

Restoration of the food web of an alpine lake following fish stocking

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Abstract

Trout stocking in the mid-1960s eliminated the calanoid copepod *Hesperodiaptomus arcticus* and other large-bodied crustaceans such as *Gammarus lacustris*, *Daphnia middendorffiana*, and *Daphnia pulex* from many alpine lakes in the Rocky Mountain Parks of Canada. *H. arcticus* frequently dominates the plankton communities of fishless lakes, preying on rotifers and nauplius larvae. Following the extirpation of *H. arcticus*, rotifers and small-bodied cyclopoid copepods dominate the zooplankton assemblages of alpine lakes.

We studied the zooplankton community of Snowflake Lake, Banff National Park, from 1966 to 1995. *H. arcticus* was eliminated following stocking of the lake with trout in the 1960s. It failed to become reestablished after the disappearance of the fish population in the mid-1980s. Several species of rotifers and small-bodied crustaceans, species originally rare or absent from the plankton, became abundant following fish stocking and remained so after the fish population declined.

In 1992, we reintroduced *H. arcticus* to Snowflake Lake. The *H. arcticus* population grew exponentially for 4 yr, but had not reached stable densities typical of unmanipulated alpine lakes by 1995. By 1994, however, even the small population of *Hesperodiaptomus* was beginning to suppress populations of rotifers, copepod nauplii, and large diatoms. Because *H. arcticus* is omnivorous, a simple model of cascading trophic interactions did not predict the outcome of trophic manipulations in this alpine lake.

In the early years of the twentieth century, many naturally fishless alpine lakes in the Rocky Mountains of western North America were stocked with non-native species of fish (Donald 1987; Bahls 1992). In the National Parks of the Canadian Rockies, fishless alpine lakes were often stocked in an attempt to attract anglers to the parks. For example, of an estimated 486 lakes in Banff National Park, 119 have been stocked at least once with fish. Most of the stocked lakes (84%) were originally fishless (Schindler and Pacas 1996). Many of the introduced fishes were not native to the

region (Nelson and Paetz 1992). In many small, ultraoligotrophic alpine lakes, the stocked fishes did not reproduce, so populations eventually died out.

In earlier years, little attention was paid to the effect of fish stocking on natural aquatic communities or to the degree to which communities were able to recover if stocked fishes did not survive. However, recent changes in the National Parks mandate, which place highest priority on maintaining ecosystems in an unimpaired state for the enjoyment of future generations, necessitate a thorough investigation of the impacts of fish stocking.

As a result of fish stocking during the past several decades, the calanoid copepod, *Hesperodiaptomus*, the cladoceran *Daphnia*, and other large zooplankton were eliminated from fishless alpine lakes and replaced by smaller copepods and rotifers (Anderson 1972; Anderson and Donald 1978). *Gammarus*, which in some lakes migrates into the epilim-

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Acknowledgments

Work in the 1960s and 1970s was supported by the Canadian Wildlife Service and Parks Canada. That in the 1990s was supported by an NSERC operating grant to D.W.S. We thank Parks Canada for expediting our work in Banff National Park.

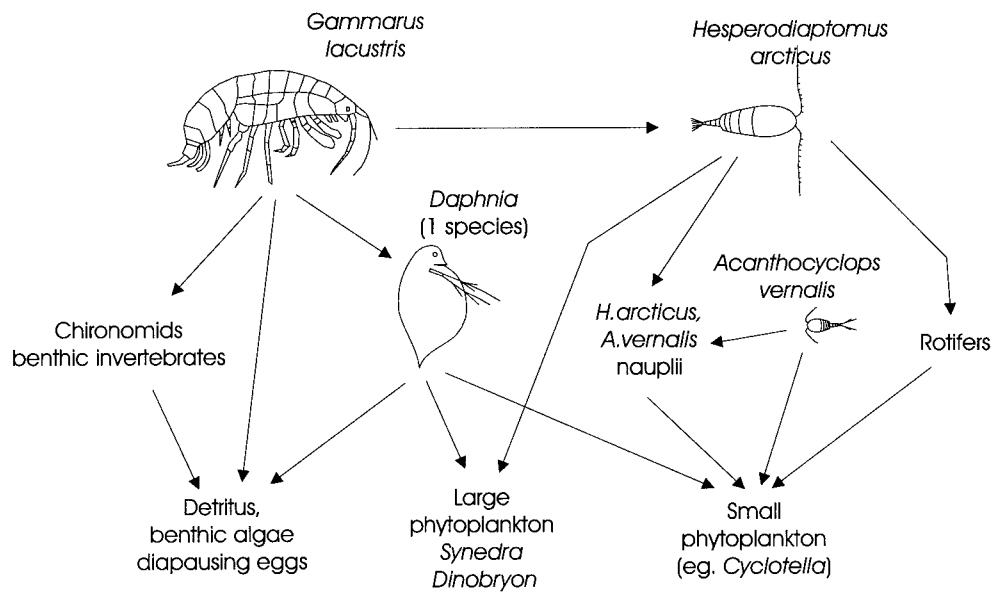


Fig. 1. The original food chain of Snowflake Lake, a typical fishless alpine lake in the Rocky Mountains of Alberta.

nion at night to prey on zooplankton, was also eliminated. In some lakes, fish reproduction failed, and the lakes became fishless again after several years. The invertebrate faunas of stocked lakes did not always recover, even in lakes where fish did not survive (Leavitt et al. 1994; Miskimmin and Schindler 1994; Paul and Schindler 1994).

In this paper, we describe long-term changes in the zooplankton community of Snowflake Lake, a small alpine lake in Banff National Park, which was stocked with fish in 1960–1966. The lake was studied from 1966–1995. *H. arcticus*, the original top pelagic predator, was eliminated by fish. It did not return to the lake, even after the fish died. Without *Hesperodiaptomus*, the zooplankton community did not recover fully. In 1992, we reintroduced *Hesperodiaptomus* in an attempt to restore the natural zooplankton community of the lake.

The zooplankton communities of Snowflake Lake and other alpine lakes in the Canadian Rockies of Alberta—Alpine lakes in the Canadian Rockies of Alberta are generally above 2,000–2,200 m. Most lie in calcareous basins and are well buffered. Average pH values are 7.5–8.0. Because they are nutrient-poor, ice-free for no more than 4 months, and have rapid rates of water renewal, alpine lakes have low algal biomass and support few zooplankton species. Most are fishless unless stocked by humans, and the food chains are very simple. The original food chain of Snowflake Lake is typical (Fig. 1). The large calanoid copepod *H. arcticus* is the dominant zooplankton in the majority (60%) of lakes in the mountain parks of the Canadian Rockies, and it is usually abundant where it occurs. It is often accompanied by a smaller calanoid copepod, such as *D. tyrelli* (Anderson 1980), cyclopoid copepods (*Diacyclops*, *Acanthocyclops*), and rotifers (Anderson 1974a). Large *Daphnia*, typically either *D. middendorffiana* or *D. pulex*, are often present in low numbers. Predation is common among the aquatic inverte-

brates in these food-limited lakes. Both *Hesperodiaptomus* and the cyclopoid copepods are predatory in later life stages, consuming one another's young as well as their own, in addition to other small crustaceans and rotifers (Anderson 1970; McNaught unpublished data). The amphipod *G. lacustris* also consumes zooplankton in these lakes (Anderson and Raasvelt 1974; Wilhelm unpubl. data). *H. arcticus* selectively preys on rotifers (chiefly *Polyarthra* and *Keratella*) and can significantly reduce the biomass of rotifers and copepod nauplii (Paul and Schindler 1994; Paul et al. 1995; McNaught unpubl. data).

In mesocosm experiments, *H. arcticus* had a strong effect on rotifers and nauplii. If these are rare, *Hesperodiaptomus* consumes large diatoms and colonial chrysophytes such as *Synedra* and *Dinobryon*, which have been observed in *H. arcticus* guts and fecal pellets.

Physical and chemical conditions in Snowflake Lake—Snowflake Lake is a small alpine lake (Table 1) located in the eastern front ranges of the Canadian Rocky Mountains in Banff National Park (Fig. 2). The lake is very oligotrophic, with total phosphorus of 3–8 $\mu\text{g liter}^{-1}$ and chlorophyll *a* (Chl *a*) of 0.1–2 $\mu\text{g liter}^{-1}$. Waters are well buffered (pH values of 7.9–8.4; alkalinities of 900–1,350 $\mu\text{eq liter}^{-1}$). Earlier information is given by Anderson (1970b, 1974b) and Anderson and Donald (1978).

In the 1990s, ice-out occurred between late June and mid-July. Depending on weather, water temperature can remain near freezing for several weeks or can rise quickly to mid-summer temperatures of 9–14°C. The maximum temperature recorded in the period of our study was 16°C, on 30 July 1994. The lake stratifies weakly in July and August, with a thermocline at 2–6 m. Bottom waters remain at 3 to 7 degrees. Stratification can be broken at any time in the ice-free season by heavy snowfall or strong winds. The lake does not restratify in the same season, except for weak diurnal

Table 1. Physical characteristics of Snowflake Lake and its drainage basin.

Feature	
NTU grid reference	11U/NH808167
Latitude, longitude	51°36'N, 115°50'W
Elevation (m)	2,320
Height of divide (m)	2,990
Drainage area (ha)	147
Lake surface area (ha)	7.1
Maximum depth (m)	12.5
Mean depth (m)	6.1
Volume ($\times 10^4$ m ³)	43.6
Median instantaneous water renewal time (days)	
Jul	45
Aug	160

thermoclines on occasional still, sunny days. The lake is usually ice-covered by late September to mid-October. Several centimeters of snow usually cover the ice within a few days after freeze-up, reaching maximum depths of 25–100 cm by April. Maximum ice thickness is 1.1–1.3 m.

Snowflake Lake is set in a limestone cirque. The catchment rises steeply to 650 m above lake level on the west side, which consists of unvegetated rock and talus. Most of the inflow water enters the lake from this area via two small streams, one of which originates as a spring at the base of a talus slope about 50 m from the lake shore. Other parts of the catchment are thinly vegetated avens meadow, or willow shrub communities (Holland and Coen 1983). The eastern edge of the lake abuts on a boggy meadow with little relief, which is largely outside the lake's catchment. The eastern shoreline of the lake is composed primarily of peat, a favorite habitat for young *Gammarus*. The lake drains to the east via a small stream.

Higher parts of the catchment typically receive 2–3 m of snow, which melts rapidly in May and June. Lake water renewal times are rapid (probably <2–3 d) during spring snowmelt. Most of the meltwater probably passes across the lake surface under ice, as described in Arctic lakes (Schindler et al. 1974; Bergmann and Welch 1985). After ice-out, flows decline, and instantaneous water renewal times are typically 24–400 d in July and August.

Fish stocking—From 1960 to 1966, Snowflake Lake was stocked with 7,500 rainbow trout, 15,000 brook trout, and 6,000 cutthroat trout (Anderson 1972; Leavitt et al. 1994). The fish did not reproduce, and many contained residual eggs from the previous year. They declined gradually. The last known fish, a brook trout, was caught in 1984. Anderson and Donald (1978) and Leavitt et al. (1994) give more information on stocking and on the growth and decline of fish stocks.

Methods

Beginning in 1966 and continuing until 1979, we carried out physical, chemical, and biological studies of Snowflake

Lake (Anderson 1970b, 1974b; Anderson and Donald 1978). The lake was sampled once in 1984. In 1990, we obtained qualitative samples from Snowflake Lake to assess the long-term effects of trout stocking and the possibility of returning the lake community to its original condition. *H. arcticus* was still absent, although *G. lacustris* and *D. middendorffiana* had returned. We monitored plankton populations in 1991 and 1992. We also carried out mesocosm experiments with *Hesperodiptomus* and nutrient manipulations to deduce what controlled rotifer and phytoplankton populations in the lake (Paul and Schindler 1994; Paul et al. 1995). In late 1992, we reintroduced *Hesperodiptomus*. We followed plankton populations until 1995. The long-term plankton record allows us to assess how fish stocking had changed the natural plankton community of Snowflake Lake, the recovery of the community after fish disappeared, and the degree to which reintroduction of *Hesperodiptomus* restored the community.

Zooplankton populations were monitored during ice-free months from 1966 to 1979 and from 1991 to 1995. In all years, zooplankton samples were collected with a 30-cm-diameter, 64- μ m mesh Wisconsin-style plankton net. From 1966 to 1979, the net was towed vertically two times through the water column from a depth of 11 m. In the 1990s, five similar tows were made on each date. The data were corrected for sampling efficiency, which was 40%. Zooplankton samples were preserved with formalin until 1979. In the 1990s, 4% sugar-formalin solution was used (Haney and Hall 1973).

Phytoplankton were sampled in 1967, 1972–1973, 1977–1979, and 1991–1995. Collection procedures for the 1960s and 1970s were described by Anderson (1968). In the 1990s, quantitative samples were collected using a 275-cm-long, 5-cm-diameter clear plastic tube and plug (DeVries and Stein 1991). The tube sampler was lowered into the water, stoppered, and quickly transferred to a 5-gal bucket. Three tube samples were combined in the bucket and mixed thoroughly. We subsampled 250 ml for phytoplankton enumeration and 1 liter for chlorophyll analysis. All phytoplankton samples were preserved with acid Lugol's solution. Samples for chlorophyll, collected from 1991 to 1995, were prepared by immediately filtering 1 liter of lake water through a Whatman GF/F glass-fiber filter. Filters were placed in a petri dish, wrapped with foil to protect them from light, and stored in a nearby creek (<6°C). Pigment samples were transported to the laboratory within 1 week and stored in a freezer until they could be analyzed.

In the laboratory, phytoplankton and small zooplankton (rotifers and copepod nauplii) were enumerated using an inverted microscope after settling several replicate subsamples (1–5 ml each) overnight. For phytoplankton, a minimum of 400 units were counted for each sample, where units were individual cells, colonies, or filaments, depending on the type of algae. Wet biomass was calculated based on geometric shapes (Rott 1981), assuming a specific gravity of one. Taxonomic identifications of phytoplankton were based on Anton and Duthie (1981), Prescott (1982), Huber-Pestalozzi (1983), Whitford and Schumacher (1984), Starmach (1985), and Krammer and Lange-Bertalot (1986, 1991). For small zooplankton, 200 individuals of each taxon were enu-

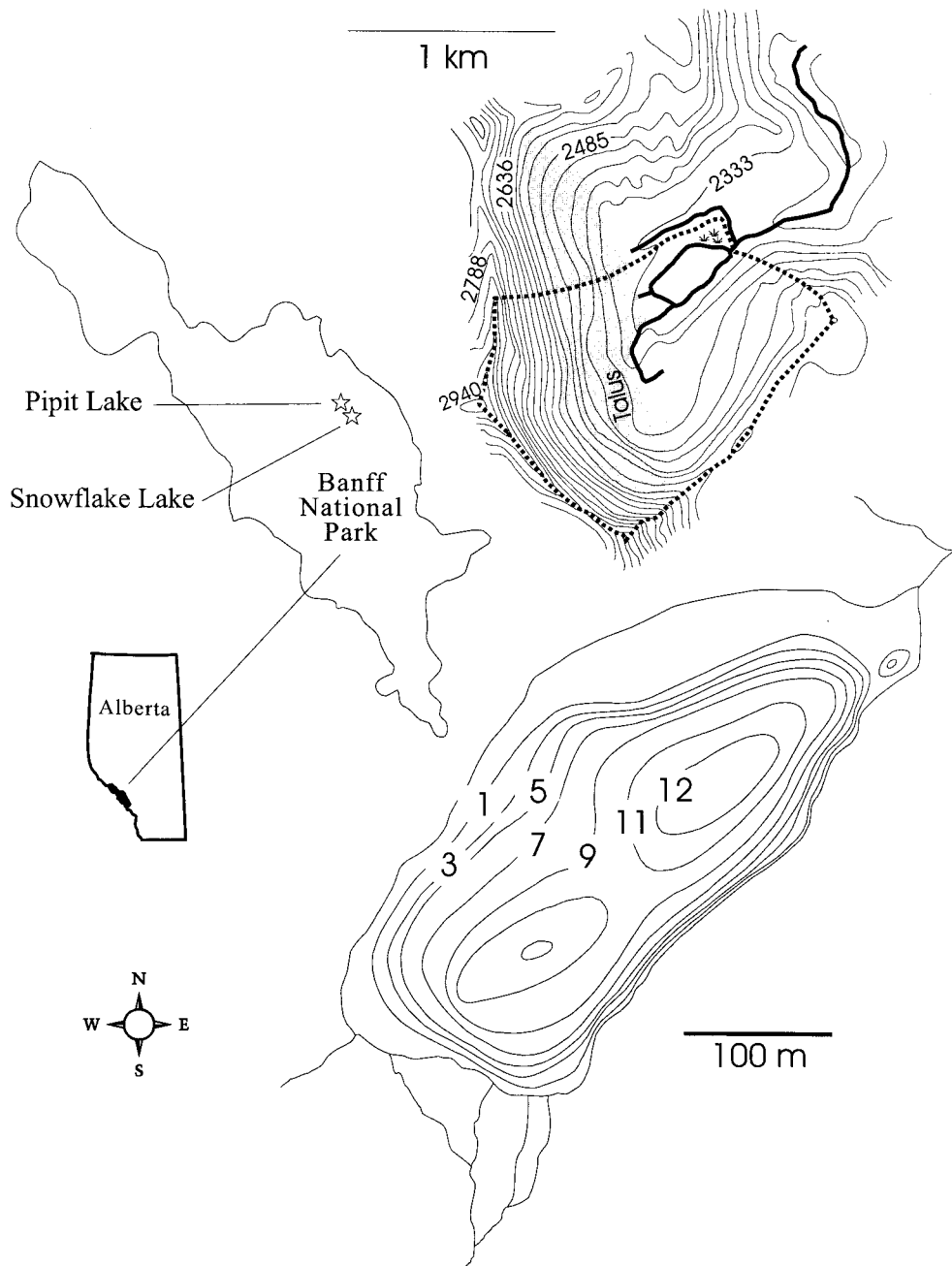


Fig. 2. The location and morphometry of Snowflake Lake and its catchment. The location of nearby Pipit Lake, included in the discussion, is also shown.

merated if possible. Large zooplankton (cladocerans and copepods) were enumerated in a Bogorov tray at $\times 50$ using a stereomicroscope. Replicate 5-ml subsamples were counted until at least 100 individuals were recorded in each major taxonomic group. Rotifera and Crustacea were identified to species using Edmondson (1959) and Chengalath et al. (1971). Copepod life stages were identified using Czaika (1982). Chlorophyll was extracted from pigment samples using 95% ethanol as described by Bergmann and Peters (1980). The Chl *a* concentration of the extract was then de-

termined spectrophotometrically using the monochromatic method (Lorenzen 1967).

After preliminary sampling in August 1990, the plankton community was studied until late July 1992 to assess the long-term changes caused by fish stocking. On 30 July 1992, we reintroduced approximately 660,000 *Hesperodiptomus* to Snowflake Lake. Animals were collected from nearby (2.5 km) Pipit Lake with a 1.25-m-diameter, 1-mm mesh plankton net towed 70 times through the water column from a depth of 15 m. At the time of sampling, the population con-

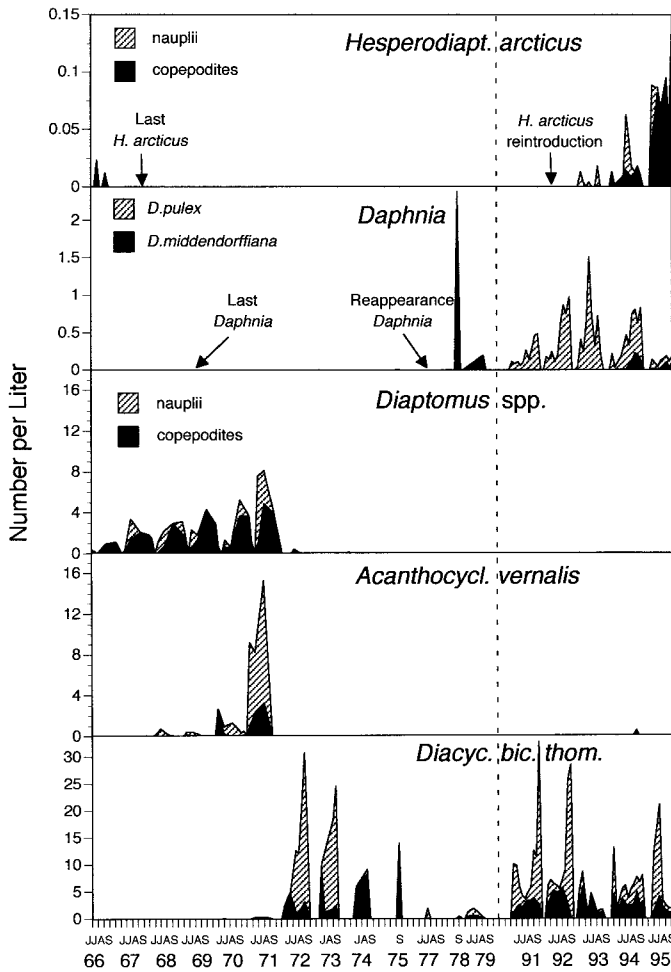


Fig. 3. Densities of crustacean zooplankton in Snowflake Lake, 1966–1995. Data for 1984 and 1990, when sampling occurred only on single occasions, are not shown. Fish were stocked in 1960–1966 and had disappeared by 1984. *Diaptomus* sp. is *D. tyrelli*. *Hesperodiaptomus* were reintroduced in 1992.

sisted largely of adults, and many of the females were gravid. Large *D. middendorffiana* were removed with 3-mm mesh, but small individuals probably escaped filtration. The copepods were transported by helicopter to Snowflake Lake in covered 20-liter buckets and immediately released into the water in deeper (>3 m) portions of the lake.

Results

Changes in the plankton community following trout stocking, 1966–1977—Predation by introduced trout rapidly eliminated large-bodied crustaceans from the zooplankton of Snowflake Lake in the 1960s. *H. arcticus* was last recorded in May 1967, and *D. pulex* was not detected after October 1968 (Fig. 3). *Chydorus sphaericus* increased briefly in 1970 then decreased to scarcely detectable levels. During the late 1960s and early 1970s, the large-bodied crustaceans were replaced by waves of progressively smaller species, including *Diaptomus tyrelli* (female: 1.2–1.9 mm) and *Acanthocyclops vernalis* (female: 1.0–1.8 mm). Eventually, the small

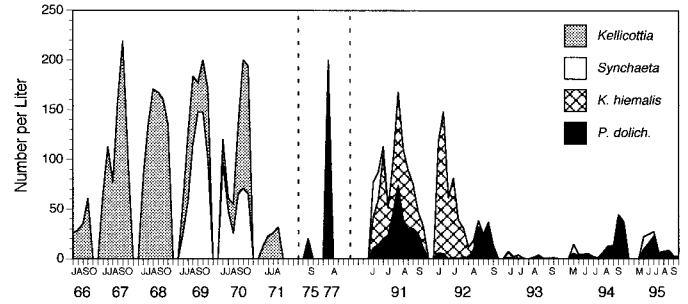


Fig. 4. Densities of rotifers in Snowflake Lake, 1966–1995.

cyclopoid copepod *Diaacyclops bicuspidatus thomasi* (female: 0.9–1.2 mm) became established as the dominant crustacean species, replacing *Diaptomus* and *A. vernalis* (Fig. 3).

The abundance and species composition of the rotifer assemblage also changed (Fig. 4). Rotifer densities were low (about 50 liter⁻¹) in 1966 when *H. arcticus* was still present in Snowflake Lake but increased by a factor of four in 1967. In 1966–1968, *Kellicottia longispina* was the only abundant rotifer. In 1969 and 1970, *Synchaeta oblonga* became an important member of the plankton community. Eventually, *Polyarthra dolichoptera* replaced both *Kellicottia* and *Synchaeta* as the most abundant rotifer. *Polyarthra* was present in small numbers in the 1960s and 1970s, but it was impossible to accurately determine densities because they had deteriorated in samples by 1995, when earlier samples were reassessed.

The phytoplankton of Snowflake Lake were assessed infrequently in the earlier period of the study. The diverse assemblage consisted of diatoms (*Cyclotella* and *Synedra*), cryptophytes (*Rhodomonas* and *Cryptomonas*), chrysophytes (*Bitrichia*, *Kephriopsis*, and *Pseudopedinella*), cyanobacteria (*Chroococcus*), and small green flagellates (*Chlamydomonas* and *Tetraedron*) (Figs. 5, 6). The composition of the phy-

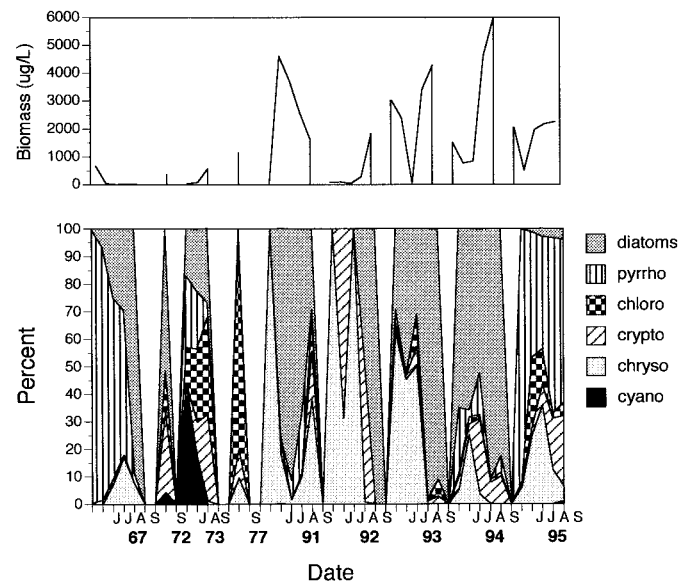


Fig. 5. Relative abundance of major phytoplankton groups, 1967–1995.

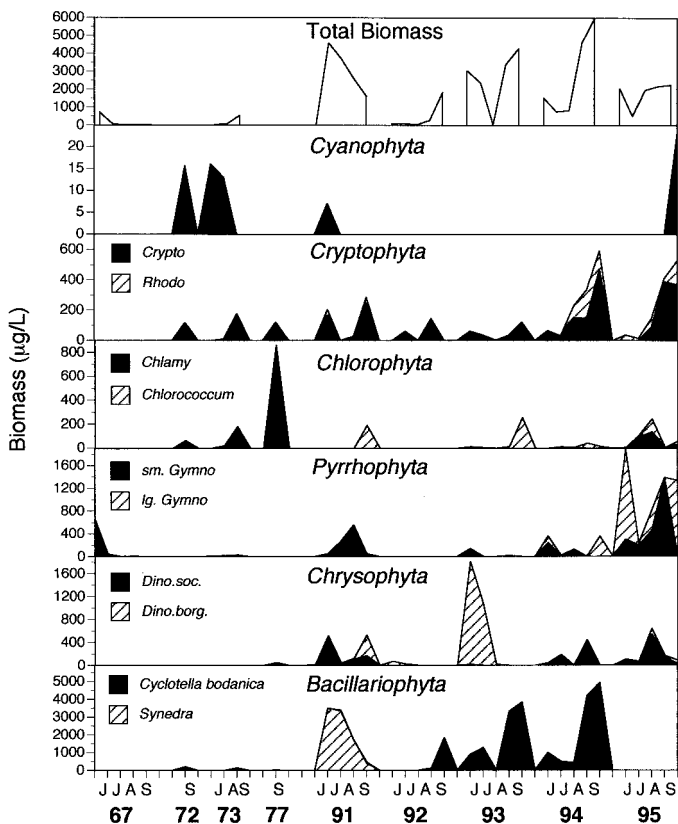


Fig. 6. Phytoplankton live biomass ($\mu\text{g liter}^{-1}$) in Snowflake Lake, 1967–1995.

toplankton community varied greatly from year to year. In 1967, the community was dominated by diatoms and dinoflagellates, whereas in 1973, the phytoplankton included chlorophytes, cryptophytes, and cyanobacteria in addition to diatoms and dinoflagellates (Fig. 5).

Changes in the plankton community following the decline and disappearance of trout, 1977–1992—All species of trout declined continuously after stocking, for there was no reproduction. Only a few large brook trout, of 420–630 g, were left by 1977 (Anderson and Donald 1978). The last fish, a brook trout, was captured in 1984. *D. pulex* reappeared in small numbers in 1975, becoming prominent by the 1990s (Fig. 3). *Keratella hiemalis* joined *Polyarthra* as a codominant of the rotifer assemblage (Fig. 4). Cyanobacteria, which constituted 15–30% of the phytoplankton assemblage in 1973–1974, were only present in trace amounts in other years (Fig. 5). *G. lacustris*, absent from samples taken in 1966–1974, began to appear in benthic samples and fish stomachs collected in 1977. *H. arcticus*, however, did not return to the lake.

Changes in the plankton community following reintroduction of Hesperodiptomus, 1992–1995—Following its reintroduction in 1992, *H. arcticus* successfully established a viable population in Snowflake Lake. Population growth was exponential, increasing about 10-fold each year (Fig. 3). In 1993, there were fewer than 0.001 individuals liter^{-1} , and in

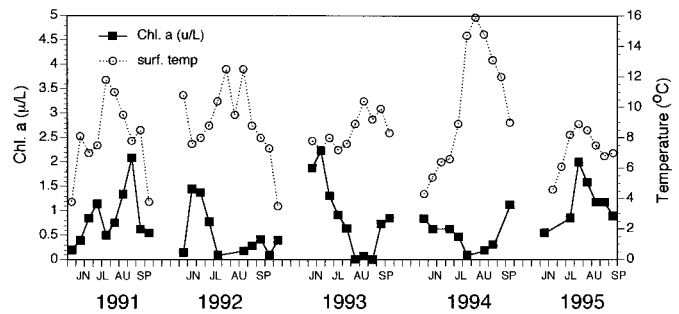


Fig. 7. Chl *a* ($\mu\text{g liter}^{-1}$) and temperature ($^{\circ}\text{C}$) in the ice-free season, Snowflake Lake, 1991–1995.

1994 and 1995, the density of *H. arcticus* copepodites reached 0.01 and 0.13 liter^{-1} , respectively. The density of *H. arcticus* in 1995 was approximately one-sixth the density (0.7 liter^{-1}) found in nearby Pipit Lake, which has a well-established population of *H. arcticus*, and one-twentieth the average density (3.2 liter^{-1}) for lakes in the Canadian Rocky Mountains (Paul and Schindler 1994).

Despite its low density, *Hesperodiptomus* caused changes to the planktonic food web of Snowflake Lake. As predicted from mesocosm experiments (Anderson 1977; Paul and Schindler 1994; Paul et al. 1995), the abundance of rotifers, particularly of *Keratella*, decreased substantially after 1992 (Fig. 4). *Keratella* density in 1995 was similar to that in nearby Pipit Lake, which contains *Hesperodiptomus*. Among the crustacean plankton, there was little detectable change in the abundance of *Diacyclops* copepodites or *Daphnia* associated with the reintroduction of *H. arcticus*. However, the late summer pulse of cyclopoid nauplii observed in 1991 and 1992 was no longer evident in 1993–1995 (Fig. 3), indicating that *Hesperodiptomus* predation was having the effect predicted from smaller scale experiments (Anderson 1970a, 1980; Paul and Schindler 1994; Paul et al. 1995; McNaught unpubl. data).

There were also changes to the phytoplankton community following the reestablishment of *Hesperodiptomus*. Algal biomass in the early 1990s was dominated by large diatoms (*Synedra* spp. and *Cyclotella bodanica*) and chrysophyceans (chiefly *Dinobryon sociale*). By 1995, dinoflagellates (*Gymnodinium* spp.) became an important component of the assemblage (Figs. 5, 6). Large diatom species disappeared in 1995, leaving the smaller *Cyclotella michiganiana* as the only abundant species. Algal species composition in 1995 was more similar to that of 1967 (a large percentage of dinoflagellates, few large diatoms) than that of 1991–1994 (small percentage of dinoflagellates, many large diatoms). These changes within the phytoplankton assemblage had little effect on chlorophyll concentrations, which ranged from <0.1 to 2.4 $\mu\text{g liter}^{-1}$ and typically exhibited two seasonal peaks, one in late June/July and the other in September (Fig. 7).

Discussion

Effects of fish stocking—The observed decrease in herbivore numbers and the shift to smaller species of crustaceans

and rotifers following fish stocking in Snowflake Lake corroborate previous studies at lower elevations (Hrbacek et al. 1961; Brooks and Dodson 1965; Carpenter et al. 1985; Vanni 1988; Vanni et al. 1990; Yan et al. 1991). Although contemporary data are not complete enough for definite conclusions to be drawn about phytoplankton during this period, paleoecological investigations of phytoplankton pigments combined with bioenergetics modelling suggest that phytoplankton increased after fish were stocked, as the result of phosphorus excretion by stocked fish (Leavitt et al. 1994).

D. tyrelli was present with *Hesperodiaptomus* in the first few years of record, while *D. bicuspidatus* were undetectable. After *Hesperodiaptomus* disappeared, successive dominance of *D. tyrelli*, *A. vernalis*, and *D. bicuspidatus*, suggested that *Hesperodiaptomus* had originally allowed *D. tyrelli* to flourish by eliminating predatory cyclopoids but that cyclopoids were able to eliminate *D. tyrelli* after *Hesperodiaptomus* was extirpated by fish. This explanation is also consistent with later recovery data, from 1996 to 1998 (Schindler and Parker unpubl. data) and smaller scale predation experiments (McNaught unpubl. data). The alternative explanation, that fish may have preyed upon smaller species of zooplankton after *Hesperodiaptomus* and *Daphnia* were eliminated, is unlikely, for examination of thousands of trout stomachs from many lakes in the region shows no evidence that cyclopoid or smaller calanoid copepods are eaten even when they are common in the plankton.

With the disappearance of *Daphnia* and *Hesperodiaptomus* in the mid-1960s, rotifer populations were no longer subject to competition or predation, and they increased dramatically. Anderson (1977) and Paul and Schindler (1994) showed that *Hesperodiaptomus* was able to control rotifer populations via predation. This is in contrast to studies at lower elevations, as discussed later (Neill 1984).

Effects of fish disappearance—The decline and disappearance of fish allowed *Gammarus* and *Daphnia* to return. *Gammarus* probably recovered from small numbers that remained in bottom sediments or in peat deposits in the littoral zone of the lake, where they would be difficult for fish to find. *Daphnia* are known to recover from diapausing eggs after many years of suppression by fish (Schindler and Comita 1972). Populations of rotifers and *Diacyclops* remained high during the 1980s, probably because *Hesperodiaptomus* remained absent from the lake.

Typically, calanoid copepod populations also recover from diapausing eggs in lake sediments (Hairston et al. 1995). However, assessments in 1994 revealed that *Hesperodiaptomus* resting eggs were absent from Snowflake Lake sediments deeper than 5 mm. The few that were found in the surface 5 mm presumably were deposited after the species was reintroduced (Parker et al. 1996). Studies of gut contents reveal that both *Gammarus* and large *Daphnia* feed at the sediment surface, consuming *Hesperodiaptomus* resting eggs (Wilhelm et al. in press, unpubl. data). *Gammarus* were abundant in the lake before stocking, and they may have kept the reserves of *Hesperodiaptomus* diapausing eggs low (Parker et al. 1996). Predation by *Diacyclops* on nauplii from any diapausing eggs that hatched may also have prevented recovery of *Hesperodiaptomus*.

Rotifer populations were low in the mid-1970s, corresponding with low populations for *Diacyclops*. *Kellicottia* and *Synchaeta*, which had been dominant in earlier years, were replaced by small populations of *Polyarthra*. However, by the early 1990s, rotifers increased in abundance despite large populations of *Diacyclops*, although *P. dolichoptera* and *K. hiemalis* predominated.

Effects of reintroducing Hesperodiaptomus—Both rotifer populations and *Daphnia* abundances declined as the *Hesperodiaptomus* population increased. In particular, *Keratella* was all but eliminated from the lake. Experimental evidence indicates that *Hesperodiaptomus* does not prey on *Daphnia*, and the decline in the latter may be due to competition between the two species after rotifers are eliminated, as discussed later. Although *Diacyclops* populations were declining by 1994–1995, they remain numerically the most abundant crustaceans in the zooplankton community.

The reintroduction caused no significant changes in phytoplankton biomass, as measured by either Chl *a* concentration or cell volume (Figs. 6, 7). However, there was a considerable shift in species from large diatoms and colonial chrysophytes to smaller diatoms and cyanobacteria. The feeding of *Hesperodiaptomus* on large phytoplankton is confirmed by gut contents, where *Synedra* and *Dinobryon* are commonly observed.

Comparison of the response of Snowflake Lake with other systems—It appears that the cold temperatures and oligotrophic conditions in alpine lakes cause responses of rotifers to predation by invertebrates to differ from those in warmer lakes. In montane lakes of coastal British Columbia, Neill (1984) concluded that invertebrate predators (*Chaoborus trivittatus* and large *Diaptomus*) could do little more than “fine tune” rotifer populations, because of high rotifer reproductive rates. In contrast, in our studies, rotifer populations were strongly suppressed by even small densities of *Hesperodiaptomus*, both in mesocosms (Anderson 1977; Paul and Schindler 1994) and in Snowflake Lake. Mesocosm experiments suggest that cold temperatures may be more important than nutrients in allowing rotifers to be suppressed. Whereas nutrient additions caused increases in phytoplankton and rotifers in mesocosms when *Hesperodiaptomus* was absent, in the presence of *Hesperodiaptomus*, rotifer numbers were no higher than in unfertilized mesocosms (Paul et al. 1995). Hatching of rotifer eggs is slower at cold temperatures (Edmondson 1965). However, few rotifers in Snowflake Lake were carrying eggs, probably because of low phytoplankton populations. Under such conditions, invertebrate predators appear to be efficient at suppressing rotifer populations.

Although *Hesperodiaptomus* did not return to Snowflake Lake after stocked fish disappeared, *Hesperodiaptomus* did return to nearby Pipit Lake (Parker et al. 1996; Schindler unpubl. data). There are several possible reasons for the difference. First, only rainbow trout were introduced to Pipit. They died out rapidly, with only a single fish caught in 1977 (Anderson and Donald 1978). Second, Pipit Lake is larger than Snowflake, with an area of 10.6 ha and a maximum depth of 20.6 m. Donald et al. (1994) found that *Hesperodiaptomus* could coexist with fish in lakes >16 m in depth.

Though *Hesperodiaptomus* was not recorded in Pipit Lake between 1968 and 1977, some animals may have escaped predation in the deeper water. Finally, sediment studies show that there was better survival of diapausing eggs in Pipit Lake than in Snowflake Lake (Parker et al. 1996), probably because Pipit Lake has a much smaller *Gammarus* population (Wilhelm unpubl. data). Parker et al. (1996) showed that diapausing *Hesperodiaptomus* eggs that were up to 25 yr old could hatch. This reserve of diapausing eggs might have allowed the *Hesperodiaptomus* population to reestablish after fish disappeared.

Comparison of the whole-lake response with that of mesocosms—Most of the effects of reintroducing *Hesperodiaptomus* on rotifers were predicted by earlier mesocosm experiments. In the presence of even low densities of *Hesperodiaptomus*, the abundance of rotifers declined. However, in mesocosm experiments, *Polyarthra* was more susceptible to predators than *Keratella* (Paul and Schindler 1994), whereas the opposite was true in the whole lake. The shift in phytoplankton from *Synedra* and *Dinobryon* to *Cyclotella* and small cyanobacteria and the general lack of effect of *Hesperodiaptomus* on phytoplankton standing crops observed in the lake were also correctly predicted by mesocosms (Paul et al. 1995). In summary, while mesocosms appear to have correctly predicted the direction in which phytoplankton and zooplankton communities would respond, they did not accurately predict the responses by all species.

Assessment of the trophic cascade in alpine lakes—Our earlier combined paleoecological/modelling study indicated that the stocking of fish initiated a weak trophic cascading response (Leavitt et al. 1994). Paleoecological pigment records indicate that after fish eliminated large zooplankton, the density of phytoplankton increased, as would be expected (Leavitt et al. 1994). The increase appeared to be due to increased nutrient recycling by fish, perhaps as the result of benthic feeding and excretion in the water column. Similar effects of fish on nutrient recycling have been observed by Lamarra (1975) and Brabrand et al. (1990).

As a result, we had predicted that reintroduction of an invertebrate predator would also initiate a cascading response, by removing rotifers that dominated the grazer community. We had believed that competing *Daphnia* could then flourish. Surprisingly, *Hesperodiaptomus* predation on rotifers did not initiate a compensatory increase in *Daphnia*. The potential cascading effect of *Hesperodiaptomus* may be weakened to some degree by its switch to phytoplankton once rotifers and nauplii are scarce. Also, *Hesperodiaptomus* nauplii feed on small phytoplankton, so that they compete directly with *Daphnia* and rotifers.

Weakening of the cascade by intertrophic level feeding may be common in high altitudes or high latitude lakes. Findlay et al. (1994) observed declines in phytoplankton populations for 2 yr after piscivorous pike were introduced into Lake 221 at the Experimental Lakes Area (ELA), which had been dominated by large yellow perch. However, several years after the introduction, phytoplankton had returned to their previous abundance, for perch fed on both large herbivorous crustaceans and the zooplankton predator *Chao-*

borus. An even more striking lack of a “cascading” response was observed in Lake 110, ELA, even though the introduction of high densities of pike caused nearly total elimination of planktivorous cyprinids, which should have resulted in an increase in large zooplankton (Elser et al. 1998). Vander Zanden and Rasmussen (1996) also identified a high degree of intertrophic level feeding in lakes of the St. Lawrence River drainage in Ontario and Quebec, illustrating that it could have significant effects on trophic cascading and contaminant accumulation.

There may also be stoichiometric constraints on *Daphnia* that prevented them from increasing enough to cause a trophic cascading response (Elser et al. 1998). Because *Daphnia* require food with low C:P ratios (<200–300:1 by moles), they were unable to increase in lakes where C:P in seston was greater than this value, even when planktivorous fishes were eliminated. While *Daphnia* were present in Snowflake Lake, they did not increase after competition from rotifers was eliminated. The C:P ratio of seston in the lake is high (>900:1), so that a strong “cascading” effect would not be expected.

High C:P in seston appears to occur when phosphorus inputs are low, light penetration is high, and thermoclines are deep, conditions that promote a high light:nutrient ratio in the mixed layer (Sterner et al. 1997). Such conditions occur in Snowflake Lake and other alpine lakes, where there is little input of nutrient or colored dissolved organic carbon, light penetration is high, and thermal stratification is absent or transient. Other lakes in the alpine and subalpine Canadian Rockies have similar high C:P ratios, and the zooplankton communities of many are similar to Snowflake, so that trophic cascading may be weak or rare.

The short ice-free season and cool midsummer temperatures unquestionably slow the response of zooplankton communities to perturbation, as shown by the several years required for the successive elimination of zooplankton species after fish were stocked and the long time required for *Hesperodiaptomus* to approach abundances typical of mountain lakes after the species was reintroduced. The full effects of reintroduction on community structure will probably not occur for several more years.

Evaluation of the restoration of Snowflake Lake—The reintroduction of *Hesperodiaptomus* was a success. The large population of *Diacyclops* present in the early 1990s, which undoubtedly preyed on *Hesperodiaptomus* nauplii (McNaught unpubl. data), has probably slowed the reestablishment of the population. As a result, >3 yr after *Hesperodiaptomus* was introduced, there are still major differences in the zooplankton community compared with that originally present in the lake. *D. tyrelli* is still absent, and *D. bicuspidatus* is still dominant, although the latter species appears to be declining. The original dominant rotifer, *Kellicottia* sp., has not returned.

In summary, while restoration of the invertebrate communities of alpine lakes following fish stocking appears to be possible, the recovery of the original community is very slow. We will continue to monitor Snowflake Lake for several more years, until the community structure has stabilized.

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Received: 9 February 1998

Accepted: 12 September 1998

Amended: 1 October 1998