Recovery of zooplankton assemblages in mountain lakes from the effects of introduced sport fish

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Abstract: Impacts of introduced fish on zooplankton assemblages of lakes may persist for decades following fish removal. We tested this hypothesis by comparing zooplankton assemblages from four categories of lakes located in western Canadian mountain parks including lakes without and with fish that differed in their fish community complexity and fish-stocking history. Zooplankton species richness was greatest in lakes with a complex community of fish and least in pristine fishless lakes. Canonical correspondence analysis showed that taxonomic shifts in zooplankton assemblages could be attributed to differences in fish-stocking history between the study lakes. In fishless lakes, larger copepods (*Eucyclops agilis*, *Diaptomus leptopus*), cladocerans (*Diaphanosoma*, large *Daphnia*), and chaoborids were abundant, whereas in the presence of fish, small crustaceans were more common and chaoborids were relatively rare. Once introduced trout were absent from lakes, recovery trajectories for zooplankton showed a general taxonomic shift towards assemblages characteristic of fishless lakes that had never been fish stocked. Based on separation between previously stocked fishless lakes and naturally fishless mountain lakes in ordination space (chi-squared distance), taxonomic recovery by zooplankton assemblages from the influence of introduced salmonids may require an average of 19 years.

Résumé : L'impact de l'introduction de poissons sur les communautés de zooplancton dans les lacs peuvent se faire sentir des dizaines d'années après le retrait des poissons. Une comparaison de communautés zooplanctoniques de quatre catégories de lacs dans les parcs montagneux de l'Ouest canadien, dont des lacs avec et sans poissons qui différaient dans la complexité de leur communauté de poissons et leur régime d'ensemencement, a permis d'éprouver cette hypothèse. La richesse spécifique du zooplancton est plus importante dans les lacs à communauté de poissons complexe et moindre dans les lacs non-pollués sans poissons. Une analyse canonique des correspondances indique que les changements taxonomiques dans les communautés zooplanctoniques peuvent être attribués à des différences dans le régime des ensemencements dans les lacs étudiés. Dans les grands lacs sans poissons, les copépodes (*Eucyclops agilis*, *Diaptomus leptopus*), les cladocères (*Diaphanosoma*, grandes espèces de *Daphnia*) et les chaoboridés sont abondants, alors qu'en présence de poissons, les petits crustacés sont plus nombreux et les chaoboridés sont relativement rares. Lorsque la truite introduite est retirée d'un lac, la trajectoire de récupération du zooplancton montre un glissement taxonomique général vers les communautés caractéristiques de lacs sans poissons qui n'ont jamais été ensemencés. D'après la séparation des lacs de montagne ensemencés et des lacs naturellement sans poissons dans l'espace réduit (distance «chi-squared»), le rétablissement taxonomique des communautés de zooplancton des effets d'une introduction de salmonidés peut requérir en moyenne une période de 19 années.

[Traduit par la Rédaction]

Introduction

Fish affect zooplankton assemblages in lakes by size-selective predation on chaoborids and large species of copepods and cladocerans (von Ende 1979; Mittelbach et al. 1995). As a result, fish predation often increases the diversity and abundance of small crustaceans. For example, zooplanktivory by introduced fish, such as rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*), and alewife (*Alosa pseudoharengus*) typically causes a size shift towards smaller invertebrate species in lakes (Brooks and Dodson 1965; Anderson 1972).

Zooplankton assemblages can show strong resilience to manipulations of complex fish communities in temperate lakes. For example, Mittelbach et al. (1995) concluded that the capacity of an altered zooplankton assemblage to return to the previous state was not restricted. Specifically, zooplankton species composition and mean body size were changed dramatically by increased planktivory by fish over a period of 7 years following the removal of the dominant predator, largemouth bass (*Micropterus salmoides*). However, the zooplankton community returned to its previous state within a few years following the reintroduction of bass. Similar compensatory dynamics within complex fish and zooplankton assemblages have been reported following the

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termination of trout stocking in a montane lake (Elser et al. 1995).

In contrast, zooplankton in pristine fishless alpine lakes can show low resilience following the extinction of introduced sport fish (Parker et al. 1996; McNaught et al. 1999). In this case, the omnivorous copepod *Hesperodiaptomus arcticus* had not recolonized an alpine lake in western Canada 26 years after trout were last stocked and 8 years after fish were last caught. Similarly, introduced trout have had profound adverse effects on zooplankton species diversity and composition in California alpine lakes (Bradford et al. 1998). Topographic barriers may impede dispersal and recovery by zooplankton species in mountain lakes compared with other lake regions where the zooplankton communities appear to be species-saturated (see Shurin et al. 2000). Therefore, we hypothesized that if introduced sport fish persist in lakes for decades before becoming extinct, their impact on zooplankton assemblages may in turn persist for decades. We tested this hypothesis by examining relationships between zooplankton and fish assemblages of fishless and fish-inhabited mountain lakes in their pristine condition and in lakes where sport fish had been stocked and subsequently become extinct.

Materials and methods

Study area

Most lakes in the national parks of the Rocky Mountains of Alberta and British Columbia, Canada, were devoid of fish at the beginning of the twentieth century (Donald 1987). Many of these lakes were subsequently stocked for several decades with salmonids. Exotic sport fish established self-recruiting populations in some lakes, while other populations were maintained by annual introductions of fingerlings. Beginning in the 1970s, sport-fish stocking was stopped for lakes that were either too remote, lacked suitable habitat conditions (e.g., winter anoxia), or supported populations of sport and other fish species maintained by natural recruitment. In 1988, sport-fish stocking was discontinued in Canadian national parks because it was deemed to be ecologically inappropriate.

Mid-summer zooplankton samples were collected over 29 years from 25 lakes situated along the Front Range of the Rocky Mountains in Jasper, Banff, and Kootenay national parks of Alberta and British Columbia, Canada. The lakes were all within the montane (1030–1500 m above sea level (ASL)) and lower subalpine (1501–1692 m ASL) ecozones (Table 1). The lakes included in this study were 0.4–32.3 ha in area with maximum depth ranging from 3 to 25 m, total dissolved solids from 39 to 278 mg·L^{-1}, and dissolved organic carbon from 1.2 to 18.5 mg·L^{-1}. Mid-summer water temperature was measured at each lake once each year from 1 to 20 August and was calculated as the mean temperature for the zone from 2 to 10 m deep or from 2 m to the maximum depth for lakes less than 10 m deep. Water samples for chemical analyses were collected near the centre of each lake at a depth of 0.4 or 5.0 m and were analyzed by methods given in Anonymous (1994).

Sampling of fish and zooplankton

Fish and zooplankton assemblages were determined for each lake in four categories: (*i*) five pristine "reference" lakes that had never been stocked or supported any fish; (*ii*) seven lakes with a relatively complex fish community of self-maintained indigenous and introduced fish (Catostomidae, Cyprinidae, and Salmonidae); (*iii*) eight lakes with only salmonid populations that were maintained by frequent stocking of hatchery-reared fish because these lakes did not have suitable spawning habitat for salmonids; and (*iv*) 13 fishless lakes that had not been stocked for 8 to 30 years and had no or few fish, including the previous eight lakes after they had not been stocked for 8 to 23 years (Table 1). In their pristine state, these 13 lakes would have been fishless (Donald 1987). Once stocking of salmonids was discontinued, 8 or more years of natural and fishing mortality reduced salmonid abundance substantially. For example, gill nets set in Kootenay Pond, Little Honeymoon, Kingfisher, Hibernia, Golden, and Marjorie lakes, 6 to 13 years after the last fish were stocked, did not yield fish of any species. However, a few old trout were caught in Upper Colfair and Dragon lakes 8 years after the last fish were stocked. Moreover, surveys of dozens of montane and subalpine lakes have shown that the maximum longevity for rainbow trout was 9 years, for cutthroat trout, 11 years, and for brook trout, 13 years (Donald et al. 1980; Donald and Alger 1986). Five of the 13 lakes (Colfair, Cutt, Dragon, Golden, and Little Honeymoon) were stocked infrequently, and their zooplankton assemblages may not have been measurably affected by the presence of fish. Zooplankton populations in these five lakes were sampled from 8 to 30 years after fish were last stocked. Only five pristine reference lakes were sampled because relatively deep, low-elevation fishless lakes (>3 m maximum depth) were rare in our study area. However, these and other lakes included in our study were representative of the small, low-elevation lakes in the region.

The status of the fish community was determined using gill nets for most of the study lakes in the 1930s (D.S. Rawson (deceased), Department of Biology, University of Saskatchewan, Saskatoon, Sask., unpublished data) and for all lakes with fish in the 1970s and early 1980s (Donald and Anderson 1982; Donald 1987). For the 13 stocked lakes, absence of natural recruitment for salmonids was determined in the 1970s and 1980s from the size and age of fish in the catches plus the presence in the catches of only hatchery-reared fish that were marked before being released into the lakes. Additional gill-net catches were made in 10 of the lakes in the 1990s to confirm fish population status. The national park stocking records were used to identify the five pristine reference lakes (no records of stocking or fish presence) and to determine the number of years stocked salmonids were present in other lakes. These records were maintained for each lake from the early 1900s to 1988 when salmonids were last stocked in the national parks. We assumed that each time fish were stocked in a lake, a significant population of trout would persist for 6 years.

Zooplankton were collected during mid-summer using Wisconsin-style plankton nets in the 1970s and early 1980s (aperture size 65 μm^2, diameter 25 cm, length 80 cm) and in the 1990s (aperture size 63 μm^2, diameter 30 cm, length 100 cm). Vertical hauls were made at a rate of 0.5 m·s^{-1} from the deepest part of the lake. Crustacean and chaoborid plankton were identified and counted, and densities per litre were determined according to the procedures outlined in Anderson (1974). The total number of zooplankton species (i.e., species richness) was considered as an index, rather than as an absolute measure, of zooplankton diversity in each lake because single-sample enumerations can seriously underestimate total species in lakes by up to 50% (Arnott et al. 1998).

Statistical analyses

A two-factor (fish presence × fish-stocking history) experimental design was used to test for the effects of fish and salmonid stocking on zooplankton species richness in the study lakes (Table 1). Four treatment combinations were made possible using two levels of fish-stocking history (salmonid stocked vs. pristine) and fish presence (fish present vs. fish absent). Specifically, five lakes (K13, K20, J392, J436, and J439) comprised the non-stocked, pristine fishless lake category. Seven lakes (Annette, Beauvert, Dog, Dorothy, Iris, Outram, and Vista) represented lakes with a relatively complex fish community. Eight lakes that were stocked frequently and sampled during active stocking in the 1970s consti-

Table 1. Morphometry, elevation, water chemistry, temperature, and fish populations of montane and lower subalpine lakes.

Lake	Latitude (north)	Longitude (west)	Morphometry Area, ha	 Maximum depth, m	Elevation, m	Chemistry TDS, mg·L^{-1}	 DOC, mg·L^{-1}	Mid-summer temperature, °C
No fish present and never stocked								
K13	50°53′	116°05′	2.5	6.0	1295	219	10.5	15.5
K20	50°50′	116°02′	0.6	3.8	1218	278	8.3	no data
J392	52°51′	118°03′	0.6	8.0	1117	212	14.9	10.0
J436	52°54′	118°19′	7.5	3.0	1455	135	18.5	no data
J439	52°55′	118°22′	7.1	3.0	1615	52	9.3	15.9
Complex community of Catostomidae, Cyprinidae, and Salmonidae								
Annette	52°54′	118°02″	28.6	23.0	1024	153	1.9	17.1
Beauvert	52°53′	118°03′	32.3	25.0	1030	135	1.2	12.4
Dog	50°48′	115°57′	15.1	4.7	1183	183	3.7	19.7
Dorothy	52°53′	118°14′	25.1	14.6	1336	145	6.8	13.1
Iris	52°52′	118°13′	5.1	13.2	1302	134	6.2	14.5
Outram	51°52′	116°48′	9.4	11.5	1460		3.3	17.8
Vista	51°14′	116°01′	6.6	6.5	1567	130	1.8	12.2
Salmonid populations maintained by introducing hatchery-reared fish								
Colfair (Upper)	52°44′	117°52′	2.9	7.5	1555	53	8.0	15.7
Copper	51°15′	155°55′	1.5	10.4	1434	86	10.5	17.1
Cutt	52°53′	118°20′	15.5	7.5	1455	62	5.9	14.4
Dragon	52°28′	117°40′	15.6	12.0	1341	100	3.0	18.2
Golden	52°53′	118°20′	13.4	10.3	1485	39	6.0	14.9
Hibernia	52°52′	118°08′	9.6	8.5	1198	158	9.9	16.9
Honeymoon (Little)	52°34′	117°41′	1.0	4.0	1310	146	9.0	19.7
Kingfisher	51°24′	116°10′	2.0	7.2	1539	113	10.7	16.0
Kootenay Pond	50°53′	116°02′	2.6	6.0	1213	234	5.4	16.1
Lost	51°28′	116°16′	0.4	5.5	1692	163	4.9	12.9
Marjorie	52°52′	118°08′	7.3	8.0	1143	179	9.0	16.7
Pilot	51°14′	115°49′	2.8	7.5	1408	202	8.2	15.6
Virl	52°52′	118°14′	3.5	6.0	1305	123	9.5	17.9

Note: TDS, total dissolved solids; DOC, dissolved organic carbon; —, stocking infrequent.

[a] LS, longnose sucker (*Catostomus catostomus*); LC, lake chub (*Couesius plumbeus*); BT, brook trout (*Salvelinus fontinalis*); WS, white sucker (*Catostomus commersoni*); MW, mountain whitefish (*Prosopium williamsoni*); RT, rainbow trout (*Oncorhynchus mykiss*); LT, lake trout (*Salvelinus namycush*); CT, cuttroat trout (*O. clarki*); BU, bull trout (*Salvelinus confluentus*).

[b] Assumes that fish were common for 6 years after each introduction of hatchery-reared fish.

tuted the salmonid-inhabited lake category, and these same eight lakes plus five other stocked lakes that were visited in the mid-1990s after salmonid stocking had been stopped were used to construct the manipulated, fishless lake category. However, the total number of samples was 14 because Kootenay Pond was sampled twice, 9 and 24 years after the last introduction of fingerlings. A 2-way ANOVA with multiple comparison (Bonferroni–Dunn) testing was performed to test for the significance of the response by zooplankton to the presence of fish and fish-stocking events. Data analysis was performed using StatView® version 5 (SAS Institute, Cary, N.C).

The zooplankton and fish taxonomic data were analyzed using canonical correspondence analysis (CCA). Species densities were $\log_{10}(x+1)$ transformed to reduce the influence of abundant taxa that otherwise dominate ordination analyses. Fish status (1, natural fishless reference; 2, complex fish community; 3, stocked with salmonids; and 4, fishless after salmonid stocking ceased) of each lake at the time of sampling was used as an environmental variable consisting of four categorical levels for the CCA. Environmental data, including fish status, lake area and maximum depth, total dissolved solids (TDS), dissolved organic carbon (DOC), and mid-summer temperature, were screened for insignificant variables by testing the significance of partial CCAs that were each performed using only one of the environmental variables (Vinebrooke and Graham 1997). Following the elimination of insignificant variables, a final CCA was performed and the significance of the ordination was determined using Monte Carlo permutation testing. Ordinations were performed using CANOCO version 3.12 (ter Braak 1991).

Simple regression analysis was performed to determine if taxonomic recovery by zooplankton assemblages from the effects of introduced sport fish could be predicted based on the number of years since a lake had last been stocked. The metric used to measure taxonomic recovery was chi-squared distance between CCA biplot coordinates for those eight salmonid-stocked lakes that were resampled 8–23 years after they had returned to a fishless state following the termination of salmonid stocking.

Results

Fish status of survey lakes

Salmonids were introduced into 13 lakes that were originally fishless by stocking one or more species including rainbow trout and brook trout (Table 1). Salmonids were present in these lakes continuously over periods of 6–51 years. The 13 lakes were sampled for zooplankton following the termination of fish stocking and the time-related reduction of their

Fish populations					
Indigenous or introduced[a]	Number of years fish abundant[b]	Mean stocking density, number·ha^{-1}	Maximum stocking density, number·ha^{-1}	Year last stocked	Year(s) plankton collected
					1996
					1996
					1997
					1995
					1996
LS,LC,BT					1994
LS,WS,MW,RT,BT					1994
LS,BT,RT					1981
LS,LC,RT					1978
LS,LC,RT					1994
LS,LC,LT,BT					1995
LS,BT,CT,BU					1994
RT	6	—	170	1971	1979
RT	35	930	2 330	1988	1973/96
RT	11	—	300	1986	1995
BT	18	—	170	1971	1979
RT	19	—	370	1986	1998
RT	51	740	1 560	1986	1970/94
BT	9	—	1 000	1966	1996
RT	45	600	5 000	1988	1973/96
BT,RT	24	560	1 115	1972	1972/81/96
BT	15	250	25 000	1972	1970/95
RT	51	1230	2 465	1986	1970/94
BT,RT	35	1240	1 785	1985	1970/96
RT	15	510	1 430	1986	1970/94

introduced fish populations (Table 1). The maximum number of fish introduced into these lakes for 1 year ranged from 170 to 25 000 fish·ha^{-1}. During the 1970s, zooplankton samples were collected from eight of these lakes when they were stocked annually at densities of 250–1240 fish·ha^{-1}.

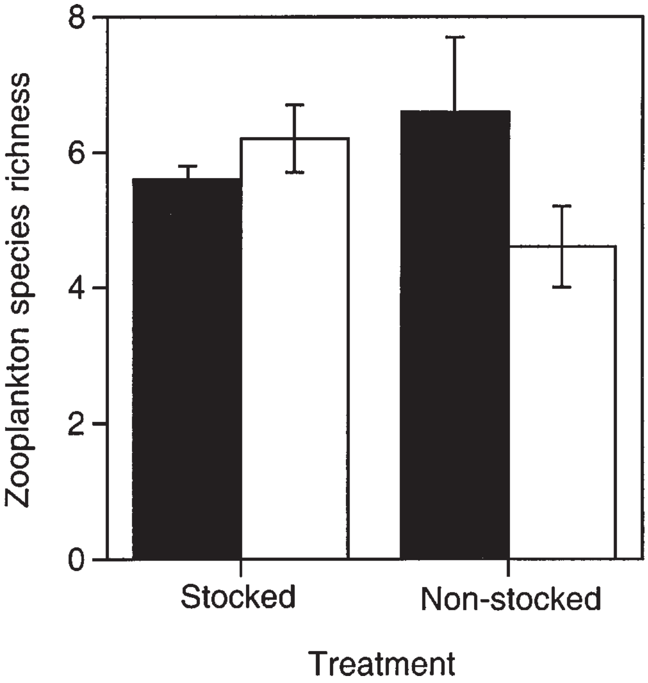
Zooplankton status

Zooplankton species richness was suppressed by salmonids in stocked lakes and, conversely, enhanced by the presence of indigenous fish species in other lakes ($F_{1,30}$ = 4.31, P = 0.04; Fig. 1). However, the mean number of copepod species was similar for lakes with and without fish (Table 2). Cladoceran species diversity was greater in lakes with a complex fish assemblage (mean 4.3 species, standard deviation (SD) = ±2.56, N = 7) compared with all fishless lakes (mean 2.4 species, SD = ±1.20, N = 18, Student's t test = 2.57, $P < 0.05$) and was intermediate for lakes with stocked salmonid populations (mean 3.3 species, N = 8). Cladoceran species diversity was similar for the two groups of lakes that did not have fish (range for mean 2.2 to 2.5 species). Chaoborid species diversity was less in lakes with a complex fish assemblage (mean 0.29 species/lake) compared with all fishless lakes (mean 1.4 species/lake, t = 3.34, $p < 0.05$). Common species were not restricted to lakes either with or without fish, although *Daphnia rosea* was more common in lakes with fish compared with all fishless lakes (10 of 15 and 1 of 19 samples, respectively, z test of proportions = 3.81, $p < 0.05$). This pattern was similar for *Bosmina longirostris* (8 of 15 samples from lakes with fish and 1 of 19 samples from lakes without fish, z = 3.16) and for *Ceriodaphnia* (7 of 15 and 1 of 19, respectively, z = 2.84).

The five "reference" lakes, which had never been stocked and did not support indigenous fish species, had high abundances of *Diaptomus leptopus*, *Chaoborus americanus*, and large *Daphnia* (Table 3). The dominant cladocerns were large *D. pulex* or *pulicaria* or *Diaphanosoma leuchtenbergianum*. The mean number of copepod and cladoceran species was 2.2 for both of these crustacean groups.

Zooplankton community composition was more diverse and variable across the seven lakes that contained complex fish assemblages (Table 2). *Diaptomus leptopus* was present in three of the seven lakes with a complex fish assemblage of indigenous and introduced species. However, in contrast to pristine fishless lakes, the dominant copepods were

Fig. 1. Effects of sport-fish stocking and fish status (fish present, solid bars; fish absent, open bars) on zooplankton species richness in the surveyed mountain lakes. Error bars represent ±1 standard error.



cyclopoids (*Diacyclops thomasi*, *Orthocyclops modestus*, or *Macrocyclops albidus*) (Table 2). The dominant cladoceran was large *Daphnia*, *Ceriodaphnia*, *Bosmina longirostris*, or *Daphnia rosea*. Chaoborids (*C. flavicans*) were found in only two of the seven lakes. The mean number of copepod and cladoceran species in these lakes was 2.7 and 4.3, respectively.

Stocked lakes had an average of 5.6 crustacean zooplankton taxa. *Diaptomus leptopus* was present in five of the eight lakes and was the dominant copepod in three lakes. In the remaining lakes, one of four other copepod species was dominant (Table 2). The dominant cladoceran taxon was a large *Daphnia* species (25%), *Ceriodaphnia*, *Bosmina longirostris*, or *Daphnia rosea*.

Eight to 12 years after salmonid stocking ceased, *D. leptopus* was present in 9 of 11 fishless lakes and was the dominant copepod in five lakes or 46% (Table 2). *Acanthodiaptomus denticornis* or *Acanthocyclops vernalis* was dominant in the other six lakes. The dominant cladoceran taxa in all of these lakes were either large *Daphnia* or *Diaphanosoma*. Chaoborids were present in all 11 lakes.

From 23 to 30 years after stocking ceased, *D. leptopus* was present in all three lakes and was the dominant copepod in two of the three lakes (Honeymoon and Kootenay Pond), *Acanthodiaptomus denticornis* was the dominant copepod in the other lake (Lost Lake, Table 2). Only large *Daphnia* or *Diaphanosoma* were the dominant cladoceran in these lakes, and all supported one or more species of *Chaoborus* (maximum four species).

Ordination analysis

A CCA of invertebrate and fish data showed a significant (P = 0.01) relationship between zooplankton assemblages and the fish-stocking histories of the study lakes (Fig. 2). The first CCA axis captured 29% of the variance contained within the species data and contrasted large-bodied zooplankton (*Chaoborus* and large daphnids) in fishless lakes from small-bodied zooplankton (*Daphnia rosea* and *Diaptomus tyrelli*) in fish-inhabited lakes. The second CCA axis accounted for 5% of the variance in the species data and separated lakes that had been stocked with fish from those that contained few or no introduced fish. Fish-stocking history was retained as the only environmental variable following screening of the data for insignificant variables.

Zooplankton assemblages changed substantially in those mountain lakes where salmonid populations were no longer maintained by annual stocking (Fig. 2). Fish-stocked lakes that had returned to a fishless state showed a common shift in ordination space towards the right (Fig. 2). Several lakes (Kingfisher, Hibernia, Kootenay, Lost, and Virl) also shifted upwards in ordination space towards the naturally fishless lakes in the upper right quadrant of the plot (Fig. 2). Chi-squared distance between CCA coordinates for salmonid-stocked lakes resampled after they had returned to a fishless state (Fig. 2) was significantly related to the number of years since the last recorded stocking event ($\log_{10}$(chi-squared distance) = 0.033 years, $r^2 = 0.76$, $F_{1,8} = 25.49$, $p = 0.001$). As a result, total chi-squared distance between the centroids representing salmonid-stocked lakes, stocked lakes that had returned to a fishless state, and pristine fishless lakes (Fig. 2*a*) equates to 18.3 years.

Discussion

Introduction of salmonid sport fish probably altered zooplankton assemblages in montane and lower subalpine lakes that were originally fishless. These fish-induced changes were evident from a comparison of zooplankton assemblages of lakes with and without fish. The plankton species found in stocked lakes were often the same species present in lakes with indigenous fish communities. However, stocked lakes contained significantly fewer zooplankton species than lakes that contained indigenous fish species. A possible explanation for greater zooplankton diversity in the presence of a native fish community is that predation on zooplankton by a variety of fish species of different sizes and feeding strategies, rather than a single species, reduced niche breadth and dominance of individual plankton species, permitting rarer species to become established in the plankton community.

Differences in zooplankton assemblages of lakes with and without fish were likely related to size-selective predation by fish on chaoborid and large crustacean plankton (Brooks and Dodson 1965; Northcote 1988; Mittelbach et al. 1995). Certainly, small species of zooplankton such as *Diacyclops thomasi*, small *Daphnia* spp., *Ceriodaphnia* spp, and *Bosmina longirostris* are often important components of the zooplankton assemblage of lakes that have fish both in our study area and elsewhere (Brooks and Dodson 1965; Evans 1986; Elser et al. 1995). However, we could not confirm the absence of chaoborids in all fish-inhabited lakes owing to their migratory behaviour and our logistical constraints that did not allow us to conduct night sampling.

Table 2. The percentage of lakes with and without fish in which zooplankton taxa were numerically dominant.

Dominant species	Length[a] (mm)	No fish (never stocked) (n = 5)	Catostomidae, Cyprinidae, and Salmonidae (n = 7)	Salmonidae stocked annually (n = 8)	No fish, number of years since last stocked	
					8–12 years (n = 11)	23–30 years (n = 3)
Copepoda[b]						
Diaptomus leptopus	1.3–2.5	100	0	37	46	67
Acanthodiaptomus denticornis	1.5–1.9	0	0	25	18	33
Acanthocyclops vernalis	0.8–1.8	0	0	13	36	0
Diacyclops thomasi	0.8–1.3	0	57	13	0	0
Orthocyclops modestus	0.8–1.3	0	29	13	0	0
Macrocyclops albidus	0.8–2.5	0	14	0	0	0
Eucyclops agilis		0	0	0	0	0
Diaptomus tyrelli	1.1–1.9	0	0	0	0	0
Cladocera[b]						
Daphnia (large species)[c]	1.3–2.3	80	29	25	82	33
Diaphansoma spp.	0.8–1.2	20	0	0	18	67
Ceriodaphnia spp.	0.4–1.0	0	13	37	0	0
Bosmina longirostris	0.5	0	29	13	0	0
Daphnia rosea	1.2–1.6	0	29	25	0	0
Chydorus sphaericus	0.4–0.7	0	0	0	0	0
Polyphemus pediculus	1.4	0	0	0	0	0
Alona spp.	0.3–0.5	0	0	0	0	0
Chaoboridae						
Chaoborus	8.0–10.2	100	29	38	100	100
Mean number of copepods		2.2	2.7	2.3	2.8	2.5
Mean number of cladocerans		2.2	4.3	3.3	2.5	2.5
Mean number of chaoborids		1.2	0.3	0.4	1.4	1.7
Mean total number of taxa		5.6	7.3	6.0	6.7	6.7

[a] From Edmondson 1959, Anderson 1968, Anderson and Fabris 1970, and our unpublished data.

[b] Rare species, those present in <5 lakes not included (*Diaptomus sicilis*, *Alonella nana*, *Acroperus harpae*, *Leptodora kindtii*, and *Graptoleberis testudinaria*).

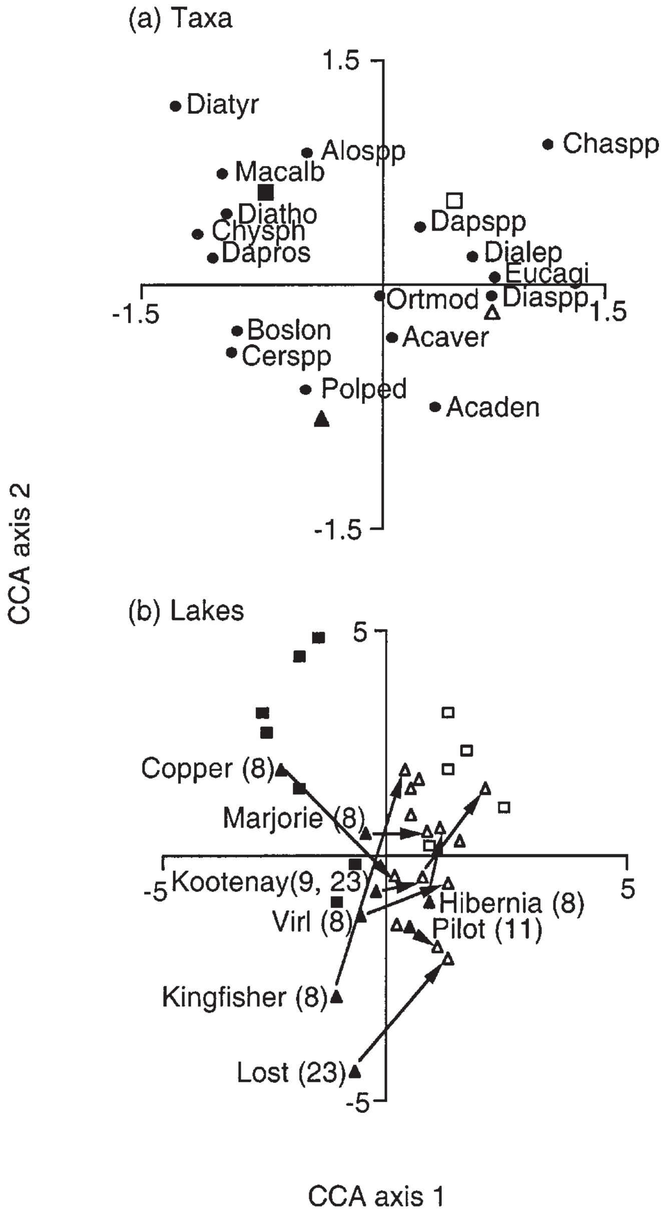
[c] *D. pulex*, *D. pulicaria*, and *D. schodeleri*.

Table 3. Mean abundances (individuals$\cdot$L^{-1}) of zooplankton taxa used in CCA with data arranged into four lake categories according to their fish status at the time of sampling.

Taxon	Fishless, never stocked (n = 5)	Catostomidae, Cyprinidae, and Salmonidae (n = 7)	Salmonid stocked annually (n = 8)	Fishless, previously stocked (n = 14)[a]
Diaptomus leptopus	4.52	0.32	8.31	6.34
Acanthodiaptomus denticornis	0	0	4.19	2.13
Diaptomus tyrelli	0	0.11	0	0
Acanthocyclops vernalis	0.04	1.52	14.93	6.11
Diacyclops thomasi	0.11	7.38	6.25	0.17
Orthocyclops modestus	0	1.60	6.35	2.09
Macrocyclops albidus	0	0.06	0.01	0.01
Eucyclops agilis	0	0.01	0	0.11
Daphnia (large species)	5.24	5.41	13.16	3.71
Diaphanosoma	2.35	0.08	0.91	3.01
Ceriodaphnia	0	4.59	12.51	0.01
Bosmina longirostris	0	2.93	7.55	0.02
Daphnia rosea	0	9.17	7.96	0.01
Chydorus sphaericus	0.01	0.17	0.06	0.01
Polyphemus pediculus	0.03	0.03	1.25	0.01
Alona	0	0.03	0.01	0.01
Chaoborus	0.49	0.02	0.04	0.16

[a] Kootenay Pond was sampled in 1981 and 1996, thus n = 14.

Fig. 2. Association of zooplankton species, mountain lakes, and fish-stocking histories of lakes based on a CCA of biological survey data from 25 mountain lakes sampled on 34 occasions. (*a*) Zooplankton taxa and centroids of the 4 categories of fish-stocking histories. Fish-stocking histories are denoted by the following symbols: non-stocked lakes with complex fish assemblage (■), salmonid-stocked lakes (▲), fishless lakes previously stocked with salmonids (△), and fishless lakes that were never stocked with fish (□). Taxa are represented by six-letter taxonomic codes (full Latin binomials appear in Table 3). (*b*) Lakes. Linear chi-squared distance vectors represent recovery trajectories for lakes that had been frequently stocked with salmonids (▲) and thereafter returned to a fishless state (△) once salmonid stocking was stopped. Numbers in brackets show the number of years since a lake had been stocked with salmonids for the trajectories.



Other whole-lake biomanipulation experiments suggest that time scales of one to two decades may be required before zooplankton assemblages become stable. In agreement, Wissel and Benndorf (1998) found that zooplankton species changed for 15 years in a lake when the fish predator was eliminated. Over this period, the dominant predator changed from a planktivorous fish (eliminated) to *Chaoborus flavicans* and then to *C. obscuripes*.

Certain dominant taxa in the fishless reference lakes were present in the stocked lakes and thus were not eliminated when salmonids were stocked. *Diaptomus leptopus* and large cladocerans were both present in 67% of the stocked lakes, with *D. leptopus* the dominant copepod in 37%. Because of the presence of these calanoid and cladoceran taxa, once fish stocking ceased the zooplankton assemblage would be positioned to recover to the type of assemblage found in a fishless environment. Our data also indicate that introduced salmonids did not reduce zooplankton species richness from that characteristic of pristine fishless lakes. A short-term study by Northcote et al. (1978) also indicated that salmonid introductions into fishless low-elevation lakes did not substantially impoverish crustacean plankton assemblages. Cutthroat trout and Dolly Varden (*Salvelinus malma*) were introduced into fishless lakes, and after 2 years, these salmonids had little effect on the number of crustacean species and their seasonal abundances. However, chaoborid abundance declined dramatically.

Rainbow trout and brook trout are not efficient planktivores, at least relative to some species such as alewife *Alosa* and lake herring *Coregonus*. These latter fish species have long slender gill rakers capable of filtering zooplankton from water. Trout are generalists, feeding on a variety of large benthic invertebrate species as well as plankton such as large individuals of *Daphnia*, *Diaptomus*, and *Eurycercus* (Neave and Bajkov 1929; Rawson and Elsey 1948; Donald and Anderson 1982). Inefficient planktivory by trout may have permitted medium- and large-sized plankters such as *D. leptopus* and *Daphnia* to persist in the presence of fish in some of the stocked montane lakes. Once trout were no longer stocked, predation on these larger species of plankton would decline and zooplankton populations could rapidly adjust to the fishless environment. When intense inter- and intra-annual sampling occurred, Arnott et al. (1998) found that individual lakes could support close to the total number of zooplankton species in a region, although most were very rare. Some of these rare species would be positioned to re-establish more abundant populations when fish were removed from the lakes in our study. Moreover, diapausing or resting eggs of crustaceans may have enabled some species to survive the impact of fish (Parker et al. 1996), especially in the five lakes that were stocked infrequently.

Recovery of extirpated species to the pristine condition would require recolonization. The rapid appearance of chaoborids after stocking ceased is not surprising. Adults of this family of flies (Diptera) could freely disperse to these lakes from nearby fishless ponds. Recolonization for crustacean species eliminated from stocked lakes, however, would be more problematic. The available mechanisms for colonization may be transport within the feathers and digestive systems of waterfowl and shorebirds (Proctor 1964; Daborn 1976) or perhaps, like amphipods, transport within the fur of semi-aquatic mammals (Peck 1975).

Large calanoid copepods (generally >2.5 mm) such as *Hesperodiaptomus arcticus* and *H. shoshone* were not found in the reference lakes, although one or both of these species are usually present in fishless subalpine and alpine lakes in our study area (Anderson 1974; Donald et al. 1994; McNaught et al. 1999). *Hesperodiaptomus* and *Chaoborus* rarely occur together in mountain lakes (Anderson and Raasveldt 1974; Anderson 1980). *Chaoborus* are most common in montane and lower subalpine ecozones (Lamontagne et al. 1994). Perhaps this disjunct distribution of *Hesperodiaptomus* and *Chaoborus* is due to competitive exclusion because both genera prey on a similar size range of zooplantkon species (Anderson 1970; Dodson 1970; Anderson and Raasveldt 1974). *Hesperodiaptomus* may have a competitive advantage in cold alpine lakes, *Chaoborus,* in relatively warm montane lakes.

Within three decades of the last year of fish stocking, all 13 fishless lakes supported chaoborids, and in six, the dominant species of cladocerans and copepods were characteristic of reference lakes. This indicates that zooplankton assemblages can recover to near their pristine condition within a few decades after fish stocking ceases and after five decades of exposure to introduced fish populations (e.g., Hibernia and Marjorie). For some lakes, however, many decades may be required for some species to re-establish their former presence and position in the zooplankton assemblage. Twenty-three years after fish were last stocked in Lost Lake, the dominant copepod in the zooplankton assemblage was *Acanthodiaptomus denticornis*, which was not present in reference lakes. For some lakes, resilience of zooplankton communities to recover from the effects of introduced sport fish may be limited. Absence of interlake connectedness or low regional zooplankton species diversity may have reduced opportunities for recolonization. Thus, the impact of long-term fish stocking on zooplankton assemblages in some lakes may be irreversible at least in terms of time scales that may be half a century or more. However, our samples from only five reference lakes may have under represented the diversity of zooplankton assemblages in pristine fishless lakes. It is possible that *Acanthodiaptomus denticornis*, a relatively small species, was the original dominant calanoid in 3 of the 13 fishless lakes, and that populations of this species were relatively unaffected by the introduction of salmonids. In at least one fishless pond near our study area that would never have been stocked with fish, *A. denticornis* was present at mean densities of 4.2 L^{-1} in June, indicating that this species can be abundant in fishless habitats (Donald 1971). In Norway, *A. denticornis* occurred in lakes with and without fish and was not identified as a species negatively affected by fish (Langeland 1982).

Although zooplankton are considered to be highly effective dispersers over vast distances (e.g., >100 km) of low-relief terrain (Shurin et al. 2000), physical dispersal barriers (e.g., mountain ranges) may impede movement of microcrustaceans between lakes in mountainous landscapes. As a consequence, biological recovery of mountain lakes from the influence of sport-fish introductions can be expected to be slow. For example, McNaught et al. (1999) reported that zooplankton in an alpine lake had not yet recovered from the effects of introduced trout after 10 years despite the aided reintroduction of an ecologically important keystone species (*Hesperodiaptomus arcticus*). In general, our findings suggest that zooplankton assemblages in mountain lakes require on average 19 years to recover once fish stocking has been stopped.

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