

The Effects of Stocking and Removal of a Nonnative Salmonid on the Plankton of an Alpine Lake

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ABSTRACT

Bighorn Lake, a fishless alpine lake, was stocked with nonnative brook trout, *Salvelinus fontinalis*, in 1965 and 1966. The newly introduced trout rapidly eliminated the large crustaceans *Hesperodiaptomus arcticus* and *Daphnia middendorffiana* from the plankton. In July 1997, we began to remove the fish using gill nets. The population comprised 261 fish that averaged 214 g in wet weight and 273 mm in fork length. Thereafter, zooplankton abundance increased within weeks. Early increases were caused by the maturation of *Diacyclops bicuspidatus*, few of which reached copepodid stages before the removal of the fish because of fish predation. *Daphnia middendorffiana*, absent when fish were present, reappeared in 1998. *Hesperodiaptomus arcticus*, which had been eliminated by the stocked fish, did not return. The proportion of large zooplankton increased after fish removal, but their overall biomass did not

change. Algal biomass was low and variable throughout the 1990s and correlated with water temperature but not with nutrient concentrations or grazer densities. Diatoms were the most abundant algal taxon in the lake, followed by Dinophyceae. Chrysophyceans and cryptophyceans were eliminated after the fish were removed. Chlorophyll *a* concentrations were unaffected. Gill netting is a viable fish eradication technique for smaller (less than 10 ha), shallow (less than 10 m deep) lakes that lack habitable inflows and outflows or other sensitive species. Further work is required to define appropriate removal methods for larger lakes and watersheds.

Key words: trophic cascading; alien species; fish eradication; lake restoration.

INTRODUCTION

In the early part of the 20th century, sport fish were widely stocked in high-elevation fishless lakes of the national parks of the Canadian Rocky Mountains (reviewed by Schindler and Pacas 1996; Schindler 2000). Many of the smaller stocked lakes did not have suitable spawning habitat, and fish populations dwindled to extinction within 2 decades, in some cases leaving the invertebrate communities of the lakes impoverished (McNaught and

others 1999; Parker and others 1996). In other alpine and subalpine lakes, introduced brook trout (*Salvelinus fontinalis*) spawned successfully, and populations were self-maintaining, although the value of these populations to regional sport fishing was variable (Rawson 1940; Donald and others 1980; Donald 1987). Bighorn Lake was one of the high alpine lakes that supported stocked brook trout.

We infer from early records that introduced fish eliminated the large crustaceans *Hesperodiaptomus arcticus* and *Daphnia middendorffiana* from the zooplankton of Bighorn Lake (Anderson 1972; Anderson and Donald 1978). When we resumed studies

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of the lake in 1991, the zooplankton community was still in an altered state. *Hesperodiaptomus* and *Daphnia* were absent, and there were few adult crustaceans observed in the plankton. In nearby fishless Snowflake Lake, we used mesocosm experiments (Paul and Schindler 1994) and a whole-lake manipulation (McNaught and others 1999) to show that *H. arcticus* is a keystone species in fishless alpine lakes, shaping the herbivorous zooplankton communities by preying on rotifers and copepod nauplii (Anderson 1977, 1980).

In keeping with changing public attitudes (Rahel 1997) and Parks Canada's mandate to maintain ecosystems in their pristine condition, stocking ceased in the mountain national parks in the late 1980s. In 1995–96, the Banff–Bow Valley Task Force was appointed by the Minister of Heritage to make recommendations for maintaining and restoring ecosystems of Banff National Park. Based on a review of the state of fisheries in Banff National Park (Schindler and Pacas 1996), the Task Force (Banff–Bow Valley Study 1996; summarized by Schindler 2000) recommended that scientific studies be undertaken to explore the feasibility of restoring aquatic communities that had been changed by the stocking of nonnative species.

The proposal to remove nonnative fishes in the parks has provoked tremendous controversy (Ritchie 2000), even though native populations of threatened bull trout (*Salvelinus confluentus*) in some of the lakes were replaced by introduced species. Several of the affected lakes in Banff National Park are internationally famous tourist destinations. Opposition has arisen from anglers, who often prefer introduced over native species, and other groups who oppose the use of fish poisons or other controversial measures to remove the fish.

In 1996, we proposed to Parks Canada that we experimentally remove brook trout from Bighorn Lake as a pilot experiment to test the feasibility of using gill nets to remove fish in larger lakes and to assess the degree to which the original aquatic communities might recover following fish removal. Gill net removal of introduced trout was being attempted elsewhere at the same time (Knapp and Matthews 1998). We began removing fish shortly after ice-out in mid-July 1997.

In this paper, we describe the brook trout population of Bighorn Lake and the long-term changes in the zooplankton and phytoplankton populations that resulted from the food web manipulations caused by the introduction and later removal of nonnative brook trout. Further, we discuss the efficacy of the removal of trout with gill nets and its applicability to other lakes.

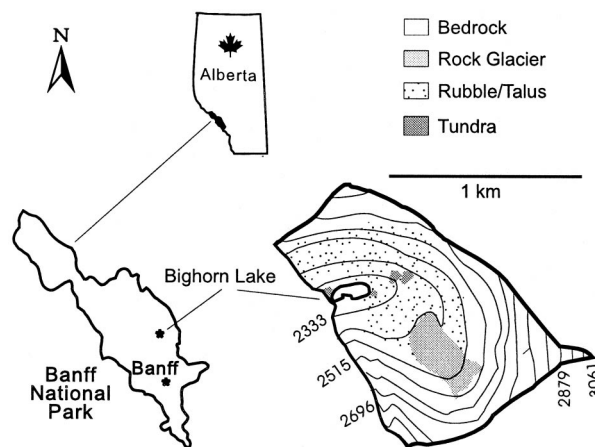


Figure 1. The Bighorn Lake watershed. Contours in m.

MATERIALS AND METHODS

Study Site

The Bighorn Lake watershed is located in the Front Ranges of Banff National Park, Canada (115°39'W: 51°28'N) (Figure 1). Because of its remote location and difficult access (it is more than 40 km from the nearest motorized vehicle access and 5 km from the nearest hiking trail), human activity in the watershed is minimal. Research activities comprised all of the human use of the basin in the last decade except for rare guided visits by small groups of tourists.

The watershed is a glacial cirque cut into stratified sedimentary bedrock that rises more than 700 m above the lake surface. Rubble and talus overlie the bedrock at lower elevations. There are 2 ha of alpine tundra in the 107-ha catchment, which is otherwise nearly barren of vegetation. A rock glacier (large, angular rock debris cemented together by interstitial ice) (Holland and Coen 1983) and several permanent snowfields are present above the lake. Lake environs are particularly windy due to the west-facing exposure of the catchment and its location at the end of a 5-km-long hanging valley.

Bighorn Lake is 2.1 ha in area, 9.2 m deep (mean depth, 3.1 m) and oligotrophic (TP 4–12 $\mu\text{g L}^{-1}$). The ice-free season is mid-June–early July through early October. Ice thickness reaches 1.75 m in late winter. Mean annual water temperature varied between 2.5 and 4.6°C in the 1990s, with midsummer surface-water maximum temperatures of 5.8–14.8°C. Under-ice temperatures average 1–2°C through the entire water column. Due to fine silt in the water, Secchi depth is shallow compared to nearby lakes, averaging 3.5 m. The lake stratifies weakly for 2–3 weeks during hot summers. Stratification does not occur during cool summers. Un-

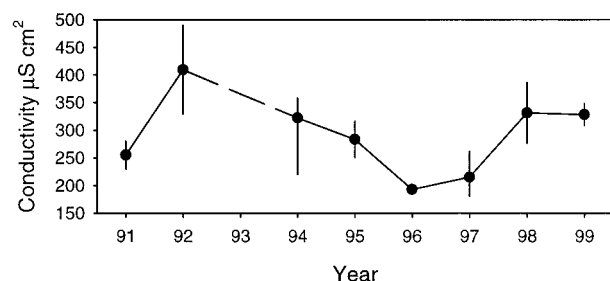


Figure 2. Mean conductivity with annual ranges. Number of samples varied between two and five per year.

like other nearby lakes, patches of *Rhizoclonium hieroglyphicum* develop between 3 and 5 m depth in the shallower western half of the lake. Otherwise, the littoral zone, which consists mostly of fractured bedrock, large boulders, and talus, is devoid of vegetation. Littoral areas to 2 m or more depth dry and/or freeze annually due to a 1–2-m drawdown over late summer and winter.

Surface outflow occurs for several weeks during and just after snowmelt, but most outflow occurs through fissures in bedrock at the west end of the lake. Most catchment runoff enters the lake via subsurface flow. Estimated water renewal rate, extrapolated from nearby basins where hydrologic flux has been measured, is 25 times per year. Conductivity (Figure 2) and concentrations of most chemical constituents are variable, probably due to a combination of high flushing rate and annually variable snowpack, rainfall, and glacier melt. Long-term average values for selected water chemistry parameters are provided in Table 1. Overall, the lake has low nutrients but relatively hard water and moderately high alkalinity.

The Original Zooplankton Community

On first sampling in 1966, the 2nd year of trout stocking, the calanoid copepod *Hesperodiaptomus arcticus* was the only species of zooplankton captured. Fish predation likely had already impoverished the zooplankton fauna by this time. The original plankton community in Bighorn Lake probably was similar to that of other fishless lakes in the area in being dominated by *H. arcticus*. In 1968, two species of cyclopoid copepod, *Acanthocyclops vernalis* and *Diacyclops bicuspidatus*, appeared in the plankton. It is probable that they were originally present in low abundance due to predation by *H. arcticus* on their nauplii, as in other nearby fishless lakes. Although no *Daphnia* were captured, other fishless lakes in the area support one species of cladoceran, usually *Daphnia middendorffiana*. Daphnids are rap-

Table 1. Selected Bighorn Lake Water Chemistry Parameters

Constituent	Mean \pm 1 SD	Unit
pH	8.00 \pm 0.29	
Alkalinity	1.37 \pm 0.20	meq L ⁻¹
Bicarbonate	81 \pm 14	mg L ⁻¹
Conductivity	281 \pm 96	μ S cm ⁻²
DOC	0.30 \pm 0.19	mg L ⁻¹
TP	7.1 \pm 2.7	μ g L ⁻¹
TN	166 \pm 87	μ g L ⁻¹
SO ₄	61 \pm 32	mg L ⁻¹
Cl	0.28 \pm 0.14	mg L ⁻¹
Ca	38 \pm 13	mg L ⁻¹
Mg	14 \pm 6.4	mg L ⁻¹
K	0.32 \pm 0.09	mg L ⁻¹
Na	0.40 \pm 0.19	mg L ⁻¹
Si	0.80 \pm 0.15	mg L ⁻¹

Means are concentration for all samples collected between 1991 and 1999 \pm 1 standard deviation. DOC, dissolved organic carbon; TP, total phosphorus; TN, total nitrogen.

idly eliminated by fish and it is likely, due to the presence of resting eggs in the sediments, that they were originally present. No rotifers were recorded in 1966, but several genera, including *Keratella*, *Notholca*, *Polyarthra*, and *Synchaeta* appeared by 1968–69. These probably were present prior to fish stocking but held at very low densities by predation by *Hesperodiaptomus*. *Gammarus lacustris* is present in all other permanent waterbodies in the vicinity that do not freeze to the bottom, but it has never been recovered from Bighorn Lake. If originally present in the lake, abundances probably were low because organic shoreline habitat is absent.

Stocking History

Bighorn Lake was fishless prior to the introduction of 2000 fingerling brook trout in both 1965 and 1966. Although park records do not report the stocking of nonnative rainbow trout (*Oncorhynchus mykiss*), several were captured in 1968. Brook trout were the only fish species present in 1977 (Anderson and Donald 1978) and later years. No brook trout recruitment occurred prior to 1977; all fish captured in test-netting that year were original stocked fish of age 13 or 14 (Anderson and Donald 1978). It was believed that due to the lack of reproductive success, the lake would return to a fishless state. We observed both juvenile and adult brook trout in the early 1990s. The age structure of the population suggests that the fish probably started to reproduce around 1980.

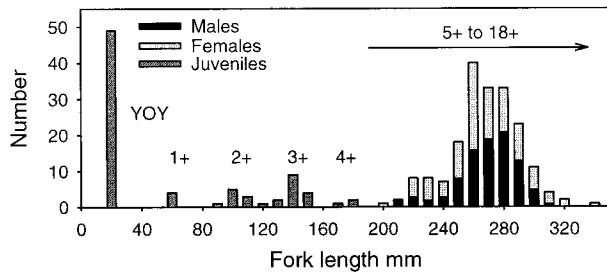


Figure 3. Estimated fork length distribution of brook trout on 6 July 1997. Juveniles captured in 1998 were assigned a fork length distribution equivalent to that of the same cohort in July 1997. Trout captured in 1999 and 2000, which were young-of-year (YOY) in 1997, were arbitrarily assigned a FL of 20 mm.

Fish Removal and Life History

Brook trout were removed with 22 35-m gangs of mixed-mesh monofilament nylon gill nets (25–100 mm stretched mesh) from 6 to 14 July 1997, then with five mixed-mesh gangs from 14 July 1997 until 1 July 1998, when an additional six mixed-mesh gangs were added (25–75 mm stretched mesh). We have continued to fish with a minimum of 10 35-m mixed-mesh gill nets through 2000. Nets were checked every day for the first 5 days, every other day for the next 5 days, and approximately once every 2–4 weeks thereafter. Deep-set gill nets were left to fish under the ice during winter. By August 2000, more than 10,000 net nights of fishing effort had been devoted to fish removal.

The fork lengths (FL) of all captured brook trout were measured to the nearest mm (± 1 mm). Weight in g (± 1 g) was determined on a portable electronic balance for all but approximately 10% of captured trout, the latter being substantially decomposed. Means of length and weight are presented as mean ± 1 standard deviation (SD). Length–weight regressions were calculated for brook trout smaller and larger than 200 mm FL that were captured between 6 and 14 July 2000. Condition is expressed as both condition factor (Bagenal and Tesch 1978) and as the ratio of actual:predicted wet weight of individual trout based on the regression equation for trout under 200 mm FL. Otoliths of 64 individuals were sectioned and then burned (Christensen 1964) prior to reading under a dissecting microscope. Aging was validated (Beamish and McFarlane 1983) for brook trout through age 5 by comparison with the size frequency distribution (Figure 3). Aging of adult brook trout was not validated except for the 1977 sample, where assessed age was consistent with year of stocking. Otoliths

were difficult to interpret for some brook trout more than 14 years of age captured in 1997.

Plankton and Water Chemistry

Zooplankton were monitored in 1966, 1968, 1971, 1972, 1977 (D.B.D. and R.S.A.), 1991, 1992 and 1994–99 (B.R.P. and D.W.S.). In all years, zooplankton were collected with a 30-cm-diameter (d.) 64- μ m mesh Wisconsin-style plankton net. Prior to 1991, the net was towed twice from 1 m above the bottom to the surface. In the 1990s five similar tows were made on each date. Zooplankton were preserved with formalin through 1977 and with sugar-formalin in the 1990s (Haney and Hall 1973). Zooplankton counts were not corrected for net efficiency. Rotifers and copepod nauplii were enumerated using an inverted microscope after settling subsamples (10%–25% of sample volume) overnight. Large zooplankton were enumerated under a stereo dissecting microscope. Sampling frequency has varied between two and five times per year in the 1990s. Access restrictions because of watershed closures due to grizzly bear (*Ursus arctos*) activity, the presence of wapiti (*Cervus elaphus*) carcasses in the basin (which attract and are aggressively defended by bears), high flows that prevented safe fording of rivers and creeks, and occasional severe weather conditions precluded implementing a strictly defined sampling regimen.

In the 1990s, phytoplankton samples were collected using a 275-cm-long 5-cm-d. clear plastic tube and plug (DeVries and Stein 1991). Three tube samples were combined and mixed thoroughly. In all, 250 ml were subsampled for phytoplankton analysis and preserved with acid Lugol's. Phytoplankton were enumerated using an inverted microscope. Wet biomass was calculated based on geometric shapes of plankton (Rott 1981), assuming a specific gravity of one. Samples for chlorophyll were prepared by filtering 1 L or more through a GF/F glass-fiber filter. Filters were placed in a petri dish, covered in foil, and stored in a creek (at less than 6°C) until transported to a laboratory for analysis. Chlorophyll *a* was extracted with 95% ethanol and the concentration determined fluorometrically. Chlorophyll *a* and water chemistry data were collected in the 1990s only.

In 1994, we collected and examined Bighorn Lake sediments to assess the occurrence of diapausing *H. arcticus* eggs. Two sediment cores were collected from Bighorn Lake with a 5.1-cm-d. trigger released gravity corer in late March 1994 following the methodology of Parker and others (1996).

Cores were held in the dark at 2°C for 2 weeks prior to analysis. Cores were extruded and sectioned at 5-mm intervals to a depth of 50 mm. The outer 3 mm of each slice was removed to avoid contamination of samples due to smearing. Core slices were diluted with GF/F filtered lake water, sonicated for 2 min, then washed through a 75- μ m nylon sieve, which was selected to retain diapausing eggs. Retained sediments were screened for *H. arcticus* resting eggs using a counting ring under a dissecting microscope. Counting efficiency was estimated at 95%–100% (Parker and others 1996).

In addition, 5.8 L of near surface sediments to a depth of approximately 6 cm (0.1 m² surface area) were collected by Ekman grab on 14 July 1997. Samples were sieved and screened for *Hesperodiaptomus* resting eggs. *Daphnia* resting eggs were not enumerated in sediment samples, but their occurrence was noted.

Collections of benthic algae and invertebrate fauna were made in 1997 through 2000, but analysis has not been completed to date.

RESULTS

Fish Population

In the 1st week of netting, 146 brook trout were caught. Approximately 90% of the fish 2 years old or older (192) were removed by October 1997. The remains of 13 mature and six juvenile brook trout were removed from the gill nets in June 1998. Because only one fish, a juvenile, was captured during the remainder of the summer, we believe that all adults were removed prior to spawning in the fall of 1998. In 1999, 48 juvenile brook trout of the 1996 cohort were captured by mid-July. One additional juvenile of the 1996 cohort was removed from gill nets in July 2000, by which time the total catch was 261 brook trout. Approximately 5700 s of electroshocking (actual pulse time) with a 3.5-amp alternating current boat-mounted shocker on 18 July 2000 failed to yield any fish, and no additional fish were caught with gill nets thereafter.

Mature brook trout averaged 273 \pm 22 mm FL and 217 \pm 46 g wet weight (Figure 3). Condition was good in juvenile fish but declined sharply with increasing length (Figure 4a and b) beyond 200 mm FL. Estimated standing stock at the start of removal on 6 July 1997 was 20.7 kg ha⁻¹.

The growth of the brook trout was relatively rapid through age 5+, averaging approximately 40 mm FL y⁻¹. Minimum size and age at maturity in 1997 were 200 mm FL and age 5+, but few fish under 230 mm FL had fully matured gonads. Fol-

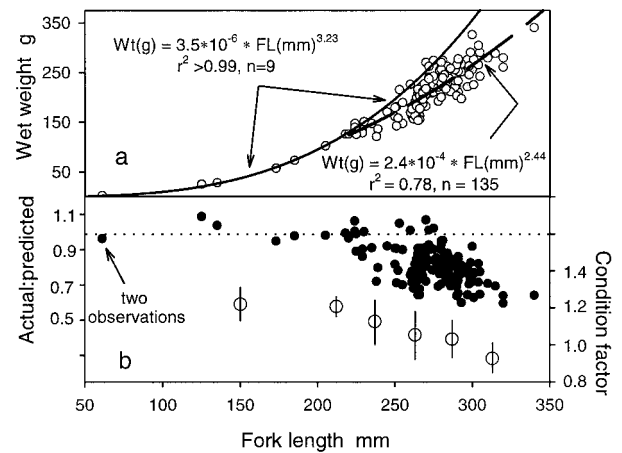


Figure 4. a Length–weight regressions for brook trout less (solid line) and greater (dashed line) than 200 mm FL. b Ratio of measured to predicted weight of brook trout, based on regression equation for trout less than 200 mm fork length (solid circles) and mean condition factor \pm one standard deviation (open hollow circles) for the following fork length ranges: 100–200 mm, 200–225 mm, 226–250 mm, 251–275 mm, 276–300 mm, and greater than 300 mm.

lowing the onset of maturity, growth rates declined, averaging less than 8 mm FL y⁻¹.

Changes in the Zooplankton Community following Trout Stocking: 1966–July 1997

H. arcticus was eliminated by trout predation within 5 years of fish stocking (Figure 5). This species, captured in plankton tows in the last year of fish stocking, was eliminated between 1968 and 1971. There was no record of *Daphnia* or any other species of zooplankton being present at first sampling 1 year after brook trout were stocked, but *Daphnia* were presumed to have been present prior to fish stocking because ephippia were recovered from lake sediments. *Diacyclops bicuspidatus* first appeared in 1968. *Acanthocyclops vernalis* were first captured in 1972 and were abundant by 1977. Low abundances of cyclopoid copepods are typical of *H. arcticus*-dominated water bodies in the area (Anderson 1974, 1977, 1980; McNaught and others 1999), but they typically increase in abundance when *H. arcticus* is eliminated (McNaught and others 1999).

By the 1990s *Diacyclops* had replaced *Acanthocyclops* as the dominant predatory crustacean. While cyclopoid nauplii were abundant, densities of adults typically were less than 1 m⁻³. Rotifers, primarily *Synchaeta* and *Polyarthra*, which were rare in 1966 and 1968, became quite abundant in the 1970s (Figure 6).

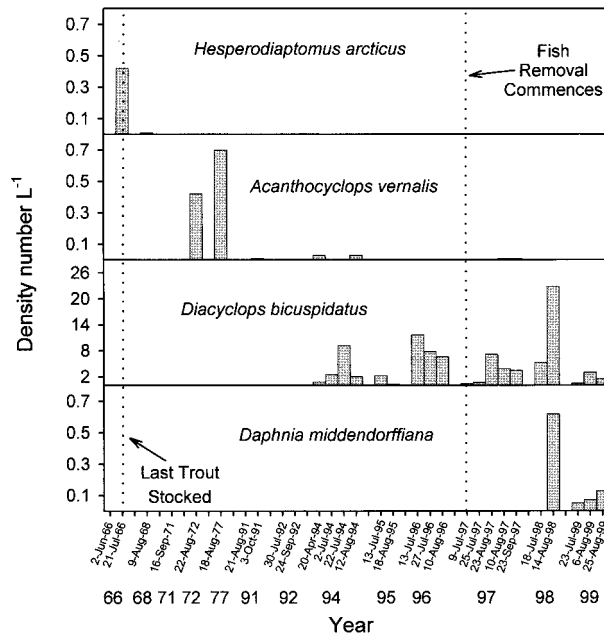


Figure 5. The densities of crustacean zooplankton in Bighorn Lake, 1968–99. No other species of crustaceans are known to be present. *Daphnia middendorffiana* is presumed to have been eliminated by trout prior to our first sampling.

Changes in the Zooplankton Community during Fish Removal: July 1997–September 1999

Despite cold water temperatures and oligotrophic conditions, zooplankton responded to fish removal within weeks. Whereas zooplankton were chiefly nauplius larvae of *Diacyclops* and the rotifers *Polyarthra* and *Keratella* when fish were present, by mid-August numerous copepodids and adults of *Diacyclops* were present (Figure 7), causing most of the shift in the size of zooplankton (Figure 8). Densities of adult *Diacyclops* increased by more than three orders of magnitude by 1998 (Figure 7) relative to preremoval years. Abundances of *Diacyclops* nauplii and eggs declined as adult numbers increased. Egg counts for *Diacyclops* averaged 35.4 per female in 1996 and 1997 combined. In 1998–99, average egg count was 10.2 eggs per female. There was little change in the abundance of *Acanthocyclops* following fish removal.

Daphnia middendorffiana were first collected in August 1998, more than a year after fish removal started. The initial density was 0.62 L^{-1} (Figure 5). We speculate that the population originated from resting eggs, which are typically produced in large numbers in lakes of the area and were present in

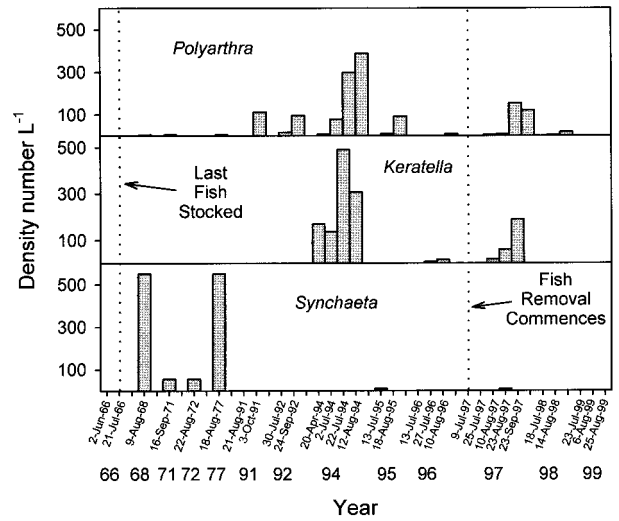


Figure 6. The densities of abundant rotifer genera in Bighorn Lake, 1968–99. *Keratella* was present at low densities in the late 1960s. Other genera captured but not included in the figure were *Brachionus*, *Euchlanis*, *Filinia*, *Kellicottia*, *Lecane*, *Lepadella*, *Monostylis*, *Mytilina*, and *Trichotria*. Abundances of these genera typically were less than 10 L^{-1} , and their occurrence was sporadic. *Notholca* was present in most collections but always at densities of less than 10 L^{-1} .

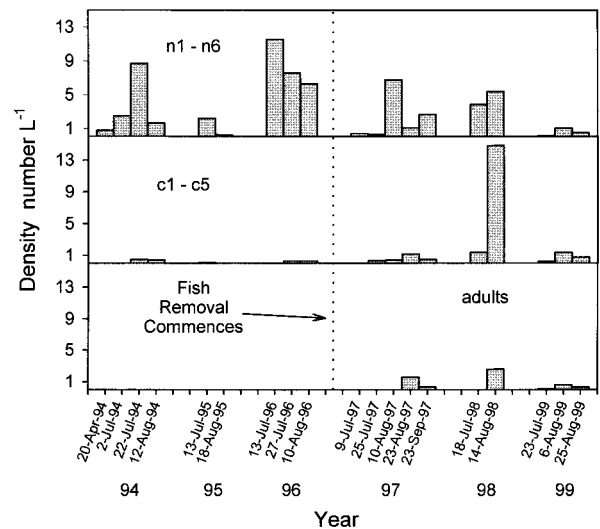


Figure 7. The densities of nauplius, copepodid, and adult *Diacyclops bicuspidatus*, 1994–99. The elimination of fish was quickly followed by increased abundance of copepodids and adult animals, suggesting that brook trout predation was responsible for the low copepodid and adult densities prior to 1997.

mud samples that we sieved in the 1990s. *Daphnia* densities fell in 1999.

In the 1990s, *Polyarthra* and *Keratella* were the most abundant genera of rotifers, together compris-

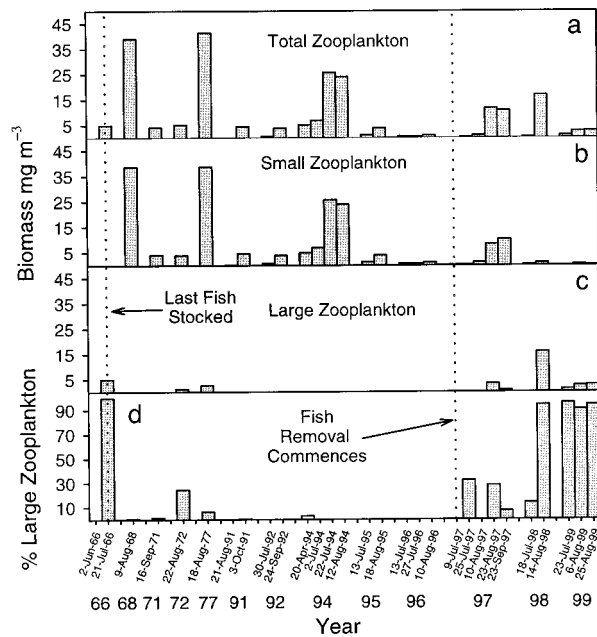


Figure 8. The biomass of zooplankton in Bighorn Lake, 1966–99; a total biomass; b biomass of small zooplankton, consisting of rotifers and nauplii; c biomass of large zooplankton, including copepodids and adults of copepod species, plus *Daphnia*; d percent of total biomass comprised of large zooplankton.

ing more than 95% of rotifer biomass. Total rotifer density was variable (Figure 6), but it was highest in the warm summers of 1994 and 1997. Overall, the total biomass of zooplankton changed little after fish removal and remained within the range observed when fish were present. There was, however, a dramatic increase in average size as a result of the reappearance of *Daphnia* and the copepodids and adults of cyclopoid copepods.

No *H. arcticus* were captured following the commencement of fish removal, and no viable *H. arcticus* resting eggs were found in the pair of sediment cores or the bulk sediment samples examined.

Changes in the Phytoplankton Community following Fish Removal

Although the shift in the average size of zooplankton was as expected from trophic cascading theory (Carpenter and others 1985), there was no detectable response by total phytoplankton populations. Total phytoplankton biomass and chlorophyll in 1997–99 remained within or exceeded the range observed in the 5 years before fish removal (Figure 9). Although plankton biomass was low in 1999, this observation was consistent with the observed correlation between annual maximum phytoplank-

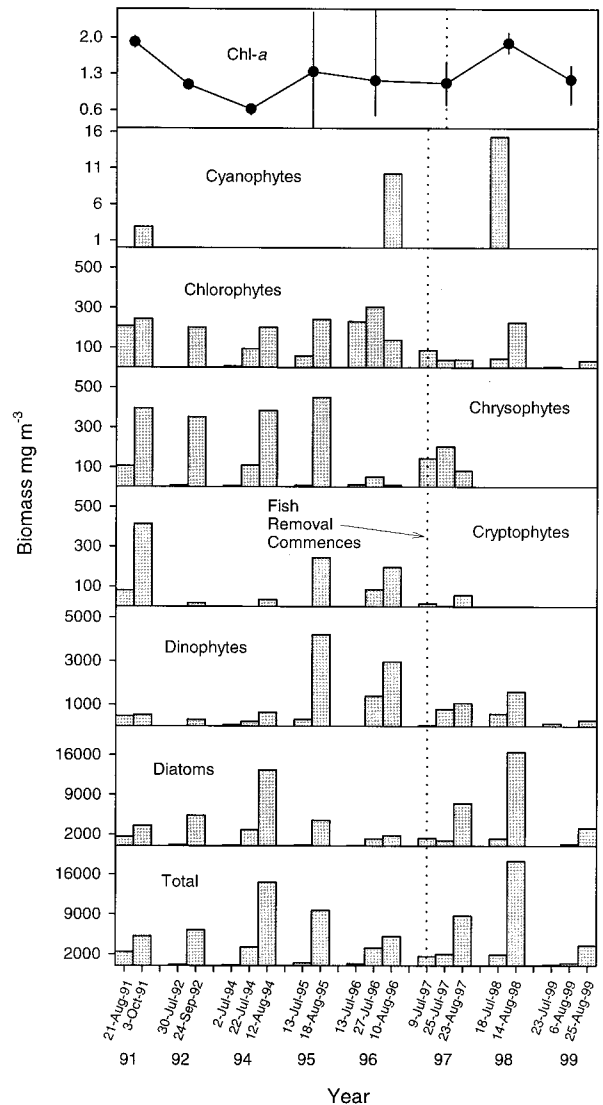


Figure 9. Phytoplankton biomass and chlorophyll *a* in Bighorn Lake in the 1990s. Annual ranges are shown for chlorophyll *a*. Ranges are less than plot symbol size in 1991 and 1992. Phytoplankton and chlorophyll *a* were not quantitatively sampled prior to 1991.

ton biomass and maximum summer surface water temperature ($r^2 = 0.72$; $P < 0.03$).

Diatoms (mostly *Fragilaria* sp.) and Dinophyceae (primarily *Gymnodinium* sp.), dominated the plankton community of Bighorn Lake throughout the 1990s, comprising greater than 75% of the biomass of the algal flora (Figure 9). The most significant food web effect of fish removal on phytoplankton may be the loss of chrysophytes (*Dinobryon* and *Mallomonas* sp.) and cryptophytes (*Rhodomonas* and *Katablepharis* sp.), which disappeared following the commencement of fish removal.

Phytoplankton species less than 25 μm in length

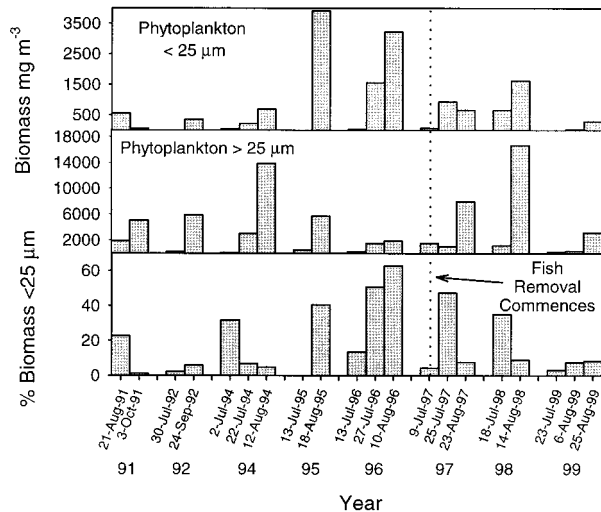


Figure 10. The biomass of small (<25 μm) and large (>25 μm) algae and the percent of total algal biomass represented by small species in the 1990s.

declined from 40%–60% to less than 10% of the phytoplankton (Figure 10) following fish removal. Small cells were also rare in the early 1990s when no *Daphnia* were present.

Nutrient Concentrations

Average annual total phosphorus concentrations in the lake increased slowly from 3 to 9 $\mu\text{g L}^{-1}$ from 1992 to 1998, then declined slightly in 1999 (Figure 11). Total nitrogen measurements were only begun in 1994, and their trend closely followed that of phosphorus, increasing from about 130 to 185 $\mu\text{g L}^{-1}$. There was no visible effect of fish removal on either nutrient.

DISCUSSION

Fish Population

Overall, the history of the introduced brook trout population in Bighorn Lake was remarkably similar to that of the same species introduced into Bunny Lake, California (Reimers 1979), a similarly cold and oligotrophic high alpine lake in the Sierra Nevada of California. Slow growth rates, among the lowest reported for Banff National Park (Mayhood and Anderson 1976) and elsewhere (Carlander 1969), poor condition, great age, and long delays prior to successful spawning, at least 14 years in Bighorn and 16 years in Bunny Lake, were common to both introduced trout populations.

Rapid improvement in the condition of most survivors following the start of the fish removal pro-

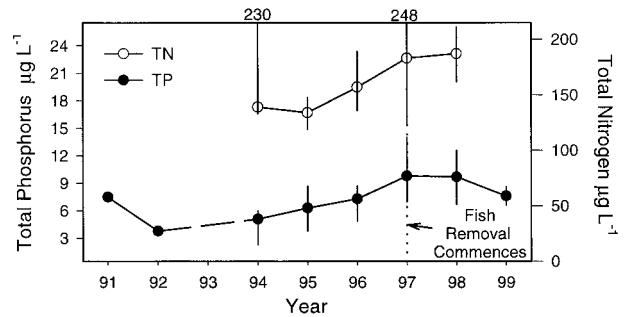


Figure 11. The concentrations of total phosphorus and total nitrogen in Bighorn Lake in the 1990s. Values are annual averages for the ice-free season with annual ranges. Sampling frequency varied between two and five times per year.

gram leads us to suggest that food limitation was primarily responsible for the slow growth rates and emaciated condition of many of the larger trout. Severe emaciation of unexploited salmonids in alpine systems has been reported elsewhere (Hofer and Medgysey 1997). Exploitation similarly led to an increase in the mean weight of stunted populations of brook trout (Donald and Alger 1989) elsewhere in the mountain parks. High elevation and cold water temperatures were considered of lesser importance in explaining the weight of brook trout in Canadian mountain lakes than the abundance of large prey species such as *Gammarus* (Donald and others 1980).

The strongly bimodal size distribution of the population (Figure 3) was similar to that of unexploited populations of arctic salmonids (Power 1978; Johnson 1976). The steep right-hand limb of the distribution curve is suggestive of a high rate of mortality as length increases, which is probably related to the increasingly emaciated condition of larger trout (Figure 4).

Zooplankton Populations

In general, the changes in the plankton community of Bighorn Lake following fish stocking and removal were similar to those observed in Snowflake Lake (McNaught and others 1999) and Pipit Lake (Anderson and Donald 1978), which were also stocked with nonnative salmonids. The loss of *H. arcticus* was expected because it cannot coexist with fish in small alpine and subalpine lakes (Donald and others 1994). The stocking of fish probably also eliminated *Daphnia*, since the genus disappeared from both Snowflake and Pipit lakes following fish stocking. Similar rapid loss of *Daphnia* and/or *Diaptomus* following fish introduction has been reported

elsewhere (Gliwicz 1967; Reimers 1979; Pechlaner 1984).

The apparent year-long delay in the reappearance of *Daphnia* may partly be an artifact of our sampling frequency ($n = 5$ in 1997 and $n = 3$ in 1998). Arnott and others (1998) found that low sampling frequency led to an underestimation of the occurrence of rare species. In our favor, Bighorn Lake is an order of magnitude smaller than the lakes studied by Arnott and others (1998). Moreover, our plankton net was larger (30-cm-diameter compared to 12.5-cm-diameter); thus, the relative volume we sampled was much larger and should have provided for better detection of recovering species. Also, the few fish that remained in the lake in 1997 may have continued to suppress the recovery of *Daphnia*, which is more vulnerable to trout predation than copepods. Furthermore, the hatching of resting eggs is strongly seasonal and generally early in the year, so that the mid-July 1997 onset of fish removal may have occurred following the hatching of most resting eggs that year. In 1998, by which time most fish had been removed, there would have been little impediment to *Daphnia* recovery. Slow response by large *Daphnia* species following food web manipulations in eutrophied lakes has been observed elsewhere (Elser and others 2000).

The strong effects of fish removal on adult *Diacyclops* abundance were not expected. Although few *Diacyclops* survived to reach adult stages prior to fish removal, the absence of this species in fish stomachs from Bighorn Lake and elsewhere in the region and the proliferation of *Diacyclops* populations in other nearby lakes with fish had led to speculation that *Diacyclops* was not an important diet item for trout in most park lakes. Clearly, however, heavy predation commenced once individuals reached the first copepodid stage, reducing their abundance to trace levels. Predation by fish on this small species (1.2 mm adult length) probably reflects the harsh conditions faced by the trout in Bighorn Lake. Stomach contents may not accurately reflect the importance of copepods in the diet of fish. In nearby Bow Lake, Campbell and others (2000) found that stable carbon isotopes indicated that zooplankton were an important component of the diet of lake trout, although they were rarely found in stomach contents. The decline in nauplii abundance following fish removal probably reflected a combination of increased cannibalism by adults on nauplii (McQueen 1969) and declining egg counts as population levels increased.

The absence of *Gammarus* from Bighorn Lake is

perplexing. It is present in all other permanent water bodies in the vicinity that do not freeze to the bottom in winter. *Gammarus* were reduced below the level of detection by introduced trout in nearby Snowflake and Pipit lakes (Anderson and Donald 1978; McNaught and others 1999) and were not recovered in trout stomachs for more than a decade after stocking. Gammarids have been eliminated by stocked salmonids in European lakes (Pechlaner 1984; Amman 1980). It is possible that *Gammarus* was eliminated by brook trout in Bighorn Lake, but this cannot be demonstrated conclusively because *Gammarus* does not leave subfossil remains in lake sediments. Alternately, the subterranean nature of the outflow may have prevented colonization by *Gammarus*. There is insufficient information to assess whether this species should be introduced to Bighorn Lake as part of our food web restoration.

H. arcticus has not returned to Bighorn Lake. Because there are at most a few viable *H. arcticus* resting eggs in the sediment and the species has not been collected in Bighorn Lake in 32 years, it has most likely been extirpated. The natural recovery of this species is uncertain, in part because *Diacyclops* has become well established. *Diacyclops* preys on calanoid copepod nauplii (Anderson 1970), and at high densities it may prevent recovery when calanoid nauplii are rare. *Hesperodiaptomus* is also known to have poor dispersal, so that its reintroduction by natural means—via transfer by waterbirds, for example—is unlikely at least in the short term. There was no recovery of *Hesperodiaptomus* in nearby Snowflake Lake until the lake was restocked with 660,000 animals (McNaught and others 1999). In Pipit Lake, where recovery of this species occurred naturally (Parker and others 1996) following loss of the stocked fish population, there remained a large pool of resting eggs in lake sediments and fish were present for only 15 years.

We plan to restock *Hesperodiaptomus* into Bighorn Lake in 2001 in an attempt to complete the restoration of the original food web of this lake. Based on results from Snowflake Lake, we predict that predation by *Hesperodiaptomus* on cyclopoid copepod nauplii and rotifers will cause further restructuring of the zooplankton and phytoplankton communities, but it will have little effect on phytoplankton biomass.

Trophic Cascade

Despite the appearance of larger zooplankton, there was little evidence for a trophic cascade in the phytoplankton of Bighorn Lake following removal of

the stocked fish population. Although adult copepod densities have increased and *Daphnia* has reappeared, to date there has been no accompanying decrease in total phytoplankton biomass or chlorophyll *a* concentration that can be attributed to fish removal. The presence or absence of fish populations has long been known to influence the size structure and abundance of zooplankton populations (Hrbacek 1962; Brooks and Dodson 1965), but our results are contrary to other studies that correlated reduced planktivorous fish abundance with decreases in chlorophyll *a* concentrations (Vanni and others 1990; Helminen and Sarvala 1997).

Some fine-scale adjustments in phytoplankton taxa have occurred—most notably, the loss of chrysophytes and cryptophytes. These taxa were lost in the same year, but prior to the reappearance of *Daphnia*, suggesting that grazing by cladocerans was not entirely responsible for their decline. It is tempting to attribute the recent decline in the relative abundance of small phytoplankton to the recovery of *Daphnia*. However, similarly low proportions of small phytoplankton species were observed several years prior to fish removal, when *Daphnia* were absent; thus, changes in proportions of large to small phytoplankton cannot be unambiguously attributed to food web effects following trout removal.

There are several possible reasons for the weak trophic cascade response in Bighorn Lake. First, Bighorn Lake is oligotrophic. Enriched lakes are thought to exhibit stronger trophic cascades than those with low nutrient concentrations (Pace and others 1999). Second, the molar carbon–phosphorus (C:P) ratios of seston generally were above 350:1—higher than the range where a strong response by *Daphnia* was expected (Elser and others 1998). Although large *Daphnia* reappeared, their densities remained low compared to warmer, more nutrient rich systems (Elser and others 2000; Schindler and Comita 1972). Further, coincident with the increase in *Daphnia*, the abundance of herbivorous rotifers and *Diacyclops* nauplii fell, thus mitigating in part the increase in *Daphnia* density. Third, the dominant *Diacyclops* is an omnivore. Nauplii are herbivorous, but the diet shifts to include small zooplankton as the animals grow. Omnivores may preclude the potential for strong cascades by feeding at multiple trophic levels (Pace and others 1999). Last, perhaps cold water temperatures imposed physiological constraints on the plankton in Bighorn Lake and prevented a strong response from occurring. Meta-analysis of 54 freshwater trophic cascades in ponds and mesocosms (Brett and Goldman 1996) suggested that although cascade responses were

widespread, a majority of studied cases had weak cascades.

Because our postremoval results only span 3 years to date, they must be considered preliminary. Nearby Snowflake Lake required about 7 years for plankton populations to adjust following both initial fish stocking and eventual restocking of *H. arcticus* (McNaught and others 1999; Anderson 1972). In eutrophication and acidification experiments at the experimental lakes area (ELA), upper trophic levels similarly required 6–8 years to recover following removal of a stress (Schindler 1998). Bighorn Lake is colder than Snowflake Lake and ELA lakes and its planktonic community may respond even more slowly. For example, it took more than 10 years for *Diacyclops* to become permanently established as the dominant zooplankton in the lake following fish introduction. Several more years of monitoring are probably required before definitive conclusions about the presence/absence or strength of any trophic cascade and the final state of recovery can be drawn.

Gill Netting as a Management Tool

Given the effort employed to eliminate trout from Bighorn Lake and other small lakes (Knapp and Matthews 1998), we speculate that removal of non-native trout with gill nets alone may be impractical for large lakes. However, we believe that the 3.0-ha size limit suggested by Knapp and Matthews may be too conservative, particularly if more and larger commercial-weight gill nets are used. Intensive commercial fishing with gill nets eliminated lake trout from Lesser Slave (1160 km²) and Touchwood lakes (29 km²) in Alberta earlier in the 20th century, although massive effort applied over several decades was required in both cases (Mitchell and Prepas 1990). We believe that shallower lakes (less than 10 m deep) of up to 10 ha should be amenable to gill net eradication of nonnative fishes over reasonably short periods, without resorting to rotenone or other poisons.

We propose that where good access is available, the intermittent deployment of gill nets, as practiced by Knapp and Matthews (1998), should be adopted to minimize gill net avoidance by salmonids in clear lakes. We have directly observed that salmonids started to avoid gill nets within a few hours after nets were set in clear alpine lakes. Thus, a series of net sets conducted days or weeks apart may remove fish more quickly than our continuous netting program.

If the restoration of substantially larger or deeper lakes is proposed, alternate methods of fish removal including, but not limited to, electrofishing, trap

netting on spawning grounds, disturbing spawning habitat, creating under-ice anoxia by the addition of nutrients (see Brunskill and others 1980 for a possible method), lake drawdown, and/or the application of piscicides should be given consideration in addition to, or as a replacement for gill nets. These alternate methods will be controversial, but they may be more practical for removing fish from certain lakes. Canadian national parks managers have previously used chemical agents in their attempt to eradicate fish from dozens of lakes.

The Bighorn Lake restoration work does not address several important issues associated with the removal of nonnative fish from lakes. For example, for lakes with habitable inlets and outlets (Bighorn Lake has neither), the removal of nonnative fish from inflowing waters and the installation of barriers to prevent their reinvasion from outflow creeks will be required. Also, selective removal of introduced fish from lakes that have one or more populations of native fish may be desirable. Further, nontarget species such as Harlequin Ducks (*Histrionicus histrionicus*) and even bears might be adversely affected by restoration activities on some water bodies. Diving birds may become entangled in gill nets and drown, and bears may lose a food resource if spawning runs of fish into shallow creeks are eliminated. Last, because organisms such as *Gammarus* may be extirpated but leave no trace of their prior existence, it will be difficult to ascertain that full food web restoration has been achieved for the many lakes that lack prestocking records of their original invertebrate communities.

Further experimental restoration work is needed to better define the practical limits of gill netting as a management tool and to provide alternate solutions for larger or otherwise "difficult" stocked lakes. A better understanding of our few remaining pristine ecosystems is also needed if we wish to undo a century of past fisheries management practices and return a small suite of lakes to their natural state.

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REFERENCES

- Amman E. 1980. Limnologische und fischereiliche Untersuchungen am Sünser See. *Österreichs Fischerei* 33:205–15.
- Anderson RS. 1974. Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains. *J Fish Res Bd Can* 31:855–69.
- Anderson RS. 1970. Predator-prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. *Can J Zool* 48:1229–40.
- Anderson RS. 1980. Relationships between trout and invertebrate species as predators and the structure of the crustacean and rotiferan plankton in mountain lakes. p 635–641. In: Kerfoot WC, editor. *Evolution and Ecology of Zooplankton Communities*. p 635–41.
- Anderson RS. 1977. Rotifer populations in mountain lakes relative fish and species of copepods present. *Arch Hydrobiol Ergeb Limnol* 8:130–4.
- Anderson RS. 1972. Zooplankton composition and change in an alpine lake. *Verh Int Ver Limnol* 18:264–8.
- Anderson RS, Donald DB. 1978. Limnological survey of some small lakes in the vicinity of the Cascade Trail, Banff National Park. Canadian Wildlife Service Manuscript Report. 162 p.
- Arnott SE, Magnuson JE, Yan ND. 1998. Crustacean zooplankton species richness: single- and multiple-year estimates. *Can J Fish Aquat Sci* 55:1573–82.
- Bagenal TB, Tesch FW. 1978. Age and growth, pp 101–136. In: Bagenal TB, editor. *Methods for assessment of fish production in freshwaters*. 3rd ed. Oxford: Blackwell Scientific Publications. 365 p.
- Banff–Bow Valley Study. 1996. Banff–Bow Valley: at the crossroads. Summary report of the Banff–Bow Valley Task Force (Page R, Bayley SE, Cook JD, Green JE, Ritchie JRB). Prepared for the Honorable Sheila Copps, Minister of Canadian Heritage, Ottawa, ON. Available from Superintendent, Banff National Park, Box 900, Banff, Alberta, T0L 0C0.
- Beamish RJ, McFarlane GA. 1983. The forgotten requirement for age validation in fisheries biology. *Trans Am Fish Soc* 112: 735–43.
- Brett MT, Goldman CR. 1996. A meta-analysis of the freshwater trophic cascade. *Proc Natl Acad Sci USA* 93:7723–6.
- Brooks JL, Dodson SI. 1965. Predation, body size and composition of the plankton. *Science* 150:28–35.
- Brunskill GJ, Graham BW, Rudd JWM. 1980. Experimental studies on the effect of arsenic on microbial degradation of organic matter and algal growth. *J Fish Res Bd Can* 28:277–94.
- Campbell LM, Schindler DW, Muir DCG, Donald DB, Kidd KA. 2000. Organochlorine transfer in the food web of subalpine Bow Lake, Banff National Park. *Can J Fish Aquat Sci* 57:1258–69.
- Carlander KD. 1969. *Handbook of freshwater fishery biology*. Volume 1. 3rd ed. Ames (IA): Iowa State University Press. 752 p.
- Carpenter SR, Kitchell JF, Hodgson JR. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–9.
- Christensen JM. 1964. Burning of otoliths, a technique for age determination of soles and other fish. *J Cons Perm Int Explor Mer* 29:73–81.
- DeVries DR, Stein RA. 1991. Comparison of three zooplankton samplers: a taxon-specific assessment. *J Plankton Res* 3:53–9.
- Donald DB. 1987. Assessment of the outcome of eight decades of

- trout stocking in the Mountain National Parks, Canada. *N Amer J Fish Manage* 7:545–53.
- Donald DB, Alger JA. 1989. Evaluation of exploitation as a means of improving growth in a stunted population of brook trout. *N Am J Fish Manage* 9:177–83.
- Donald DB, Anderson RS, Mayhood DW. 1994. Coexistence of fish and large *Hesperodiaptomus* species (Crustacea: Calanoida) in subalpine and alpine lakes. *Can J Zool* 72:259–61.
- Donald DB, Anderson RS, Mayhood, DW. 1980. Correlations between brook trout growth and environmental variables for mountain lakes in Alberta. *Trans Am Fish Soc* 190:603–10.
- Elser JJ, Chrzanowski TH, Sterner RW, Mills KH. 1998. Stoichiometric constraints on food web dynamics: a whole lake experiment on the Canadian Shield. *Ecosystems* 1:120–36.
- Elser JJ, Sterner RW, Galford AE, Chrzanowski TH, Findlay DL, Mills KH, Paterson MJ, Stainton MP, Schindler DW. 2000. Pelagic C:N:P stoichiometry in a eutrophied lake responses to a whole-lake food-web manipulation. *Ecosystems* 3:293–307.
- Gliwicz ZM. 1967. Zooplankton and temperature–oxygen conditions of two alpine lakes of the Tatra Mountains. *Pol Arch Hydrobiol* 14:53–72.
- Haney JF, Hall DJ. 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera. *Limnol Oceanogr* 18:331–3.
- Helminen H, Sarvala J. 1997. Responses of Lake Pjhaejaervi (southwestern Finland) to variable recruitment of the major planktivorous fish, vendace (*Coregonus albula*). *Can J Fish Aquat Sci* 54:32–40.
- Hofer R, Medgysey N. 1997. Growth, reproduction and feeding of dwarf arctic char, *Salvelinus alpinus*, from an alpine high mountain lake. *Arch Hydrobiol* 138:509–24.
- Holland WD, Coen GM. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol 1: Summary. Alberta Inst of Pedology publ no. M-83-2.
- Hrbacek J. 1962. Species composition and the amount of zooplankton in relation to the fish stock. CSAV. *Rad Mat Prir Ved* 72:116.
- Johnson L. 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, arctic char, *S. alpinus* and associated species in unexploited lakes of the Canadian Northwest Territories. *J Fish Res Bd Can* 33:2459–88.
- Knapp RA, Matthews KR. 1998. Eradication of nonnative fish by gill netting from a small mountain lake in California. *Restor Ecol* 7:207–13.
- McNaught AS, Schindler DW, Parker BR, Paul AJ, Anderson RS, Donald DB, Agbeti M. 1999. Restoration of the food web of an alpine lake following fish stocking. *Limnol Oceanogr* 44:127–36.
- McQueen DJ. 1969. Reduction of zooplankton standing stocks by predaceous *Cyclops bicuspidatus thomasi* in Marion Lake, British Columbia. *J Fish Res Bd Can* 26:1605–18.
- Mayhood DW, Anderson RS. 1976. Limnological survey of the Lake Louise Area, Banff National Park: part 2—the lakes. Canadian Wildlife Service Manuscript Report. 273 p.
- Mitchell P, Prepas E, editors. 1990. Atlas of Alberta lakes. Edmonton (Alberta): University of Alberta Press.
- Pace ML, Cole JJ, Carpenter SR, Kitchell JF. 1999. Trophic cascades revealed in diverse ecosystems. *TREE* 14:483–8.
- Parker BR, Wilhelm FM, Schindler DW. 1996. Recovery of *Hesperodiaptomus arcticus* populations from diapausing eggs following elimination by stocked salmonids. *Can J Zool* 74:1292–7.
- Paul AJ, Schindler DW. 1994. Regulation of rotifers by predatory calanoid copepods (subgenus *Hesperodiaptomus*) in lakes of the Canadian Rocky Mountains. *Can J Fish Aquat Sci* 51:2520–8.
- Pechlaner R. 1984. Historical evidence for the introduction of Arctic charr into high-mountain lakes of the Alps by man. In: Johnson L, Burns BL, editors. Biology of the Arctic charr. Proceedings of the International Symposium on Arctic Charr, Winnipeg, Manitoba, May 1981. Winnipeg. (MB): University of Manitoba Press. p 549–57.
- Power G. 1978. Fish population structure in arctic lakes. *J Fish Res Bd Can* 35:53–9.
- Rahel FJ. 1997. From Johnny Appleseed to Dr. Frankenstein: changing values and the legacy of fisheries management. *Fisheries* 22:8–9.
- Rawson DS. 1940. The eastern brook trout in the Maligne River system, Jasper National Park. *Trans Am Fish Soc* 70:221–35.
- Reimers N. 1979. A history of a stunted brook trout population in an alpine lake: a lifespan of 24 years. *Calif Fish Game* 65:196–215.
- Ritchie C. 2000. Non-natives can be better. *Real Fishing* 6:5.
- Rott E. 1981. Some results from phytoplankton counting inter-calibrations. *Schweiz Z Hydrol* 24:15–24.
- Schindler DW. 2000. Aquatic problems caused by human activities in Banff National Park. *Ambio* 29:401–7.
- Schindler DW. 1998. Replication versus realism: the need for ecosystem-scale experiments. *Ecosystems* 1:323–34.
- Schindler DW, Comita GW. 1972. The dependence of primary production upon physical and chemical factors in a small, senescing lake, including the effects of complete winter oxygen depletion. *Arch Hydrobiol* 69:413–51.
- Schindler DW, Pacas C. 1996. Cumulative effects of human activity on aquatic ecosystems in the Bow Valley of Banff National Park. In: Green J, Pacas C, Bayley S, Cornwell L, editors. Ecological outlooks project. A cumulative effects assessment and futures outlook of the Banff–Bow Valley. Prepared for the Banff–Bow Valley Study. Ottawa (Ontario): Department of Canadian Heritage.
- Vanni MJ, Luecke C, Kitchell JF, Magnuson JJ. 1990. Effects of planktivorous fish mass mortality on the plankton community of Lake Mendota, Wisconsin: implications for biomanipulation. *Hydrobiologia* 200–201:329–36.