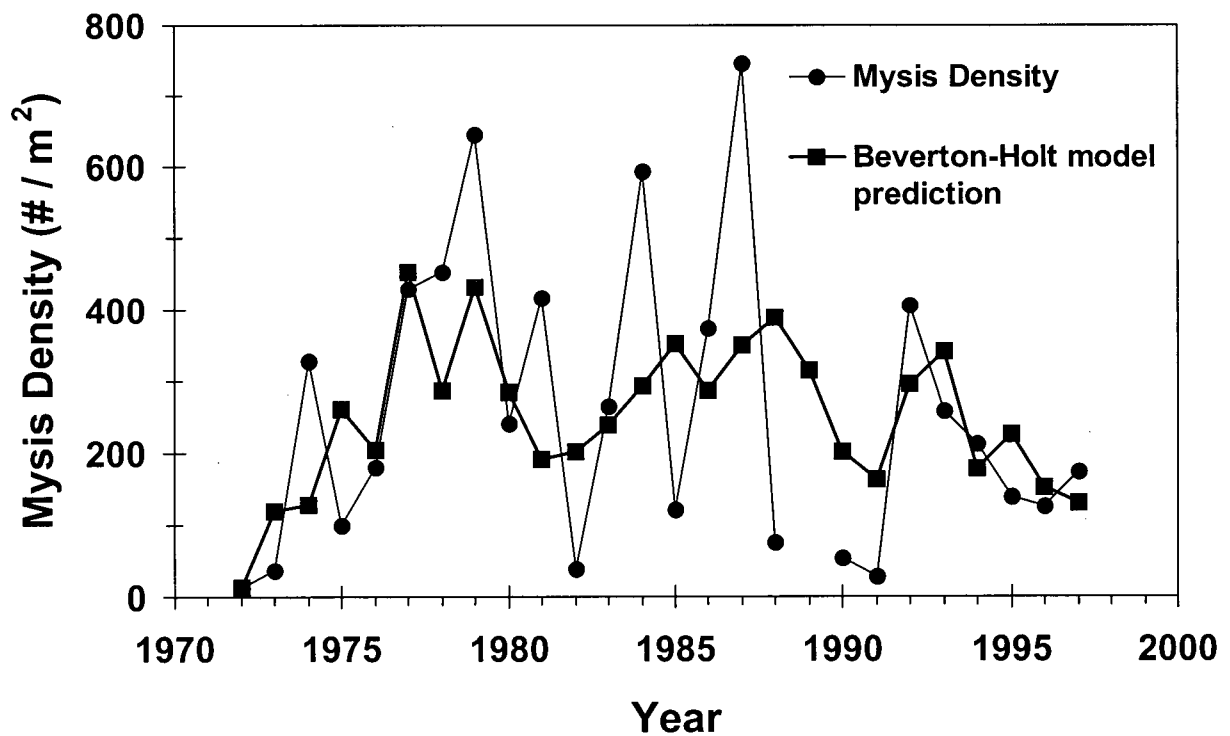


Fig. 37. Beverton-Holt model prediction of *M. relicta* density, including flow-related mortality, and actual *M. relicta* annual average density time series.

Regulation of flow by the Duncan and Libby Dams has caused the spring peak flow through Kootenay Lake to be lower than it was historically, and shifted flow to the autumn and winter (Fig. 2). This may have decreased *M. relicta* mortality in spring and summer since dam operations began. *M. relicta* densities rose in the early 1970's over the same period that spring peak flows declined. In the early 1980's spring peak flows increased and *M. relicta* densities declined, although they were still very erratic. *M. relicta* densities increased again in the late 1980's, coincident with lower flows, but declined during the higher flow years 1990-1991. Densities were high in 1992, a low flow year. However, spring peak flows rose each year from 1992 to 1997, with the exception of a slight decrease in 1994. Spring peak flows in 1996 and 1997 were as high as those seen in 1963, 1964, and 1970. High snow packs in 1996 and 1997, combined with spring flow releases intended to encourage white sturgeon spawning, caused the unusually high spring flows in these years.

Kokanee Abundance

Spawner Abundance

Kokanee spawner returns to Meadow Creek and the Lardeau River have varied by an order of magnitude since the early 1960's (Fig. 38 a). Returns in the early 1970's were almost 4 million in the Lardeau River, and 3 million in Meadow Creek. In the 1980's returns to both tributaries declined, and this trend continued until 1991. Initially the Lardeau River runs were larger than those in Meadow Creek, but from 1986 onward this pattern was reversed (fish were not monitored in the Lardeau River in 1985).

Spawner returns to both tributaries increased during the fertilization experiment, and by 1997 the combined run was 1.45 million fish. Lardeau River runs in 1995 and 1996 were lower than in 1993 and 1994. However, since the majority of kokanee in the main lake spawn as they turn age 4, the fish returning in 1995 were mainly the product of the 1991 run, which was

extremely low in the Lardeau River. Similarly, the 1996 run resulted from the 1992 run, which was also low. The spawner runs in 1995 and 1996 were about four and two times larger than the runs that produced them, respectively.

The number of kokanee spawners returning to West Arm and South Arm tributaries followed different trajectories than the North Arm stocks (Fig. 38 b). West Arm spawner numbers were erratic in the early 1970's, and peaked at almost 50,000 in 1975. Numbers then declined until 1979, but then generally increased until 1995. Spawner numbers in the South Arm tributaries have historically been lower than in the North or West Arms. The total peak count observed has never been above 10,000 fish in any of the years sampled between 1969 and 1997. In the late 1980's numbers declined to less than 1,000 fish, and numbers did not increase during the fertilization experiment.

Kokanee Abundance and Total Phosphorus Load

Annual total phosphorus (TP) loads to Kootenay Lake averaged 940 t from 1960 to 1996, and ranged from 167 t in 1993 to 3829 t in 1968. Expressed in areal terms the average was $2.4 \text{ gPm}^{-2}\text{yr}^{-1}$, and the range was 0.42 to $9.6 \text{ gPm}^{-2}\text{yr}^{-1}$. From 1960 to 1972 the phosphorus loading was consistently above the "dangerous" limit (Fig. 16). Between 1973 and 1978 loads fluctuated around the limit lines; they were at "safe" levels from 1979 to 1996, with the exception of 1988 and 1996 when loads were above the "admissible" limit line.

Spawner abundance in the Lardeau River was highly positively correlated with TP load, for loads between 0 t and 1000 t (Fig. 39). Beyond 1000 t the number of kokanee returning to spawn declines to levels no higher than observed for phosphorus loads less than 500 t. The regression of spawner abundance on 4-year average TP load where loads were between 0 t and 500 t was:

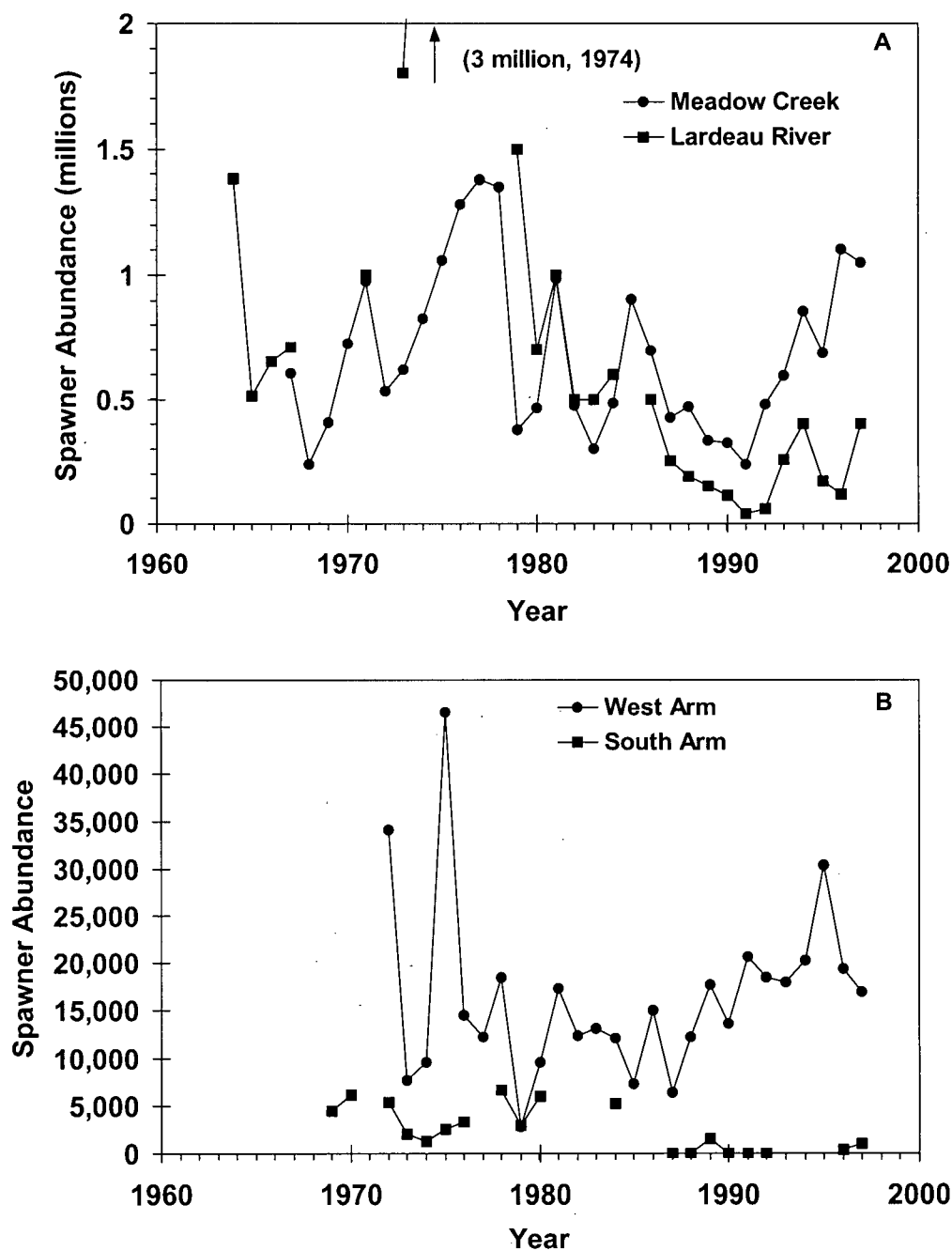


Fig. 38. A) Kokanee spawner returns to Meadow Creek (channel, and creek above and below channel) and the Lardeau River from 1964 to 1997. B) Kokanee spawner returns to the West Arm spawning channels (Kokanee Creek and Redfish Creek) and to West Arm and South Arm creeks from 1969 to 1997. Data were unavailable for the South Arm for some years.

$$\text{Kokanee Spawners (millions)} = -1.080 + 0.005 \text{ TP load}$$

with $r^2 = 0.55$, $F = 20.46$, $p = 0.0004$, and $n = 17$. The regression of spawner abundance on 4-year average TP load where loads were between 0 t and 1000 t was:

$$\text{Kokanee Spawners (millions)} = -0.836 + 0.004 \text{ TP load}$$

with $r^2 = 0.83$, $F = 87.40$, $p < 0.0001$, and $n = 19$. These regressions are shown to indicate the pattern between kokanee spawner abundance and phosphorus load. The high significance of the relationships suggest that the pattern is too strong to have occurred by chance. However, the points are not independent because the data come from a single lake. The error terms of the regression for loads less than 500 t are autocorrelated, with a first order autocorrelation value of 0.292. The Durbin-Watson test was inconclusive for the regression for loads less than 1000 t; the first order autocorrelation value was 0.182. No attempt was made to correct for autocorrelation since phosphorus loads and kokanee returns are inherently autocorrelated. While the relationship between phosphorus load and kokanee returns is very strong, there is still the chance that both phosphorus loads and kokanee spawner returns could be correlated with other variables, such as long term climate change, that may have similar effects on loads and kokanee.

Kokanee Abundance and *M. relicta* Density

Kokanee abundance and *M. relicta* density were not correlated prior to the fertilization (Fig. 40). During the fertilization period, from 1992 to 1996, the two species were negatively correlated:

$$\text{Kokanee Spawners (millions)} = 1.124 - 0.002 \text{ Mysis Density}$$

($r^2 = 0.45$, $F = 4.54$, $p < 0.12$, $n = 5$). However, the same caveats mentioned above for kokanee abundance and TP load, regarding non-independence of data points and autocorrelation, also apply to this relationship.

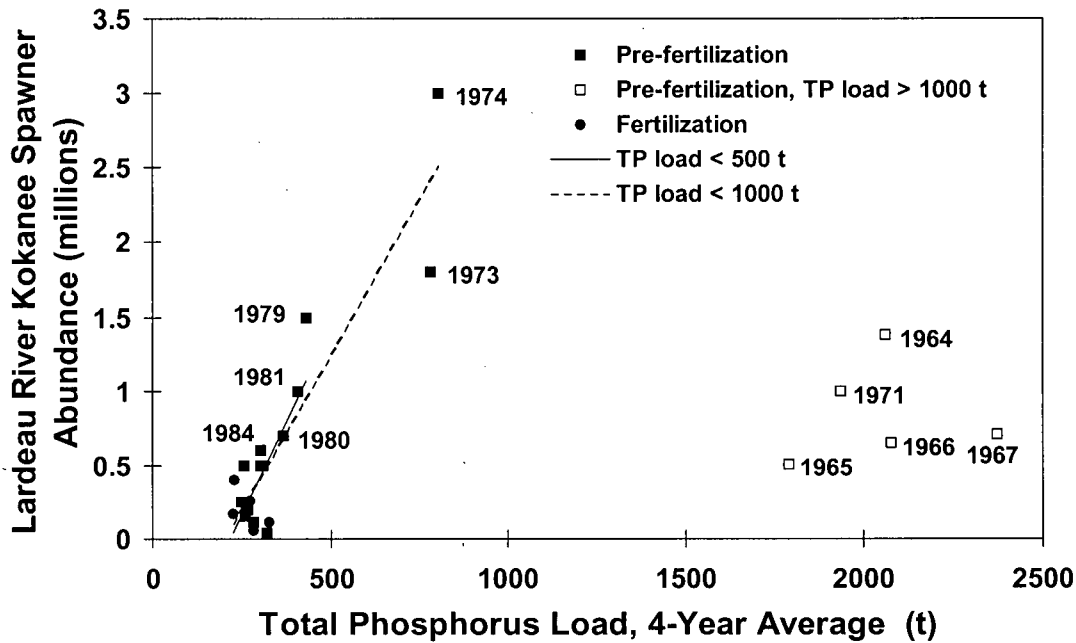


Fig. 39. Lardeau River kokanee spawner escapement plotted against the annual total phosphorus load to Kootenay Lake between 1964 and 1996. Loads of 500t to 1000 t span the range of potential “dangerous” TP loads based on Vollenweider and Dillon’s (1974) criteria, which vary with hydraulic retention time. White squares indicate data that were omitted from regressions because TP loads were well above the “dangerous” limit.

Hydroacoustic Density

The total abundance of kokanee in Kootenay Lake, as estimated from the detailed autumn hydroacoustic surveys, correlates well with the increasing trend in spawner returns to Meadow Creek, and the Lardeau River. Whole-lake kokanee abundance increased from 8.5 million in 1992 to 35.6 million in 1994 (Table 5; Mr. Dale Sebastian and Mr. George Scholten, B.C. Ministry of Environment, Lands and Parks, 780 Blanshard St., Victoria, B.C., V8V 1X4, unpublished data). Abundance dropped to 25.3 million in 1995, rose again to 34.9 million in 1996, and dropped back to 26.2 million in 1997. These estimates represent the age 0+ to 2+ age classes only, since most 3+ kokanee would already have left the lake to spawn in August or early September, before the surveys were done.

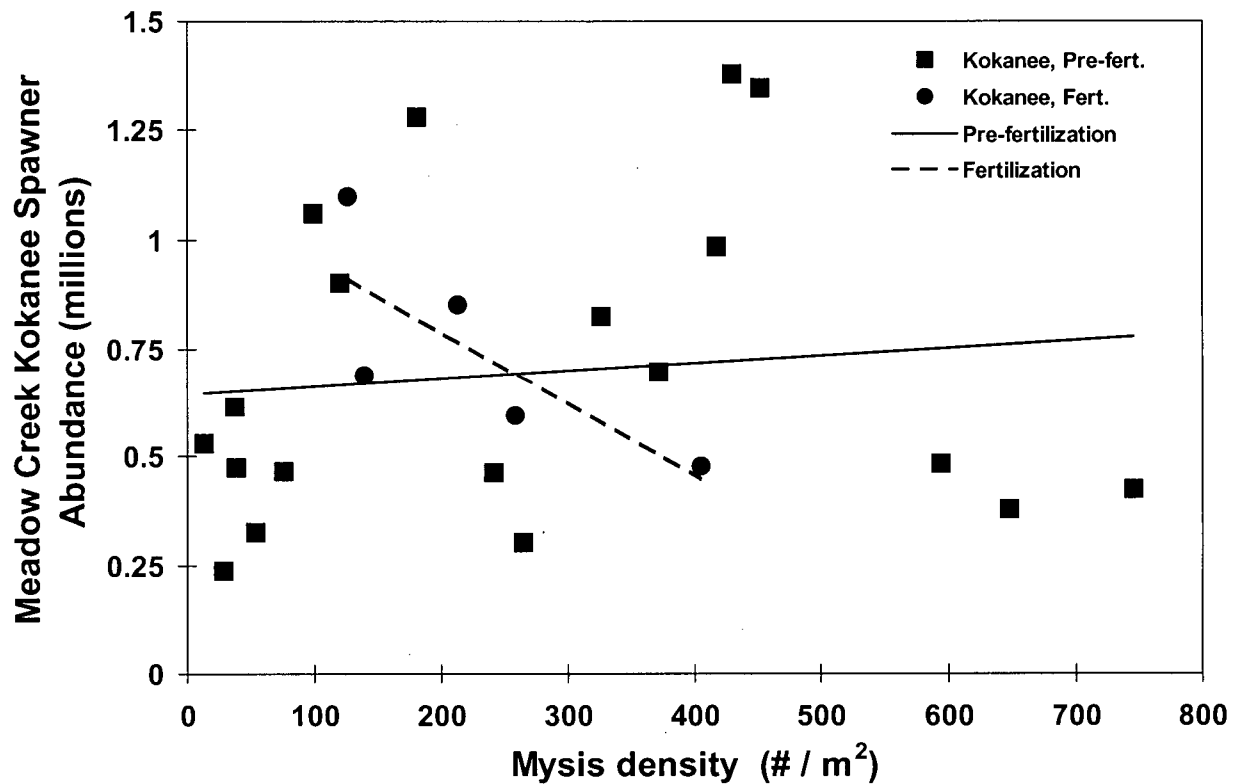


Fig. 40. Meadow Creek kokanee spawner escapement plotted against *Mysis relicta* density (May-October average) between 1972 and 1996 (*M. relicta* data for 1989 were unavailable).

Table 5. Total abundance of age 0+, 1+, and 2+ kokanee in Kootenay Lake in autumn, estimated from hydroacoustic transects. Confidence intervals estimated from Monte Carlo simulation procedures.

Year	Abundance (millions)	95% Confidence Interval
1992	8.53	7.48 – 9.75
1993	10.9	9.57 – 12.5
1994	35.6	32.1 – 38.7
1995	25.3	22.8 – 27.5
1996	34.9	31.7 – 38.3
1997	26.2	23.8 – 29.3

Kokanee Horizontal Distribution Along Productivity Gradient

Kokanee density along the length of the lake showed similar patterns between years (Fig. 41). Fry distribution was usually skewed toward higher densities in the North Arm, particularly in June, July, and August. The majority of fry produced in Kootenay Lake originate from Meadow Creek, and the Lardeau River, and emigrate into the lake from April to June. Apparently it then takes several months for fry to swim southward, and distribute themselves more evenly along the lake. Thus fry in the South Arm should tend to be older than fry in the North Arm. I discuss the implications of this for patterns of fry size-at-age in greater detail in the section on kokanee fry otoliths (p. 81). Assuming that fry swim at one body length per second, for 5 hours per day, always in a southward direction, I calculated that a fry that emigrated into the North Arm of the lake in May should be able to reach the bottom of the South Arm by September (Table 6). This estimate seems reasonable, given that swimming estimates of $0.4 \text{ km} \cdot \text{d}^{-1}$, and $1 \text{ km} \cdot \text{d}^{-1}$ have been observed for sockeye fry dispersal in rearing lakes (Burgner 1991). In 1992, 1995, and 1997 fry in Kootenay Lake were evenly distributed along the lake by September. However, in 1993, 1994, and 1996 there were still more fry in the North Arm in September. It is possible that fry movements adjust to food availability so as to produce an ideal free distribution relative to a gradient of zooplankton production, such that all fry experience a similar growth rate (MacCall 1990), even though the density of fry is greater in the fertilized end of the lake. However, since I do not have detailed information on the length of time that fry spend actively swimming at different times of the year, and in different years, it is impossible to calculate an accurate estimate of the time fry would need to distribute themselves evenly in the absence of a zooplankton production gradient.

Table 6. Potential distance travelled south along Kootenay Lake by fry migrating into the lake from the Meadow Creek Channel in May.

Month	Fry Fork	Average	Hours	Distance	Distance	Cumulative
	Length	Speed	Travelling	Per Day	Per Month	Distance
	(mm)	(m·s ⁻¹)	(hr·day ⁻¹)	(km·day ⁻¹)	(km·month ⁻¹)	(km)
May	25	0.025	5	0.45	13.95	13.95
June	28	0.028	5	0.50	15.12	29.07
July	30	0.03	5	0.54	16.74	45.81
Aug.	45	0.045	5	0.81	25.11	70.92
Sept.	50	0.05	5	0.90	27.00	97.92

Age 1+ to 3+ kokanee distribution was generally even along the lake (Fig. 41). In some months more fish were detected in the North Arm than in the South Arm (e.g., June and August 1993, June 1995) but the pattern was not consistent across months within a given year. At other times more age 1+ to 3+ fish were detected in the South Arm (e.g., August 1992, July 1993, July 1994).

Kokanee trawl catches along the lake show roughly the same pattern as the hydroacoustic distributions (Fig. 42), indicating that the decibel level cut-off chosen to separate fry and older fish targets in the hydroacoustic analyses was accurate. The trawl densities are biased toward fry in all months except September, when stepped oblique layers were trawled through the entire depth range where kokanee were located. In other months trawling was optimized to capture fry, as a minimum sample size was needed for both size and diet analyses. Trawl densities probably underestimate age 1+ kokanee in all months, as the net is inefficient at capturing this size class (pers. comm., Mr. Dale Sebastian, B.C. Ministry of Environment, Lands and Parks). This is likely due to a combination of the mesh size of upper part of the net allowing age 1+ fish to pass

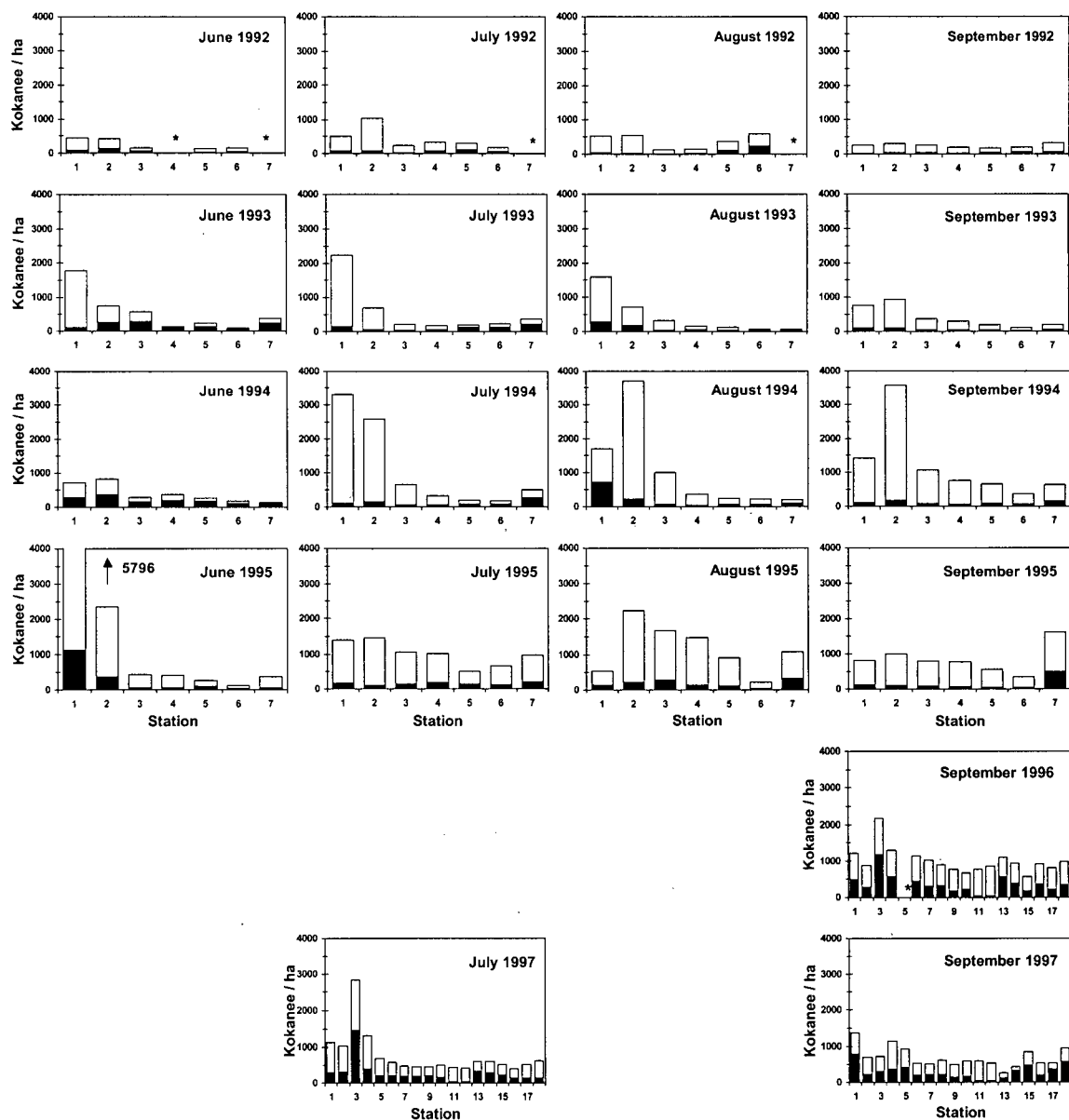


Fig. 41. Hydroacoustic density of fry, and age 1+ to 3+ fish along the length of Kootenay Lake from June to October, 1992 to 1997. Fry density shown in white, and density of age 1+ to 3+ fish combined shown in black. An asterisk indicates stations that were not sampled.

through, and the swimming ability of 1+ fish allowing them to orient themselves to swim through. While fry are small enough to pass through the same size of mesh or smaller, they appear to be less able to swim through, and instead tumble back into the cod end of the net.

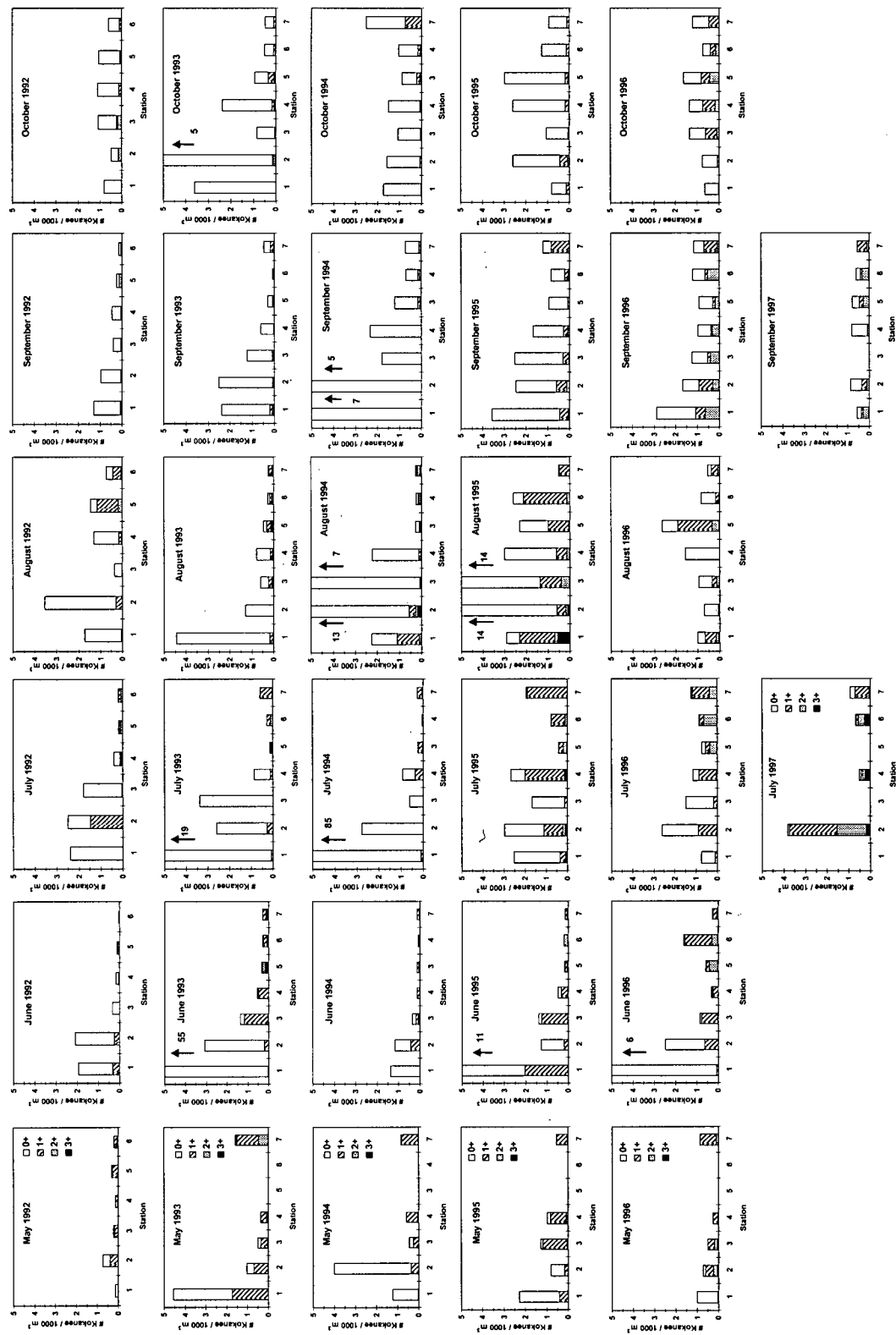


Fig. 42. Density of kokanee caught in trawls in from 1992 to 1997, by month and station along the length of the lake. From 1993 to 1996 stations 5 and 6 were not sampled in May. In 1997 trawls were conducted in July and September only. No trawls were conducted at stations 1, 3, and 5 in July, or at station 3 in September.

Gerrard Rainbow Trout Abundance

Rainbow trout spawner abundance increased during the fertilization experiment (Fig. 43). The peak count ranged from 219 to 344, similar to the 1957-1991 average of 285 fish. Because Gerrard trout usually do not spawn until they are about six years old it was expected that there would be a time lag in the response of trout spawner numbers to any benefits of fertilization. Although in this thesis I am focusing on the first 6 years of fertilization, it is notable that in spring 1998 the peak count was 367 fish. In 1999 the peak count was over 400, and trout were also observed spawning in sub-optimal habitat downstream of the Gerrard site, where silty inputs from Mobbs Creek would cause lower egg survival.

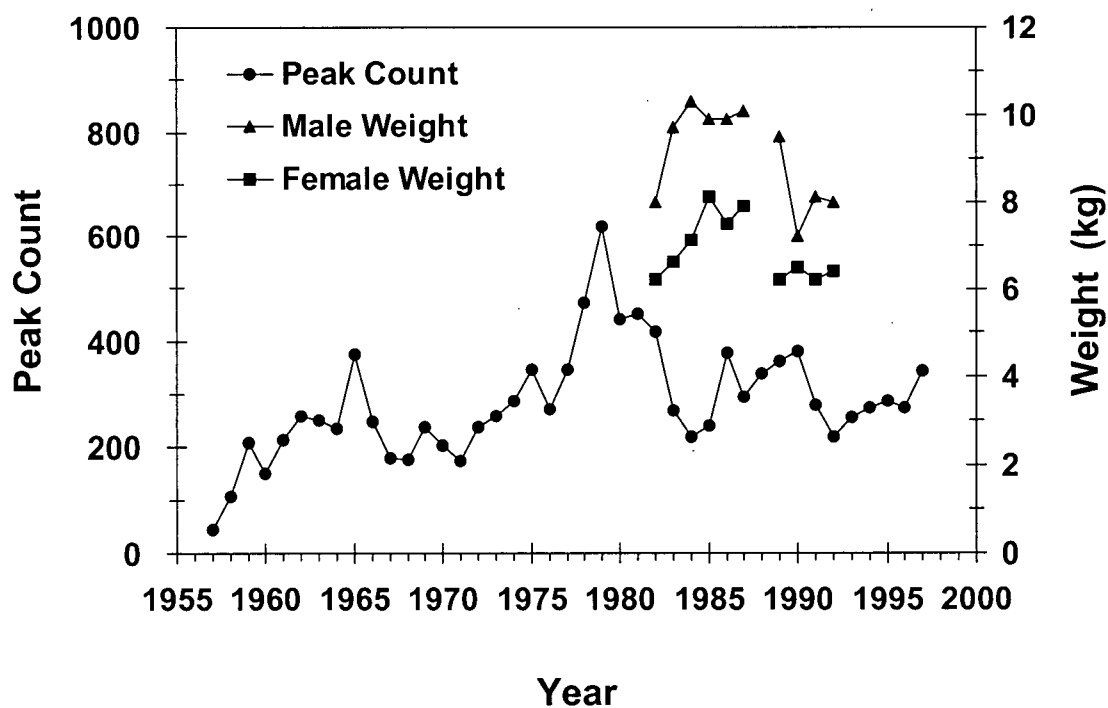


Fig. 43. Gerrard rainbow trout spawner returns and weight (for years when water levels permitted trapping) at the Lardeau River spawning ground, 1957 to 1997.

Bull Trout Abundance

It was not possible to obtain an estimate of bull trout abundance in Kootenay Lake, although the collection of this sort of data has attracted increasing interest in recent years. In a survey of Kootenay Lake tributaries, as many as 200 bull trout were counted in some tributaries (pers. comm., Mr. Donald Miller, Kootenay Wildlife Services, Harrop, B.C., and Mr. Albert Chirico, B.C. Ministry of Environment, Lands and Parks, Nelson, B.C.). Experienced anglers suggest that Kootenay Lake may contain twice as many bull trout as Gerrard rainbow trout. Anglers also report that bull trout catches have been very good during the fertilization experiment, suggesting that the bull trout population may be following a trajectory similar to that of the rainbow trout.

Production

Potential Phytoplankton Production

Potential annual primary production of wet weight phytoplankton biomass in Kootenay Lake was $170,000 \text{ mg}\cdot\text{m}^{-3}$. From 1992 to 1996 the average growing season algal biomass in Kootenay Lake was $751 \text{ mg}\cdot\text{m}^{-3}$ (data from Station 2 in the North Arm, and Station 6 in the South Arm). Phytoplankton in Kootenay Lake had a potential annual P/B ratio of 227. This is higher than the average of 113 noted by Wetzel (1983) for freshwater ecosystems, but well within the range of 9-359. Averaged over the growing season from April to October, the daily P/B ratio would be 1.08 d^{-1} .

Microzooplankton (Rotifers)

Rotifer eggs were not counted for this study, so it was not possible to calculate rotifer production rates. However, based on the standing stock biomass observed, and a range of P/B values from the literature (Makarewicz and Likens 1979), I calculated potential rotifer

production (Table 7). For comparison, the combined production (wet weight) of the macrozooplankters *L. ashlandi*, *D. bicuspidatus thomasi*, and *Daphnia* spp. in 1994, 1995, and 1996, was 2802 mg·m⁻³, 3073 mg·m⁻³, and 2220 mg·m⁻³, respectively. Thus, macrozooplankton production probably exceeded rotifer production in all of the years in which rotifers were studied.

Table 7. Potential rotifer production in Kootenay Lake, based on average seasonal average biomass (wet weight) observed in 1994 - 1996, and growing season P/B ratios from other north temperate lakes (Makarewicz and Likens 1979).

		P/B ratios				
Year		8.2	14	26.3	64.6	85.7
Production / Season	1994	179	306	575	1413	1875
(April-Oct., mg·m ⁻³ ·season ⁻¹)	1995	284	485	912	2239	2970
	1996	215	367	689	1693	2246

Macrozooplankton

Body Size

Zooplankton body size data for each month and station sampled from 1992 to 1997 are shown in Fig. 44. Values shown are the average dry weight of an individual of a particular species, calculated from the measurement of up to 30 individuals per sample. The average size of individuals of each species does not appear to have changed from 1992 to 1997, with the exception of *Daphnia*. The average size of *Daphnia* was greater in 1992 than in subsequent years, particularly during the peak biomass months of August and September (Fig. 45). In 1992 average individual weights (station averages) ranged from 15 to 33 µg in August, and from 25 to

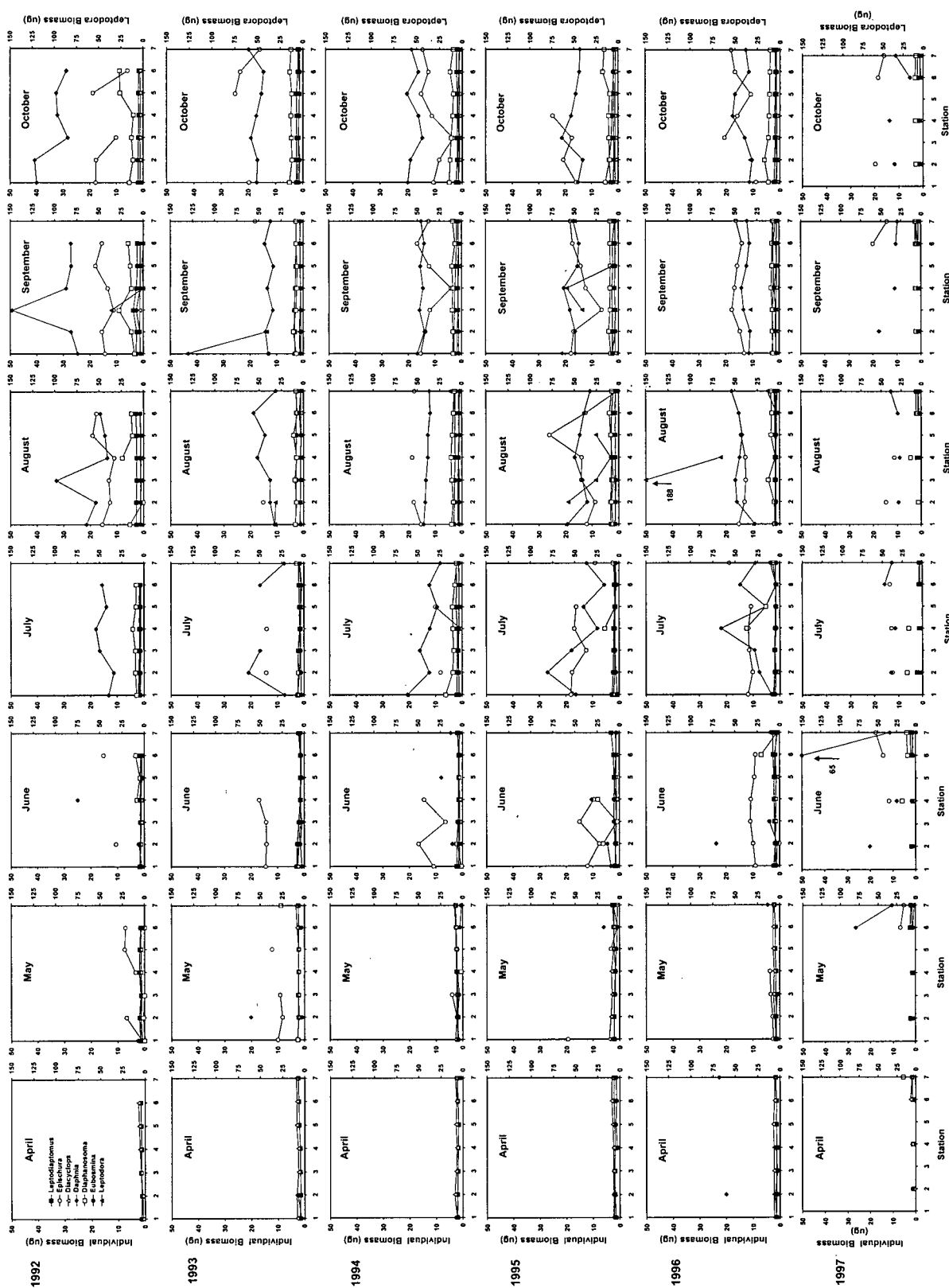


Fig. 44. Zooplankton species size data (biomass dry weight) plotted by month and station for 1992 - 1997.

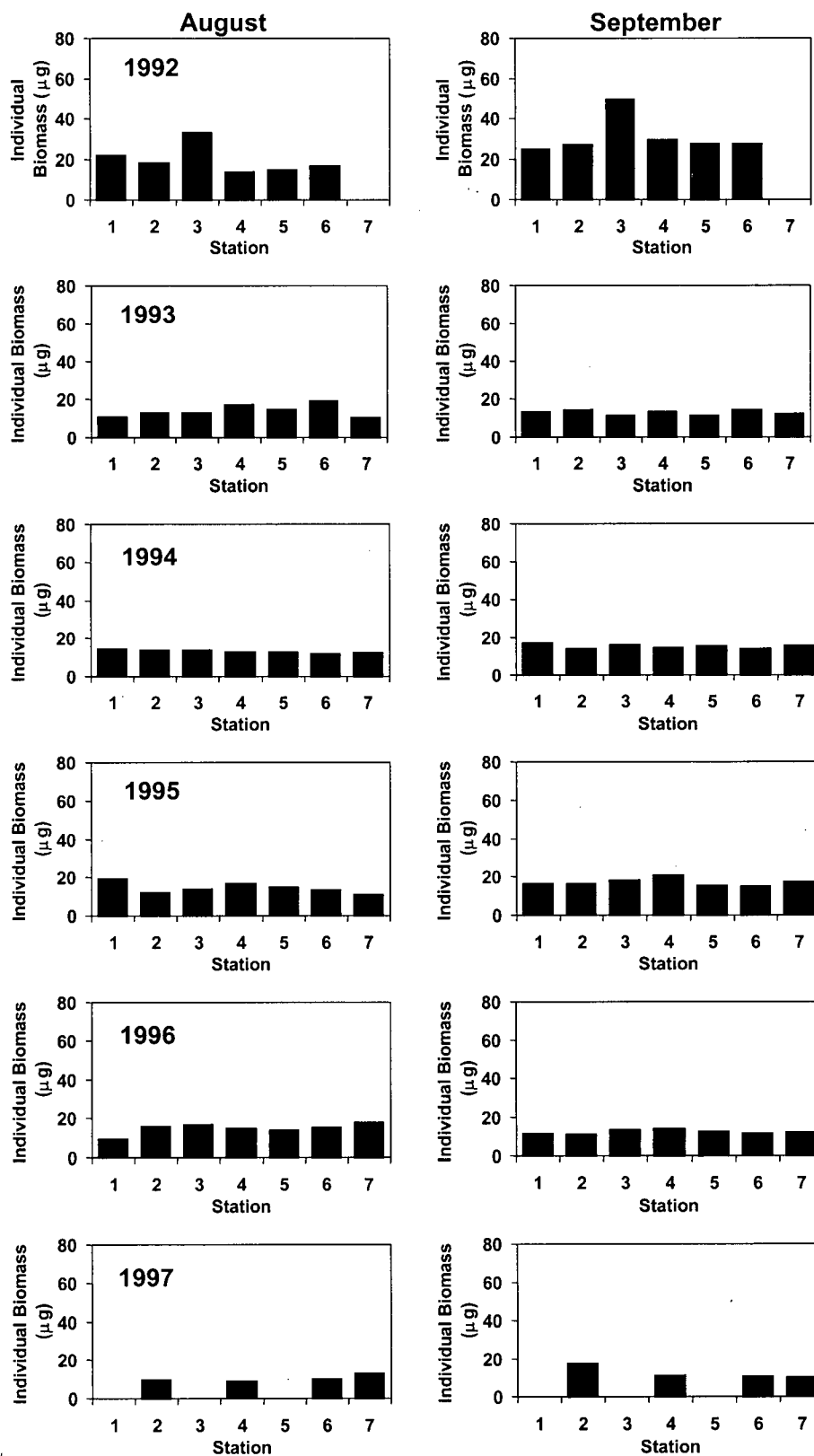


Fig. 45. *Daphnia* spp. size data (biomass dry weight) for August and September, 1992 - 1997.

49 μg in September. From 1993 onward the average individual weight in August and September did not exceed 21 μg at any station. Like the abundance data, the body size data do not show any clear spatial trends along the phytoplankton biomass gradient (Fig. 44). In August and September 1992 *Daphnia* individual biomass was higher at Station 3 than at other stations, but Stations 1 and 2, which were closer to the fertilization site, showed individual biomasses similar to the South Arm of the lake (Fig. 45). From 1993 to 1997 *Daphnia* size was similar at all stations along the length of the lake.

Fecundity

Growing season average fecundities are presented for the most common copepod species, *L. ashlandi*, and *D. bicuspidatus thomasi*, and for *Daphnia* spp. *L. ashlandi* had higher numbers of eggs per water volume in 1993 and 1994 in comparison with years before and after (Table 8). The number of eggs per female was approximately 10 from 1992 to 1994, then increased from 1995 to 1997. The number of eggs per capita and the proportion of females gravid were similar in all years except 1996, when both these variables were lower.

For *D. bicuspidatus thomasi* the number of eggs per water volume was lower in 1992 than in subsequent years (Table 9). The number of eggs per female increased from 9 in 1992 to about 10 in 1993, and 11 or higher from 1994 onward. The number of eggs per capita was 0.21 eggs·individual⁻¹ in 1992. This value was higher from 1993 to 1995, declined to 0.30 eggs·individual⁻¹ in 1996, then increased again to 0.47 eggs·individual⁻¹ in 1997. The proportion of females gravid showed a similar pattern, with a low value occurring in 1992 and the lowest value, 0.08, in 1996.

In the case of *Daphnia* spp., the number of eggs per water volume declined steadily from a high of 0.69 eggs·L⁻¹ in 1992 to 0.24 eggs·L⁻¹ in 1997 (Table 10). Fecundity per gravid female was over 3 eggs·female⁻¹ from 1992 to 1995, then declined to below 3 eggs·female⁻¹ in 1996 and

1997. The number of eggs per capita and the proportion of females gravid were also lower in 1996 and 1997 than in previous years.

Table 8. Fecundity data for *L. ashlandi*. Data presented are growing season (April - October) averages (bi-weekly samples at six stations in 1992, bi-weekly samples at seven stations from 1993-1996, and monthly samples at four stations in 1997). Data shown are the number of eggs per volume (eggs·L⁻¹), number of eggs per gravid female (eggs·gravid female⁻¹), per capita egg number (eggs·individual⁻¹), and the proportion of females gravid.

Year	Eggs per Volume	Eggs per Gravid Female	Eggs per Capita	Proportion Females Gravid
1992	1.30	10.00	0.29	0.12
1993	2.72	9.80	0.37	0.16
1994	2.07	9.92	0.30	0.13
1995	1.69	11.36	0.32	0.15
1996	1.41	12.73	0.20	0.05
1997	1.53	13.72	0.36	0.18

Seasonal Observations (Temporal and Spatial)

There were no consistent trends in fecundity along the length of the lake for *L. ashlandi* (Fig. 46), *D. bicuspidatus thomasi* (Fig. 47), or *Daphnia* spp. (Fig. 48), from 1992 to 1997. Due to a miscommunication about counting methods, fecundity data were not recorded for some stations in most months of 1993. The data available for 1993 are shown for reference but I will not comment on them further with regard to seasonal patterns.

Table 9. Fecundity data for *D. bicuspidatus thomasi*. Data presented are growing season (April - October) averages (bi-weekly samples at six stations in 1992, bi-weekly samples at seven stations from 1993-1996, and monthly samples at four stations in 1997). Data shown are the number of eggs per volume (eggs·L⁻¹), number of eggs per gravid female (eggs·gravid female⁻¹), per capita egg number (eggs·individual⁻¹), and the proportion of females gravid.

Year	Eggs per Volume	Eggs per Gravid Female	Eggs per Capita	Proportion Females Gravid
1992	1.14	8.96	0.21	0.13
1993	2.30	10.10	0.53	0.22
1994	2.72	10.51	0.46	0.18
1995	2.85	11.52	0.64	0.22
1996	2.74	11.47	0.30	0.08
1997	2.79	11.94	0.47	0.27

In May, June, and July, 1992 *L. ashlandi* females carried more eggs per female in the North Arm (Fig. 46). However, this trend was not seen in other months. The number of eggs per water volume was higher in the South Arm in May, 1992, but there was no trend in other months. In May and June, 1994, May, 1995, and May, 1997 the number of eggs per water volume was higher in the South Arm. The proportion of females gravid was higher in the South Arm in June, 1994, and the number of eggs per female was higher in the South Arm in May, 1997. There were no trends in fecundity in 1996.

Table 10. Fecundity data for *Daphnia* spp. Data presented are July - October averages (bi-weekly samples at six stations in 1992, bi-weekly samples at seven stations from 1993-1996, and monthly samples at four stations in 1997). Data shown are the number of eggs per volume (eggs·L⁻¹), number of eggs per gravid female (eggs·gravid female⁻¹), per capita egg number (eggs·individual⁻¹), and the proportion of females gravid.

Year	Eggs per Volume	Eggs per Gravid Female	Eggs per Capita	Proportion Females Gravid
1992	0.69	3.06	0.60	0.20
1993	0.61	3.40	0.51	0.15
1994	0.57	3.10	0.54	0.16
1995	0.56	3.63	0.68	0.19
1996	0.48	2.75	0.30	0.12
1997	0.24	2.16	0.33	0.14

Like *L. ashlandi*, *D. bicuspidatus thomasi* showed higher numbers of eggs per female in the North Arm in May and June, 1992 (Fig. 47). In June, 1992 there were also higher eggs per water volume, and a higher proportion of females gravid in the North Arm. These trends were not seen in other months. In May of 1994, females again carried more eggs in the North Arm, but no other trends were seen in this or other months. In May, 1995 *D. bicuspidatus thomasi* had higher eggs per capita in the North Arm, and from June to September there were higher numbers of eggs per water volume in the North Arm. In May and June, 1996 females in the North Arm carried higher numbers of eggs, and there was a higher number of eggs per water volume in the North Arm in June. There were no trends in other months. In May, 1997 *D. bicuspidatus*

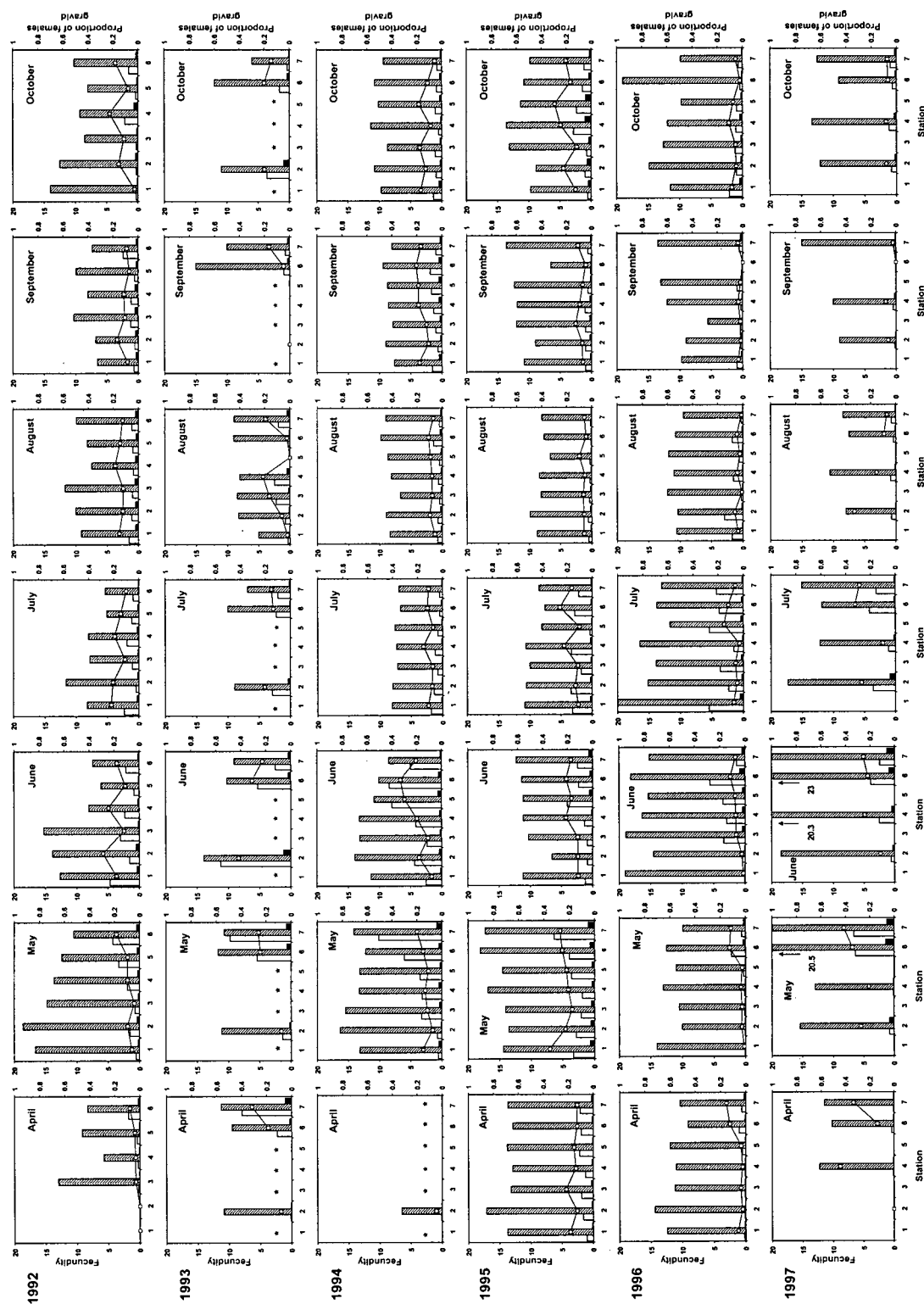


Fig. 46. *Leptodiaptomus ashlandi* fecundity for 1992-1997, plotted by month and station. Data shown are the number of eggs per volume (eggs·L⁻¹, white bar), number of eggs per gravid female (eggs·gravid female⁻¹, hatched bar), per capita egg number (eggs·individual⁻¹, black bar), and the proportion of females gravid (white square with black line). An asterisk indicates that fecundity data were not recorded for zooplankton at a station.

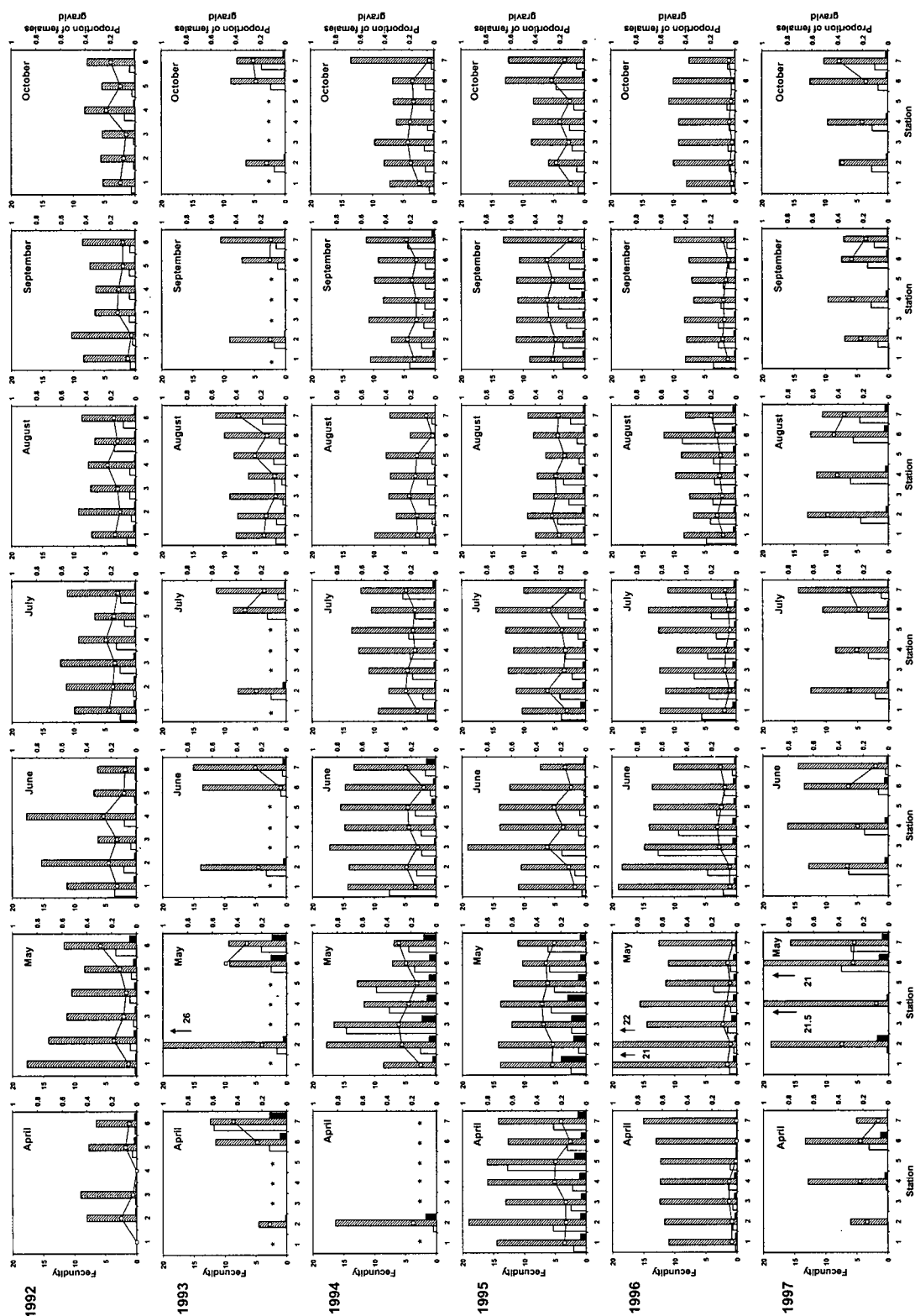


Fig. 47. *Diacyclops bicuspidatus thomasi* fecundity for 1992-1997, plotted by month and station. Data shown are the number of eggs per volume (eggs L^{-1} , white bar), number of eggs per gravid female ($\text{eggs gravid female}^{-1}$, hatched bar), per capita egg number ($\text{eggs individual}^{-1}$, black bar), and the proportion of females gravid (white square with black line). An asterisk indicates that fecundity data were not recorded for zooplankton at a station.

thomasi had higher numbers of eggs per water volume in the South Arm, but this pattern was reversed in June, and there were no trends in this or other variables in other months.

There were very weak trends for *Daphnia* spp. to have higher eggs per capita, and a higher proportion of females gravid in the North Arm in August and September, 1992, but these patterns were not seen in July or October (Fig. 48). These trends were seen again in 1994, but only in July. In all months in 1995 (July - October) there was a trend toward more eggs per capita in the North Arm. In 1996 *Daphnia* spp. showed no fecundity trends, except for a weak tendency for more eggs per capita and a higher proportion of females gravid in the North Arm in September. Finally, in 1997 there was again a higher proportion of females gravid in the North Arm in September, but there were no trends in the other fecundity variables.

Lack of spatial and temporal patterns of fecundity response to fertilization could mean either that there was no clear P/B response, or that the response was concentrated in the body growth component of production. I was not able to measure changes in body growth rates directly, but lack of change in mean size suggests growth rates also did not change substantially.

Zooplankton Production Estimates

The seasonal average P/B ratio and mean daily turnover time of *L. ashlandi* did not show any consistent trends along the lake in 1992 - 1997 (Fig. 49). P/B values ranged from a minimum of 3.32 at Station 4 in 1997, to a maximum of 9.22 at Station 6 in 1992. Turnover times ranged from a minimum of 18.22 days at Station 6 in 1992, to a maximum of 57.23 days at Station 4 in 1996.

For *D. bicuspidatus thomasi*, seasonal P/B ratios and mean daily turnover time also did not show any clear trends along the lake over the 1992 - 1997 period (Fig. 50). The minimum P/B ratio, 2.22, and maximum turnover time, 75.56 days, were seen at Station 2 in 1992. The

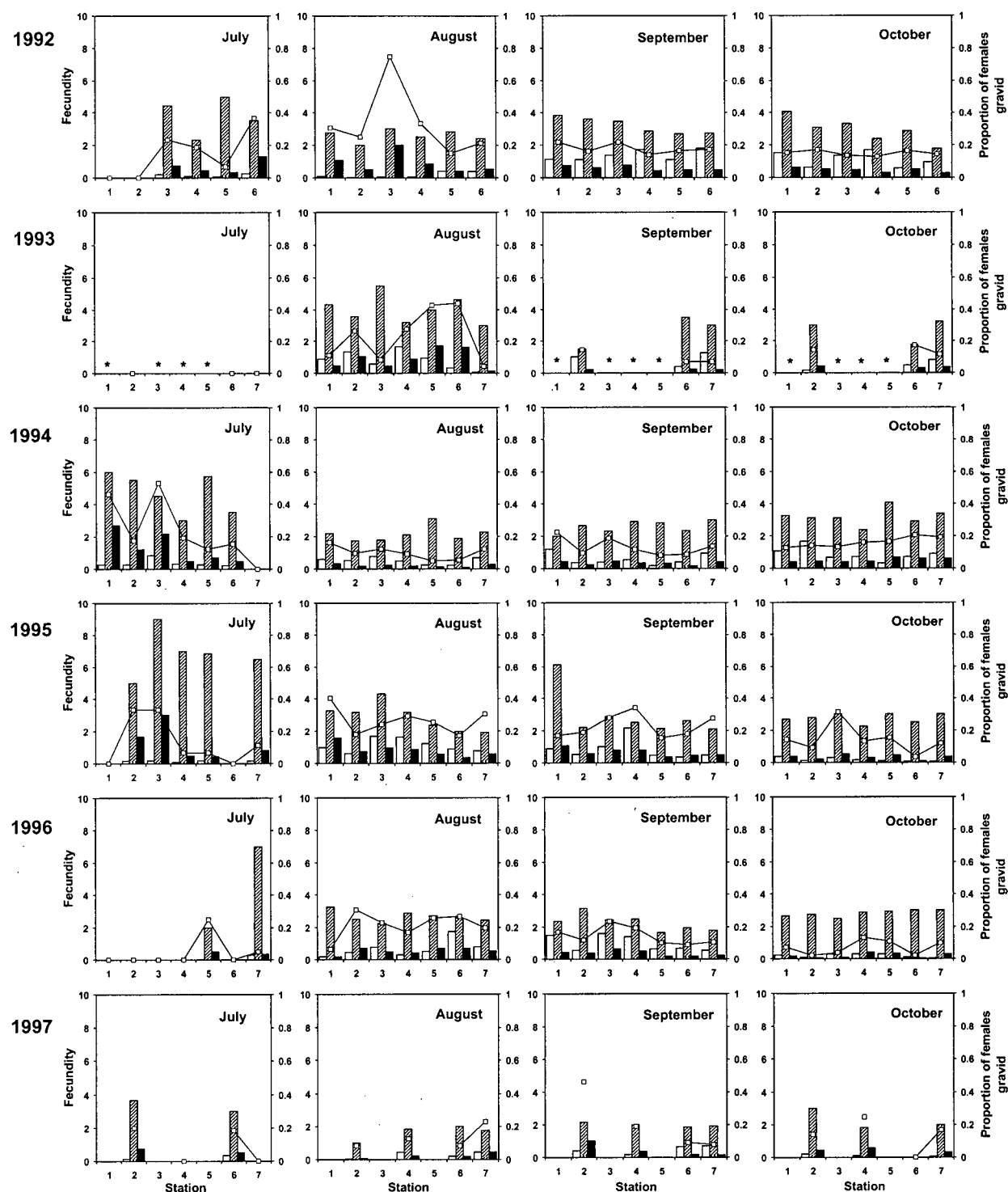


Fig. 48. *Daphnia* spp. fecundity for 1992-1997, plotted by month and station. Data shown are the number of eggs per volume ($\text{eggs} \cdot \text{L}^{-1}$, white bar), number of eggs per gravid female ($\text{eggs} \cdot \text{gravid female}^{-1}$, hatched bar), per capita egg number ($\text{eggs} \cdot \text{individual}^{-1}$, black bar), and the proportion of females gravid (white square with black line). An asterisk indicates that fecundity data were not recorded for zooplankton at a station.

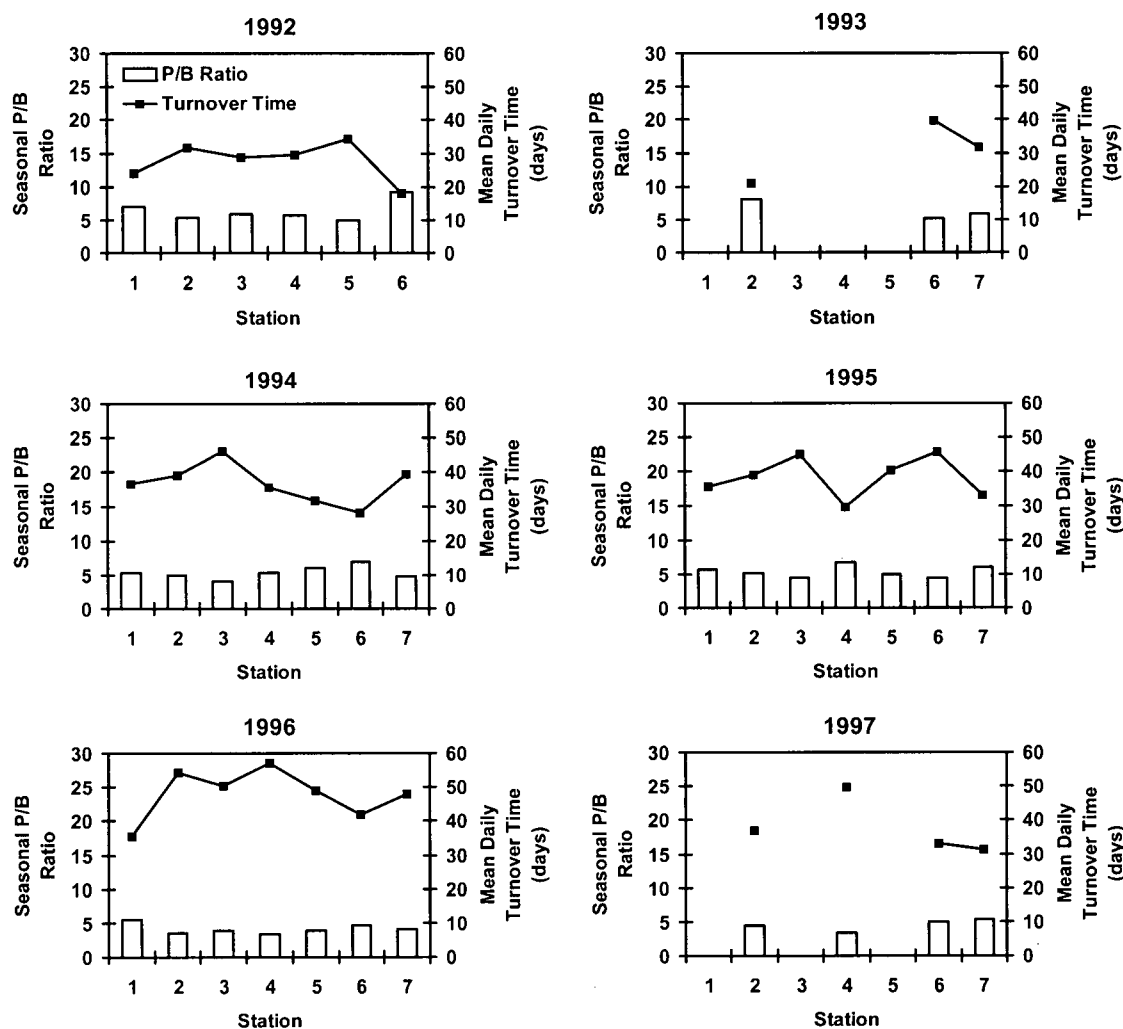


Fig. 49. Seasonal average P/B ratios, and mean daily turnover time for *L. ashlandi* for 1992 - 1997, plotted by station.

maximum P/B ratio, 10.39, and minimum turnover time, 19.35 days, were observed at Station 4 in 1995.

Daphnia spp. also showed no consistent trends along the lake for the seasonal average P/B ratio, nor the mean daily turnover time (Fig. 51). However, *Daphnia* spp. P/B ratios were approximately double those of the copepods, and the turnover times were about half those seen for copepods. P/B values ranged from 4.27 at Station 7 in 1997, to 20.45 at Station 4 in 1995. The turnover time ranged from 9.45 days at Station 6 in 1992, to 38.68 days at Station 7 in 1997.

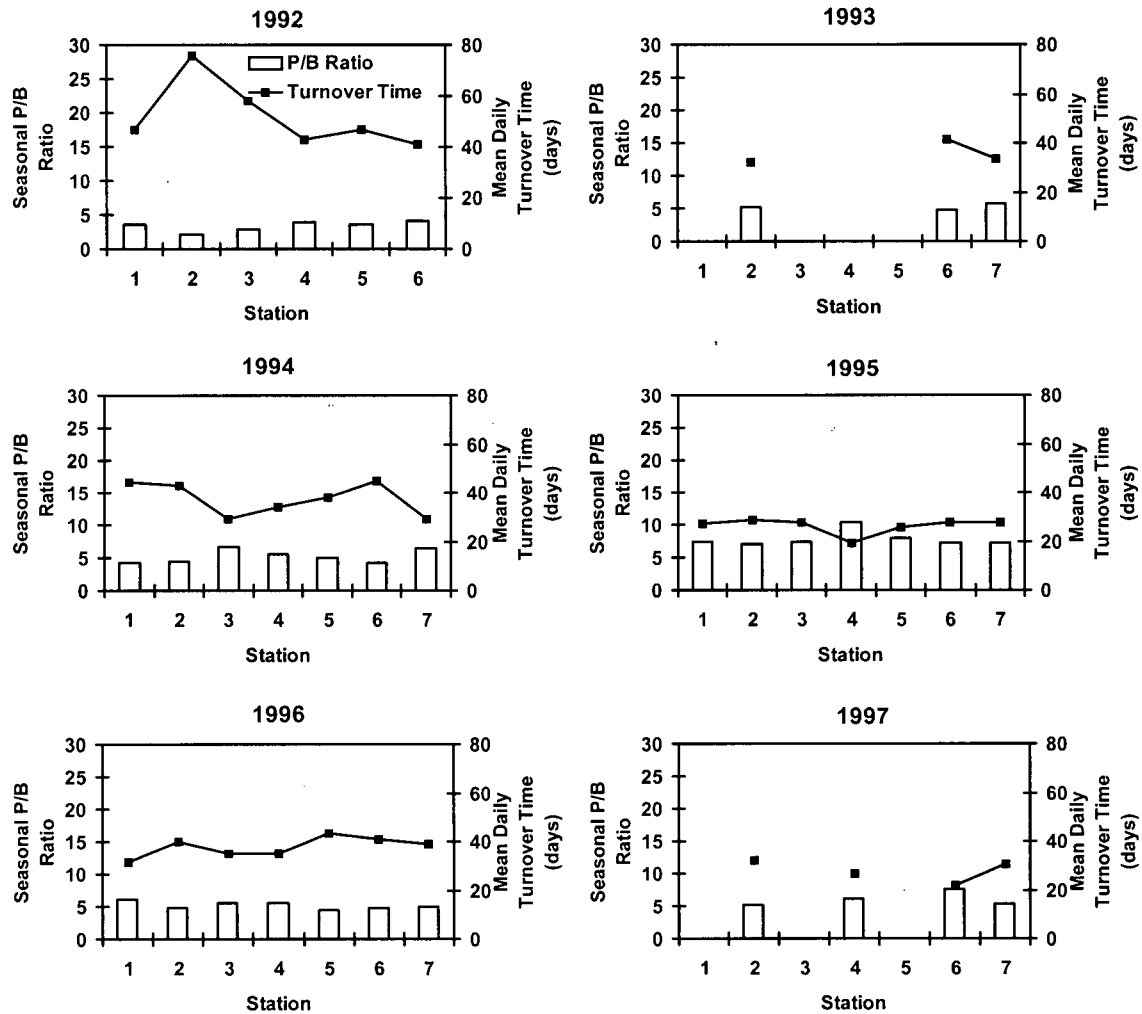


Fig. 50. Seasonal average P/B ratios, and mean daily turnover time for *D. bicuspidatus thomasi* for 1992 - 1997, plotted by station.

The seasonal production values calculated for Kootenay Lake macrozooplankton are comparable to values in the literature (Wetzel 1983). Growing season standing stock biomass was relatively high, and similar to data for eutrophic lakes. Production was similar to oligotrophic and mesotrophic lakes (there was a great deal of overlap between these lake types). Turnover times were similar to those seen in other north temperate lakes, although in some years turnover times in Kootenay Lake were longer than usual for this lake type. On a lake-wide basis *L. ashlandi* was most productive in 1993, with the highest values seen for both daily average P/B

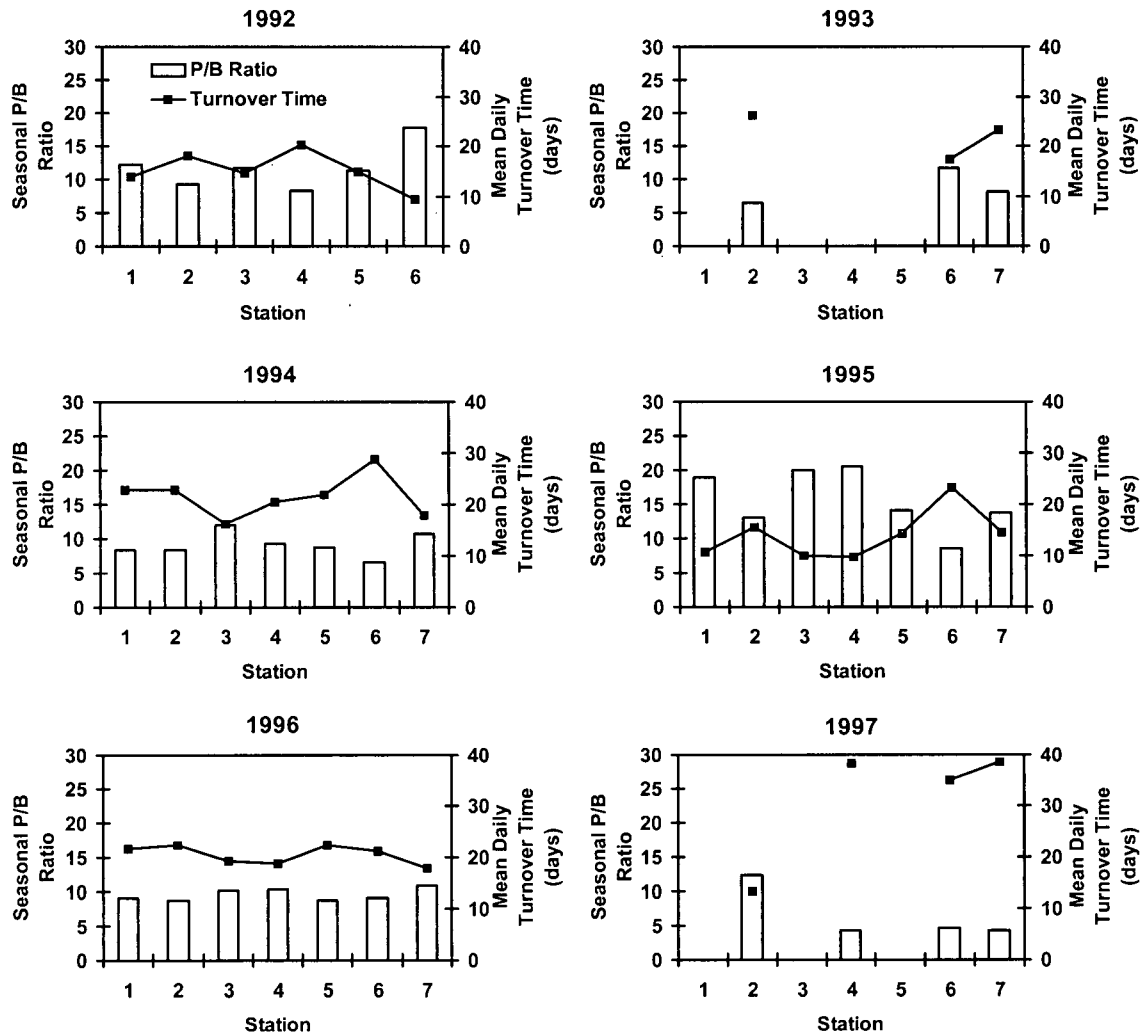


Fig. 51. Seasonal average P/B ratios, and mean daily turnover time for *Daphnia* spp. for 1992 - 1997, plotted by station.

and seasonal average P/B, as well as the highest standing stock biomass, and shortest turnover time (Table 11). Production declined for the next three years, and *L. ashlandi* was least productive in 1996, when the lowest P/B ratios occurred. Production was also low in 1997; the amount of new biomass produced was the lowest in the six year period, and the standing stock biomass was the second lowest, but the resulting P/B ratios were slightly higher than in 1996.

Table 11. Production data for *L. ashlandi*. Data presented are whole-lake May - October averages (bi-weekly samples at six stations in 1992, bi-weekly samples at seven stations from 1993-1996, and monthly samples at four stations in 1997). Data shown are total seasonal biomass production, $\sum_{t_0}^{t_n} B_{new}$ (mgm^{-3} , i.e., the sum of the new biomass produced during each time interval), average biomass produced per day, \overline{B}_{new} ($\text{mgm}^{-3}\text{day}^{-1}$), average standing stock biomass during the season, \overline{B}_{mean} (mgm^{-3}), daily average P/B ratio, $P/B_{DailyAverage}$ (days^{-1}), mean daily turnover time (days), and seasonal total P/B ratio, $P/B_{SeasonalAverage}$. All biomasses are dry weight.

Year	$\sum_{t_0}^{t_n} B_{new}$	\overline{B}_{new}	\overline{B}_{mean}	P/B	Turnover	P/B
				Daily Average	Time	Seasonal Average
1992	57.30	0.31	9.12	0.03	28.98	6.28
1993	103.68	0.51	14.40	0.04	28.06	7.20
1994	77.81	0.41	13.89	0.03	34.08	5.60
1995	59.67	0.30	11.85	0.03	39.93	5.03
1996	53.19	0.27	12.32	0.02	45.17	4.32
1997	42.84	0.26	9.69	0.03	37.33	4.42

The production of *D. bicuspidatus thomasi* increased from 1992 to 1995, when highest P/B ratios and maximum new biomass (dry weight) were seen (Table 12). In 1996 the standing stock biomass was the highest observed, but the seasonal average P/B was the second lowest. In 1997 the P/B ratios increased, but since the standing stock biomass was the lowest seen the amount of new biomass produced was the lowest since 1992. The peak year for *D. bicuspidatus thomasi* production, 1995, corresponds with the peak year for nanoplankton biomass.

Table 12. Production data for *D. bicuspidatus thomasi*. Data presented are whole-lake May - October averages (bi-weekly samples at six stations in 1992, bi-weekly samples at seven stations from 1993-1996, and monthly samples at four stations in 1997). Data shown are total seasonal biomass production,

$\sum_{t_0}^{t_n} B_{new}$ (mgm^{-3} , i.e., the sum of the new biomass produced during each time interval), average

biomass produced per day, \bar{B}_{new} ($\text{mgm}^{-3}\cdot\text{day}^{-1}$), average standing stock biomass during the season,

\bar{B}_{mean} (mgm^{-3}), daily average P/B ratio, $P/B_{DailyAverage}$ (days^{-1}), mean daily turnover time

(days), and seasonal total P/B ratio, $P/B_{SeasonalAverage}$. All biomasses are dry weight.

Year	$\sum_{t_0}^{t_n} B_{new}$	\bar{B}_{new}	\bar{B}_{mean}	P/B	Turnover	P/B
				Daily Average	Time	Seasonal Average
1992	36.42	0.20	11.51	0.02	57.50	3.17
1993	69.91	0.35	11.72	0.03	33.87	5.96
1994	71.67	0.38	11.57	0.03	30.83	6.20
1995	87.02	0.43	11.35	0.04	26.21	7.67
1996	85.15	0.44	16.05	0.03	36.77	5.30
1997	62.70	0.38	9.70	0.04	25.51	6.47

Daphnia spp. production was relatively high in 1992, and peaked in 1995 with a seasonal average P/B ratio of 15, and daily average P/B ratio of 0.08 day^{-1} (Table 13). In 1997 the seasonal average P/B ratio dropped to 5, and the daily average P/B ratio dropped to 0.03 day^{-1} , about one third of the 1995 values. Over the six-year period the standing stock biomass (dry weight) declined fairly steadily from 28 mgm^{-3} to 7 mgm^{-3} . In combination with the P/B ratios, this resulted in a drop in the annual new biomass produced from 310 mgm^{-3} in 1992 to 37 mgm^{-3} in 1997. Because of the lack of pre-fertilization production data, it is not possible to tell if *Daphnia* spp. production is following a long term trend of decline. Alternatively, production may have increased during the

Table 13. Production data for *Daphnia* spp. Data presented are whole-lake May - October averages (bi-weekly samples at six stations in 1992, bi-weekly samples at seven stations from 1993-1996, and monthly samples at four stations in 1997). Data shown are total seasonal biomass production, $\sum_{t_0}^{t_n} B_{new}$ (mgm^{-3} , i.e., the sum of the new biomass produced during each time interval), average biomass produced per day, \bar{B}_{new} ($\text{mgm}^{-3}\cdot\text{day}^{-1}$), average standing stock biomass during the season, \bar{B}_{mean} (mgm^{-3}), daily average P/B ratio, $P/B_{DailyAverage}$ (days^{-1}), mean daily turnover time (days), and seasonal total P/B ratio, $P/B_{SeasonalAverage}$. All biomasses are dry weight.

Year	$\sum_{t_0}^{t_n} B_{new}$	\bar{B}_{new}	\bar{B}_{mean}	P/B	Turnover	P/B
				Daily Average	Time	Seasonal Average
1992	310.47	1.71	27.80	0.06	16.30	11.17
1993	112.06	0.55	12.03	0.05	21.68	9.32
1994	130.73	0.68	13.55	0.05	19.79	9.65
1995	160.59	0.80	10.38	0.08	12.99	15.48
1996	94.04	0.48	9.53	0.05	19.76	9.87
1997	36.79	0.22	6.91	0.03	31.00	5.32

first years of fertilization, and may gradually be returning to pre-fertilization levels as predator (kokanee and *M. relicta*) abundance and consumption of *Daphnia* spp. increase. *Daphnia* spp. production peaked in 1995, the year of peak nanoplankton biomass, as was the case for *D. bicuspidatus thomasi*. The annual peak in density and biomass for both these species occurs in late summer (August and September), unlike *L. ashlandi*, which usually peaks earlier, in July.

Bias in *Daphnia* spp. Z_{biom} Caused by Kokanee Fry Size Selective Predation

Size selective predation on *Daphnia* spp. by kokanee fry caused Z_{biom} (biomass mortality rate) due to kokanee fry to be higher than Z_{num} (numbers mortality rate) due to fry (Table 14). Individual *Daphnia* biomass in fry stomachs averaged over 25 μg at both stations. At the same time the average weight of *Daphnia* in the lake was 11.95 μg and Station 2, and 13.04 μg at Station 6. Bias in Z_{biom} occurred at both stations, but was greater at Station 2 because of the higher fry density, and larger proportion of standing stock biomass consumed there. Although size selective fry predation on zooplankton causes a bias in the mortality rate assumed in the calculation of zooplankton production, the actual mortality caused by fry is very small relative to the standing stock biomass of zooplankton. *M. relicta* consumes a much higher proportion of the standing stock biomass than do kokanee, and older age classes of kokanee (1+ - 3+) consume a higher proportion of zooplankton standing stock than fry (see Table 19). It is unlikely that the differential bias in Z_{biom} caused by kokanee fry along the lake is enough to obscure a pattern of higher zooplankton production in the fertilized end of the lake.

Table 14. Mortality rates of *Daphnia* biomass and numbers due to kokanee fry at Stations 2 and 6 in August 1995. B_{con} is the *Daphnia* spp. biomass consumed by fry per hectare, B_{indiv} is the average biomass of individual *Daphnia* in fry stomachs, N_{con} is the numbers consumed per hectare, and N is *Daphnia* spp. density per hectare.

Station	B_{con}	B_{indiv}	N_{con}	N	Z_{num}	Z_{biom}	Ratio
	(mg/ha)	(μg)	(#/ha)	(#/ha)			($Z_{\text{biom}}/Z_{\text{num}}$)
2	15,759	27.83	566,259	5.88×10^8	0.00096	0.002	2.08
6	2,059	25.17	81,804	1.08×10^9	0.000076	0.0001	1.32

Enclosure Experiment

The zooplankton enclosure experiment was attempted in order to estimate the population growth rate of zooplankton species in the absence of predation. It was considered possible that zooplankton populations in the main body of the lake were suppressed by predation by fish and *M. relicta*, and if so the populations would increase to the carrying capacity set by food availability once in the safety of the enclosures. This would allow the measurement of the component of mortality due to predation in the main lake. Fecundity estimates from the enclosures were to be used as a check against the fecundity data collected in the routine zooplankton sampling, which may have been biased due to egg loss during sampling with the Clarke-Bumpus net.

The zooplankton populations failed to thrive in the enclosures, but the reasons for this are unclear. It may be that pollutants from motor boats at the nearby marina increased the mortality rate of zooplankton in the enclosures. Temperature may have been a factor, since the enclosures were only 4 m deep (the maximum possible at the location), so zooplankton would not have been able to migrate down to cooler water and lower their metabolic rates to conserve energy. Alternatively, the phytoplankton (which was expected to come in to the enclosures through the mesh, since it had 193 μm holes) may not have been of the same composition as in the main lake and may have had a lower proportion of grazeable algae. In each of the three sets of enclosures the density of *Daphnia* spp. and *D. brachyurum* never reached the levels seen in the main lake over the same time period, and densities only increased for a few sample dates before declining below the initial levels. Daily average P/B ranged from 0.004 - 0.009 day^{-1} for the 3 sets of enclosures, resulting in turnover times ranging from 115 - 244 days. Daily average P/B ratios for *D. brachyurum* ranged from 0.002 - 0.036 day^{-1} , while turnover times ranged from 27 - 465 days. *D. brachyurum* production was not calculated for the main lake samples but the enclosure

values are of the same order of magnitude as the enclosure values for *Daphnia* spp., and are likely low relative to natural populations.

Kokanee Growth

Time Series Changes in Size

Kokanee spawner size in the fall trawls was similar from 1985 to 1991 (Fig. 52). Spawner size increased from 1992 to 1995, then decreased in 1996 and 1997 to the lowest sizes seen in this time series (1985 to 1997). In 1990 the age 2+ year class grew more than in previous years, but this cohort grew less in 1991, so the average final size was similar to previous years. The cohort which emerged in 1989 (black triangles) grew more than previous cohorts in its 1+ and 2+ years (1990 and 1991) resulting in larger size at age 3+ than seen for previous cohorts. Similar patterns were seen for the 1990, 1991, and 1992 cohorts. However, the growth rates of the 1993 and 1994 cohorts were lower than the 1989 to 1992 cohorts, particularly in the 2+ and 3+ years. Kokanee size-at-age began to increase prior to the fertilizer experiment, and began to decline in the fourth year of fertilization (1995). Kokanee growth rates appear to be negatively correlated with kokanee abundance. As the population reached very low densities in 1990 and 1991, size-at-age began to increase. As the population increased, kokanee growth rates declined to below pre-fertilization levels. There appears to be a trade-off between kokanee abundance and individual size in Kootenay Lake, probably due to intraspecific competition for zooplankton. Similar responses have been seen for kokanee in Idaho lakes (Rieman and Myers 1992). However, in Kootenay Lake the total biomass of kokanee (age 0+, 1+, and 2+) in September has increased during the fertilization experiment, from approximately 130 t in 1992, to 136 t in 1993, 258 t in 1994, and 187 t in 1995. Kokanee biomass was about 519 t in 1996 and 386 t in 1997 (All biomass estimates were calculated from the total abundance estimate for the lake, multiplied by the average individual weight in September for each age class, and accounting for the fraction

that fry and older fish comprised in September hydroacoustic sampling; older fish were fractioned into 1+ and 2+ classes based on relative abundance in trawl catches). In other words, although individual kokanee size-at-age has declined as abundance increased, the decrease in size did not fully “compensate” for the increase in numbers. Therefore, there is now greater kokanee biomass available to prey on zooplankton and on *M. relictus*, to compete with *M. relictus* and with other fish species for zooplankton, and as prey for trout and other predatory fishes.

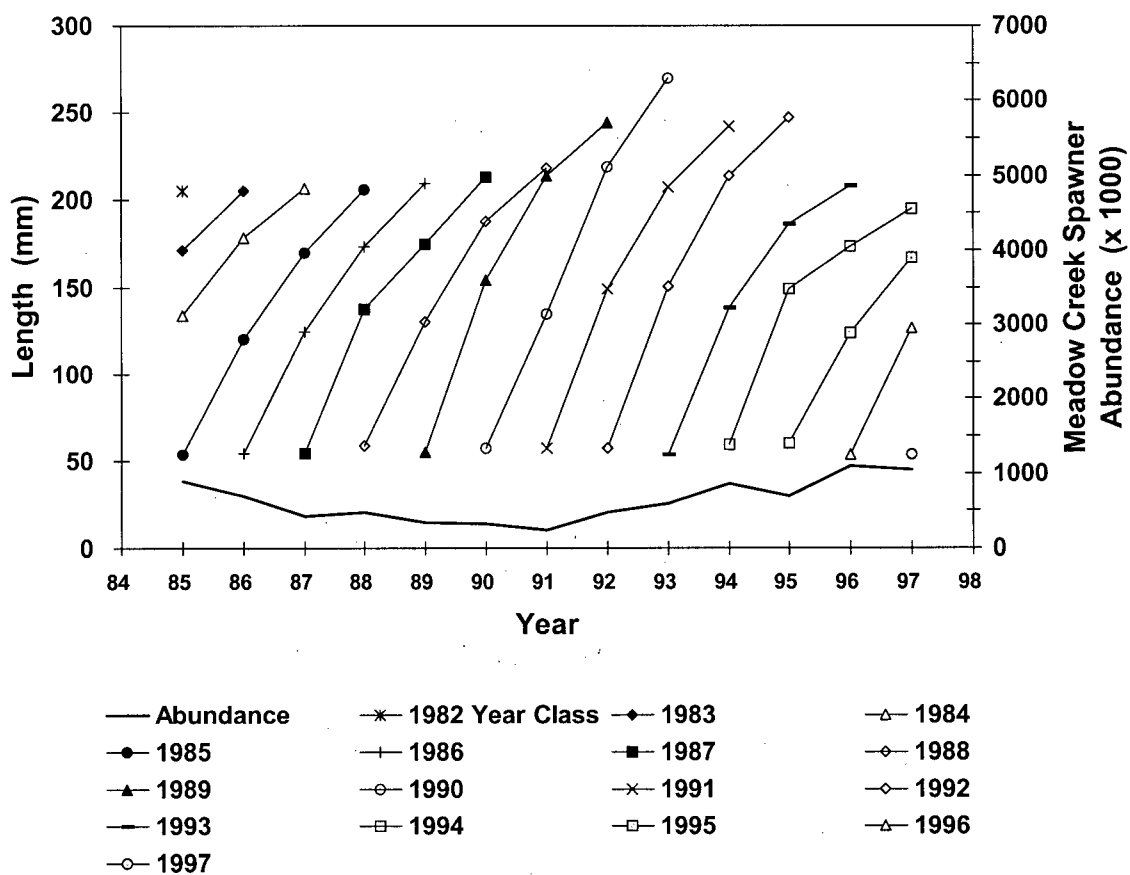


Fig. 52. Kokanee length-at-age observed during autumn (near the new moon closest to October 1) plotted with Meadow Creek spawner abundance (1985 to 1997). Lengths of kokanee aged 0+ to 2+ are from fish captured in the major autumn trawl series. Lengths of age 3+ kokanee are from fish measured at the Meadow Creek spawning channel.

The observed changes in kokanee spawner size are also related to shifts in the age of spawning, according to otolith-based ages of kokanee spawners at Meadow Creek. Historically kokanee have returned to spawn at age 3+ (i.e., just as they are about to turn 4). However, in 1992 there was a shift toward more kokanee returning to spawn at age 4+, and this probably contributed to the increase in average spawner size (Table 15). In 1993, the year with the highest average spawner size on record, there was still a high proportion of age 4+ spawners, but also an increase in the proportion of age 2+ spawners. In 1994 the proportion of 2+ spawners reached 42%, and spawner size declined. The proportion shifted toward age 4+ spawners again in 1995, although more than 25% of the fish were 2+, and the average size rebounded somewhat. In 1996, the last year for which otoliths have been analyzed, over 40% of spawners were age 2+, and spawner size declined further.

Table 15. Contribution of different age classes to the kokanee spawner run at Meadow Creek channel from 1989 to 1996. Ages were determined from readings of sagittal otolith annual growth rings.

Year	Kokanee Spawner Age Proportions (%)				
	2 (1+)	3 (2+)	4 (3+)	5 (4+)	6 (5+)
1989	0	13.4	86.6	0	0
1990	0	0	92.5	7.5	0
1991	0	0	100	0	0
1992	0	0	82	18	0
1993	0	14.7	62.4	22.9	0
1994	0	41.9	52.7	5.4	0
1995	1.6	26	55.7	13.6	3.1
1996	4.1	41.5	42.2	10.2	2

More detailed size-at-age data are available from 1992 to 1996, when trawls were conducted monthly from May until October, and 1997, when trawls were done in July and September (Fig. 53). Data points are the average size of the age class at each station sampled in each month, and the x-axis scale is the day of the year. There is a gap in the data points between each year of sampling, since no sampling was conducted during the winter. It appears that there was very little growth during the winter, since fish in the fall of a given year were about the same size as fish in the same cohort the following spring. Fish growth in the 0+ and 1+ year classes was quite linear; the growth rate (slope of curve) did not decline as fish grew larger across the season. However, this result may be an artifact of size selective predation. If the smallest fish in a year class had a higher predation mortality rate, this would have caused the average size of the remaining fish to increase. This would cause the observed growth relationship to become more linear, even if individual fishes' growth rates declined with increasing size.

Von Bertalanffy growth curves are plotted in Fig. 53 for the 1991 to 1996 cohorts. However, the curves are fitted to all four years of growth for the 1992 to 1994 cohorts only, so the remaining curves are inaccurate. For the three years where the data are complete, the within-season data show the same pattern as seen in the autumn data in Fig. 52. Growth rates of age 1+ and 2+ kokanee were higher for the 1992 cohort than for the 1993 and 1994 cohorts, resulting in successively smaller spawners during this period. Although the data for the 1989 to 1990 cohorts are incomplete, the body size of the year classes for which data are available suggest that growth rates were higher for these cohorts than for subsequent cohorts.

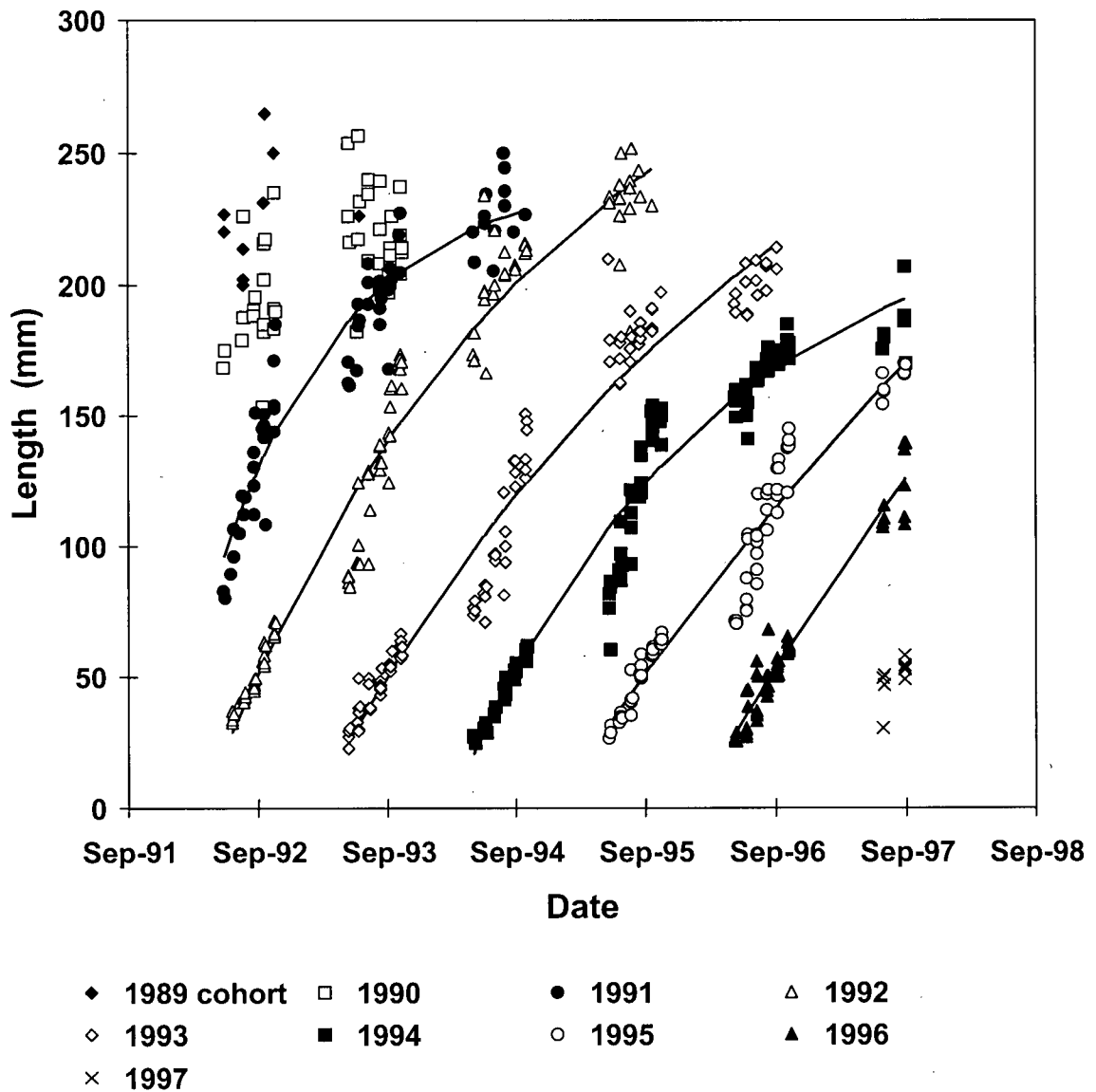


Fig. 53. Von Bertalanffy growth curves showing length-at-age of trawl-caught kokanee from May to October (near the new moon each month) of 1992 to 1997. Data points are average size at each station in each month sampled. In 1997 trawls were conducted in July and September only.

Within-Season Patterns in Size

I compared the length-at-age and weight-at-age of the four main age classes of kokanee along the productivity gradient, and through each growing season from 1992 to 1997. The data are presented grouped by age class, with six years of data shown on each page. Therefore data for different ages of a particular cohort appear on different pages, since it was important to

determine whether particular age classes consistently experienced differential growth along the productivity gradient. Kokanee fry grew from about 27 mm to over 60 mm each year, during the period from May to October (Fig. 54). Fry in the South Arm were over 70 mm by October 1992, but fry this large were not observed in subsequent years. In all years there was a tendency for fry in the South Arm to be larger than those in the North Arm. Extreme examples of this can be seen in September 1992, July 1993, and June, July and August 1996. As the data are plotted, if fry were of similar sizes at all stations within a given month, the plots would look like a staircase across the season, rather than a continuous diagonal line of points. This pattern of increased size in the unfertilized end of the lake may result from fry in the South Arm being older than those in the North Arm, as discussed in the section on kokanee horizontal distribution (p. 129). Alternatively, the lower density of fry in the South Arm may allow them to have higher growth rates because of lower intraspecific competition. I examine this possibility in more detail in the subsequent section on the analysis of kokanee fry age from daily growth rings (p. 170).

Age 1+ kokanee were about 70 to 80 mm long in May of each year, and grew to about 150 mm by October (Fig. 55). The size of age 1+ fish in October has decreased slightly during the fertilization experiment, from highs of about 170 mm in 1992, and 1993, to less than 150 mm in 1996 (and probably 1997, although sampling was only done in July and September). Age 1+ fish do not show a consistent trend toward larger size at either end of the lake.

Age 2+ kokanee length increased from about 170 mm to about 200 mm between May and October (Fig. 56). This age class was over 200 mm by fall in 1993, and 1994, but sizes in 1996 and 1997 decreased, and age 2+ reached only about 175 mm length. Age 2+ kokanee size may also be affected by increased intraspecific competition.

Age 3+ kokanee showed minimal change in length between May and September (Fig. 57). In 1992 too few fish were caught to see a trend in size, and in 1993 sizes were very variable

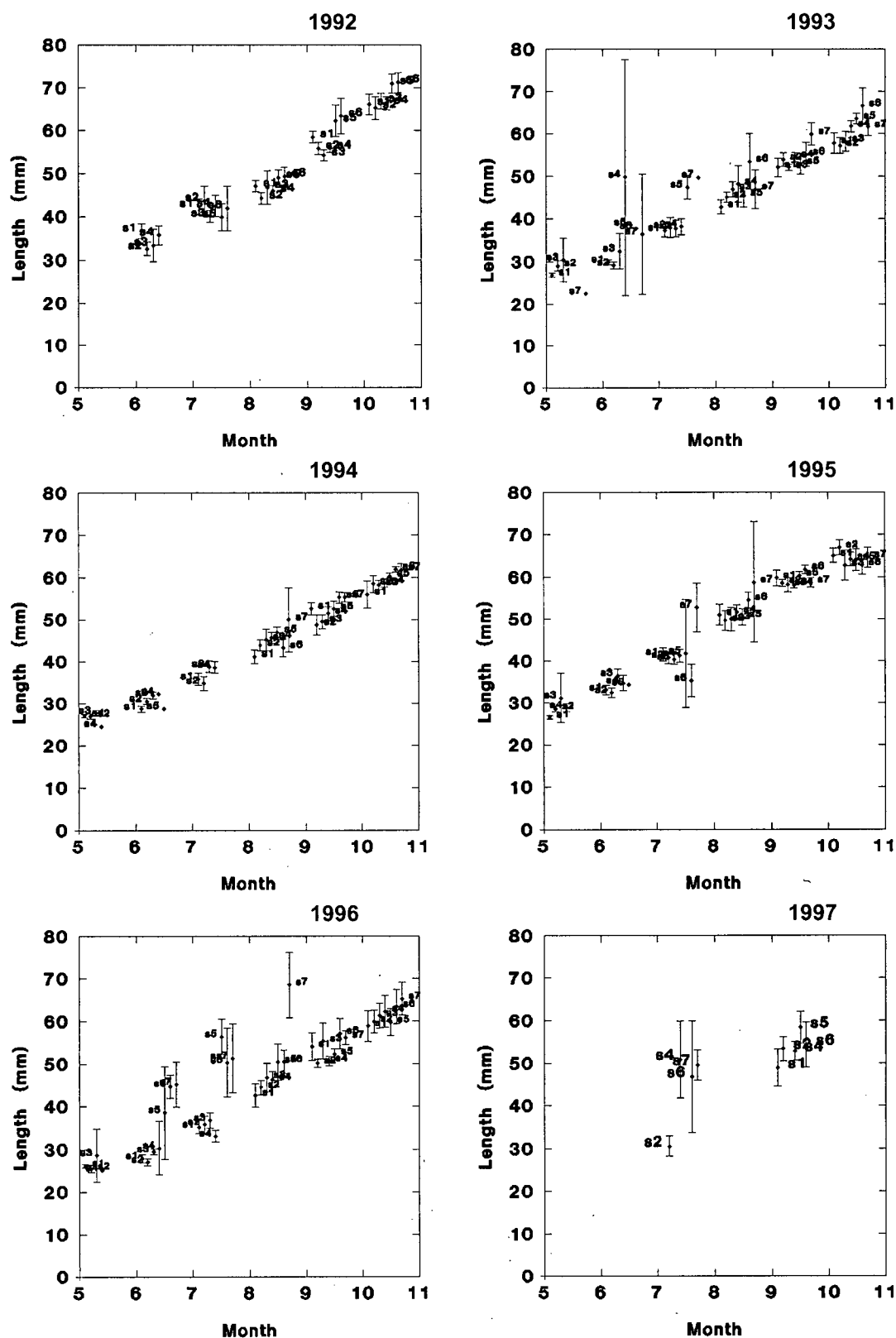


Fig. 54. Length of age 0+ kokanee caught in trawls from 1992 to 1997. Error bars are two times the standard error of the mean. Labels s1 to s7 indicate sampling station. The point symbols are staggered within each month to make the error bars more visible.

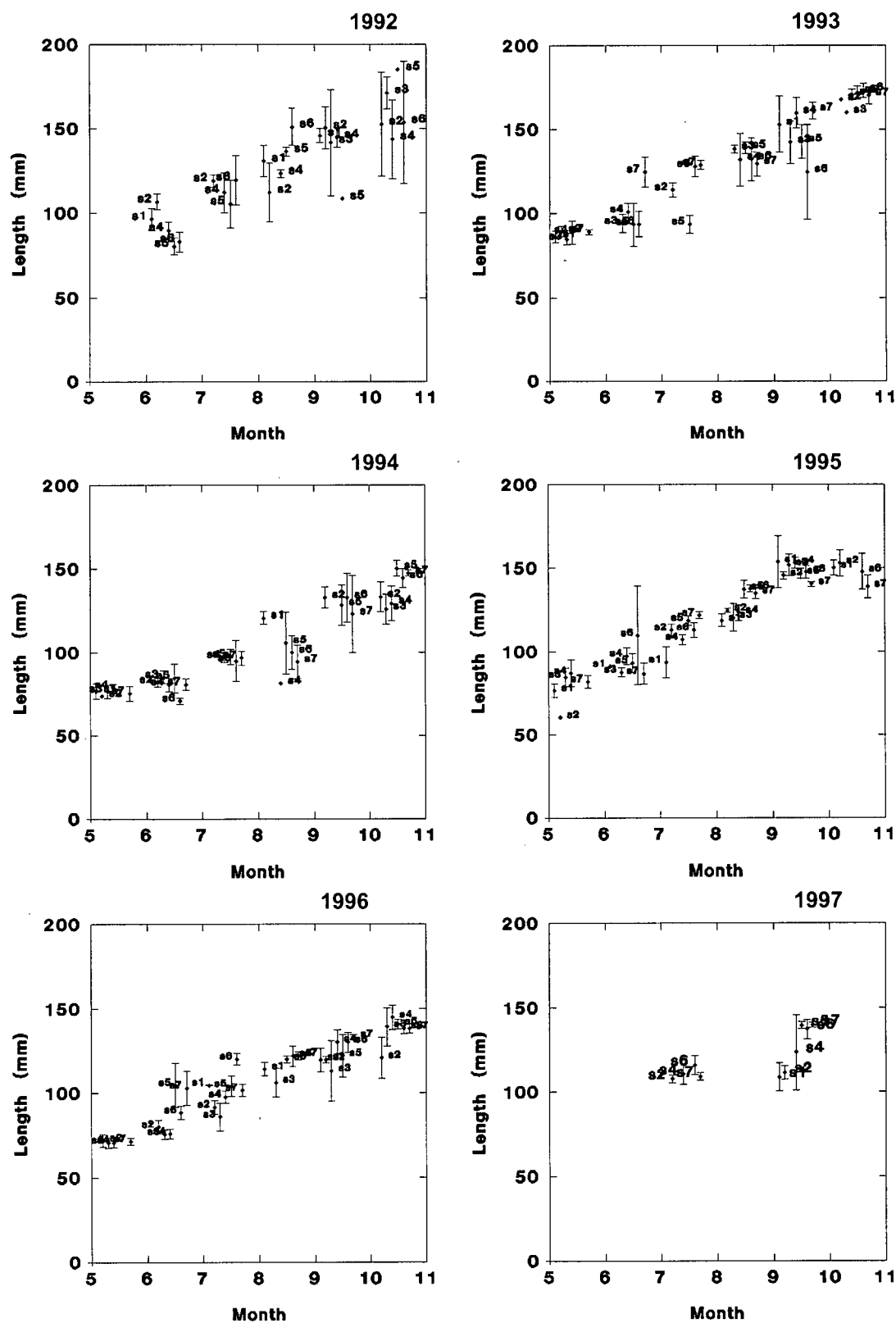


Fig. 55. Length of age 1+ kokanee caught in trawls from 1992 to 1997. Error bars are two times the standard error of the mean. Labels s1 to s7 indicate sampling station. The point symbols are staggered within each month to make the error bars more visible.

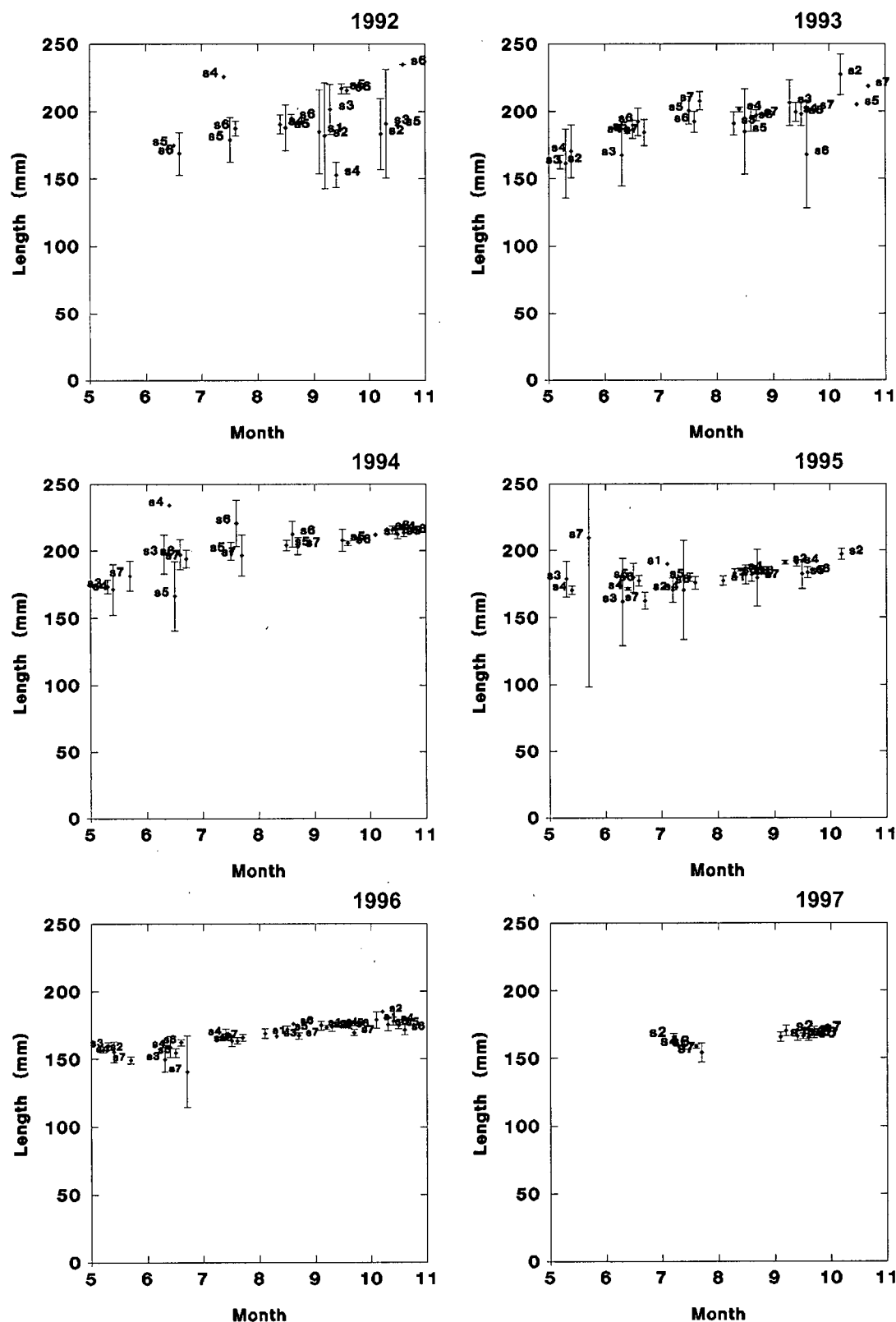


Fig. 56. Length of age 2+ kokanee caught in trawls from 1992 to 1997. Error bars are two times the standard error of the mean. Labels s1 to s7 indicate sampling station. The point symbols are staggered within each month to make the error bars more visible.

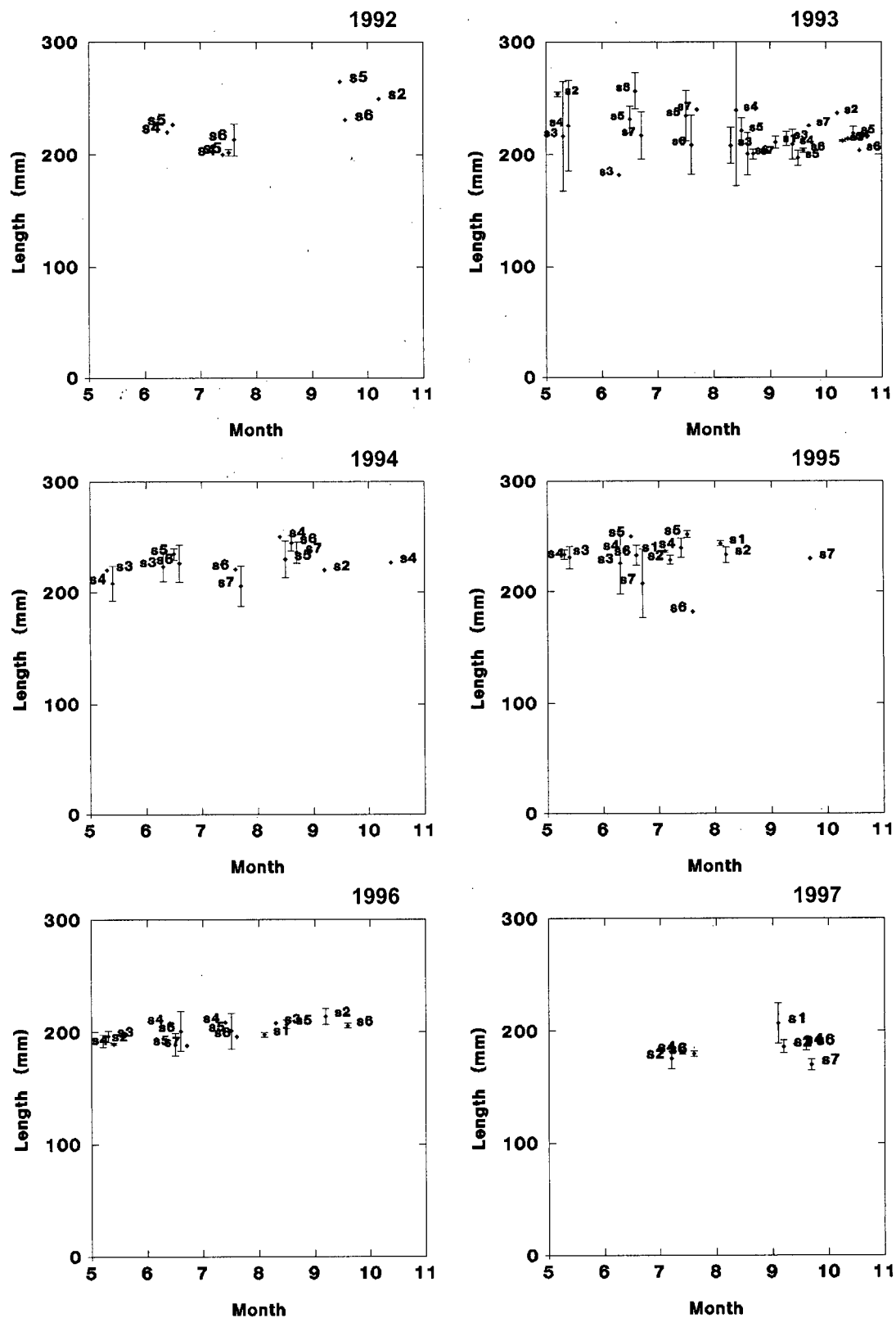


Fig. 57. Length of age 3+ kokanee caught in trawls from 1992 to 1997. Error bars are two times the standard error of the mean. Labels s1 to s7 indicate sampling station. The point symbols are staggered within each month to make the error bars more visible.

across the year. In 1994 lengths increased from about 210 mm to 240 mm. Sizes were similar throughout 1995, and fish were about 230 mm long. Age 3+ fish were smaller in 1996 and 1997, as noted for the growth curve plots (Fig. 52), and reached lengths of about 210 mm in 1996, and 190 mm in 1997.

Kokanee fry weight followed similar patterns over time and space as fry length. Kokanee fry weight increased from about 0.2 g in May to over 2 g by October (Fig. 58). In 1992 fry weight was over 3 g at the end of the growing season, but fry grew to only 2 - 2.5 g in subsequent years. Fry tended to weigh more toward the south (unfertilized) end of the lake (e.g., September 1992, June, July and August 1996, September 1997). As for fry length, this longitudinal pattern may result from fry in the South Arm being older, or having had higher growth rates, and will be considered in the section on the analysis of kokanee fry age from daily growth rings (p. 170).

Age 1+ kokanee weighed about 5g each spring (Fig. 59). In 1992 this age class grew from about 10 g in May to about 50 g in October, and in 1993 age 1+ kokanee reached about 55 g. In subsequent years growth declined, and age 1+ fish only reached about 30 g by October. Age 1+ fish showed some tendency for larger size in the South Arm (e.g., August 1992, June, July, and August 1996, September 1997) but this trend was not consistent across years or months (e.g., August 1994, September and October 1995).

Age 2+ kokanee weight declined during the fertilization experiment, as was seen for length (Fig. 60). In 1992 to 1994 this age class grew from about 50 g in May to about 120 g in October. Average size in October was about 90 g in 1995, and 60 g in 1996. October size was probably similar in 1997, since age 2+ fish weighed less than 60 g in September. This age class did not show consistent trends in size along the lake.

Age 3+ kokanee weight declined during the fertilization experiment, as was the case for length (Fig. 61). Age 3+ kokanee were not consistently caught in trawls, especially in the early years of the experiment, because their densities were low relative to other age classes. Despite erratic catches, it is clear that age 3+ fish generally weighed between 100 g and 150 g between 1992 and 1995, but weighed from 70 g to less than 100 g in 1996 and 1997. Age 3+ kokanee do not appear to be larger in the South Arm of the lake, but small sample sizes would probably obscure such a trend.

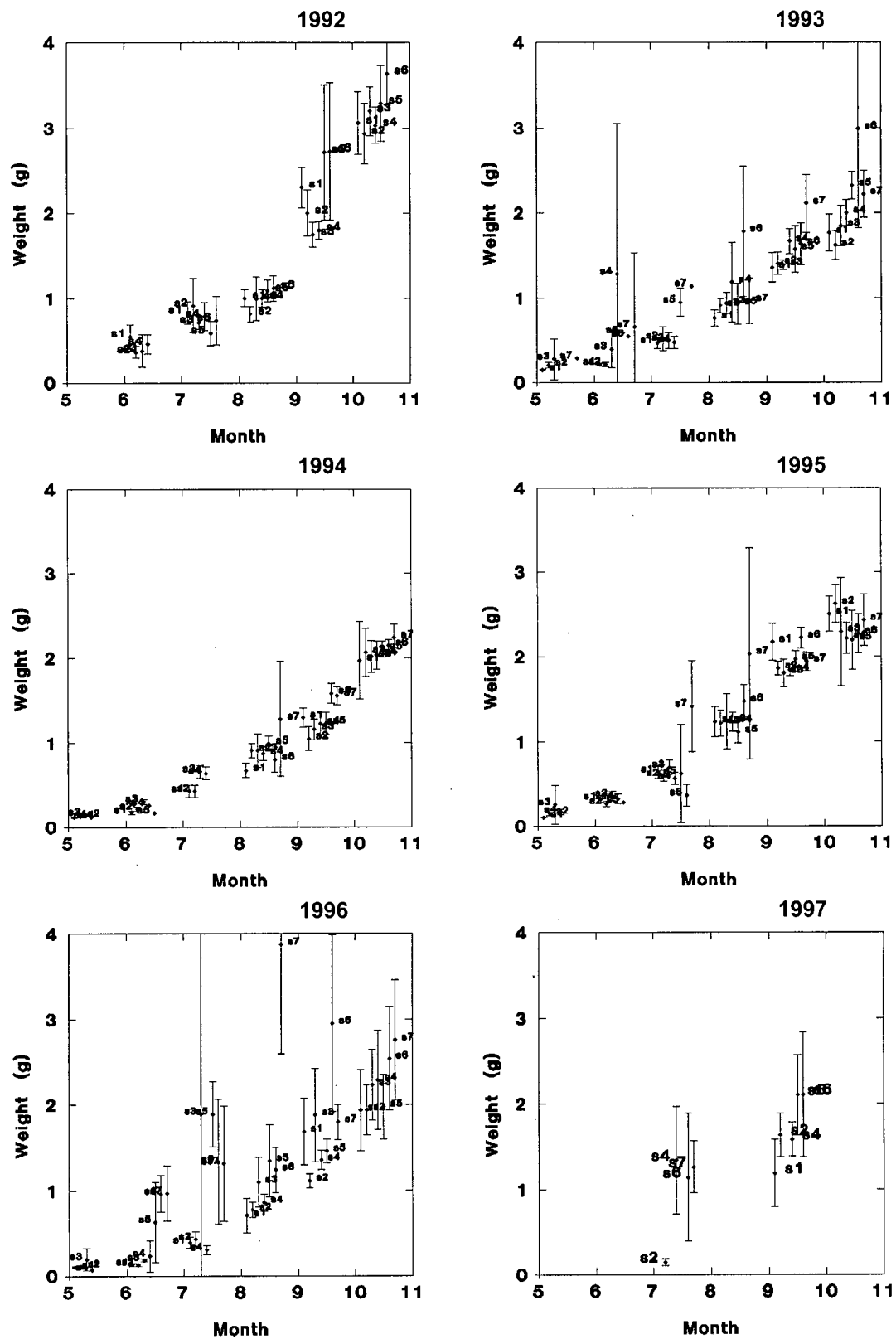


Fig. 58. Weight of age 0+ kokanee caught in trawls from 1992 to 1997. Error bars are two times the standard error of the mean. Labels s1 to s7 indicate sampling station. The point symbols are staggered within each month to make the error bars more visible.

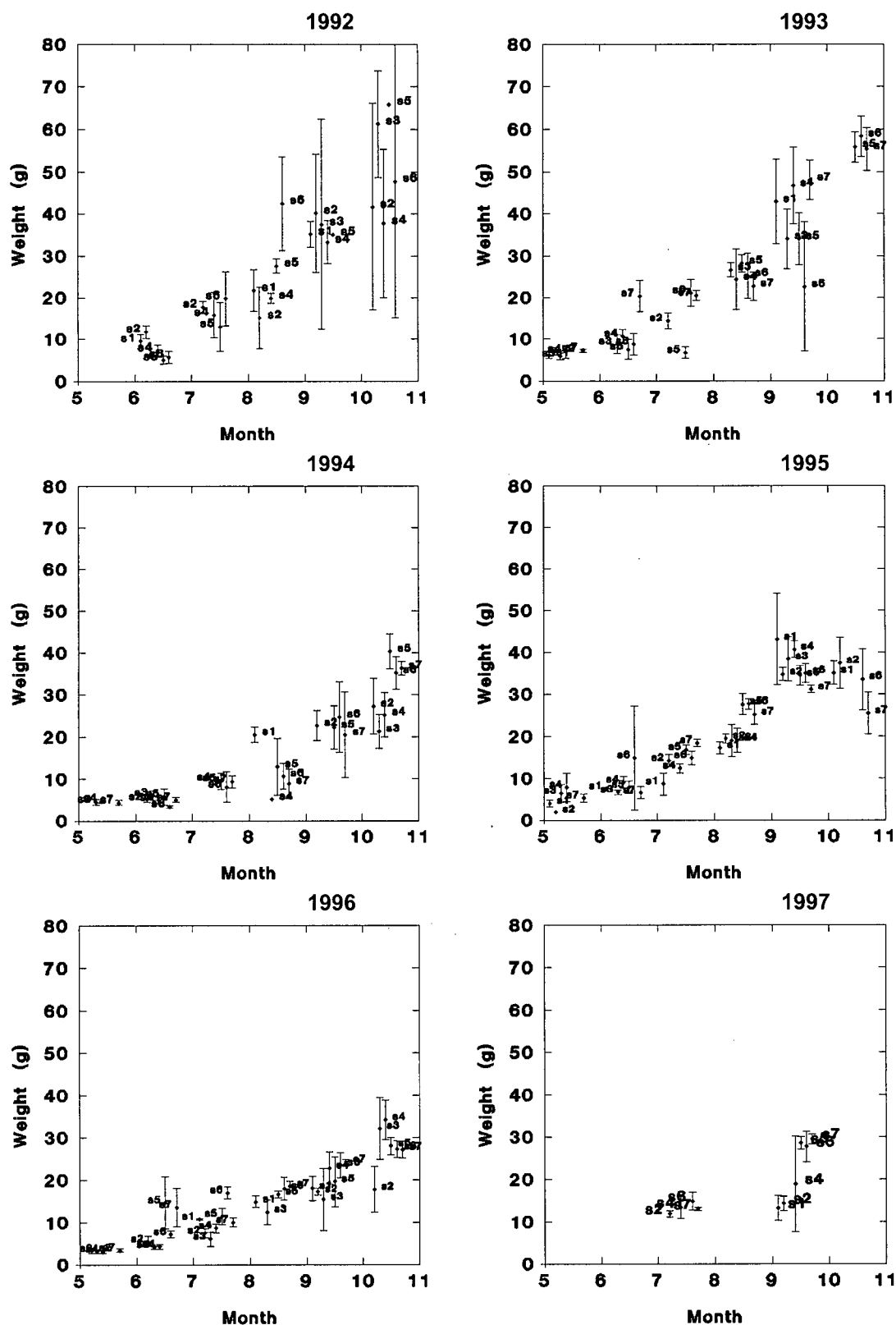


Fig. 59. Weight of age 1+ kokanee caught in trawls from 1992 to 1997. Error bars are two times the standard error of the mean. Labels s1 to s7 indicate sampling station. The point symbols are staggered within each month to make the error bars more visible.

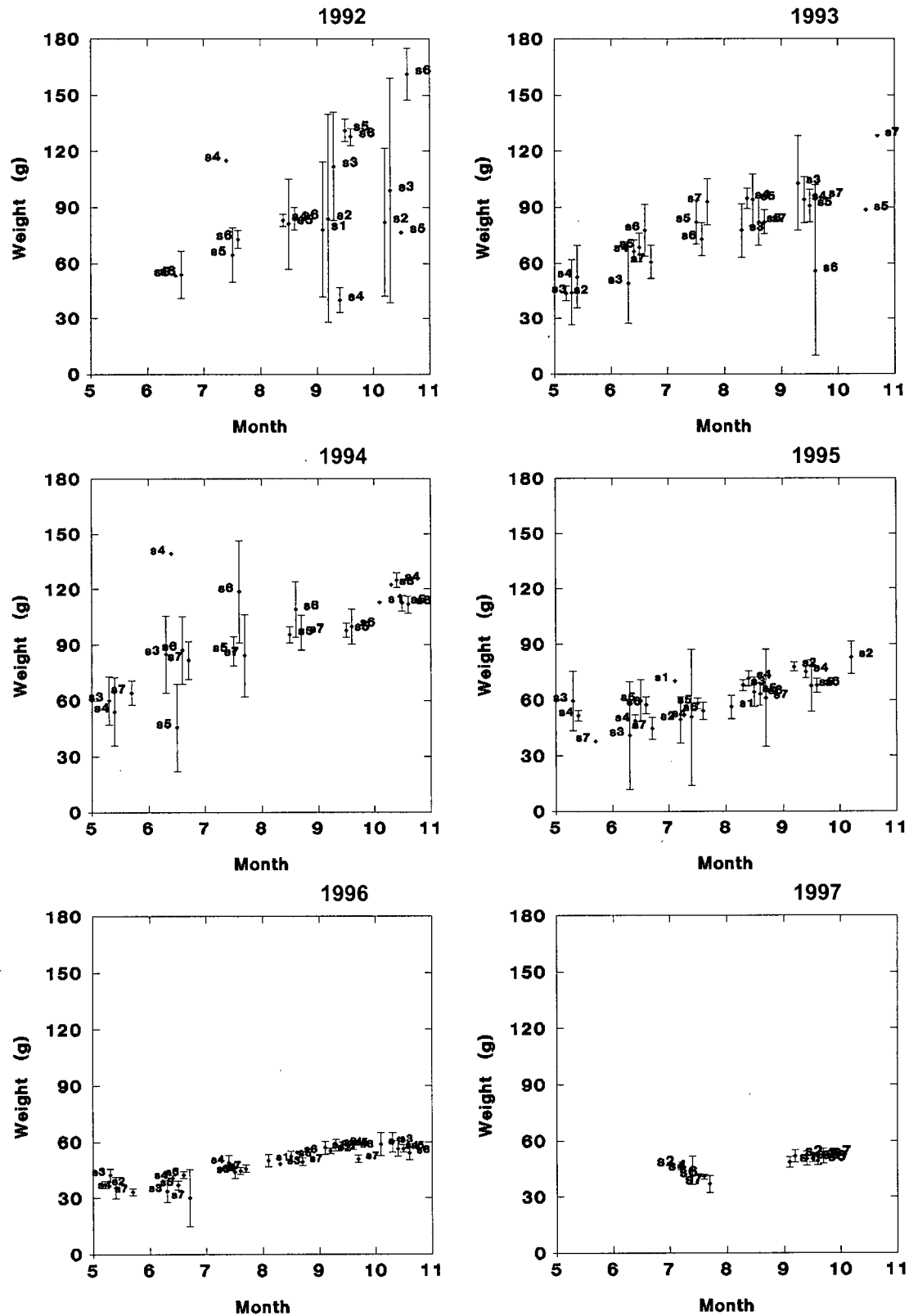


Fig. 60. Weight of age 2+ kokanee caught in trawls from 1992 to 1997. Error bars are two times the standard error of the mean. Labels s1 to s7 indicate sampling station. The point symbols are staggered within each month to make the error bars more visible.

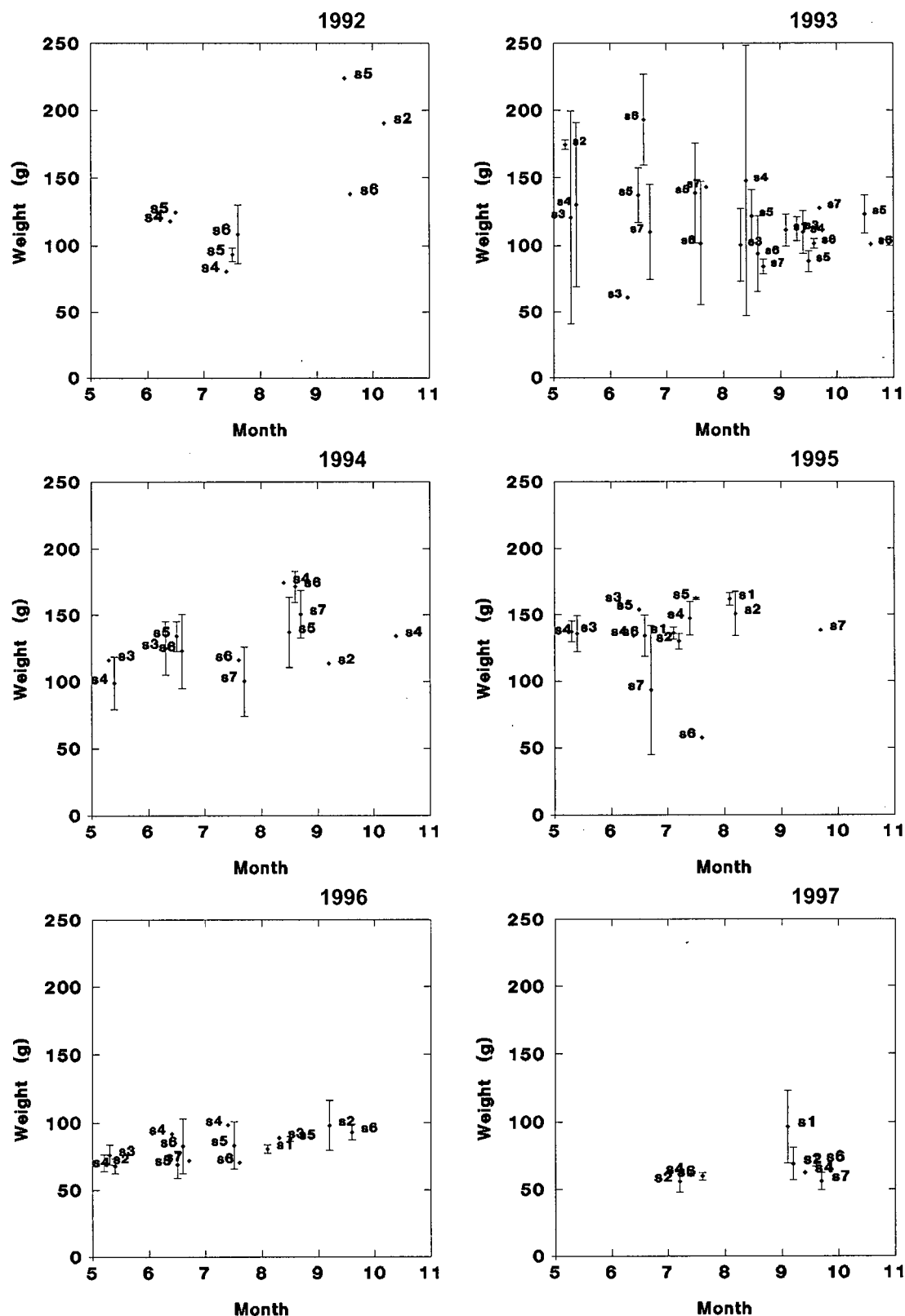


Fig. 61. Weight of age 3+ kokanee caught in trawls from 1992 to 1997. Error bars are two times the standard error of the mean. Labels s1 to s7 indicate sampling station. The point symbols are staggered within each month to make the error bars more visible.

Otolith Analysis of Kokanee Fry Size-at-Age Along Productivity Gradient

Larger size of fry in the South Arm compared to those in the North Arm (Fig. 54) seems to be caused by fry in the South Arm being older, rather than having higher growth rates. I compared body size with age in days, back-calculated from otolith daily rings, and found that when fry were larger they were also older. All fry had a similar relationship of length to age (days since emergence), and of weight to age. This suggests that kokanee fry had similar growth rates in the fertilized and unfertilized ends of the lake. South Arm fry tended to be larger because they tended to have had more days in the lake to grow.

Kokanee fry at Stations 2 and 6 had similar lengths in September 1993, and 1995 (Fig. 62). However, fry at Station 6 tended to be larger than those at Station 2 in September 1994, and 1996. In 1993 and 1995 the lengths of fry at Stations 2 and 6 were not significantly different (Table 16); all length and ring count distributions were normal). Back-calculated ages (ring counts) also did not differ (Fig. 63). In 1994 and 1996 both length and age were significantly greater at Station 6.

Table 16. Comparison of length and daily ring counts of kokanee fry at Stations 2 and 6 in September of 1993 to 1996.

Year	Length (mm)			Ring Count (days since emergence)		
	Station 2	Station 6	Prob.	Station 2	Station 6	Prob.
1993	53.87	55.09	0.46	116.80	112.33	0.44
1994	48.76	55.28	<0.0001	93.80	108.75	0.005
1995	59.00	61.26	0.08	118.45	120.65	0.65
1996	50.68	53.96	0.02	97.20	105.75	0.049

Note: All sample sizes for length were 30 fry, except Station 6, 1993 (n=9), and Station 6, 1996 (n=39). All sample sizes for ring counts were 10 otoliths, except Station 6, 1993 (n=9).

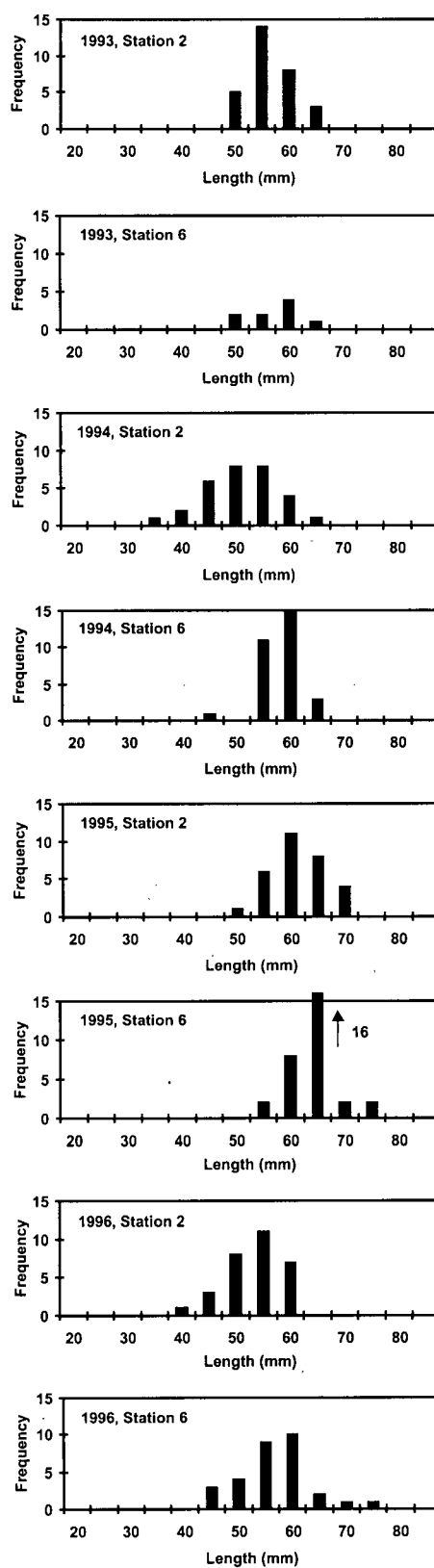


Fig. 62. Length frequency histograms of kokanee fry for which otolith-based days-since-emergence was calculated.

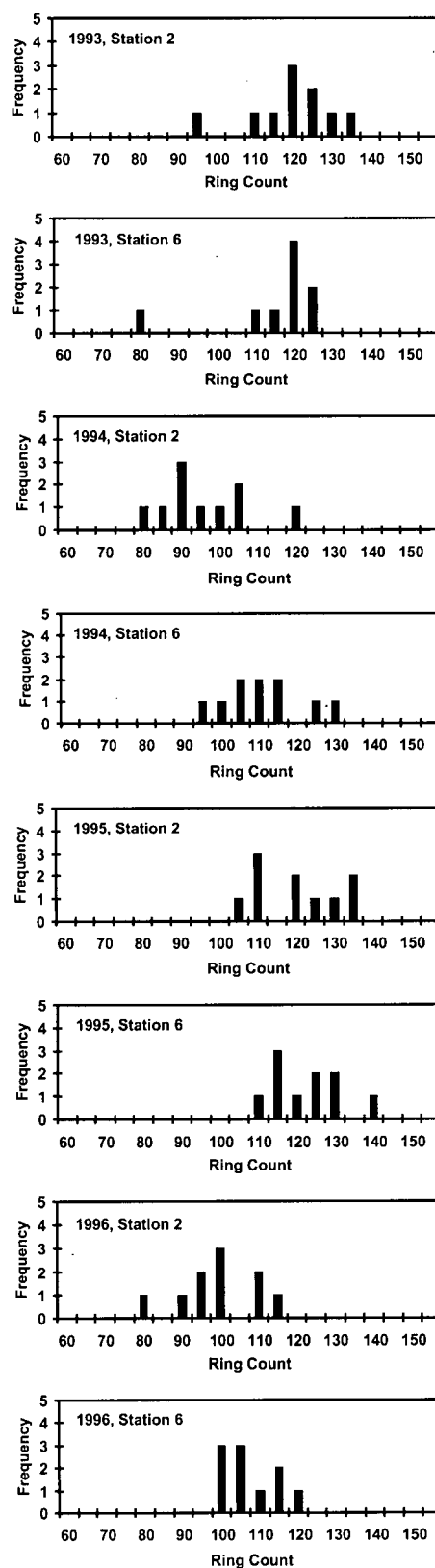


Fig. 63. Daily ring count frequency histograms of kokanee fry for which otolith-based days-since-emergence was calculated.

All kokanee fry at Stations 2 and 6 in September 1993 to 1996 had similar relationships of fork length to age (Fig. 64), and wet weight to age (Fig. 65). This suggests that kokanee fry follow an ideal free distribution (MacCall 1990), and move south along the length of the lake to give a distribution that results in all fry having similar growth rates. Fry that are larger are also older, and therefore have had more days to reach their greater size, rather than having grown faster than smaller fry.

Autumn trawl data from 1988 to 1991 indicate that fry in the South Arm of Kootenay Lake tended to be larger than North Arm fry even prior to fertilization (Fig. 66). Fry at the most northern station sampled (near present Station 3) were significantly smaller than fry at other stations in 1988 to 1991 (single factor ANOVA, $p < 0.05$ in each year). The North Arm tributaries produced the majority of fry entering the lake during that time period (as is still the case) so most fry in the South Arm would have originated from the North Arm. Similar to the pattern observed during fertilization, fry caught in the South Arm would have tended to be older and therefore larger than fry in the North Arm. Otoliths were not sampled from fry prior to fertilization so it was not possible to back-calculate the ages or relative growth rates of fry along the lake at that time. Also, since hydroacoustic sampling of kokanee density and distribution was only done in the autumn prior to 1992, it is not possible to know whether kokanee fry distribution along the lake in spring and summer was as skewed as has been observed during fertilization. It is possible that the distribution of fry along the lake evened out earlier in the season in the absence of fertilization, and that kokanee fry are now staying longer in the North Arm longer than prior to fertilization.

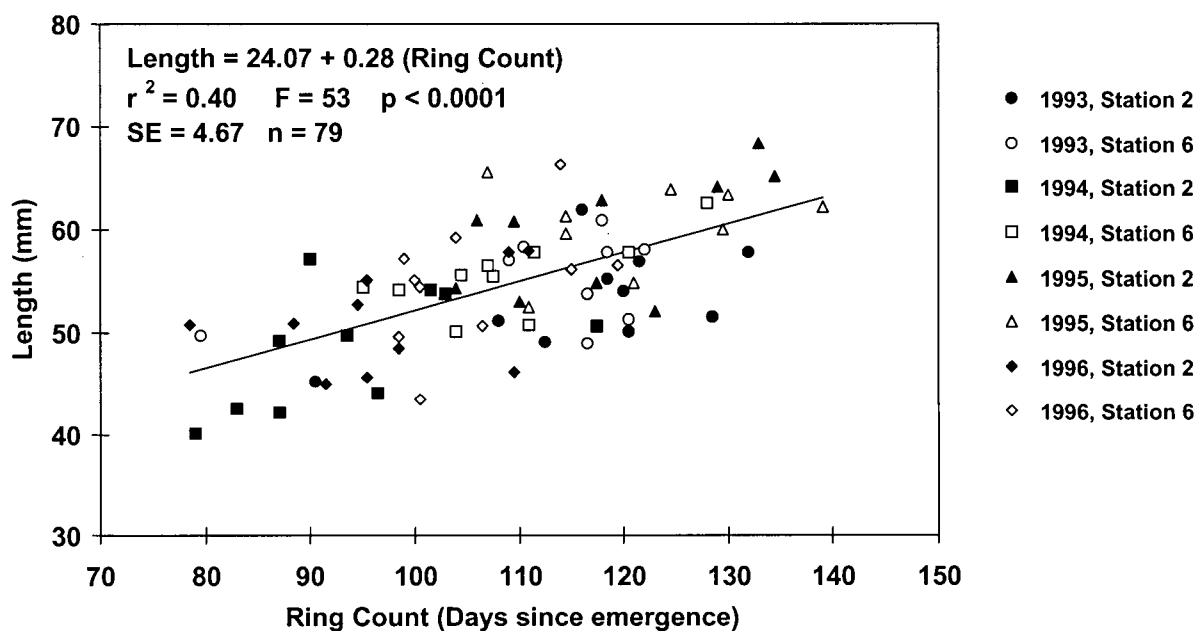


Fig. 64. Regression of fork length on otolith-based days-since-emergence for fry at Stations 2 and 6, in September of 1993 to 1996. Statistics are the coefficient of determination (r^2), F-statistic (F), its probability (p), standard error (SE), and sample size.

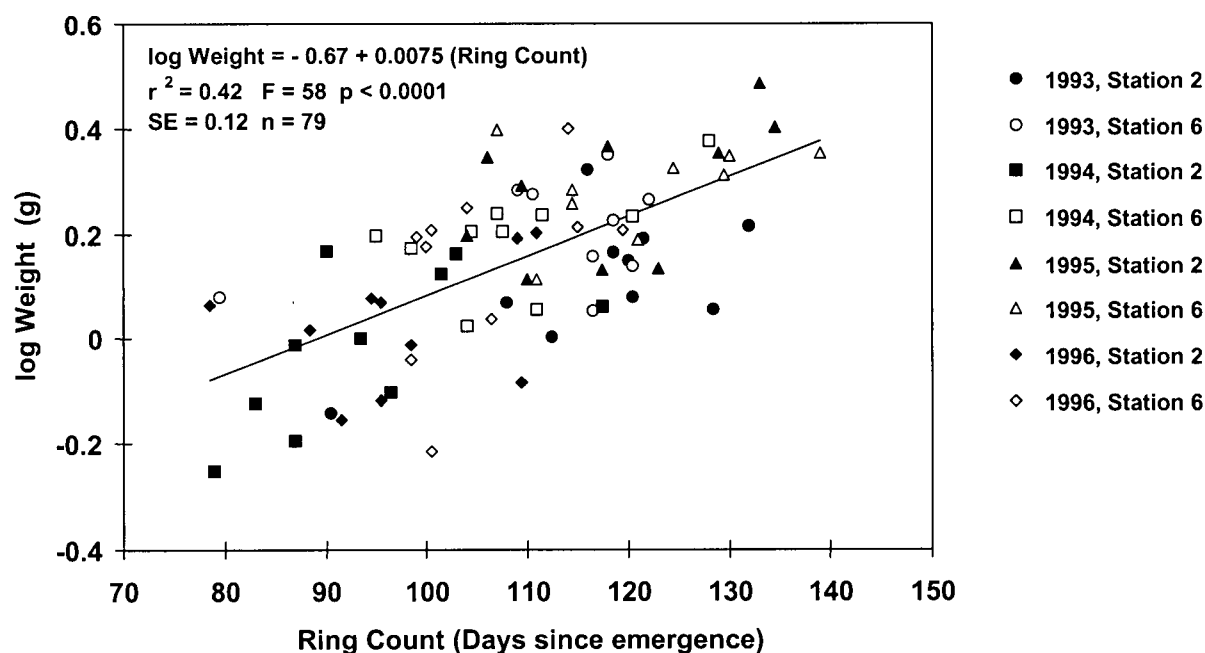


Fig. 65. Regression of log wet weight on otolith-based days-since-emergence for fry at Stations 2 and 6, in September of 1993 to 1996. Statistics are the coefficient of determination (r^2), F-statistic (F), its probability (p), standard error (SE), and sample size.

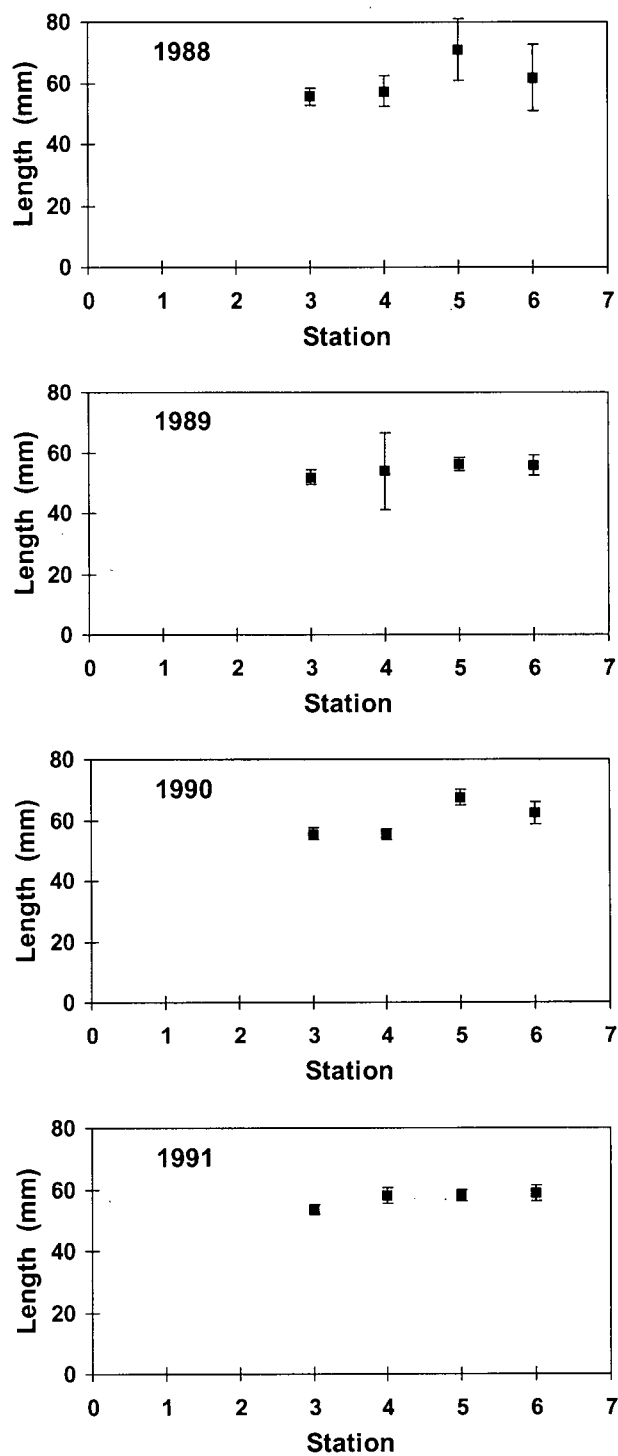


Fig. 66. Fork length of kokanee fry caught along the length of Kootenay Lake in autumn 1988 to 1991. Error bars are 95% confidence intervals.

Kokanee Fecundity

Body size and fecundity were highly correlated in Meadow Creek spawners (Fig. 67). As spawner size increased in the early 1990's fecundity also increased, rising from 191 eggs·female⁻¹ to a peak of 408 eggs·female⁻¹ in 1993. As spawner size declined during the fertilization experiment, fecundity also decreased, down to 187 eggs·female⁻¹ in 1997.

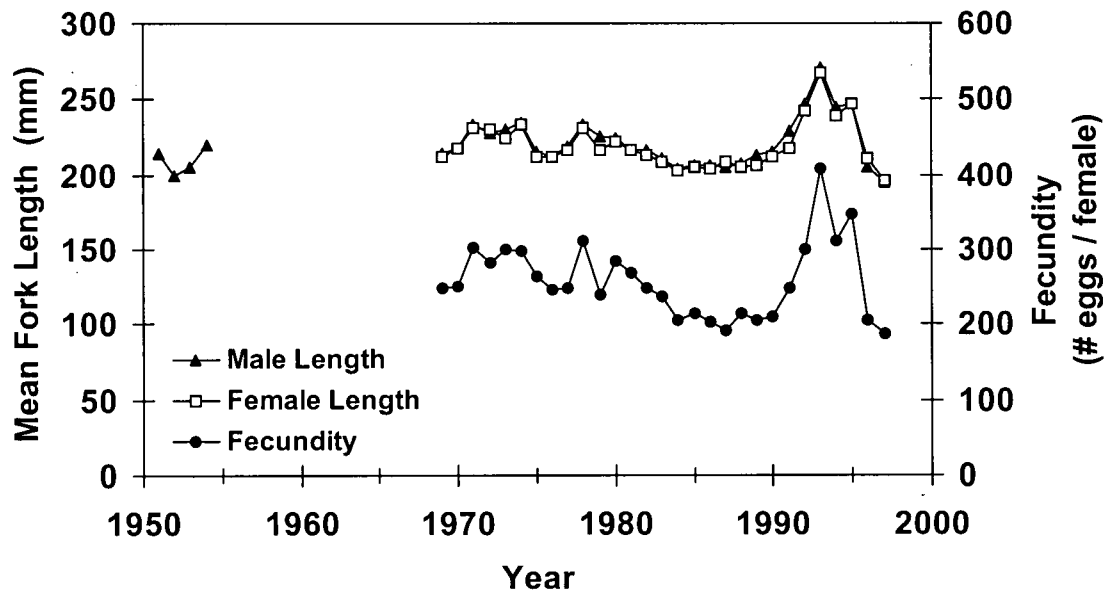


Fig. 67. Average size and fecundity of kokanee spawners at the Meadow Creek channel from 1951 to 1997.

Changes in spawner size and fecundity have affected egg deposition and fry production at the Meadow Creek channel (Fig. 68). Egg deposition and fry production both increased in 1992, and peaked in 1993, when over 120 million eggs were deposited, and 28 million fry emigrated to the lake. Egg deposition then decreased as size (and fecundity) declined, to a low of 55 million in 1997. Fry production tracked this decline, decreasing to 9 million in 1996, but increased slightly in 1997 to 12 million (spring 1998 outmigration). Egg-to-fry survival rates in the Meadow Creek channel are much higher than rates for fish in un-enhanced creeks and rivers, generally ranging from 25% to 45%.

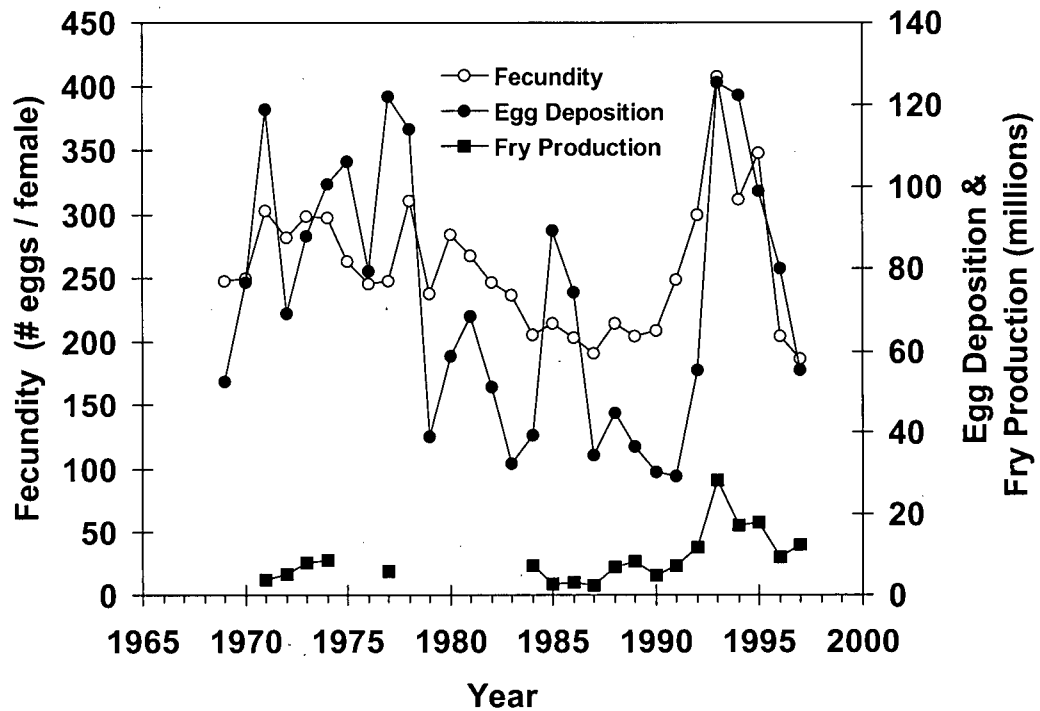


Fig. 68. Meadow Creek kokanee spawner fecundity, egg deposition and fry outmigration, 1969 to 1997. Fry production is measured in the spring, and is derived from the eggs that were deposited the previous fall. Therefore, for example, fry production measured in spring 1997 is plotted as a 1996 value on the X-axis.

Gerrard Rainbow Trout Size

Rainbow trout spawner size was not monitored from 1992 to 1997 because of high water levels at the Gerrard spawning site. Historically, female trout spawners have weighed about 6 kg to 8 kg, while males have weighed 7 kg to 10 kg (Fig. 43). Additional data on rainbow trout spawner size were obtained from Birchgrove Marina fishing derby records (Fig. 69). Maximum weights showed a slight decline from the early 1980's to 1995. Maximum weight in the derby increased in 1996 and 1997, but was still below values from the 1980's, when the winning fish was usually over 10 kg. Average weight data up to 1989 are not comparable to later data because a size limit of 4.53 kg was imposed in 1990. Average size declined from 1991 to 1994, from about 7 kg to 4 kg. Average size then began to increase, and reached 7 kg again in 1997.

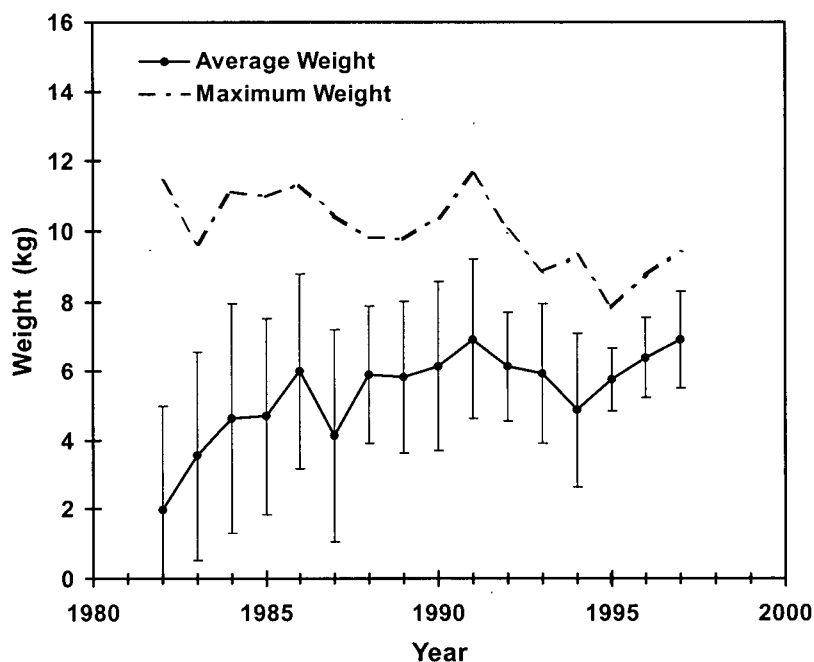


Fig. 69. Average and maximum weight of rainbow trout caught in Kootenay Lake. Data are from the annual fishing derby held by the Birch Grove Marina, and from fish turned in at other marinas along the lake. Error bars are 1 standard deviation. The Birch Grove Derby started a 10 lb. (4.53 kg) limit in 1990.

Bull Trout Size

Limited data on bull trout size were also obtained from Birchgrove Derby records (Fig. 70). Very few bull trout were entered in the competition in 1988, but from 1989 to 1994 the maximum size was between 6 kg and 8 kg, and the average was between 3 kg and 5 kg.

Diet and Consumption

M. relicta Consumption

M. relicta consumes a large proportion of the macrozooplankton standing stock, but the pattern of consumption along the lake is uncertain. *M. relicta* distribution data are extremely variable. Spatial data along the lake for 1992 – 1994 show that *M. relicta* sampled in deep hauls were distributed evenly along the lake, or were more dense in the South Arm (Kootenay Lake Fertilization Database, unpublished data). Mysids usually consumed only a small proportion of

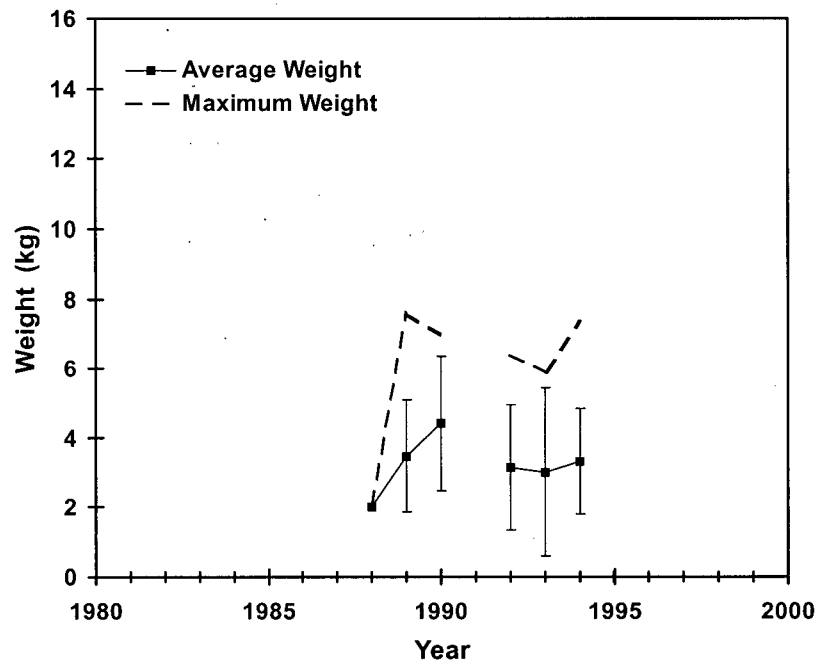


Fig. 70. Average and maximum weight of bull trout caught in Kootenay Lake. Data are from the annual fishing derby held by the Birch Grove Marina, and from fish turned in at other marinas along the lake. Error bars are 1 standard deviation. The Birch Grove Derby started a 10 lb. (4.53 kg) limit in 1990.

copepod standing stock per day, with an average consumption rate of 0.007 d^{-1} (that is, 0.7% per day), but showed a maximum consumption rate of 0.5 d^{-1} , or 50% per day (Fig. 71). The consumption rate of cladocerans by *M. relicta* was higher, with an average rate of 0.14 d^{-1} , and maximum rate of 1.0 d^{-1} . *M. relicta* also consumed a high proportion of *Daphnia* spp., at an average rate of 0.13 d^{-1} , and with a maximum rate of 1.0 d^{-1} . *M. relicta* preferred *Daphnia* spp. from July to October, when they were readily available. These data do not show a tendency for *M. relicta* to crop higher proportions of zooplankton in the fertilized end of the lake. If this were the case, *M. relicta* cropping could suppress an increase in zooplankton biomass which could otherwise occur due to higher phytoplankton biomass in the North Arm. The extremely high consumption values that occurred in 1992, and early 1993, are almost certainly not realistic. They are probably partly the result of sampling error for *M. relicta*, which usually shows quite

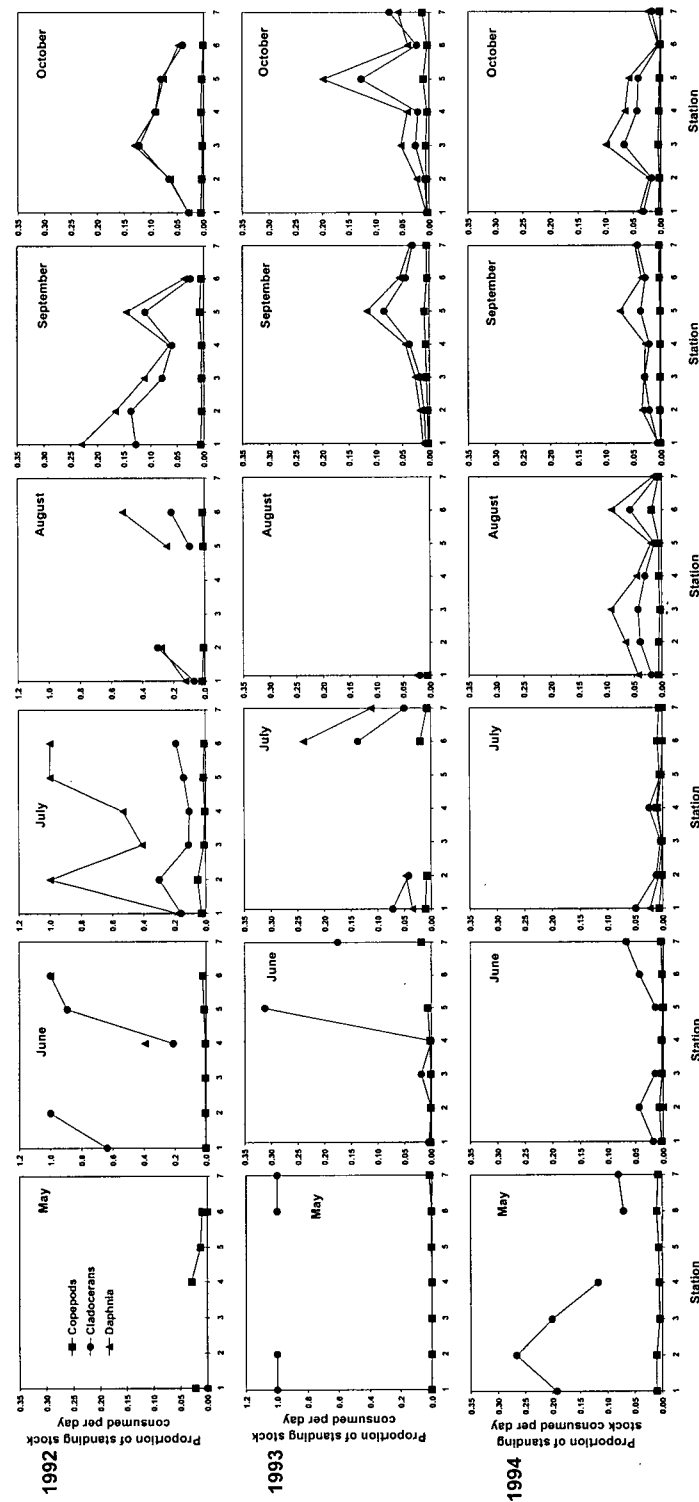


Fig. 71. Consumption by *M. relicta* of macrozooplankton along the lake in 1992 to 1994. Rates shown are the proportion of macrozooplankton standing stock biomass contained in guts of *M. relicta* when captured, and may underestimate total daily consumption. Note that the Y-axis scale was expanded for June and July 1992, and May 1993 to show higher consumption rates in those months. *M. relicta* and zooplankton were not sampled at Station 7 in 1992. Missing stations in 1993, and 1994 occur when *M. relicta* data were not available.

variable densities along the lake, compounded by the fact that *M. relicta* densities were higher in 1992 than in subsequent years. Also, accurate estimation of *Daphnia* spp. abundance is difficult early in the season when these individuals are very rare. Since *M. relicta* preys preferentially on *Daphnia* spp., mysids begin to show a high proportion of *Daphnia* spp. in their diet when this species is rarely observed in the plankton hauls. The combination of relatively rare *Daphnia* spp. plus occasional overestimation of mysid density probably resulted in over estimation of consumption rates.

In contrast to my analysis, Smokorowski (1998) commented that *M. relicta* were more abundant in the North Arm, and calculated that *M. relicta* consumed a higher proportion of zooplankton standing stock in the fertilized end of the lake. Smokorowski did a bioenergetic analysis using data from Stations 2 and 6 for 1992 and 1995. While *M. relicta* densities were higher in the North Arm in the years that Smokorowski used for her analyses (see p. 119), densities were higher in the South Arm for at least two of the years in my analysis.

Kokanee Diet

Diet analyses concentrated on kokanee fry, since adequate growth in the first year in the lake may be critical for overwinter survival. Stomachs of kokanee fry caught after dusk contained from less than 1% up to 19% of fish body weight (Fig. 72). Data shown are the wet weight zooplankton biomass in the stomach after dusk, relative to the fish's wet weight. Fry stomachs at all stations contained less than 5% of fish body weight in May, June and July of 1993 and 1994. The proportion of body weight in stomachs increased dramatically in August and September of 1993 and 1994. It is likely that the same pattern occurred in 1992 and 1995, although only August and September data were analyzed. In 1993 and 1994 fry stomach content

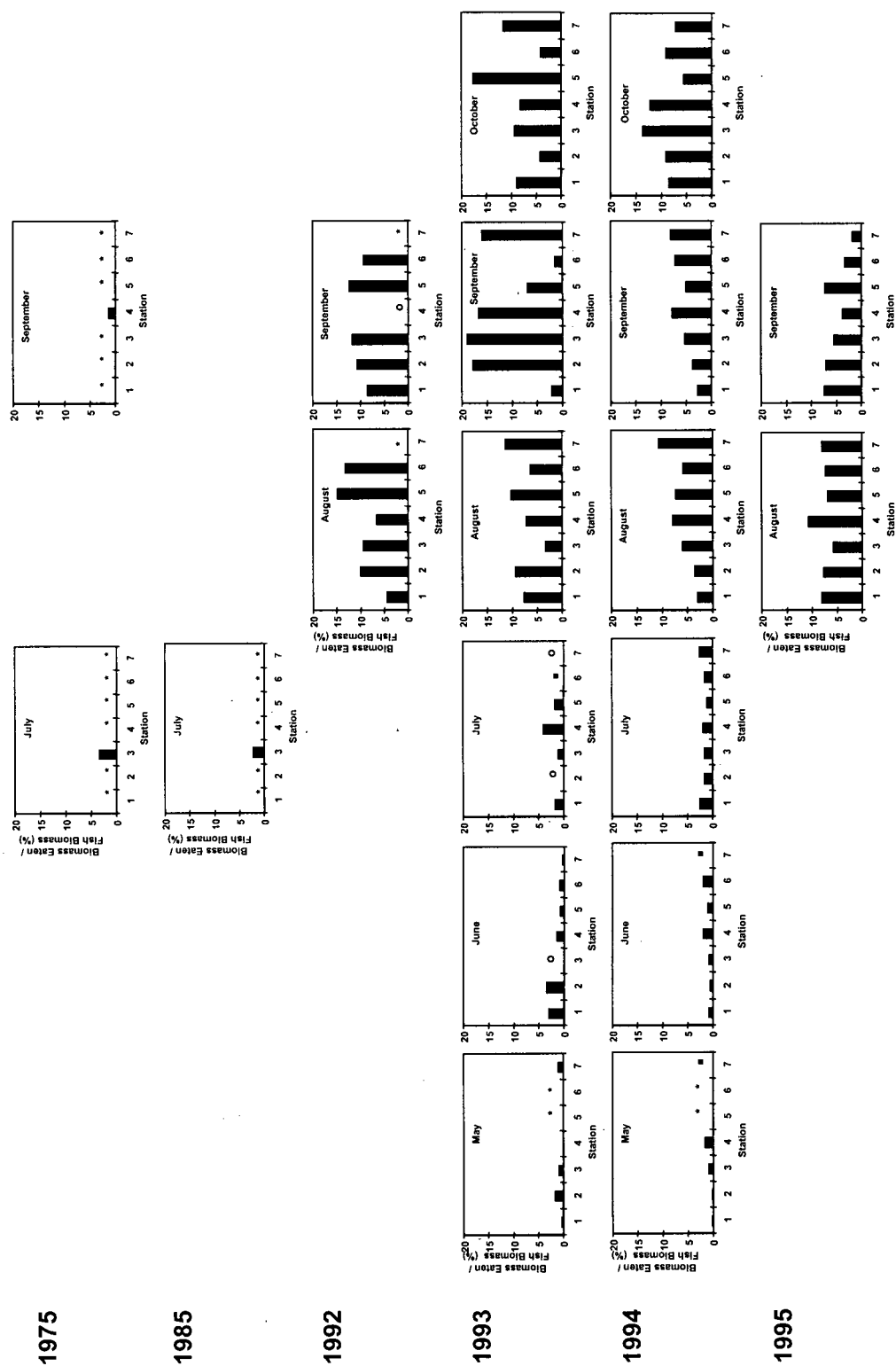


Fig. 72. Diet of kokanee fry in 1975, 1985, and 1992 - 1995. The amount of zooplankton eaten is shown as the biomass of zooplankton present in the gut at dusk, as a percentage of the fish's weight. An asterisk indicates stations that were not sampled, a black square indicates stations where no fry were caught, and an open circle indicates stations where fry were caught but not analyzed because of poor preservation.

weights continued to be a large proportion of fish weight in October, indicating that zooplankton were providing a good food source into early autumn.

In August and September 1992 fry stomach contents were between 4% and 15% of fish weight, with peaks in August at Stations 5 and 6. In August 1993 stomach contents were 3% to 11% of body weight, with no trend along the lake. Stomach contents were more variable in September 1993, ranging from 2% to 19%, again with no pattern along the lake. In August and September of 1994 fry stomach contents were 3% to 11% of fish weight. In both months there was a trend for stomach contents of South Arm fry to be a higher proportion of fish weight, but this pattern reversed in October. In August 1995 fry stomach contents were 6% to 8% of fish weight, evenly along the lake. In September 1995 the pattern was the opposite to the previous year, with stomach contents representing a higher proportion of fish weight in the North Arm, and ranging from 2% to 8%. In summary there was no consistent trend for stomach contents of fry in the fertilized end of the lake to be a higher proportion of fish weight.

In comparison with the historical samples obtained for 1975 and 1985, kokanee fry during the fertilization experiment appeared to obtain a similar amount of food in July. In September fry probably obtained more food in 1992 to 1995 than had fry in September 1975. Zooplankton density in Kootenay lake was very low in 1975, at 5 individuals·L⁻¹ (Fig. 27), and the proportion of cladocerans was less than 1% (Fig. 28). In 1985 zooplankton density averaged 27 individuals·L⁻¹, including 1.4% cladocerans. It is unclear whether fry in September 1985 may have obtained as much food as fry between 1992 and 1995. While total zooplankton was high in 1985, the proportion of cladocerans was low, so there would have been relatively few *Daphnia* spp. available. *Daphnia* spp. density in 1985 was 0.37 individuals·L⁻¹, compared with the range of 7.4% to 12.6% between 1992 and 1995.

For all ages of kokanee, it must be stressed that the stomach contents sampled represent only the zooplankton in the stomach at the end of the day. All age classes likely also feed actively at dawn, and 1+, 2+, and 3+ fish probably feed for most of the day, potentially in schools. Fry may also be feeding in schools during the day, or they may be spending the time between dawn and dusk in deeper water, to avoid predation. Kokanee feeding behaviour is dealt with in more detail in the section on kokanee vertical migration (p. 200). The proportion of body weight consumed per day by fry is probably at least double that sampled, and the proportion could be considerably higher for older kokanee. Furthermore, although kokanee fry appeared to consume a similar proportion of their body weight at all locations along the lake, it is possible that fry at one end of the lake may be spending less time feeding than fry at other locations. The consequence of such differences for analysis of the effects of fertilization are also considered in the vertical migration section.

Sample sizes of kokanee older than fry were small and highly variable between stations, so it was not possible to compare the diet of these age classes along the lake. However, I pooled age 1+ kokanee from different stations and compared the proportion of body weight found in the stomach at dusk in June and August, 1992 to 1995 (Fig. 73). Age 1+ kokanee stomachs contained from 1% to 1.7% of body weight in June, and contained slightly more in June 1992 than in later years. Fish consistently contained more food relative to their size in August, as was seen for fry. In August age 1+ kokanee stomachs contained from 2.8% to 7.1% of their body weight, with the maximum occurring in August 1992. Comparing kokanee fry diet in August across different years, fry also contained the most food in 1992. In September 1993 fry also contained large amounts of food, but data on 1+ fish were not available to compare this pattern.

Since few age 2+ kokanee were caught in trawls, I pooled the fish caught by year, and tried to sample fish from a range of stations and months. Age 2+ kokanee stomachs contained

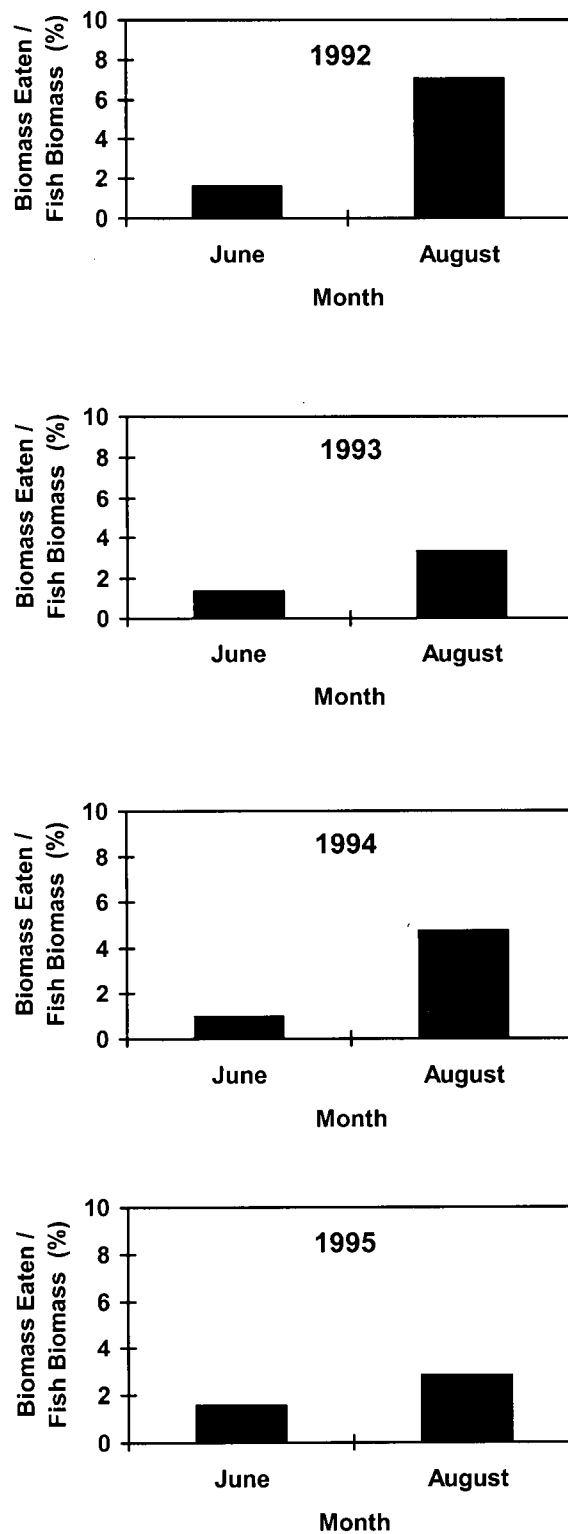


Fig. 73. Diet of age 1+ kokanee in June and August of 1992 - 1995. The amount of zooplankton eaten is shown as the biomass of zooplankton present in the gut at dusk, as a percentage of the fish's weight. Because of small sample sizes data were pooled from all stations where age 1+ fish were caught.

from 1.4% to 3.8% of fish body weight (Fig. 74). As was the case for fry and age 1+ fish (August data), age 2+ kokanee stomachs contained the highest proportion of body weight in 1992. Age 2+ stomachs also contained a relatively high proportion of body weight in 1994, similar to 1+ fish.

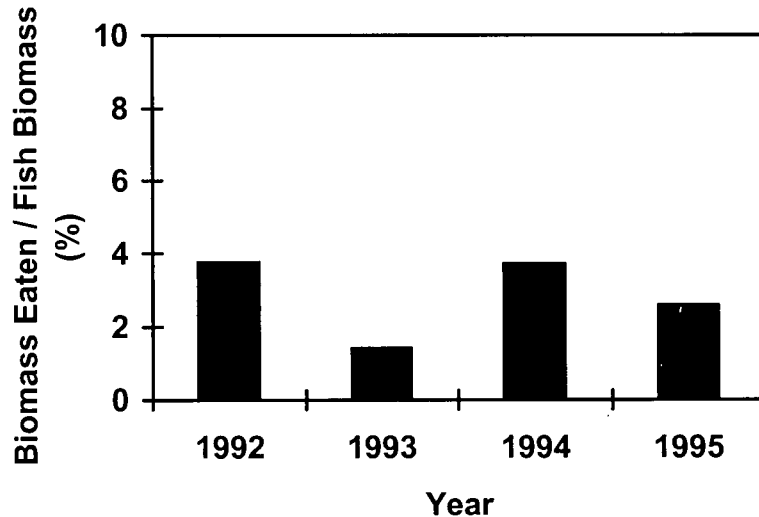


Fig. 74. Diet of age 2+ kokanee from 1992 to 1995. The amount of zooplankton eaten is shown as the biomass of zooplankton present in the gut at dusk, as a percentage of the fish's own biomass. Because of small sample sizes data from all months and stations available were pooled.

Insufficient age 3+ kokanee were caught and adequately preserved for analysis of this age class. However, one 3+ kokanee from August 1993, Station 4, was examined, and its stomach contents were 0.8% of its body weight. The proportion of body weight contained in kokanee stomachs declines with increasing age, as would be expected from an asymptotic growth curve.

Daphnia spp. made up a very large proportion of kokanee fry diet during the months that *Daphnia* spp. were available (Fig. 75). In August and September, 1992 to 1995, about 75% of the

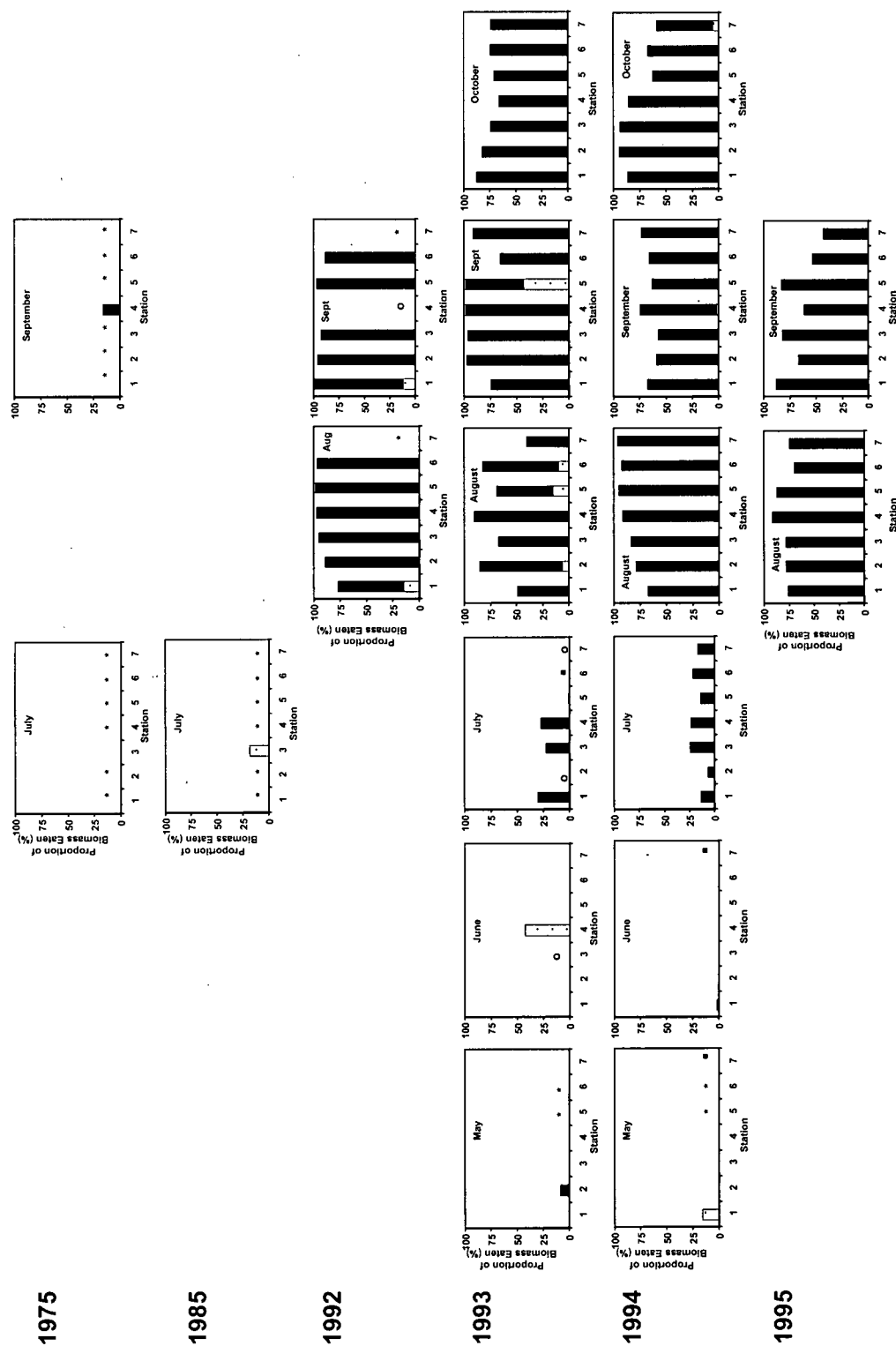


Fig. 75. Proportion of *Daphnia* spp. biomass (black bars), and *M. relicta* biomass (shaded bars), relative to total biomass in the diet of kokanee fry in 1975, 1985, and 1992 - 1995. An asterisk indicates stations that were not sampled, a black square indicates stations where no fry were caught, and an open circle indicates stations where fry were caught but not analyzed because of poor preservation.

food in kokanee fry stomachs was *Daphnia* spp. In these months *Daphnia* spp. made up about 10% of zooplankton density (Fig. 31), but peaked at 50% to 80% of zooplankton biomass, (Fig. 32). Kokanee fry prefer *Daphnia* spp. even more than would be expected based on *Daphnia*'s proportion of zooplankton biomass. *Daphnia* spp. made up only 16% of the biomass in fry stomachs in September 1975, in contrast to diet data for the fertilization experiment. I do not have accurate biomass estimates for zooplankton in 1975, but cladocerans made up less than 1% of zooplankton biomass in that year (Fig. 28), so *Daphnia* spp. biomass was substantially lower than during the fertilization experiment. *M. relicta* were rarely observed in fry stomachs, but were observed more often in fry in 1992 and 1993 than in subsequent years. This trend may relate to the decline in *M. relicta* density since 1992.

Age 1+ kokanee also ate a large proportion of *Daphnia* spp. when these species were available (Fig. 76). *Daphnia* spp. made up over 25% of age 1+ diet in June 1992, but were rarely seen in stomachs in June 1993 to 1995. In August *Daphnia* spp. made up about 75% of age 1+ diet, and about 90% in August 1992. *M. relicta* were seen in the stomachs in both months in all four years, and were 2% to 22% of stomach content biomass. The proportion of *M. relicta* did not show any trends that might be related to the decline in *M. relicta* density.

The proportion of *Daphnia* spp. in age 2+ kokanee was highest in 1992, at 92% (Fig. 77). *M. relicta* were seen in age 3+ kokanee diets in all years. However, the presence of over 99% *M. relicta* in 1994 stomachs is likely the result of a small sample size. Several of these fish contained only 1 mysid, and no zooplankton, while one fish contained 37 zooplankton, and 96 mysids. In comparison, the one age 3+ kokanee that was analyzed contained 5232 zooplankton, and one mysid.

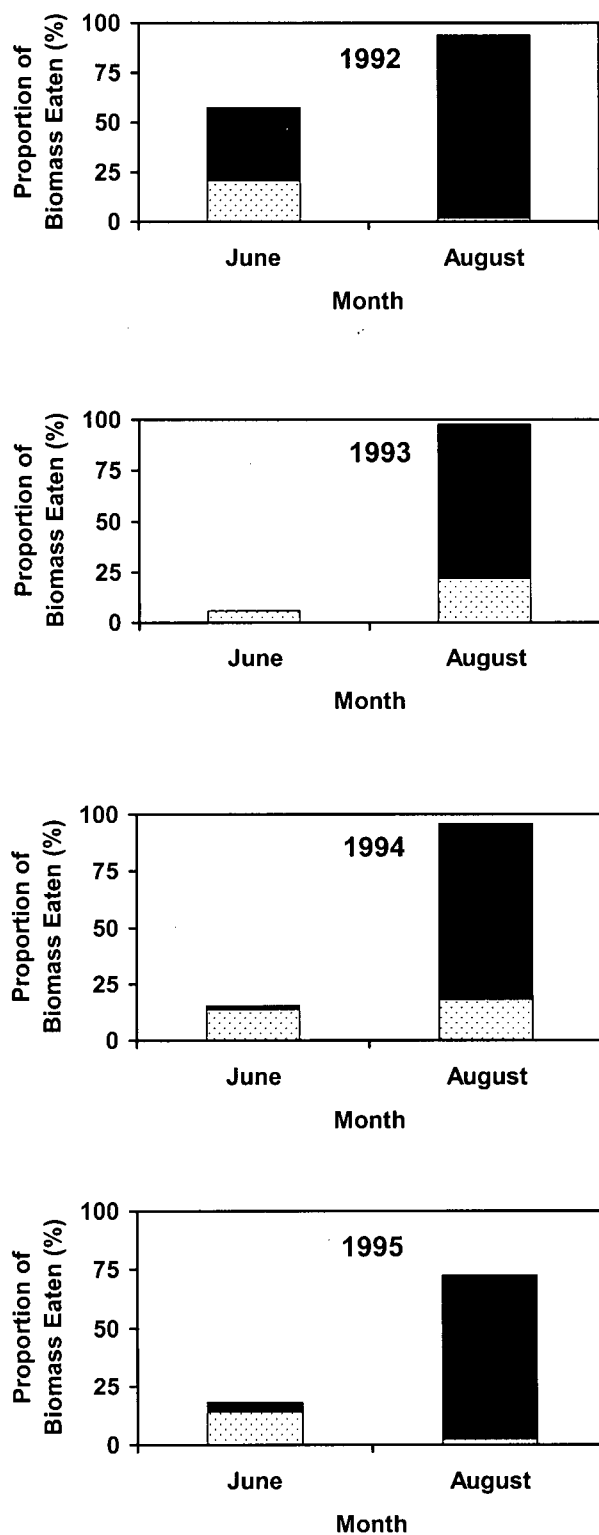


Fig. 76. Proportion of *Daphnia* spp. biomass (black bars), and *M. relicta* biomass (shaded bars), relative to total biomass in the diet of age 1+ kokanee in June and August of 1992 - 1995. Because of small sample sizes data from all stations were pooled.

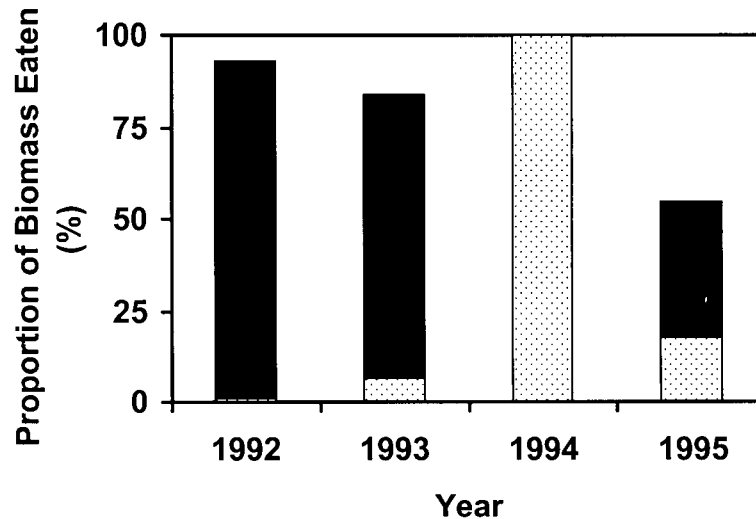


Fig. 77. Proportion of *Daphnia* spp. biomass (black bars), and *M. relictus* biomass (shaded bars), relative to total biomass in the diet of age 2+ kokanee from 1992 to 1995. Because of small sample sizes data from all months and stations were pooled.

Size Selective Predation on Macrozooplankton

Kokanee fry consistently chose zooplankton prey larger than the average available in the standing stock (Fig. 78). Copepods in fry stomachs often averaged 10 μg , while the average copepod in the lake was less than 5 μg (Fig. 44). The average size of copepods in the diet was increased by the preference of fry for *E. nevadensis*, which usually weighed between 10 μg and 20 μg in net haul samples. However, fry also tended to choose the older stages of all copepod species. Cladocerans in the diet tended to be *D. brachyurum*, and averaged 10 μg to 70 μg in August and September 1992, and from 5 μg to 40 μg in subsequent years. Individual *D. brachyurum* in net hauls averaged 4 μg and 10 μg in 1992, and less than 5 μg from 1993 onward. *Daphnia* spp. in the diet averaged 40 to 80 μg in 1992, and about 25 μg to 45 μg in

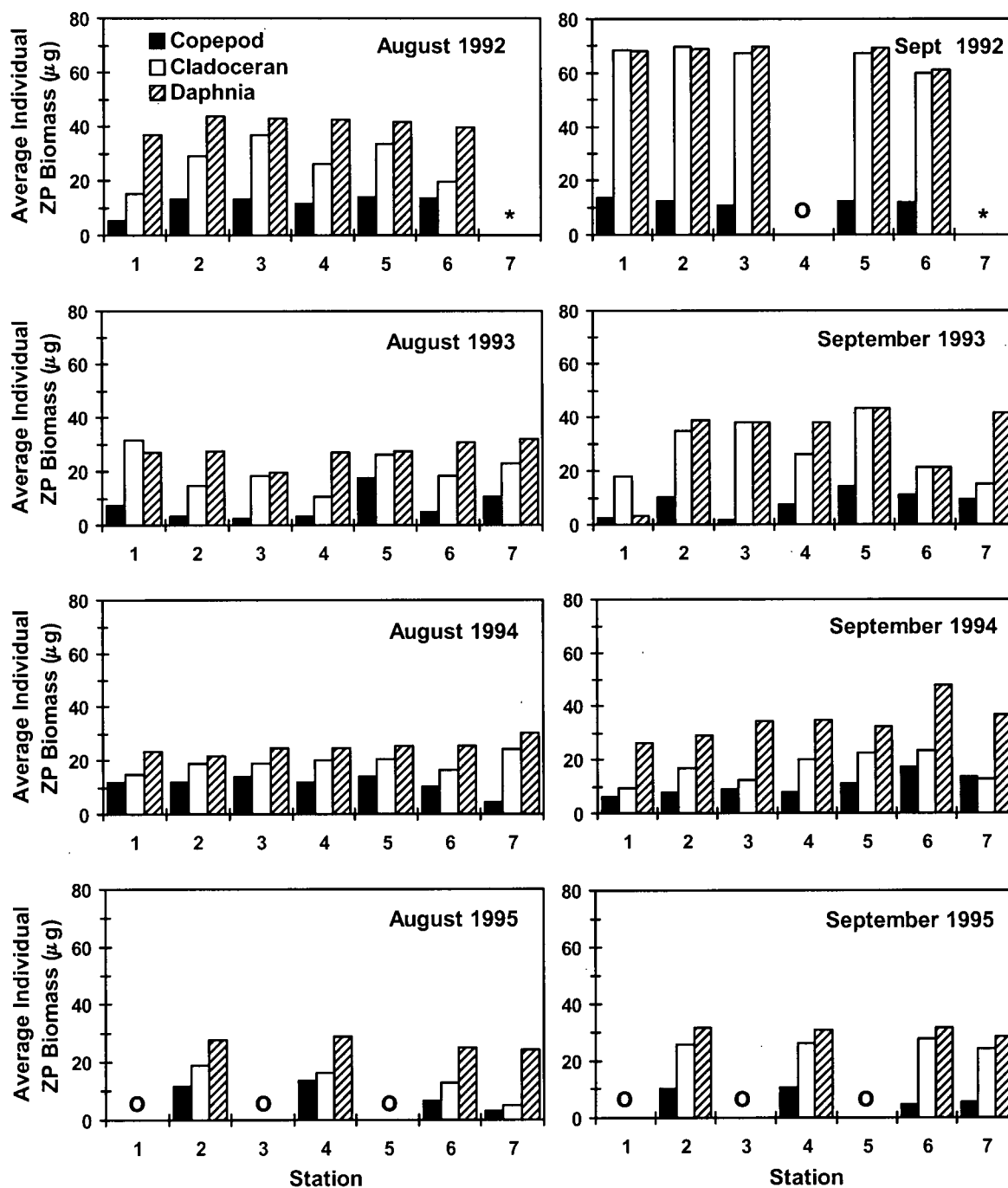


Fig. 78. Average size of individual zooplankton eaten by kokanee fry in August and September of 1992 to 1996. Zooplankton are grouped as copepods, *Daphnia* spp., and "other cladocerans".

subsequent years. In 1992 *Daphnia* spp. in the lake averaged between 15 μ g and 50 μ g.

From 1993 to 1995 the average in the lake was about 17 μ g. In summary, fry chose copepods twice as large as the average in the lake, cladocerans two to eight times larger, and *Daphnia* spp. 1.5 to three times larger. The implications of kokanee prey size selectivity for zooplankton production are examined in the section on kokanee diet and bias in zooplankton production calculations (p.152). I did not examine the size selectivity of older kokanee in detail, but sizes observed in the diets of age 1+ to 3+ fish were comparable to those observed in fry.

Kokanee Consumption

Kokanee consumption of zooplankton appeared to be relatively unimportant in comparison with consumption rates by *M. relictus* (Table 19). In 1994, seasonal consumption to prey biomass ratios for kokanee fry were consistently below 0.2. Consumption ratios for age 1+ kokanee were lower, with a maximum of 0.08 for *Daphnia* spp. Age 2+ and 3+ kokanee combined had the highest consumption ratios of the kokanee, with 0.02 for copepods, 0.02 for cladocerans, and 0.19 for *Daphnia* spp. Ratios of kokanee consumption to standing stock biomass of *M. relictus* increased with increasing kokanee age. Fry consumed a very small fraction of *M. relictus* biomass, while age 2+ and 3+ kokanee consumed 0.18 of the juvenile *M. relictus* standing stock biomass in a five month period, and 0.05 of the adult *M. relictus* standing stock biomass.

Age 1+ consumption of zooplankton and *M. relictus* is likely underestimated, since the proportion of age 1+ fish vs. older fish in the hydroacoustic surveys was estimated from the proportion of ages in the trawl catch. The trawl net is inefficient at catching 1+ kokanee. Age 2+ and 3+ consumption is likely overestimated, for the same reason. Age 1+ kokanee consume a greater proportion of their body weight per day than age 2++ fish, but since they are smaller their actual consumption of zooplankton biomass is similar to or less than that of older fish. Age 1+

kokanee contained an average of 6 mg of copepods, 36 mg of cladocerans, and 36 mg of *Daphnia* spp., while older fish contained 5 mg, 112 mg, and 110 mg, respectively.

Kokanee fry consumed relatively more zooplankton in the North Arm of the lake, because of their skewed density distribution (Fig. 79, see also Fig. 41). This pattern was most apparent in August 1992, when *Daphnia* spp., and cladoceran consumption rates were each 0.017 d^{-1} . In all subsequent months consumption rates were an order of magnitude less. Consumption rates were highest for *Daphnia* spp., followed closely by other cladocerans. Rates for copepods were always less than 0.0005 d^{-1} . Fry consumed *M. relicta* at seven of the stations shown from 1992 to 1994, but the highest rate observed was 0.0002 d^{-1} .

Rainbow Trout and Bull Trout Diet

Diet was sampled in 139 rainbow trout, and 137 bull trout caught by anglers who turned the stomachs in to marina operators between 1988 and 1994. On average rainbow trout fork length was 66 cm, and weight was 5.4 kg. Bull trout averaged 56 cm, and 3.4 kg. Angled rainbow trout contained a wide range of food types: kokanee, other fish (species unidentifiable), *M. relicta*, terrestrial insects, and benthos (Fig. 80). Bull trout contained kokanee, whitefish, other fish, and *M. relicta*, but did not contain terrestrial insects or benthos. Almost 40% of rainbow trout contained kokanee, and 17% of rainbows contained other fish, some of which may have been kokanee. *M. relicta* and other food types were found in less than 10% of rainbow trout. Smaller proportions of bull trout contained kokanee (31%) and other fish (11%), and less than 1% of bull trout contained *M. relicta*. High proportions of both species had empty stomachs: 36% of rainbow trout, and 61% of bull trout. Twice the proportion of bull trout contained tapeworms (7%) than did rainbow trout (3%).

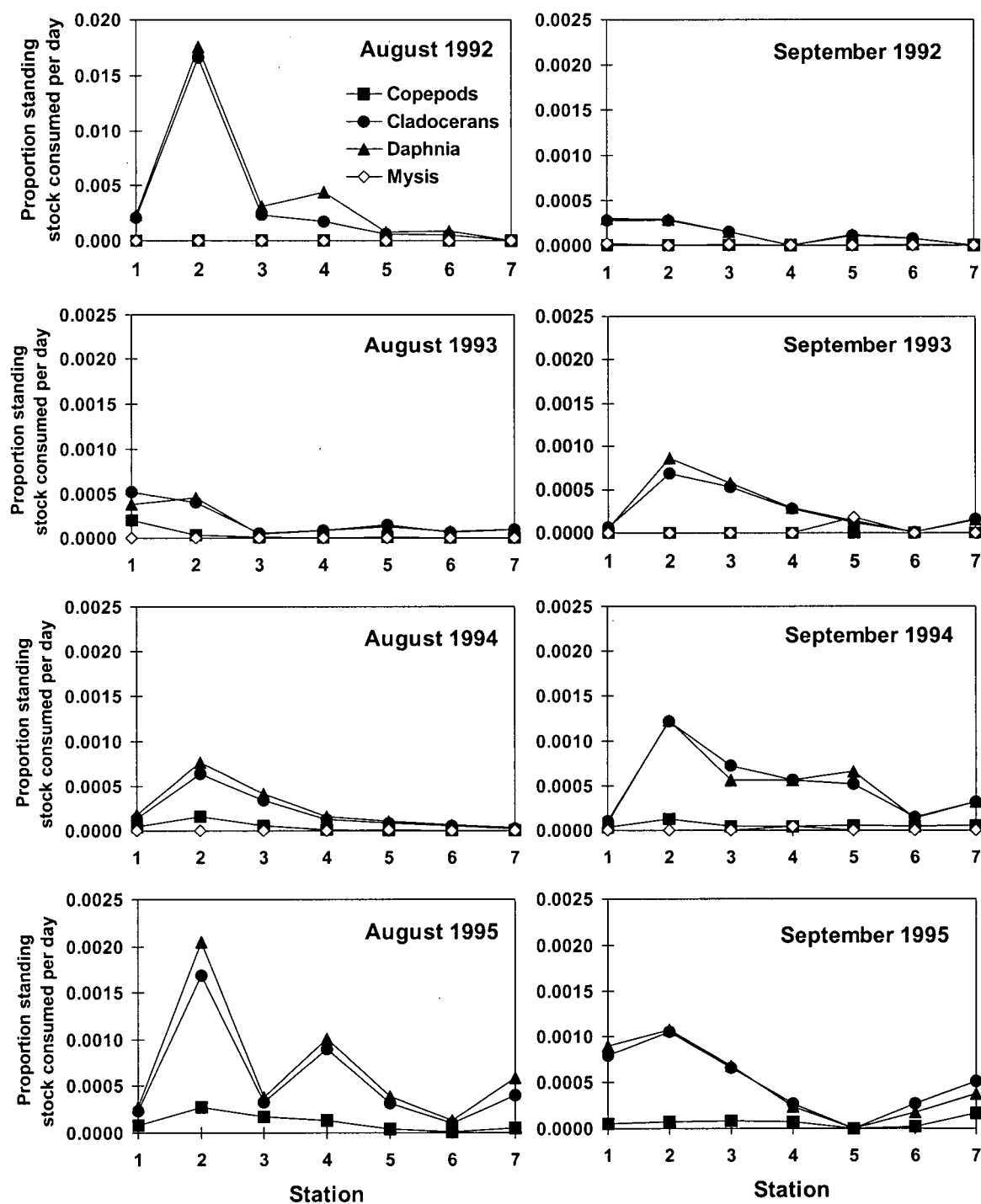


Fig. 79. Consumption by age 0+ kokanee of zooplankton and *M. relicta* along the lake in August and September of 1992 to 1995. Data for *M. relicta* are for 1992 to 1994 only. Note expanded Y-axis scale for August 1992 only.

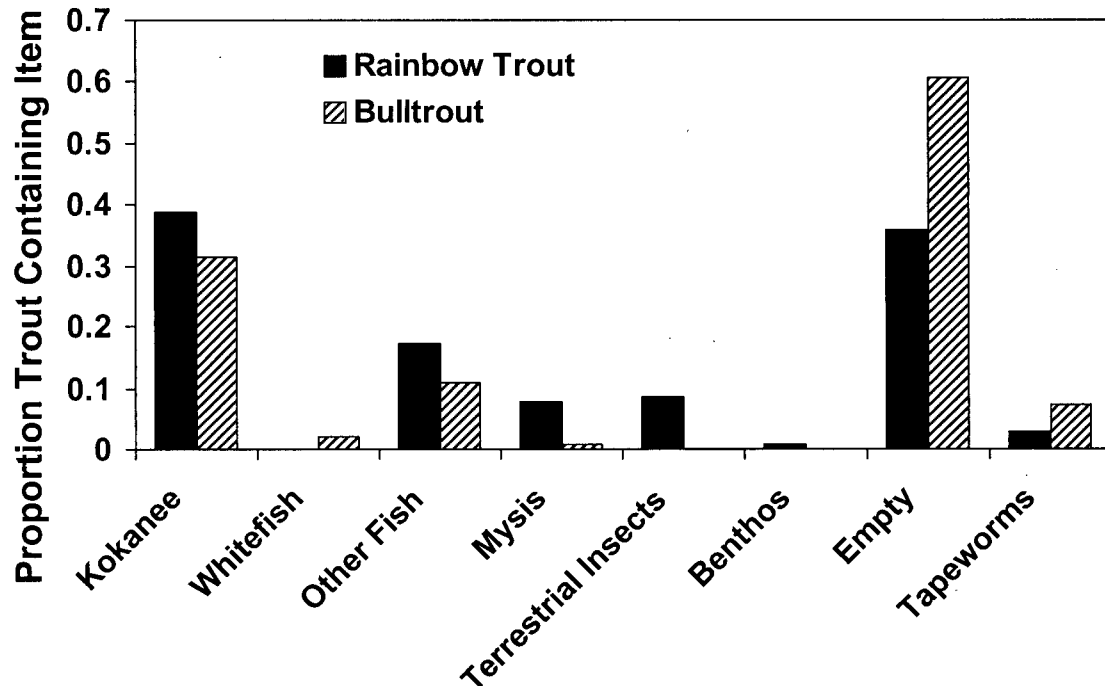


Fig. 80. Frequency of occurrence of different types of prey in stomachs of angled rainbow trout and bull trout. Bars show the proportion of fish that contained each food type. The 'other fish' category is fish that could not be identified because they were too digested.

I also calculated the average number of each type of food item in the stomachs of each trout species, including trout that had empty stomachs. On average a rainbow trout contained 0.72 kokanee, 0.2 other fish, 1.03 mysids, 1.06 terrestrial insects, and 0.04 benthic organisms (Fig. 81). The average bull trout contained 0.53 kokanee, 0.03 whitefish, 0.4 other fish, and 0.01 mysids. A potential source of bias in these diet estimates arises from the fact that the fish in the sample were caught by angling, and were probably feeding actively when they were captured. These fish likely contained fewer food items than the average rainbow trout or bull trout in the lake. Some trout would be satiated and not actively feeding, and would be less likely to be caught by anglers. Thus, these diet estimates likely underestimate the average stomach contents of trout in the lake. The kokanee observed in trout stomachs were predominantly age 1+,

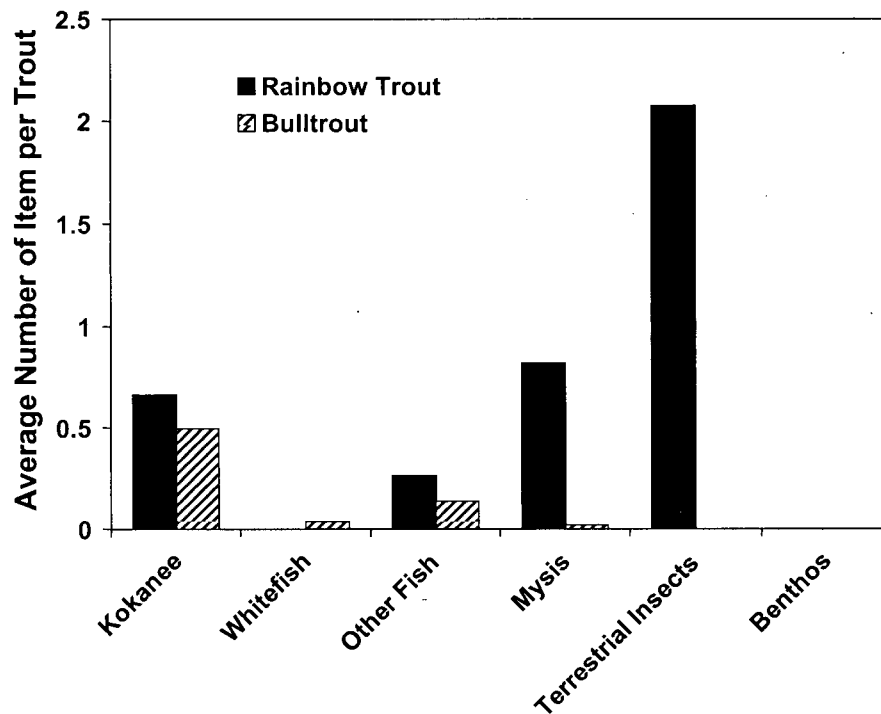


Fig. 81. Average stomach contents of angled rainbow trout and bull trout, including fish that had empty stomachs. The 'other fish' category is fish that could not be identified because they were too digested.

but this was compensated for by the increase in other fish from 0.18 to 0.26.

and occasionally 2+. The smallest kokanee seen was about 65 mm, in a trout caught in March 1990, and was probably a small age 1+ kokanee early in the season. It is possible that younger age classes of trout, which are not as actively pursued by anglers, may prey upon kokanee fry.

I compared trout size and diet before and during the fertilization experiment. Prior to 1992, rainbow trout averaged 70 cm (fork length), and 5.6 kg (n=101). Rainbow trout caught between 1992 and 1994 tended to be smaller, and averaged 54 cm, and 4.6 kg (n=38). Likewise, bull trout were 65 cm, and 3.5 kg prior to fertilization (n=35), and 52 cm, and 3.3 kg during fertilization (n=102). The proportion of rainbow trout containing kokanee declined from 41% to 31%, but the proportion of rainbows containing other fish increased from 15% to 24%. Rainbow

trout contained an average of 0.75 kokanee prior to fertilization, and 0.65 kokanee during fertilization, but this was compensated for by the increase in other fish from 0.18 to 0.26.

The proportion of bull trout containing kokanee before and during fertilization decreased from 43% to 27%, but was somewhat balanced by an increase in the proportion of bull trout containing other fish, from 6% to 13%. The average number of kokanee per bull trout declined from 0.65 kokanee to 0.49 kokanee, while the number of other fish was steady at 0.14. The proportions of bull trout containing other types of food, and the amount of each of these items per trout, were similar before and during fertilization.

Kootenay Lake Pelagic Ecosystem Ecopath Model

Most of the organisms in the Kootenay Lake food web are omnivorous (Table 17), and feed on more than one trophic level. The highest trophic level included in the model is 4.3, occupied by bull trout (Table 18). The upper levels of the food web have the highest ecotrophic efficiencies (the higher the EE, the lower the proportion of production that goes to detritus). Mysids have low EE values, which may reflect the limited amount of predation fish are able to impose because of *M. relicta*'s strategy of hiding in dark water by day. *M. relicta* is able to sustain its biomass even though its production to consumption ratio (P/Q) was the highest permitted by the software (0.5), and despite export mortality of about 25% of its standing stock biomass per year (shown as emigration). *Daphnia* spp. has the highest EE of the macrozooplankton, followed closely by other cladocerans, while that of copepods is half as large.

The Kootenay Lake model balanced using empirical values for phytoplankton, rotifer, zooplankton, *M. relicta*, and kokanee biomass. Empirical values for zooplankton production, and kokanee production and consumption also functioned well. This is somewhat surprising given that there were many potential biases in the calculation of zooplankton production, and

Table 17. Diet matrix for Kootenay Lake pelagic Ecopath model.

	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11
1	Bull Trout	0.050										
2	Rainbow Trout	0.050										
3	Kokanee 2++	0.200	0.200									
4	Kokanee 1+	0.300	0.300									
5	Kokanee 0+	0.200	0.200									
6	<i>M. relicta</i> (adult)	0.100	0.150	0.100	0.100							
7	<i>M. relicta</i> (juvenile)	0.100	0.140	0.100	0.100	0.050						
8	Copepod Zooplankton			0.100	0.100	0.200	0.200	0.200	0.050			
9	Cladoceran Zooplankton			0.025	0.025	0.025	0.025	0.025	0.025	0.025		
10	<i>Daphnia</i> Zooplankton			0.675	0.675	0.725	0.680	0.675	0.050	0.025		
11	Rotifers						0.095	0.100	0.050	0.025		0.005
12	Phytoplankton								0.825	0.925	1.000	0.605
13	Detritus											0.390
	Import		0.010									
	Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

kokanee consumption was based on stomach content data, which probably doesn't reflect all the food eaten. Nevertheless, observed kokanee production fits well with the stomach content data.

According to the empirical data available, and EcoPath model output, biomass mortality of zooplankton is due mainly to *M. relicta* consumption (Table 19). Biomass mortality of *M. relicta* caused by predation, is due mainly to kokanee, but this mortality is relatively small in comparison with *M. relicta*'s production to biomass ratio (P/B).

Table 18. Output from Ecopath model of Kootenay Lake pelagic ecosystem, including trophic level designation, production to biomass ratios (P/B), consumption to biomass ratios (Q/B), ecotrophic efficiency (EE), production to consumption ratio (P/Q), and net migration from system. All values were calculated for the growing season, May to October, using 1994 data.

Group name	Trophic Level	Biomass (t km ⁻²)	P/B (6 mo. ⁻¹)	Q/B (6 mo. ⁻¹)	EE	P/Q	± Net migration (t km ⁻² 6 mo. ⁻¹)
Bull Trout	4.3	0.257	0.4	2.4	0.952	0.167	0
Rainbow Trout	4.1	0.193	0.4	2.2	0.853	0.182	0
Kokanee 2+ & 3+	3.2	0.361	0.7	5.5	0.852	0.127	0
Kokanee 1+	3.2	0.16	2.15	5.4	0.908	0.398	0
Kokanee 0+	3.1	0.12	1.77	9	0.981	0.197	0
<i>M. relicta</i> (adult)	3	3.88	4	8	0.104	0.5	1.2
<i>M. relicta</i> (juvenile)	3	1.08	5	10	0.159	0.5	0.4
Copepods	2.2	10	6	42	0.498	0.143	0
Cladocerans	2.1	2	10	70	0.757	0.143	0
Daphnia	2	7	10	70	0.794	0.143	0
Rotifers	2	0.88	64.5	650	0.553	0.099	0
Phytoplankton	1	15	113	-	0.774	-	0
Detritus	1	100	-	-	0.197	-	0

Table 19. Growing season biomass mortality for each prey type (Z, biomass of prey i consumed by predator j, divided by standing stock biomass of prey i, B), partitioned by predator, calculated from EcoPath model output. Production to biomass ratios of prey (P/B) are shown for comparison with Sum Z (sum over all predators).

	Prey \ Predator		1	2	3	4	5	6	7	8	9	10	11		
		Predator Biomass (t km^{-2})	0.26	0.19	0.36	0.16	0.12	3.88	1.08	10	2	7	0.88		
		Predator Q/B	2.4	2.2	5.5	5.4	9	8	10	42	70	70	650		
		Prey Biomass (t km^{-2})												Sum Z	P/B
1	Bull Trout	0.26	0.12											0.12	0.40
2	Rainbow Trout	0.19	0.16											0.16	0.40
3	Kokanee 2++	0.36	0.34	0.24										0.58	0.70
4	Kokanee 1+	0.16	1.16	0.80										1.95	2.15
5	Kokanee 0+	0.12	1.03	0.71										1.74	1.77
6	<i>M. relicta</i> (adult)	3.88	0.02	0.02	0.05	0.02								0.11	4.00
7	<i>M. relicta</i> (juvenile)	1.08	0.06	0.06	0.18	0.08	0.05							0.43	5.00
8	Copepod Zooplankton	10.00			0.02	0.01	0.02	0.62	0.22	2.10				2.99	6.00
9	Cladoceran Zooplankton	2.00			0.02	0.01	0.01	0.39	0.14	5.25	1.75			7.57	10.00
10	<i>Daphnia</i> Zooplankton	7.00			0.19	0.08	0.11	3.02	1.04	3.00	0.50			7.94	10.00
11	Rotifers	0.88						3.35	1.23	23.86	3.98		3.25	35.67	64.50
12	Phytoplankton	15.00								23.10	8.63	32.67	23.07	87.47	113.00

Comparison of Kokanee Vertical Migration at Two Points on the Fertilization Gradient

Kokanee fry showed vertical migration patterns similar to those of older kokanee at Stations 1 and 4 in July and August 1994. Fry did not appear to migrate to deeper waters in midday, as has been observed for Okanagan Lake kokanee fry (Levy 1991). There were no obvious differences in the time spent near the surface by fry or older kokanee at dawn or dusk at the two stations.

Data were collected between July 21 and August 2, 1994. During this time sunrise ranged between 5:08 a.m. and 5:25 a.m., and sunset ranged between 8:46 p.m. and 8:28 p.m. Sampling started 1.5 hours before sunrise or sunset, and continued until 1.5 hours after. Secchi disk depth was less at Station 1 than Station 4, and the depth at which light was completely attenuated was also shallower at Station 1 (Table 20.), so kokanee would have had to come closer to the surface to feed visually at Station 1. In contrast, the UV-B₃₁₀ downwelling attenuation coefficient was greater at Station 4, indicating that kokanee would have had to come to slightly shallower depths at Station 4 to make use of UV light for feeding. UV-B absorption is related to dissolved organic carbon content of water. The attenuation coefficients observed in Kootenay Lake are relatively low in comparison with other north temperate water bodies. Silver Lake (northeast Ontario) had an attenuation coefficient of 0.68 m, while the Welland Canal, and Bay of Quinte (Lake Ontario) had values of 4.94 m, and 22.18 m respectively (Scully and Lean 1994). Water temperature at the surface and at 20 m were similar at Stations 1 and 4, so fish metabolic rates should have been similar relative to depth at the two stations. The total zooplankton density, and *Daphnia* spp. density were higher at Station 4 than at Station 1 in July. The same pattern was seen in August, although densities increased at both stations (Fig. 32). These data suggest that in spite of fertilization the amount of food available for kokanee was lower at the north end of the lake. In contrast, the densities of kokanee fry and older kokanee

were higher at Station 1. The density of kokanee fry may not have been as extreme at the time the hydroacoustic survey was done as the numbers here suggest. In August, fry density at Station 1 was 985 individuals \cdot ha $^{-1}$, and density of older kokanee was 712 individuals \cdot ha $^{-1}$ (see also Fig. 41). This ratio of fry to older kokanee better reflects the ratio of the two age groups indicated from the vertical migration data, which was collected at the end of July, and early August.

Table 20. Limnological conditions at Stations 1 and 4 during the kokanee vertical migration hydroacoustic survey, July 21 to August 2, 1994.

Variable	Station 1	Station 4
Secchi depth (m)	3.5	5.0
Depth of Complete Light Attenuation (m)	11	19
UV-B ₃₁₀ Downwelling Attenuation Coefficient, K _{d310} (m)	3.23	4.42
Surface Water Temperature (°C)	21	22
Water Temperature at 20 m (°C)	14	13
Total Zooplankton Density (Individuals \cdot L $^{-1}$)	28	35
<i>Daphnia</i> spp. Density (Individuals \cdot L $^{-1}$)	0.11	0.68
Kokanee Fry Density (Individuals \cdot ha $^{-1}$)	3179	263
Kokanee 1+ - 3+ Density (Individuals \cdot ha $^{-1}$)	116	73

Kokanee at Stations 1 and 4 were usually at between 10 m and 20 m at 3:30 a.m. (Fig. 82 and Fig. 83). Kokanee began to move upward as surface light levels increased, but this pattern was obscured because of large differences in the time the fish began to surface on the west and east sides of the lake. Kootenay Lake is narrow, and the high mountains on either side cause shadows across the lake on the east side at dawn, and on the west side at dusk. This effect can

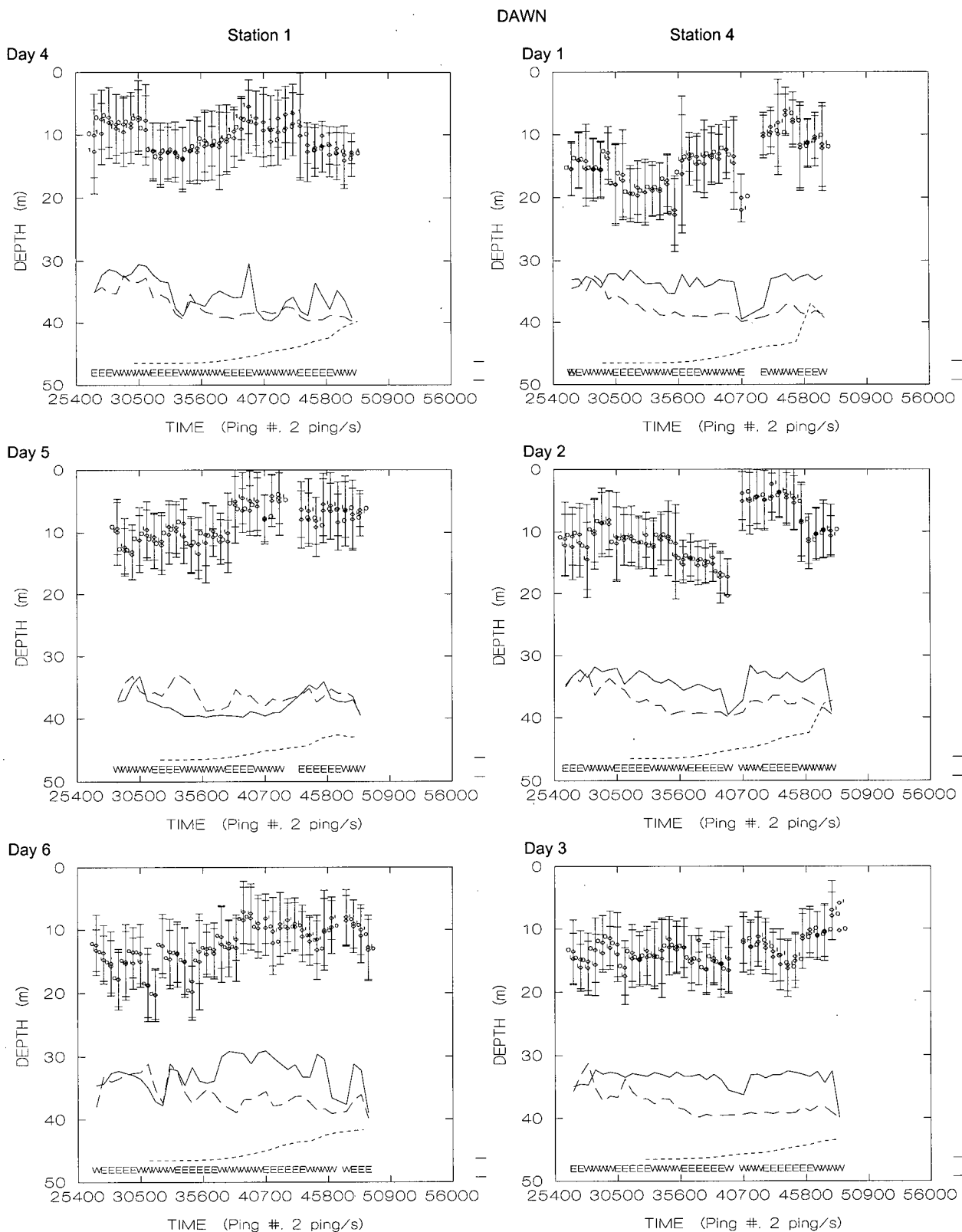


Fig. 82. Vertical movement of kokanee at dawn at two locations along the lake productivity gradient (days 1-6 of study). Average depths of fry (O) and of older kokanee (1) are shown with 95% confidence intervals. Dashed line is fry density, solid line is density of older kokanee. W and E indicate westward or eastward direction of boat travel across the lake. Fine dashed line is light intensity. X-axis time period is from 3:31 a.m. to 7:47 a.m.

DAWN

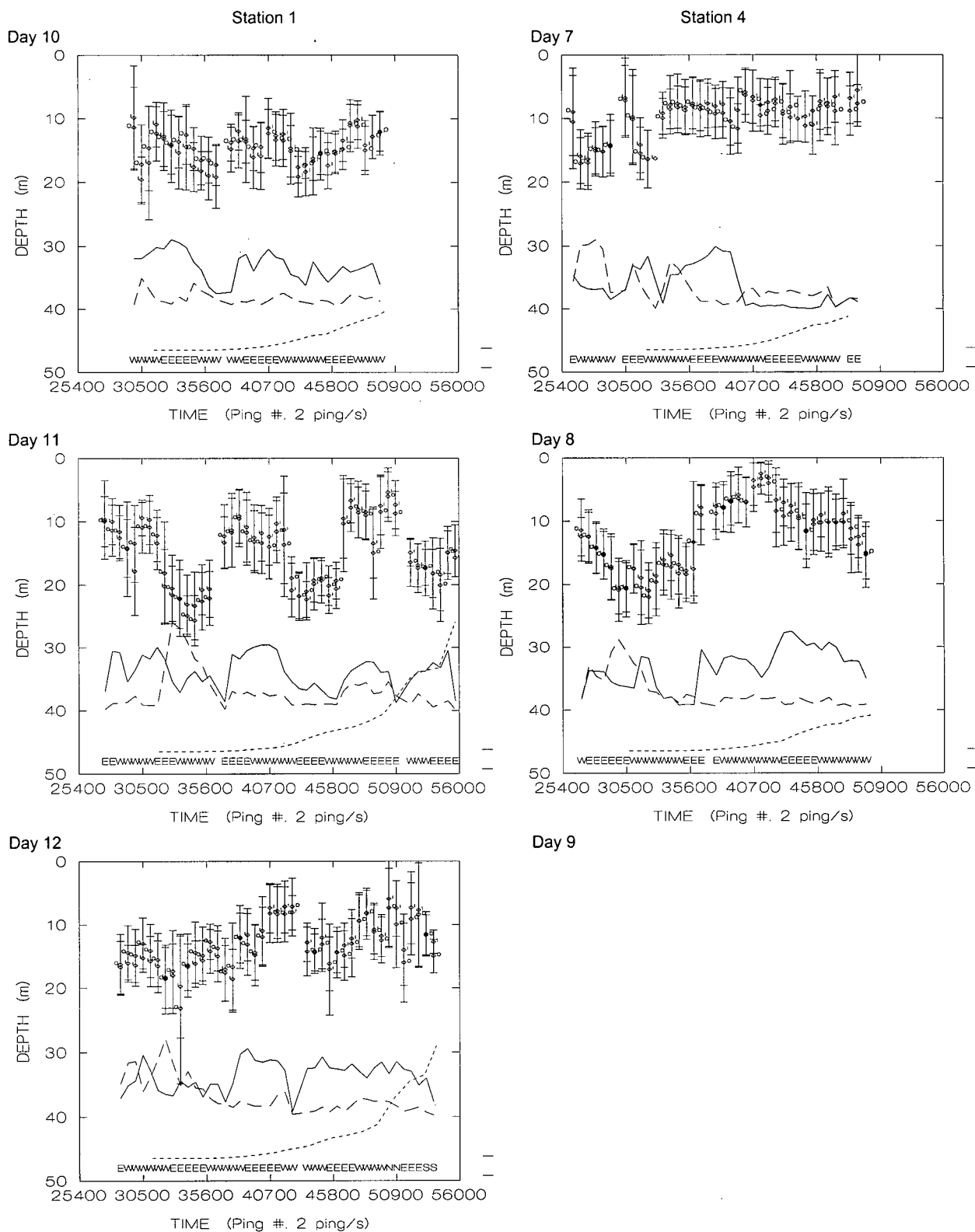


Fig. 83. Vertical movement of kokanee at dawn at two locations along the lake productivity gradient (days 7-12 of study). No sampling was done at Station 4 on Day 9 at dawn because of technical problems with the boat. Average depths of fry (O) and of older kokanee (I) are shown with 95% confidence intervals. Dashed line is fry density, solid line is density of older kokanee. W and E indicate westward or eastward direction of boat travel across the lake. Fine dashed line is light intensity. X-axis time period is from 3:31 a.m. to 7:47 a.m.

be seen in the sigmoidal fluctuations in the light values, which flattened out as the boat moved eastward at dawn. The combination of the boat moving into shadow, plus the overall increasing light levels, caused the light readings to plateau. The apparent effect on kokanee of different light levels across the lake is particularly visible in the Dawn, Station 1, Day 11 plot (Fig. 83). On Days 11 and 12 at Station 1 we continued sampling longer than the usual 1.5 hours after sunrise, until surface light levels were as high as $820 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, but still saw no evidence of fry migrating downward. Short gaps in data collection (e.g., Dawn, Station 4, Day 1, at ping # 40700) occurred when I had to switch to a new DAT tape and calibrate it. The decreases in average numbers of fish observed at these times are artifacts caused by the gap in echosounder data collection. As I became more experienced I was able to get a new tape started in under 10 minutes, so only 1 or 2 data points were lost.

The differences in depth distribution of kokanee on different sides of the lake may also be the result of seiche activity. Our vertical temperature profile data were collected only in the middle of the lake, so we would not have been able to detect horizontal differences in temperature across the lake. However, there was a thunderstorm the evening before sampling was done at Dawn, Station 5, Day 5, and there is little evidence of cross-lake differences in fish vertical distribution on this day. The highest waves we observed during the sampling period were about 1 m, during midday, on July 27. In general weather conditions during the survey were very stable, hot, and dry, and hazy, due to forest fire smoke moving northward from Washington and Idaho. It is unlikely that the cross-lake differences in kokanee vertical distribution were the result of temperature and seiche effects.

At dusk the pattern of kokanee descending toward the thermocline was seen fairly consistently, and correlated well with decreasing surface light intensity (Fig. 84 and Fig. 85). At Station 4 fish began to descend at about 7:50 p.m. (Ping # 142900). At Station 1 the time of

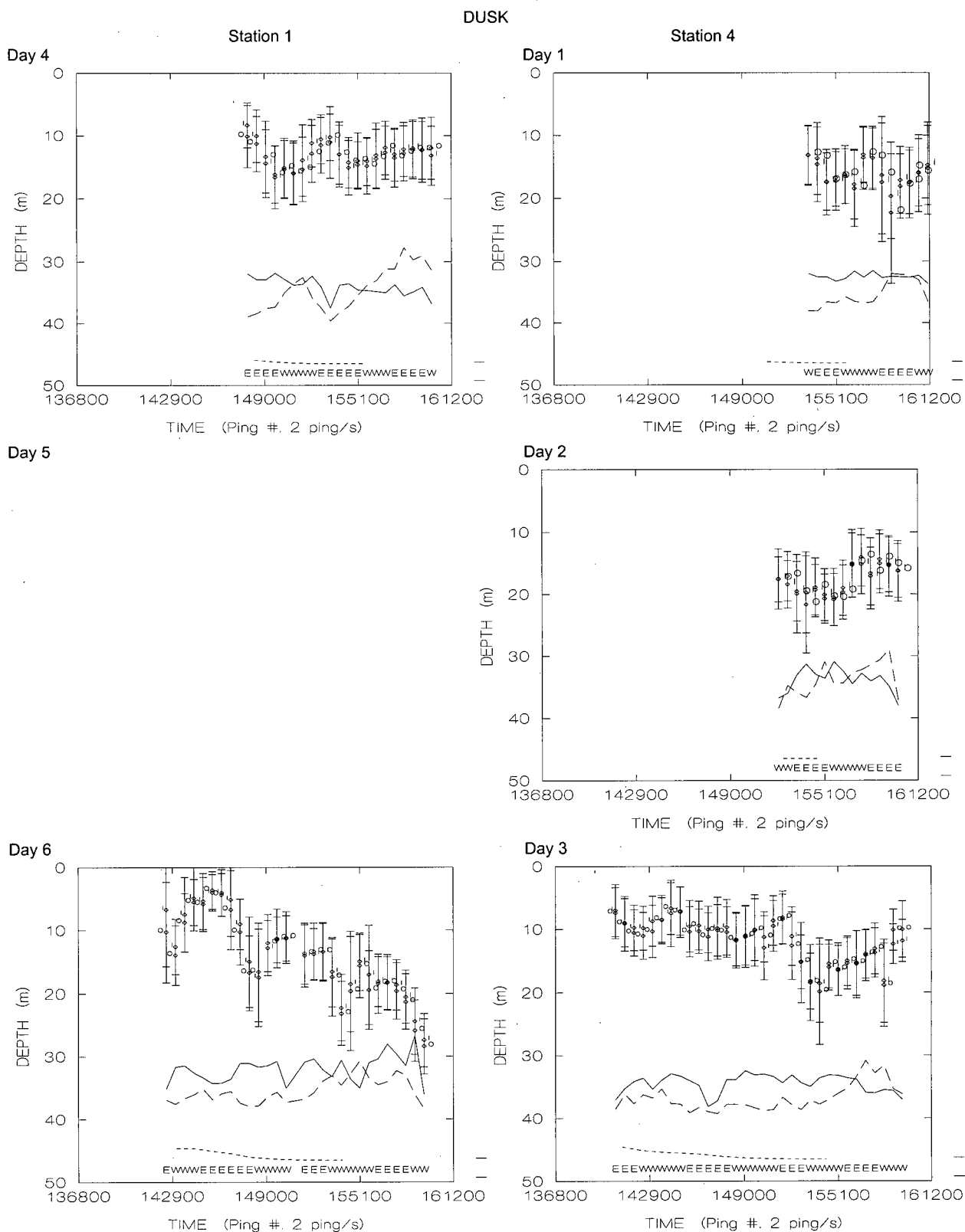


Fig. 84. Vertical movement of kokanee at dusk at two locations along the lake productivity gradient (days 1-6 of study). No sampling was done at Station 1 on Day 5 at dusk because of an electrical storm. Average depths of fry (O) and of older kokanee (1) are shown with 95% confidence intervals. Dashed line is fry density, solid line is density of older kokanee. Fine dashed line is light intensity. W and E indicate westward or eastward direction of boat travel across the lake. X-axis time period is from 7:00 p.m. to 10:23 p.m.

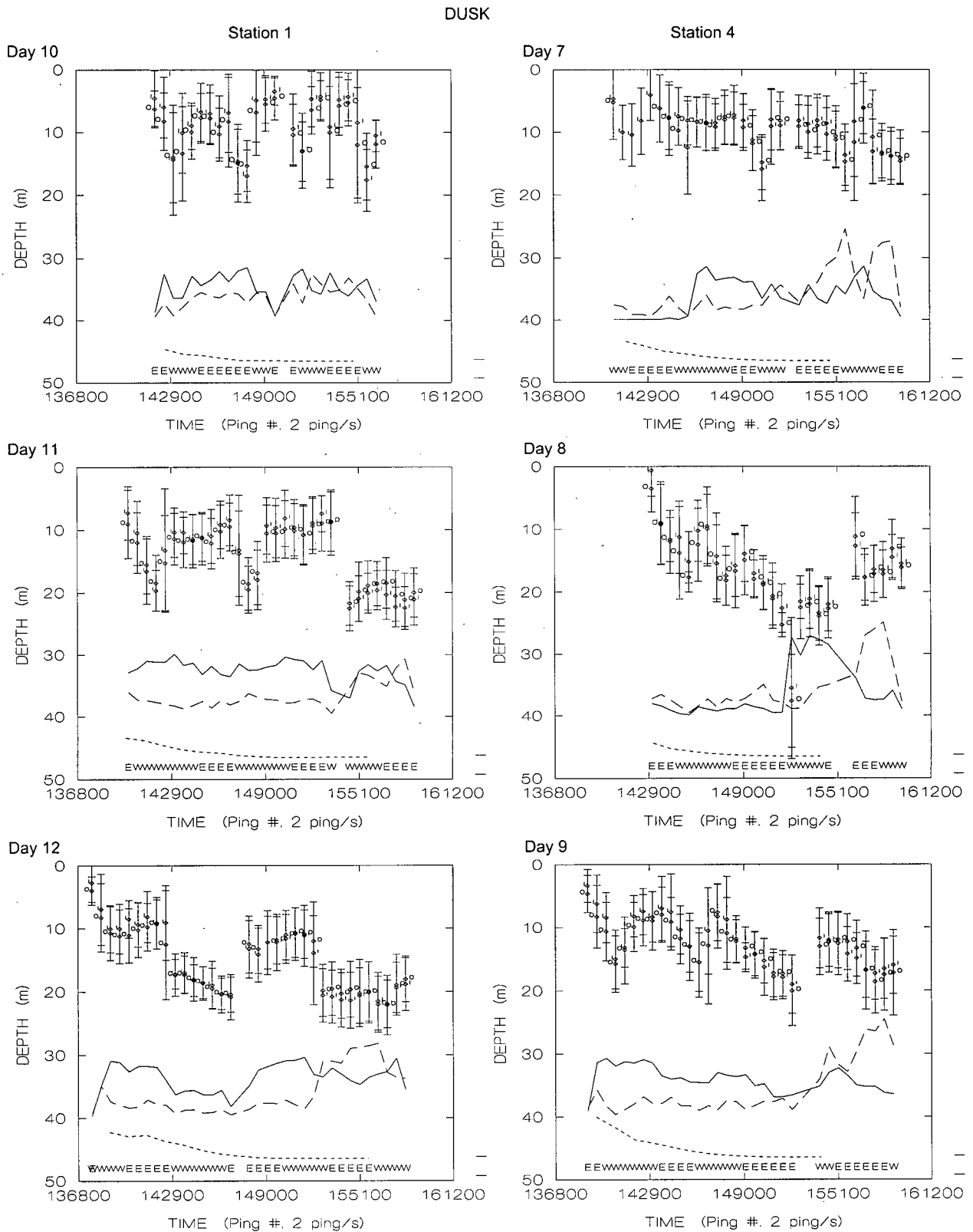


Fig. 85. Vertical movement of kokanee at dusk at two locations along the lake productivity gradient (days 7-12 of study). Average depths of fry (O) and of older kokanee (I) are shown with 95% confidence intervals. Dashed line is fry density, solid line is density of older kokanee. Fine dashed line is light intensity. W and E indicate westward or eastward direction of boat travel across the lake. X-axis time period is from 7:00 p.m. to 10:23 p.m.

descent was later than at Station 4 on Days 6, 10, and 11, but earlier on Day 12. The difference in time of descent between the two Stations was not consistent. Data are missing for the early part of the dusk sampling at Station 1 on Day 4, and 6, and Station 4 on Day 1 and 2. Data were not collected at these times because of technical problems with deployment of the upward-looking transducer and fin, and with the cable system. Occasionally the fin would flip over, so we had to pull in the cable and re-deploy the fin, or maneuver the boat so as to cause the fin to flip back over. On several evenings it was necessary to launch the fin very slowly while re-taping the hydroacoustic cable to the metal cable, to prevent tension on and damage to the hydroacoustic cable. For the parts of these evenings where sampling was done the data appear similar to days when the complete dusk period was sampled. It was not possible to extend the survey over additional days because the hydroacoustic equipment was rented, and borrowed for a limited time period.

Fry appear to be forming schools at dawn, and breaking out of schools at dusk. Individual fry counts started to decline prior to sunrise on most days (Fig. 82 and Fig. 83). The decline was usually complete by 5:00 a.m. (Ping # 35600). The decline in observed numbers of fry may result from fry forming schools, and becoming "invisible" to dual-beam analyses. Fry counts began to increase starting at 9:00 p.m. (Ping # 152000), about 30 minutes after sunset, on most days (Fig. 84 and Fig. 85). As fry leave schools and swim as individuals, they would become detectable to dual-beam analysis, and fry counts would increase.

An examination of the chart paper data collected at the same time as the electronic data offers further evidence that kokanee are forming schools at dawn, and breaking out of schools at dusk. I examined the chart papers for the relative frequency of schools during the dawn and dusk periods. The chart data include all hydroacoustic targets, including "hits" on schools, but it is not possible to ascertain the size of an individual target. For example, a large fish that was

oriented at an oblique angle to the sounder would produce only a weak target strength, and could be confused with a fry. Nevertheless, schools appear as large blobs compared with narrower specks for individual fish. On all days that fry numbers declined at sunrise, the number of targets on the chart paper decreased, but the number of schools (very large targets) increased. Likewise, on all days that fry numbers increased after sunset, the number of targets on the chart paper increased, and the number of schools decreased. In addition, I never observed large numbers of targets in deeper water by day, separate from another group of targets at the surface. This would be expected if fry were moving to deeper water between feedings periods at dawn and dusk, that is, doing a double diel vertical migration, as seen in Okanagan Lake by Levy (1991). These results suggest that the average depths obtained from the electronic data give a good estimate of average fry depth, and that fry in Kootenay Lake did not migrate to deeper water in midday during the July-August period.

Kokanee fry appear to be spending the same amount of time near the surface, and the same amount of time in schools, at the two stations examined along the fertilization gradient. The timing of school formation and break-up may be a better indicator of the time that fry spend feeding than the timing of fry vertical migration. Fry in schools may be making a trade-off between decreased feeding efficiency, and increased survival rates due to reduced predation risk while in schools. Given that fry densities were higher at Station 1 than Station 4, and zooplankton densities were lower, it would have been reasonable to expect that fry might actually spend more time out of schools (and feeding more intensively) at Station 1, even though it is closer to the fertilization site. However, there was no apparent difference in the timing of school formation or break-up at Stations 1 and 4. In addition, the surface light levels were very low at the time of the increases and decreases in fry density at dusk and dawn. This suggests that kokanee fry begin forming schools as soon as light levels permit, and leave schools only

when low light levels make it difficult to orient with other fish, regardless of the density of competitors, or of zooplankton. The lack of a downward migration by fry in midday may relate to the high numbers of fry in Kootenay Lake at the time of sampling. If fry are easily able to find large numbers of other fry to form schools, the trade-off between growth and survival may be better met by staying in surface waters to feed in the day, rather than seeking refuge in deeper water, but obtaining much less food.

Kokanee Survival Rate

Meadow Creek channel kokanee egg-to-spawner survival rates ranged from 0.35 % and 2.90 % for the cohorts spawned between 1969 and 1991 (Fig. 86). Some fish in the 1991 to 1994 cohorts may not yet have returned to spawn, so these survival estimates are incomplete. No fish from the 1995 to 1997 cohorts had returned to spawn at the time this study was completed, so no survival estimates are possible for these cohorts. Spawner ages were confirmed by otolith analysis from 1985 onward, so for the 1977 to 1982 cohorts the age of spawners was otolith-corrected for at least some return years, and for the 1983 cohort onward all return years had otolith-corrected ages.

The survival rate appeared to fluctuate cyclically, with peaks for the 1972, 1982 and 1991 year classes. The highest survival rate seen was for the 1991 year class, at 2.90%. Since the final possible year of spawners (age 5+) for this cohort had not returned by the time of this study, the survival rate may still increase slightly.

High kokanee survival rates occurred for several year classes born during El Niño periods, such as 1972-1973, 1982-1983, and 1991-1992 (Mayell 1997). However, survival rates were low for the year classes associated with the El Niño of 1986-1987, and rates began to rise during the strong La Niña cold period of 1988-1989. It is too early to tell if survival rates are correlated with the El Niños that occurred in 1993, 1994, and 1997-1998, or with the La Niñas of

1995-1996, and 1999. I examined the time series graphs for flow (Fig. 2), zooplankton density (Fig. 27), *M. relicta* density (Fig. 35), and kokanee spawner abundance (Fig. 38), but could not see any consistent correlations with El Niño events.

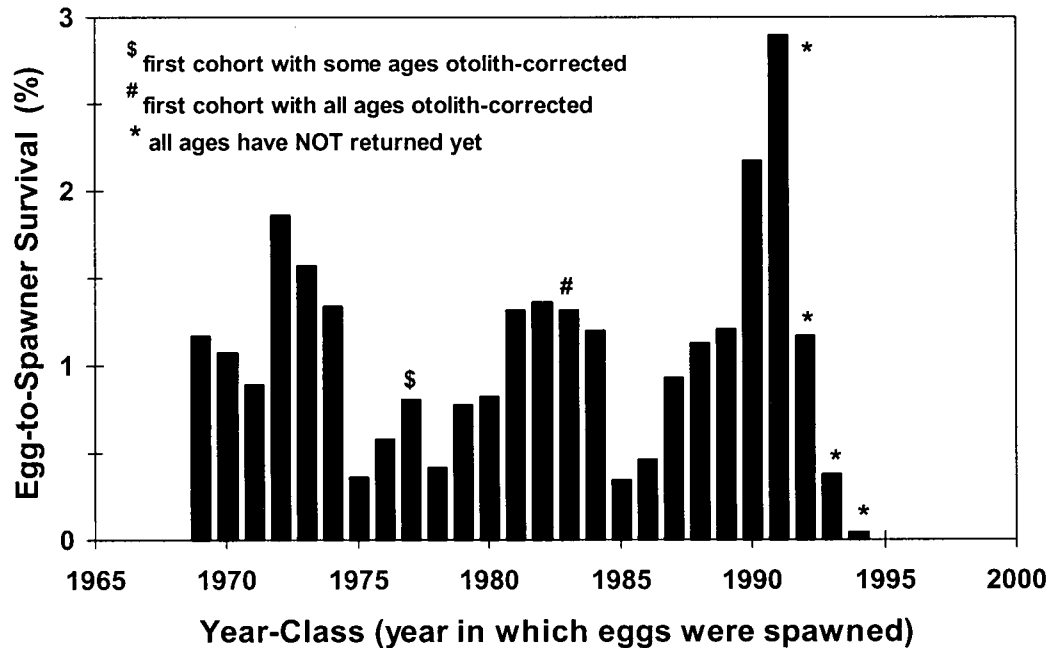


Fig. 86. Kokanee egg-to-spawner survival rate for years classes spawned from 1969 to 1994 at the Meadow Creek spawning channel.

Summary of Patterns in Abundance and Production

Time Series Trends

1. Total dissolved phosphorus and dissolved ortho-phosphate increased in 1995 and 1996, then decreased in 1997. The natural total phosphorus load from the Kootenai River was lower than average from 1992 to 1994, but was high in 1996 and 1997.
2. Phytoplankton biomass in Kootenay Lake increased during the first five years of fertilization, then decreased in 1997.

3. Rotifers showed no trends in density or biomass from 1994 to 1996.
4. Rotifer production was probably lower than macrozooplankton production.
5. No major macrozooplankton species shifts were observed, but *Daphnia* spp. were present in higher proportions than in the eutrophic period in the 1960's. *E. nevadensis* was not seen from 1972 - 1992, and *D. kenai* was not seen in this study.
6. Macrozooplankton abundance was higher during this study than the long term average, but not higher than some years in the 1980's.
7. There was an increase in the proportion of cladocerans in years 1-5 of fertilization (1992-1996), but a decrease in year 6 (1997). (Note: the proportion of cladocerans increased to 9% in 1998, similar to values seen from 1992-1996).
8. *Daphnia* spp. individuals were larger in 1992 than in subsequent years. There was no change in the average individual size of other species.
9. *L. ashlandi* and *D. bicuspidatus thomasi* showed increases in the number of eggs per gravid females during the fertilization experiment (growing season averages). In contrast, *Daphnia* spp. showed decreases eggs per gravid female over the six year period, with the exception of 1995. *Daphnia* spp. also showed decreases in the eggs per water volume over the six year period.
10. Whole-lake seasonal average P/B ratios: the new biomass produced of *L. ashlandi* decreased from 1993 onward, while P/B decreased from 1993 to 1996, and was also low in 1997. The new biomass of *D. bicuspidatus thomasi* increased from 1992 to 1996, then declined in 1997 to the 1994 level. P/B increased from 1992 to 1995, a year with increased Kootenai River flow (Libby Dam outflow). *D. bicuspidatus thomasi* P/B decreased in 1996, then increased in 1997. *Daphnia* spp. P/B peaked in 1995, but dropped in 1997 to half the P/B seen in most

years, and one third of peak P/B, while standing stock biomass declined fairly steadily from 1992 to 1997.

11. *M. relicta* densities were low immediately prior to the start of fertilization, increased to 405 individuals·m⁻² in 1992, then steadily declined from 1993 to reach 126 individuals·m⁻² in 1996; densities rose slightly in 1997.
12. Kokanee spawner returns to both major tributaries increased during the fertilization experiment, and hydroacoustic density estimates increased from about 8 million to about 25 million fish (age 0+ - 2+).
13. Rainbow trout spawner abundance increased during the fertilization experiment.

Patterns Along Gradient

1. Total dissolved phosphorus (TDP) concentrations showed no trends along the length of the lake in 1992 - 1995. In 1996 there was a trend toward higher TDP concentrations in the South Arm (unfertilized) of the lake from April to July. This trend disappeared from August onward. In 1997 the same trend was seen, but TDP concentrations were lower than in 1996.
2. Biomass of smaller, grazeable algae was higher in the fertilized end of the lake from 1992 to 1996. In 1997 there was no difference in grazeable algal biomass along the length of the lake, and the grazeable algal biomass was the lowest observed during the fertilization experiment.
3. Rotifers showed no trends in density or biomass or along the gradient in any of the years they were sampled (1994-1996).
4. There were no consistent trends in the density or biomass of copepods, *Daphnia* spp., or other cladocerans along the phytoplankton gradient, in any of the years studied (1992-1997).
5. There were no trends in individual zooplankton size along the phytoplankton gradient, despite differences in fish density along gradient.

6. There were no consistent trends in zooplankton fecundity or P/B ratios along the gradient for any of the three species considered.
7. *M. relicta* density along the fertilization gradient has not shown a consistent pattern over the six years of fertilization (Lasenby et al. 1998).
8. *M. relicta* production was higher in the North Arm, as evidenced by faster growth rates, greater female size, and higher fecundity (Smokorowski 1998).
9. Kokanee fry distribution tended to be skewed toward higher densities in the fertilized end of the lake in spring and early summer, but fry distribution along the lake was even by autumn.
10. Age 1+, 2+, and 3+ kokanee were evenly distributed along the lake.
11. Kokanee fry tended to be larger in the unfertilized end of the lake, but otolith analyses showed that larger fish were also older, so size-at-age was similar throughout the lake.
12. Kokanee spawner size in the fall trawls was similar from 1985 to 1991. Spawner size and fecundity increased from 1992 to 1995, then decreased in 1996 and 1997. The shift in kokanee size appears to be density dependent, but is also related to shifts in age of spawning (larger spawners were age 4+, smaller spawners were age 2+).
13. Zooplankton mortality due to kokanee fry predation was higher in the fertilized end of the lake, due to the skewed fry distribution, but mortality due to kokanee fry was very small compared with mortality due to *M. relicta*.
14. The consumption rate of zooplankton by *M. relicta* was higher in the fertilized end of the lake in 1992, and 1995 (Smokorowski 1998).
15. Kokanee fry appear to spending the same amount of time feeding, and vulnerable to predation, at different points along the gradient (according to vertical migration hydroacoustic data).

CHAPTER 5: DISCUSSION

Food Web Patterns

The time series changes in abundance and production of different trophic levels observed from 1991 to 1997 are summarized in Fig. 87. The values shown are those described earlier in this chapter, but are scaled to allow all levels of the food web to be shown on one plot (e.g., actual abundance values were divided by a common denominator that allowed all values for a given trophic level to fit onto 1/10 of the Y-axis, since there were 10 patterns to be shown). There is fairly close tracking of abundances through the food web, suggesting bottom-up control. Nanoplankton abundance correlates well with nutrient load, while netplankton abundance correlates better with in-lake nutrient concentrations. Cladoceran density correlates well with changes in nanoplankton abundance, and better than with netplankton abundance. *M. relicta* density does not correlate well with changes in cladoceran abundance, nor with changes in phytoplankton abundance. Between 1991 and 1992 *M. relicta* abundance increased as cladoceran abundance increased. However in subsequent years *M. relicta* abundance was better correlated, negatively, with outflow. *M. relicta* abundance may be limited in high flow years by flow effects rather than prey abundance as described in Chapter 3 (p.120). Kokanee fry abundance (estimated from hydroacoustic data) correlates fairly well with changes in cladoceran abundance, but this pattern is weaker for older kokanee. Rainbow trout spawner abundance correlates well with the abundance of older kokanee, time-lagged by one year.

Time series data for production are less reliable than for abundance. I assumed that phytoplankton abundance over time was a good reflection of phytoplankton production. Zooplankton density and biomass along the spatial fertilization gradient were not correlated with phytoplankton abundance, and zooplankton did not appear to exert strong top-down control on

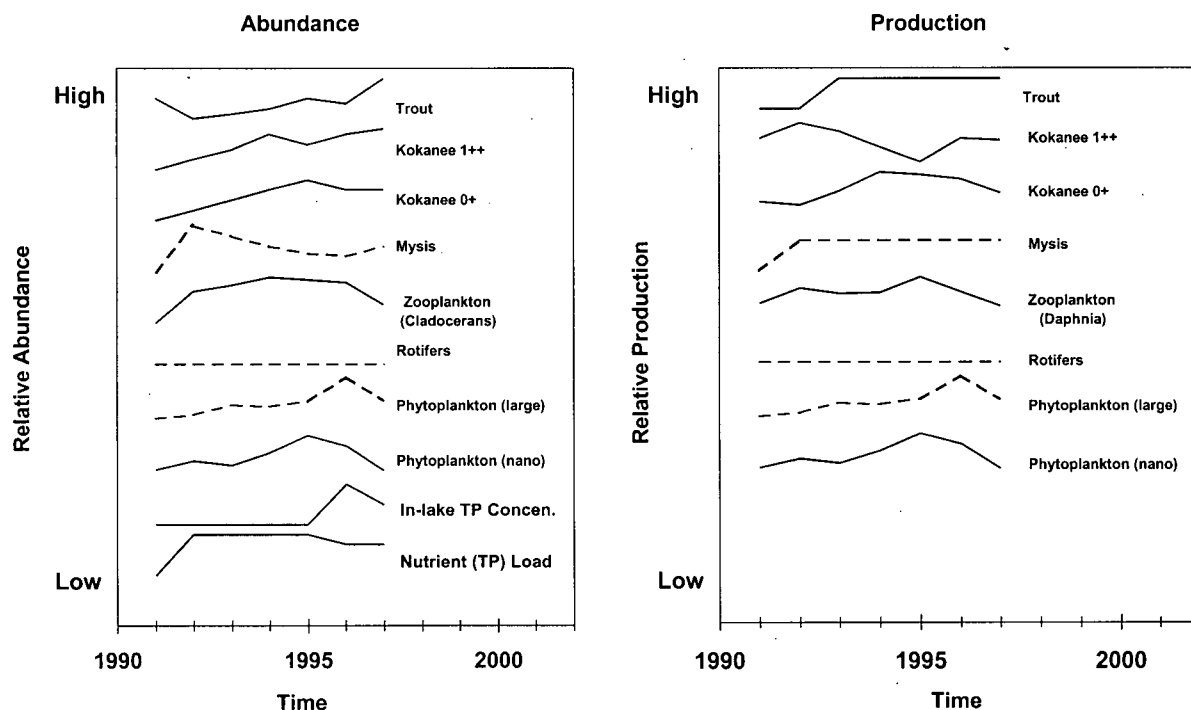


Fig. 87. Observed time series patterns of abundance (biomass of phytoplankton, rotifers and macrozooplankton, and density of *M. relicta*, kokanee and trout) and production (growth) in Kootenay Lake from 1991 to 1997, by trophic level. Dashed lines indicate organisms whose increase in abundance, production or both could indicate that fertilization was not beneficial to kokanee.

phytoplankton, so increased phytoplankton biomass should be a reflection of increased phytoplankton production, mainly in response to changing nutrient loads. Zooplankton production values are the actual annual P/B ratios for *Daphnia* spp., and these correlate well with the proposed production values for nanoplankton. I assumed that *M. relicta* production has increased during the fertilization experiment, based on the findings of Smokorowski (1998), but I do not have detailed annual values for this component of the food web.

Fry production tracks *Daphnia* spp. production fairly well, although fry production increased in 1993 and 1994, while *Daphnia* spp. production decreased slightly (Fig. 87). Fry production declined slightly in 1995, a year with high *Daphnia* spp. production. Both fry and *Daphnia* spp. production decreased in 1996 and 1997. I calculated the biomass production of kokanee fry as the biomass of fry present in the autumn, estimated from hydroacoustic density

and average size in trawls. However, this estimate does not take into account the biomass produced during the year that is lost due to mortality, since I do not have estimates of fry consumption by trout. The biomass production of older kokanee was estimated using the same data as for fry, but I calculated the change in biomass of the 1+ year class, versus the biomass of the same year class the year before (when the fish were fry). I calculated the change in biomass of the 2+ year class versus its biomass the year before (at age 1+). Age 3+ fish were not considered, since they were not generally observed in the autumn surveys. Again, these estimates are of net production, not gross production, since I did not correct for the biomass lost to consumption by trout. Net production of older kokanee does not correlate with any of the trophic levels below it, although it does correlate negatively with the abundance of rainbow trout over time (Fig. 87). Increased rainbow trout abundance and consumption may have been significant enough to remove a large proportion of the kokanee biomass produced in 1994 and 1995. Alternatively the use of pooled hydroacoustic estimates of the density of older kokanee, combined with trawl estimates of age frequency and size, may have resulted in over or underestimates of biomass production.

I have shown the trend in trout production as a simple one-time increase in 1992, since I do not have accurate information on changes in mature trout size from year to year, and because information on changes in size of small trout is unavailable (Fig. 87). Rainbow trout spawner abundance increased fairly steadily during the experiment, and individual size has stayed the same or increased slightly, based on angling records. Likewise, bull trout numbers and size appear to have increased. Meanwhile, trout mortality due to angling should not have changed markedly during the experiment, due to low catch limits. Trout production should have increased relative to the pre-fertilization period, since we see more biomass of trout in the lake, and the removal of trout biomass by anglers has probably remained constant.

The patterns of abundance and production observed along the length of Kootenay Lake were not as clear cut as the potential food web scenarios described in Chapter 2 (Fig. 13). The actual outcome appears to be a mix of bottom-up and top-down effects. There remains uncertainty about the responses of *M. relicta* and trout, and in turn, about the effects these food web components could have had depending on their distribution in the lake. Despite the increased fertilizer nutrient load to the North Arm, nutrient concentrations along the lake were similar (Fig. 88). Both nanoplankton and netplankton abundances were higher in the North Arm. Rotifer abundance appeared to be similar along the lake. Likewise, macrozooplankton abundance did not show a longitudinal trend. *M. relicta* abundance along the lake was uncertain. Kokanee fry abundance was higher in the North Arm in the early part of the summer, but evened out by September, and this appears to be the result of a skewed initial distribution rather than a response to fertilization. The abundance of older kokanee was evenly distributed along the lake. The abundance of trout along the lake was not sampled, but may be important for a complete understanding of the effects of fertilization.

Nanoplankton and netplankton production was probably higher in the North Arm of the lake (Fig. 88). Rotifer production was probably similar along the gradient, and my calculations suggest that there was no trend in macrozooplankton production along the lake. *M. relicta* production was higher in the North Arm, as evidenced by faster growth rates, greater female size, and higher fecundity (Smokorowski 1998). The production of kokanee fry biomass would have been higher in the North Arm in the early part of the summer, since fry growth rates along the lake were similar, and there were more fry in the North Arm. This production pattern would have disappeared by late summer, when fry were evenly distributed along the lake. Production of older kokanee was similar along the lake, based on equal densities, and equal size-at-age along the lake. Trout production along the lake is uncertain.

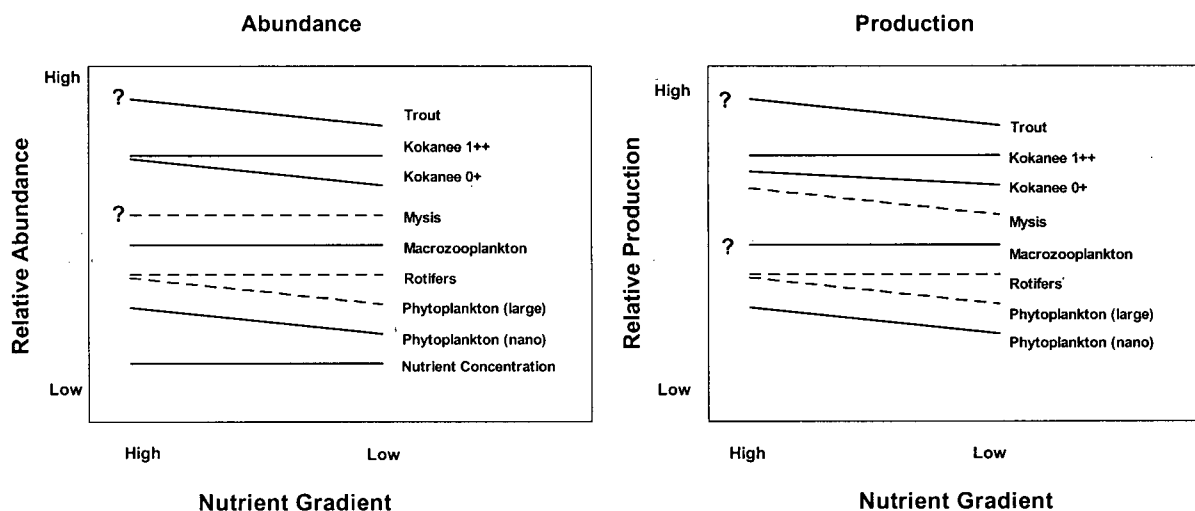


Fig. 88. Observed patterns of abundance (biomass of phytoplankton, rotifers and macrozooplankton, and density of *M. relicta*, kokanee and trout) and production (growth) along the length of Kootenay Lake, by trophic level. Dashed lines indicate organisms whose increase in abundance, production or both in the fertilized end of the lake, could indicate that fertilization was not beneficial to kokanee. Question marks indicate patterns which were uncertain.

Differences in Food Web Structure Along the Fertilization Gradient

The patterns in the food web along the length of Kootenay Lake during nutrient additions (Fig. 88) do not exactly match any of the four hypothetical scenarios proposed in Chapter 2. One possible outcome, not proposed in the hypothetical set of food web patterns, was that fertilization might have no measurable effects whatsoever, and that any patterns observed in the lake would have occurred regardless of whether the nutrient additions had occurred. The lack of pattern in zooplankton and adult kokanee abundance and production along the fertilizer gradient are consistent with this “no effect” hypothesis. However, the patterns observed at other trophic levels, in combination with information on physical factors operating during the experiment, offer further insight into the fate of nutrient additions in the Kootenay Lake food web.

That nanoplankton and netplankton abundance was higher in the fertilized end of the lake, but macrozooplankton abundance was not, indicates that abundance did not increase at all levels of the food web in response to nutrient additions (Fig. 88). Thus, we can reject the simple “Bottom-Up, No Top-Down Response” scenario (Fig. 13) that predicts increases in abundance at all trophic levels. The increase of nanoplankton biomass in the fertilized end of the lake, and relatively low proportion of cyanobacteria in the phytoplankton, indicate that the added nutrients did not get shunted into the microbial loop. The lack of a gradient in rotifer abundance along the lake also suggests that the microbial loop components of the food web did not dominate the classical food web. Thus, we can also reject the “Bottom-Up, Blue-Green Algae Response” scenario. Rotifer abundance was similar to that in other lakes, but macrozooplankton production was probably higher than rotifer production. Considerable evidence suggests that rotifers are unlikely to predominate in lakes that contain large *Daphnia*, due to exploitative competition and mechanical interference (Gilbert 1988). However, predation on daphnids by fish or *Chaoborus* may indirectly allow rotifer abundance to increase (Lynch 1979). An enclosure experiment in a small British Columbia lake showed that rotifers were out-competed by crustacean zooplankton, even in the presence of nutrient additions (Neill 1984). However, if *Daphnia* was removed from enclosures, rotifers increased, and increased even more if nutrients were also added. When phosphorus and nitrogen were added to Lake Hymenjaure, Sweden, abundance of the rotifer *Conochilus unicornis* increased relative to a control lake, but no other rotifer species responded (Persson 1978). In the context of Kootenay Lake, these studies suggest that *Daphnia* should be able to outcompete rotifers even during nutrient additions, unless *Daphnia* populations are suppressed, for example by extremely high predation.

From a management standpoint, it is more important that we be able to distinguish between a “Top-down, *Mysis* Increase” scenario, and a “Top-down, Kokanee Increase” scenario.

The abundance patterns of these two scenarios are similar up to the level of macrozooplankton response (Fig. 13). Nutrient concentrations are expected to be similar along the lake, while nanoplankton abundance increases in the fertilized end of the lake, due to weak grazing pressure by macrozooplankton, which show no trend in abundance along the lake (due to predation). The main difference between the two scenarios is whether kokanee or *M. relicta* are responsible for grazing down macrozooplankton in the North Arm. In terms of production, the two scenarios are also the same up to the macrozooplankton level, with nanoplankton and macrozooplankton showing increased production in the North Arm. Neither scenario matches the observed macrozooplankton production pattern of no difference along the lake. It is possible that compounded biases in the calculation of zooplankton production obscured a trend toward increased production in the fertilized end of the lake (see p.64). In the "Top-Down, Mysis Increase" scenario *M. relicta* shows increased production in the North Arm, and also increased abundance, due to limited predation mortality from fish. During the experiment there was increased *M. relicta* production in the North Arm, but the abundance of *M. relicta* along the lake in different years was variable (Lasenby et al. 1998). In the "Top-Down, Kokanee Increase" scenario *M. relicta* abundance and production show no trend along the lake, while kokanee abundance and production are both higher in the North Arm. The observed data for *M. relicta* are consistent with the production aspect of the "Top-Down, Mysis Increase" scenario, but also with the abundance aspect of the "Top-Down, Kokanee Increase" scenario. The observed data for older kokanee are consistent with the "Top-Down, Mysis Increase" scenario, both in terms of abundance and production trends along the lake. Kokanee fry abundance is consistent with the "Top-Down, Kokanee Increase" scenario early in the year, but by autumn fry distribution is even along the lake, consistent with the "Top-Down, Mysis Increase" scenario. Fry production along the lake matches the "Top-Down, Mysis Increase" scenario, in terms of production per unit

biomass. However, since there are more fry in the North Arm in early summer, total production of fry biomass would be higher in the North Arm.

Two main factors complicate our ability to distinguish which of these two scenarios is most similar to the observed patterns. First, *M. relicta* density may have been suppressed by increased mortality due to high water flows. In this case *M. relicta* abundance might be lowered throughout the lake, despite increased production in the North Arm. Second, if trout concentrate in the North Arm they could crop down increased kokanee production, and we would see even abundance of kokanee along the lake (as predicted in the "Top-Down, *Mysis* Increase" scenario). In this case we should still see higher kokanee production per unit biomass, as well as higher trout production, in the fertilized end of the lake. Alternatively, if kokanee in the North Arm spend less time feeding in order to obtain the same amount of food, and therefore spend less time vulnerable to predation, survival rates in the North Arm should be higher. This should eventually result in increased kokanee abundance (numbers) in the North Arm, which we did not see (this would be a bottom-up, ratio-dependent response caused by the "refuge" of decreased feeding time). However, the mobility of kokanee, and the reliance on a single monthly hydroacoustic transect at each station for distribution, may have limited our ability to accurately determine the distribution of older kokanee. Data on trout abundance and production along the fertilization gradient were not collected during this experiment, so it is not possible to determine whether trout distribution along the lake, and consumption of kokanee have obscured the "Top-Down, Kokanee Increase" scenario.

It may be that the actual scenario is a blend of the "Top-down, *Mysis* Increase" scenario that has been masked by increased *M. relicta* mortality due to high water flows, and a "Top-Down, Kokanee Increase" scenario that is at some stage between increasing kokanee abundance, and transfer of this biomass to trout. If we assume that there was error in the calculation of

zooplankton production, *M. relicta* production along the gradient is consistent with the hypothesis that mysids grazed down new macrozooplankton production and kept zooplankton abundance similar along the gradient, and allowed increased phytoplankton abundance in the fertilized end of lake. If high water flows suppressed *M. relicta* abundance, kokanee would have faced less competition from *M. relicta*, and would have been able to graze on the remaining zooplankton along the length of the lake. As kokanee abundance increased because of decreased competition for food, the mortality of mysids due to kokanee predation would have increased, compounding the flow-related mortality. Increased kokanee production throughout the lake could then be transferred to trout. If there were a time-lag in trout response because of their longer reproductive time, this would explain the lake-wide increase in kokanee abundance, and the increase in trout spawner abundance.

Competition Between Kokanee and *M. relicta*

It is important to note that the critical factor in this blended scenario is that flow effects must decrease the competitive effect of mysids on kokanee. The competitive interaction of kokanee and *M. relicta* can be illustrated through competition isoclines, which shift with changes in each species' carrying capacity, and the competitive influence of each species on its competitor (Fig. 89 and Fig. 90). The intersection of the two species' isoclines is the competitive equilibrium toward which the species' abundances will move. *M. relicta* and kokanee carrying capacity at time 1 are K_1 , and K_2 respectively. The competitive effect of *M. relicta* on kokanee is a_{21} , and the effect of kokanee on *M. relicta* is a_{12} . *M. relicta* carrying capacity at time 2 is K_1' , and so forth. The number of *M. relicta* at time 1 is $N_1 = K_1 - a_{12} * N_2$, and the number of kokanee at time 1 is $N_2 = K_2 - a_{21} * N_1$.

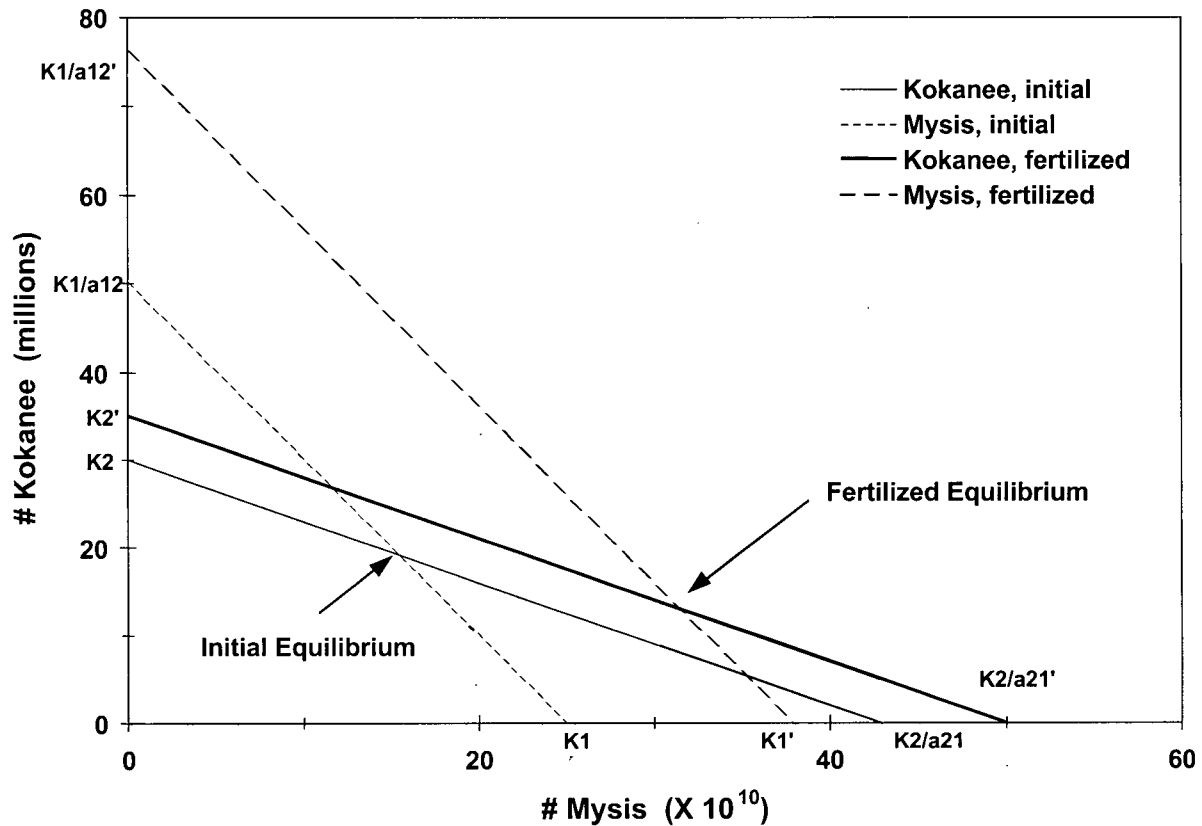


Fig. 89. Kokanee-*M. relicta* competition isoclines showing shift in competitive balance that the AEA workshop predicted due to fertilization. Kokanee abundance would be lower than initially, while *M. relicta* abundance would increase. Note: abundances are approximate, and were chosen for ease of scale.

The Kootenay Lake Fertilization Response model predicted that nutrient additions would benefit both kokanee and *M. relicta*, but that *M. relicta* would benefit substantially more from fertilized conditions. At time 1, kokanee and *M. relicta* abundances will be moving toward, or be at, the Initial Equilibrium point (Fig. 89). At time 2, nutrient additions are in progress, and the isocline of each species has increased ($K1'$ and $K2'$ are higher than $K1$ and $K2$). The abundances of kokanee and *M. relicta* will move toward the new Fertilized Equilibrium point. At this point kokanee abundance will be lower than at the Initial Equilibrium, and *M. relicta* abundance will be higher than it was initially.

The observed changes in abundance indicate that the equilibrium has shifted in the opposite direction to that predicted (Fig. 90). The kokanee isocline is higher, presumably due to

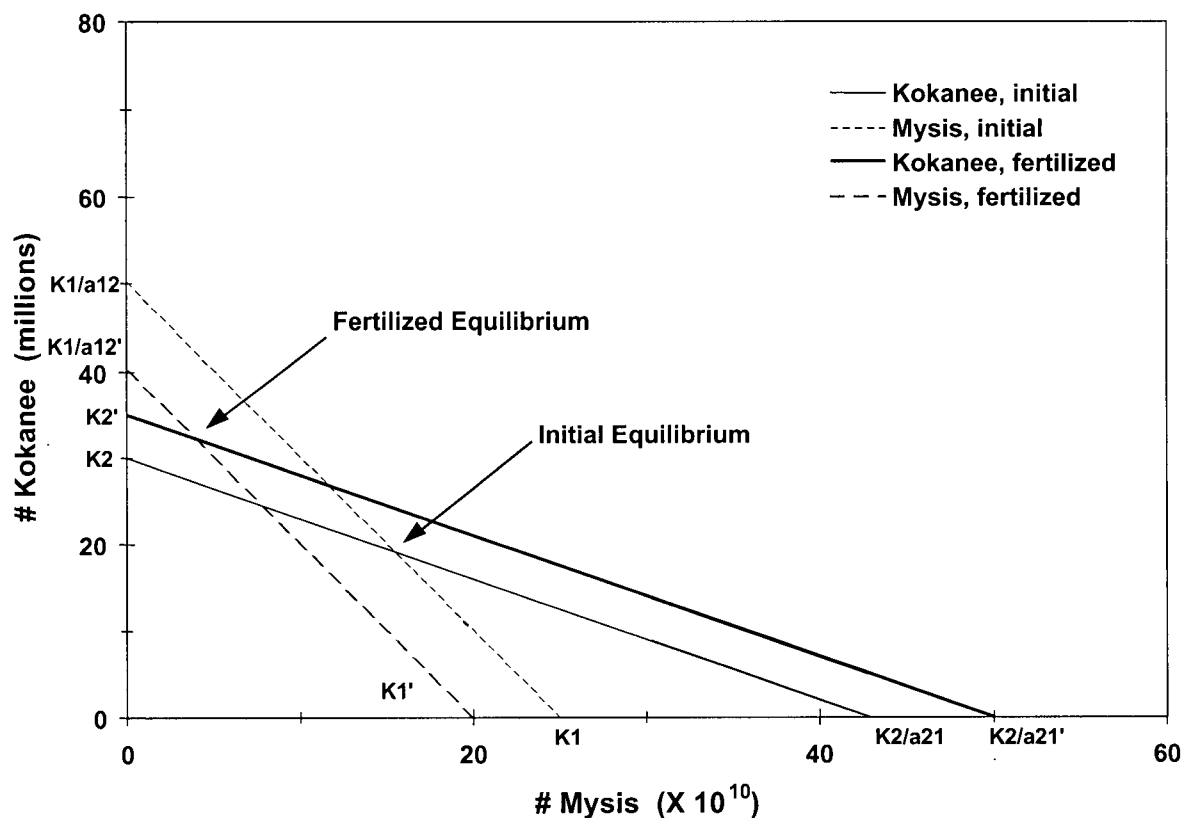


Fig. 90. Kokanee-*M. relicta* competition isoclines showing observed shift in competitive balance during fertilization experiment. Kokanee abundance is higher than initially, while *M. relicta* abundance is lower. The shift may have resulted from effects of increased nutrient loads on kokanee and *M. relicta*, and the effect of high flows on export mortality of *M. relicta*. Note: abundances are approximate, and were chosen for ease of scale.

nutrient additions, while the isocline of *M. relicta* is lower than at the start of the experiment. The abundances of the two species have shifted toward the Fertilized Equilibrium, at which kokanee abundance is higher than initially, and *M. relicta* abundance is lower. The combination of increased kokanee carrying capacity (because of fertilization, or increased nutrient inputs in high flow years) and decreased competition from *M. relicta* (because of increased export mortality) results in a shift in competitive advantage toward kokanee. Kokanee are better able to avoid being flushed out of the lake in high flow years, so the kokanee population is able to increase in response to increased resources. The relationship between kokanee and *M. relicta* is

actually more complex than a simple competitive interaction, because the two species also have a predator-prey relationship. If *M. relicta* abundance is depressed because of high export mortality, and kokanee abundance increases in response to increased nutrient loads, predation by kokanee may be substantial enough to keep *M. relicta* abundance down for an extended time period, even if flows decrease. This predator-prey interaction is not defined in the competition equations, but is implicit in the calculation of what *M. relicta* abundance would be seen at a given kokanee abundance, and vice versa.

Other Factors Affecting Distribution of Kokanee and *M. relicta*

Factors other than those directly related to food web effects may have influenced the distribution of kokanee and *M. relicta* along the gradient, and this could have obscured the abundance and production patterns seen during fertilization. Historically, kokanee fry distribution was probably always skewed toward higher fry densities in the North Arm of the lake in spring and early summer (see p.129). Without pre-fertilization spring and summer distribution data it is difficult to determine how quickly fry moved southward in the past, and whether intraspecific food competition affected fry dispersal rates. Fry dispersal rates in Kootenay Lake are comparable with rates observed for *O. nerka* in other lakes (Burgner 1991), and it does not appear that fry are lingering in the fertilized end of the lake longer than in the absence of nutrient additions. That the distributions of older age classes of kokanee along the lake were fairly even suggests that fry distribution was not substantially altered by nutrient additions.

It was considered possible that physical gradients along the lake could affect kokanee distribution. For example, river water entering the lake as an interflow at the thermocline might reach a considerable distance down the lake, and influence kokanee behaviour. I examined vertical profiles of temperature, and specific conductance along the length of Kootenay Lake for

April to October, 1992 to 1995. There were no patterns in these variables that suggested the effects of deep water interflows would affect kokanee distribution at more than a short distance from river mouths.

It was suggested that *M. relicta* distribution might be altered by the effect of a deep-water counter current. The prevailing winds in the summer are from the south, so water in the epilimnion should "pile up" toward the north end of the lake, then cycle back under, just above the thermocline. This circulation could then trigger a reverse circulation of hypolimnetic water that would move southward near the thermocline, and northward near the bottom of the lake. Since mysids are usually located in deep water, and often near the bottom of the lake for the majority of the day, they would tend to be shifted northward. The different distributions of mysids along the lake in different years suggests that a deep-water counter-current is not consistently affecting *M. relicta* distribution in Kootenay Lake. (I also consulted hydrology researchers in the U.B.C. Civil Engineering Department who predicted that in a lake as deep as Kootenay there might actually be a third cell of circulating water near the bottom of the hypolimnion, with its water moving southward near the bottom of the lake. They suggested that in any case the velocity of a water current near the bottom of the lake would be extremely small, and should not affect the distribution of an organism the size of *M. relicta*).

Changes in Zooplankton Abundance, and Kokanee Size and Abundance Prior to Fertilization

Positive changes in zooplankton density, and in kokanee spawner size occurred before fertilization started. Also, kokanee spawner size and numbers in 1992 were higher than would have been expected given only one season of nutrient additions. As I reported earlier, the 1991 and 1992 average annual zooplankton densities from the old sampling program likely underestimate the density of cladocerans, particularly *Daphnia*, since sampling did not continue

through the summer peak. However, the decline and increase of zooplankton immediately prior to the beginning of fertilization were reasonably well tracked (Fig. 27). Flows in 1990 and 1991 were higher than in the previous eight years, and *M. relicta* densities were low. It is possible that a combination of increased natural loading, and decreased predation allowed zooplankton densities to increase coincident with the onset of fertilization. It is difficult to predict what would have happened from 1992 to 1994 in the absence of nutrient additions, since these were low flow years, with relatively low natural nutrient loads.

Kokanee spawner numbers and size began to increase in 1992, and sizes were unusually large until 1995. The sudden increases in numbers and size in 1992 are attributable to the fact that a large proportion of spawners in 1992 were age 4+, rather than the usual 3+ (Table 15). These were fish that would normally have spawned in 1991, thus contributing to the extremely low spawner run in that year. These fish may have been too small to spawn successfully in 1991, so they opted to spend an entire extra year in the lake. This would have increased the mortality of this year class, since the fish would have spent another year vulnerable to predation, but resulted in the survivors being unusually large. There was also a high proportion of age 4+ spawners in 1993 (18%), but by 1994 there was a shift toward age 2+ spawners, and smaller sizes. The downward shift in spawner size may result from density dependent effects, as observed for kokanee in Idaho lakes (Rieman and Myers 1992). As productivity in Kootenay Lake increased, more fish would have been able to obtain enough food to reach a threshold for survival, so numbers would increase, but sizes would be limited by intraspecific competition for food. Although fish in the lake in the early years of fertilization would have been able to grow larger because of increased food resources, and lack of competition, as numbers increased, average size would drop back to historical levels. Increased lake productivity would therefore result in more kokanee rather than bigger kokanee.

Changes in spawner size have had predictable effects on fecundity, with very high numbers of eggs deposited in the early years of the experiment, and declines as spawner size decreased. The number of fry produced in Meadow Creek declined between 1993 and 1997, but is still near long-term average. Numbers may have been bolstered by high egg-to-fry survival in the Meadow Creek channel (where gravel is of optimal size, and is scarified to remove silt each summer prior to the arrival of spawners). Egg-to-fry survival at Meadow Creek improved steadily from 1985 to 1991. However, egg-to-fry survival in the Lardeau River is not enhanced, so it will be important to monitor kokanee returns there in comparison with Meadow Creek to assess the impact of decreased spawner size on kokanee abundance.

Management Implications for Kootenay Lake

As fertilization has coincided with rebounding kokanee stocks in Kootenay Lake it would be prudent for managers to continue to add nutrients, provided that monitoring efforts are continued. There continues to be uncertainty about the response of *M. relictus* to enriched conditions, and in the absence of a natural flow regime with a large spring freshet there is the chance that mysid populations may increase given the opportunity of several consecutive low flow years. Rehabilitation measures for sturgeon in the Kootenai River, such as increased flows in spring to encourage spawning, should benefit kokanee. Potential river fertilization could also benefit kokanee more than *M. relictus*, provided that it is coupled with high flows to maintain *M. relictus* mortality rates.

If funding can be assured it would be extremely informative to vary the location of fertilizer application in the lake for several years at a time. Kokanee stocks are now strong enough that a stock collapse is unlikely even if it turns out that the North Arm application is essential for early fry growth and survival. Movement of the fertilizer site would test the power

of the experimental design. It could also test the effect of higher nutrient loads on South Arm kokanee spawner runs, which have remained low throughout the experiment.

Continued monitoring of the Kootenay Lake ecosystem is essential, since there may be as yet undiscovered environmental “side” effects of fertilization. For example, *M. relicta* may undergo genetic shifts toward individuals better able to avoid export mortality, or predation by kokanee, through altered timing of vertical migrations. Several additions to the monitoring program would be extremely informative. Hypolimnetic water sampling to track the build-up of nutrients in the hypolimnion would be useful for comparison with treatments of other lakes. Hypolimnetic nutrient concentrations could provide an early warning that a lake is near to being replenished with nutrients, and that surface loading rates should be decreased the following year, thus avoiding excessive algal blooms. Better data on the distribution of *M. relicta* would have clarified the outcome of the Kootenay Lake experiment. A concerted effort was made by members of the research group to extract mysid distribution patterns from the hydroacoustic data, but thus far these efforts have been unsuccessful. As hydroacoustic techniques become more advanced it would be valuable to re-visit their potential for assessing mysid distribution. Finally, it may be possible to extract information on trout distribution from the hydroacoustic data collected to monitor kokanee. Currently these data are analyzed with a decibel level cut-off that excludes targets the size of trout, in order to facilitate kokanee population estimates. It would be worthwhile to re-analyze a sub-sample of transects to see if hydroacoustic sample sizes are adequate to estimate trout distribution along the lake.

Management Considerations for Restoration of Large Lakes Affected by Hydroelectric Dams or Exotic Species Introductions

Several other large interior British Columbia Lakes have experienced serious declines in kokanee salmon stocks in recent years (Fig. 91). In the Arrow Lakes Reservoir decreases in

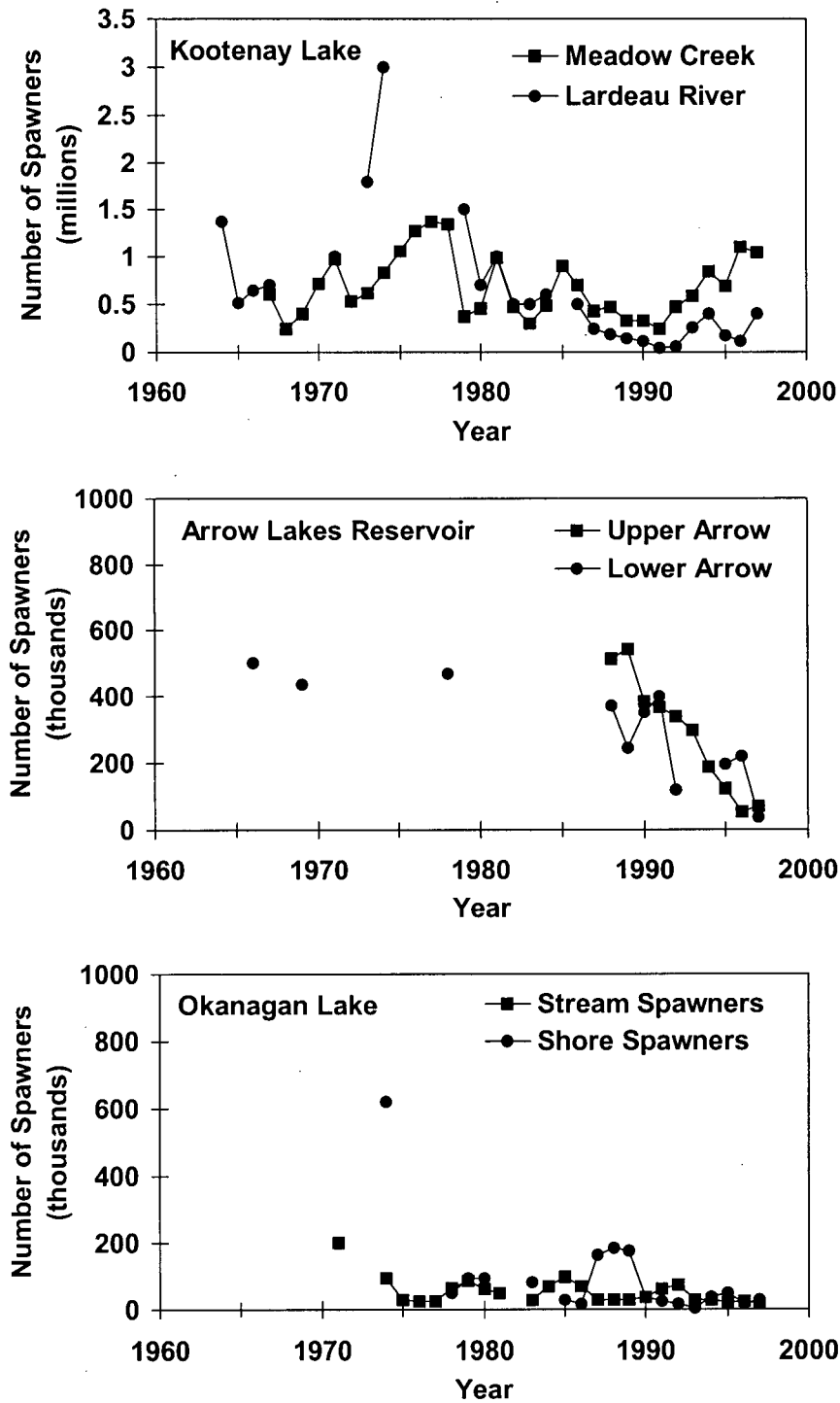


Fig. 91. Kokanee spawner numbers in Kootenay Lake (Meadow Creek and Lardeau River), in Upper and Lower Arrow Lakes, and Okanagan Lake (stream spawner peak counts, and shore spawner index counts). Data for the Arrow Lakes from Pieters et al. (1998) and data for Okanagan Lake from Ashley et al. (1998). Note: Kootenay Lake data are plotted in millions, while Arrow Lakes and Okanagan Lake data are plotted in thousands.

kokanee abundance have been attributed to the effects of hydroelectric dams, and also to the competitive impacts of introduced *M. relicta* (Pieters et al. 1998). Kokanee in Okanagan Lake have also declined since the early 1970's, although the reasons for this are difficult to specify (Ashley et al. 1998). The abundance of shore spawning kokanee in Okanagan Lake is particularly critical, and in 1998 no shore spawners were observed, despite extensive monitoring efforts (pers. comm., Mr. Steve Matthews, B.C. Ministry of Environment, Lands and Parks, Penticton, B.C.). Fertilization of Upper Arrow Lake began in 1999, seven years after the fertilization of Kootenay Lake started. An extensive monitoring program began on Okanagan Lake in 1996. To date recovery efforts have focused on decreasing the competitive effect of mysids, such as harvesting mysids with trawl nets.

The results of the Kootenay Lake experiment provide some guidelines and suggestions for recovery efforts on other large lakes. If similar fertilization programs were attempted on other lakes the outcomes might be similar to those on Kootenay Lake, insofar as the new lakes were similar to Kootenay Lake in morphology, flow regime, food web composition, and initial states of the populations. Kootenay Lake is large, long, steep-sided, and deep, with relatively linear flow from the two main inflows to the outflow (see Carmack et al. (1986) for description of water circulation patterns in Kootenay Lake). The lake's hydrograph is altered by hydroelectric dams both upstream and downstream. The lake has a four-level food web, including *Daphnia* as a prominent cladoceran zooplankter, kokanee as the main pelagic planktivore, and rainbow trout and bull trout as the predominant piscivores. The most notable exotic species is *M. relicta*, although other introduced fish species inhabit the lake in much lower numbers than the native kokanee. Kootenay Lake had a relatively very good historical data set, including water flow (hydrograph) and nutrient loading data, which made it possible to calculate natural nutrient loads over time (Larkin 1998).

The greater the differences between Kootenay Lake and a candidate lake for fertilization, the greater the uncertainty of the outcome in comparison with the patterns observed in Kootenay Lake. A monitoring program should be designed with increased effort toward areas of greatest uncertainty. For example, the north ends of Upper Arrow Lake, and Okanagan Lake have greater proportions of littoral zone than Kootenay Lake, so kokanee fry may spend more time in nearshore waters when they first enter the lake, if shelter is available from predators. If so, fertilization of the pelagic waters may have little impact on the early feeding and survival of fry.

The Arrow Lakes Reservoir has a more altered hydrograph than Kootenay Lake, with extreme level fluctuations, and rapid changes in discharge. Added nutrients may be flushed out more or less quickly than in a more natural system. The Arrow Lakes also receive a greater contribution of inflow from local tributary streams (30%), as opposed to only 10% in Kootenay Lake (Pieters et al. 1998). Monitoring of flow and nutrient inputs from these tributaries has added to the complexity of the Arrow Lakes experiment. Okanagan Lake experiences less impact from dams than Kootenay Lake, but water level fluctuations may still have adverse effects on kokanee, such as leaving eggs stranded in shoreline areas if water levels are lowered after spawning has occurred (Ashley et al. 1998). Okanagan Lake also has a much longer hydraulic retention time than Kootenay Lake or the Arrow Lakes Reservoir. The storage of nutrients in the hypolimnion should be more of a factor in this lake than in Kootenay and the Arrow Lakes Reservoir. Hypolimnetic monitoring was not conducted on Kootenay Lake, so it was not possible to monitor the potential replenishment of hypolimnetic nutrient stores, but this monitoring is being done in the Arrow Lakes program.

Turbidity may also be a factor in the outcome of fertilization experiments that involve exotic species. It is uncertain whether increased turbidity would give an advantage to kokanee

or to mysids. Kokanee may be more impacted by turbidity, since they feed visually, during daylight hours. However, mysids may rely on light as well as tactile cues in feeding on zooplankton. If mysids had to come closer to the surface to feed efficiently they would incur higher metabolic costs because of warmer water temperatures, and could also face greater kokanee predation.

Top-down / bottom-up food web theory predicts that outcomes would be different in systems with three or five trophic levels than in a four level system such as Kootenay Lake. In a lake with very heavy fishing pressure on piscivores, the fishery may act as a fifth trophic level, suppressing the fourth level, and freeing up the third (kokanee) to prey more heavily on the second (zooplankton). This could result in reduced grazing pressure on phytoplankton, and greater phytoplankton standing stocks than in a four-level system. This may have ramifications for management, if increased phytoplankton biomass is sufficient to affect aesthetic values. Ney (1996) notes that the optimal phosphorus loading for maximum fish standing stock is higher than the optimal loading for other uses such as drinking water, or recreation. The food web structure may in turn affect the optimal phosphorus load for a lake. Active programs to stock predators (trout) may cause mortality of kokanee to increase faster than can be balanced by increased kokanee production. In the case of the Arrow Lakes Reservoir the stocking of rainbow trout and bull trout has been suspended during the fertilization program thus far.

Finding a valid experimental design will probably continue to be difficult, as was the case for Kootenay Lake. If control and replicate lakes are available, and funds allow, a BACI design could be used. However, it is unlikely that managers could risk unforeseen environmental and economic impacts on the replicate lakes. If a gradient design is chosen the lake should have a linear shape that should allow graded effects of nutrient additions. I would recommend against using a gradient design without baseline data along the potential gradient.

Otherwise there is an implicit assumption that conditions along the gradient are statistically identical prior to fertilization. Variable flow and nutrient inputs from different tributaries in different years may cause gradient effects in a non-fertilized lake. Without baseline data it is difficult to tell if patterns observed along gradient (or lack of patterns) are correlated with fertilization treatment, or would have occurred regardless. The movement of fish along the gradient is also a problem with this design. The distribution of piscivores should be monitored hydroacoustically to determine the differential top-down impacts of the top trophic level along the gradient.

Ideally, there should be a commitment from funding agencies, prior to the commencement of monitoring, that funding will be available for at least five years, so that data can be collected for at least one life cycle of the top trophic level (e.g., trout in Kootenay Lake reproduce at approximately age 6). This will increase the chance that time-lagged effects will be apparent before nutrient loading is stopped or altered. Without adequate monitoring it is impossible to know if the experimental treatment is doing more harm than good, nor is it possible to manage adaptively, learning about the system, and changing to a new policy if the current one is inadequate. In addition to testing whether nutrient additions are environmentally beneficial, monitoring allows a test of whether or not fertilization is economically viable. Finally, a commitment to funding will allow staff to be hired on a longer-term basis, with more job security, which should decrease staff turnover, preserve "institutional memory" about the system, and improve the consistency of methods over time.

Total Phosphorus Load and Kokanee Abundance

The close relationship between total phosphorus (TP) load and kokanee spawner abundance in Kootenay Lake suggests that TP loading rates may be useful as a rough guideline in the design of fishery restoration experiments. The regression slope for the kokanee-TP load

plot for loads less than 1000 t is slightly lower than the slope of the plot for loads less than 500 t (Fig. 39). This may be the beginning of a curvilinear relationship as phosphorus load increases. It is possible to describe all the points on the graph with a quadratic function, although no Lardeau River kokanee data are available for TP loads between 1000 and 1500 t. A curve like this suggests that there may be an optimal TP load that will maximize spawner abundance for a particular lake. Ney (1996) shows a similar relationship for fish standing stock in southeastern U.S. reservoirs and phosphorus concentration, but points out that the phosphorus concentration necessary to maximize standing stock may be over the threshold for maintaining "clear water" for other uses such as recreation or drinking water.

The relationship between kokanee spawner abundance and TP load has practical implications for management of Kootenay Lake. The unit response of kokanee to changes in TP load could be used to predict responses to future nutrient loads, with the caveat that both TP load and kokanee could both be correlated with other variables affecting the ecosystem (e.g., flow-related mortality of *M. relictus*, and resultant decreases in competition for zooplankton). The relationship between kokanee spawner abundance and TP load is probably lake-specific and should not be used to predict spawner numbers in other lakes, since values for the regression came only from Kootenay Lake. It might also be possible to predict the amount of kokanee produced through the addition of a given amount of fertilizer. Thus, the cost of each additional fish could be estimated, and the efficacy of nutrient additions evaluated from a cost-benefit perspective.

It would be very informative to use the approach of Lee and Jones (1991) to analyze abundance or yield and TP load data for an array of *fertilized* lakes. This would provide a spatially replicated, comparative regression of the effect of nutrient additions on yield, as opposed to the effect of total TP load. If TP in fertilizer is more bioavailable than natural TP, the

slope of the regression line would be steeper. Less fertilizer TP would be needed to correct the effects of nutrient losses caused by upstream impoundments, or lack of salmon carcasses due to high harvest rates.

Conclusions

Six years of nutrient additions to Kootenay Lake have increased our knowledge of the critical processes involved in the transfer of nutrients through the food web, and have improved our ability to predict the outcome of fertilization in similar aquatic systems. However, the project has raised new questions about the efficacy of different experimental designs for whole-lake management experiments. In addition, the results emphasize the potential role of factors independent of food web processes, such as water flow and natural nutrient loading, in the outcome of large-scale food web experiments. Additional experiments on lakes that have experienced disturbances similar to Kootenay Lake may give further insight into the degree that the results of the Kootenay Lake fertilization experiment can be generalized to other aquatic systems.

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