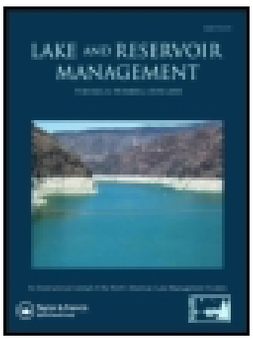

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Rotenone for exotic trout eradication: nontarget impacts on aquatic communities in a mountain lake

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ABSTRACT

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Rotenone is widely used in lake and reservoir management for the eradication of exotic fish. However, nontarget effects of rotenone on freshwater organisms such as zooplankton and macroinvertebrates are of concern because of the ecological importance of these organisms in aquatic food webs as a resource base for fish, especially when rotenone is applied to lakes prior to native fish reintroduction. The objective of our study was to determine the effects of rotenone on nontarget zooplankton and macroinvertebrate species assemblages in a headwater mountain lake where rotenone was applied to remove exotic brook trout (*Salvelinus fontinalis*; Banff, AB Canada). We found strong negative rotenone impacts on the community structure and density of crustacean zooplankton, and to a lesser extent on macroinvertebrates, lasting for at least 1 yr after the rotenone treatment. Our study offers 2 unique insights that differentiate from rotenone studies on other lakes: (1) the persistent and almost complete eradication of crustacean zooplankton in the following summers, 11 months after rotenone treatment, and (2) a considerable shift in the macroinvertebrate community composition, likely resulting from combined effects of both nontarget rotenone effects on taxon density and trophic interactions associated with the eradication of brook trout from the lake. We advocate that assisted recolonization in the restoration of aquatic food webs could play an important role in facilitating nontarget aquatic community recovery following lake rotenone treatment.

KEYWORDS

Aquatic community reestablishment; exotic fish removal; mountain lake; nontarget impacts; rotenone

Worldwide introductions of nonnative freshwater fish have caused biodiversity decline and local extinction of invertebrates and fish through predation, competition, and disease transmission (Gozlan et al. 2010). In mountain lakes, introductions of nonnative trout have caused species extirpations and substantial changes to aquatic communities (Donald 1987, Knapp et al. 2001, Parker et al. 2001, Pister 2001, Winder et al. 2001, Schindler and Parker 2002, Tiberti et al. 2014). Rotenone is an effective piscicide that is widely employed as a management tool to remove invasive fish species (Rytwinski et al. 2019); it blocks the reoxidation of nicotinamide adenine dinucleotide (NADH), which inhibits cellular respiration (Horgan et al. 1968). However, the nontarget effects of rotenone on freshwater organisms have been poorly documented, especially in vulnerable mountain lake ecosystems that were extensively stocked with nonnative trout historically.

Nontarget effects of rotenone on freshwater organisms such as zooplankton and macroinvertebrates are of concern because of the ecological role of these organisms in aquatic food webs as a resource base for vertebrate consumers such as fish (e.g., Sanchez-Hernandez et al. 2019), especially when rotenone treatment is done prior to

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native fish reintroduction. Crustacean zooplankton tend to be highly sensitive to rotenone (mountain lakes: Anderson 1970, McGann 2018, other types of lakes: Kiser et al. 1963, Beal and Anderson 1993, Peterson et al. 2011, Dalu et al. 2015). However, the reestablishment of crustacean zooplankton communities following rotenone treatment can be variable across aquatic ecosystems (1 month to 3 yr: Vinson et al. 2010), with longer recovery times in mountain lakes (Anderson 1970). Macroinvertebrate communities can also be negatively impacted by rotenone (Vinson et al. 2010), especially gill-respiring insect larvae (Booth et al. 2015). Macroinvertebrate communities tend to recover more rapidly than crustacean zooplankton, within the first year following rotenone application (Melaas et al. 2001, Blakely et al. 2005, Vinson et al. 2010), potentially because of a combination of smaller initial impact due to higher tolerance (Dalu et al. 2015) and higher dispersal capacity (Vinson et al. 2010). However, there are many treatment-related, environmental, and biological factors (e.g., concentration of the treatment, invertebrate's morphology and life history, presence of refugia in the lake, and distance from colonization source) that can affect zooplankton and macroinvertebrate community reestablishment following rotenone application to aquatic ecosystems (Vinson et al. 2010).

Mountain lake ecosystems may be particularly vulnerable to nontarget rotenone effects on the reestablishment of zooplankton and macroinvertebrates. The absence of upstream lakes and steep outflow gradients with natural barriers such as cascades or waterfalls may prevent recolonization from flowing water, while the geographical isolation as well as the short ice-free period may reduce probabilities of overland dispersal (Sarnelle and Knapp 2004, Li et al. 2019). Despite this, only a handful of studies have addressed the nontarget effects of rotenone on crustacean zooplankton in mountain lakes (Anderson 1970, McGann 2018), and there are presently no studies on nontarget effects of rotenone on macroinvertebrate communities in these ecosystems.

Our study objective was to determine the nontarget effects of rotenone on zooplankton and macroinvertebrates and their early reestablishment in a headwater mountain lake in the Canadian Rockies. Following the findings of Anderson (1970) for 2 other mountain lakes that are located at a similar latitude and ecozone as our study lake, we predicted a drastic and immediate decrease in the density of crustacean zooplankton taxa within 3 weeks following the rotenone treatment, and that this response would be followed by full reestablishment of cladoceran density, partial reestablishment of cyclopoid copepod density, and some presence of calanoid copepods in the following summer. For macroinvertebrates, we predicted a response similar to results reported by studies in the laboratory (Dalu et al. 2015), and in nonmountain lakes and mountain streams (Vinson et al. 2010): a small initial impact of rotenone treatment on community composition and density, especially on gill-breathing taxa (e.g., Trichoptera and Ephemeroptera), but full recovery of pre-rotenone community composition and structure within the first year because of high dispersal capacity of terrestrial adults and the presence of survivors remaining after rotenone.

Study site

The focus of our study was Hidden Lake, Banff National Park, Canada (Table 1), a high-elevation mountain lake in the Canadian Rockies that received rotenone treatment during the summers of 2018 and 2019 to eradicate nonnative brook trout (*Salvelinus fontinalis*) that were introduced and established in the 1970s, leading to the extirpation of a population of Westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). It is unknown whether the Westslope cutthroat trout was native or introduced in Hidden Lake, but a sustainable population was present since at least 1920. The ultimate conservation objective was to restock Hidden Lake with Westslope cutthroat trout. The rotenone treatment was done according to Montana State (USA) rotenone policy in the absence of a Canadian equivalent. This policy recommends 2 rotenone treatments for brook trout eradication because their spawning is not perfectly synchronous and because brook trout eggs in the gravel are not susceptible to rotenone (MFWP 2017). Moreover, several fish and traces of environmental DNA from brook trout were

Table 1. Characteristics and location of Hidden Lake, which received rotenone treatment in 2018 and 2019, and of other mountain lakes in Banff, Kootenay, and Yoho Canadian National Parks that were used for spatial comparisons of macroinvertebrate and zooplankton communities with Hidden Lake. Ecological lake history of fish stocking is from Messner et al. (2013), but for Hidden Lake it comes from S. Humphries (pers. comm.). Horizontal lines separate lakes by treatment (rotenone, reference with fish, and reference fishless), and lakes are listed from high to low elevation for each treatment.

Lake	Latitude	Longitude	Elevation (m)	Area (ha)	Maximum depth (m)	Ecological history of exotic brook trout stocking (pre 1975)
Hidden	51°29′3.95"N	116°6′26.03"W	2279	11.80	32.0	Historical Westslope cutthroat trout population since at least 1920, displaced by brook trout. The provenance of the brook trout is unclear.
Helen	51°21′57.74"N	116°10′42.49"W	2400	2.48	15.0	Historically fishless; stocked with brook trout
Temple	51°41′3.70"N	116°24′49.00"W	2207	3.25	12.0	Historically fishless; stocked with brook trout
Margaret	51°34′52.86"N	116°22′16.97"W	1808	18.00	22.0	Historical Westslope cutthroat trout population displaced by brook trout stocking
Ross	51°26′25.40"N	116°19′46.13"W	1735	6.61	21.5	Historically fishless; stocked with brook trout
Mud	51°26′25.40"N	116°10′34.61"W	1600	7.20	7.2	Stocked with brook trout; longnose dace present
McNair	51°24′23.18"N	116°9′27.61"W	1532	1.66	4.0	Stocked with brook trout
Olive	50°40′24.10"N	115°56′14.39"W	1470	1.66	3.5	Historical Westslope cutthroat trout population displaced by brook trout stocking
Cobb	50°39′40.28"N	115°52′41.41"W	1260	2.29	8.0	Stocked with brook trout
Dog	50°46′49.30"N	115°55′46.31"W	1185	11.50	4.7	Diverse fish assemblage; stocked with brook trout
Sentinel	51°20′2.40"N	116°13′14.88"W	2274	2.21	6.0	Never stocked, fishless
Annette	51°22′6.49"N	116°12′31.61"W	1898	4.98	14.5	Stocked with Westslope cutthroat and rainbow trout, Now fishless

detected between the 2 rotenone treatments in summer 2018 and 2019 (Derry A, unpubl. data).

Hidden Lake is relatively small (11.8 ha), situated at treeline at an elevation of 2279 m, with an outflow of approximately 1 km via Hidden Creek, into Corral Creek (Parks Canada 2020). The waters are typical for the area with low nutrients (e.g., total nitrogen <0.02 mg/L, total phosphorus 0.0012 mg/L), near neutral to alkaline pH (8.38), low temperature (6.3 C in Aug), and high dissolved oxygen (9.48 mg/L). The ice-free period at Hidden Lake is typically from 1 July to 20 October. There is no piscivorous forage base for the brook trout other than cannibalism of their young (Parks Canada 2020).

The rotenone formulation applied to Hidden Lake (21–22 Aug 2018 and 13 Aug 2019) was Nusyn-Noxfish and contained 2.5% rotenone active ingredient. The theoretical rotenone concentration of Hidden Lake once it penetrated the thermocline by pumping was 30 ppb and 25 ppb in 2018 and 2019, respectively (Parks Canada 2020).

Materials and methods

Description of datasets

Crustacean zooplankton

For crustacean zooplankton, we assessed the effects of rotenone on the density of 3 dominant species: the cyclopoid *Acanthocyclops vernalis*, the calanoid *Leptodiaptomus tyrelli*, and the cladoceran *Daphnia pulicaria*. Long-term patterns were examined with historical data on the density of the 3 dominant crustacean zooplankton species in Hidden Lake collected in early August from 2014 to 2018, and these were compared with post-rotenone treatment samples from early August 2019 (11 months after the first rotenone application) and early August 2020 (11 months after the second rotenone application). A second dataset was collected to understand short-term impacts of rotenone on the developmental stage of the 3 focal crustacean zooplankton species, which would affect differences in the potential for reproduction in relation to the timing of rotenone treatment. For the second dataset, crustacean zooplankton were sampled in Hidden Lake in mid July 2018 (5 weeks before the first rotenone application), early September 2018 (3 weeks after the first rotenone application), and early August 2019 (11 months after the first rotenone application).

Macroinvertebrates

For whole macroinvertebrate communities, Hidden Lake was sampled in mid July 2018 (5 weeks before the first rotenone application), early September 2018 (3 weeks after the first rotenone application), and late July 2019

(11 months after the first rotenone application). To partition seasonal variance and to determine whether the range of responses observed in Hidden Lake to rotenone treatment was different from the range of community variation observed between lakes in the region, samples from Hidden Lake were compared with 11 Rocky Mountain lakes that did not receive rotenone treatment (9 lakes with brook trout populations and 2 fishless lakes) in Banff, Kootenay, and Yoho National Parks, Canada (Table 1). In mountain lakes, there is an interaction between the presence of exotic trout and lake elevation, such that zooplankton communities in higher elevation lakes with brook trout are more similar to zooplankton communities in lower elevation lakes with exotic trout than communities in higher elevation lakes without exotic trout (Messner et al. 2013, Redmond et al. 2018). A similar interaction between exotic trout presence and lake elevation was suspected for macroinvertebrate communities as for zooplankton communities (Knapp et al. 2005, Tiberti et al. 2014). Thus, we included high- and low-elevation lakes with exotic trout in our comparisons with the high-elevation, rotenone-treated Hidden Lake. However, for fishless lakes, only high-elevation fishless lakes were included in the spatial analyses of macroinvertebrates because the low-elevation, fishless lakes do not represent the fishless state expected in Hidden Lake; at the higher elevation, we had data available for only 2 fishless lakes. The 11 reference lakes were sampled for macroinvertebrate communities at the same seasonal sampling periods of Hidden Lake, but only in 2018 (mid Jul and early Sep 2018).

Field and laboratory

Crustacean zooplankton

For the long-term zooplankton dataset, crustacean zooplankton were collected each year (2014–2020) during an index period between 4 and 11 August using full water column tows at the deepest point of the lake with a 30 cm diameter, 243 µm mesh plankton net. Samples were preserved immediately with 95% ethanol and later enumerated under a dissecting microscope. We generated subsamples using a Folsam plankton splitter and enumerated at least 200 individuals per sample. Samples with fewer than 200 individuals were counted in their entirety. Taxonomic keys used included Brooks (1957), Wilson (1957), Smith and Fernando (1978), Thorp and Covich (2010), and Haney et al. (2013). Since members of the *Daphnia pulex* species complex cannot be reliably distinguished using morphological characteristics, we verified the identification of *D. pulicaria* using sequences from 2 mitochondrial DNA loci, cytochrome oxidase I (COI) and ND5, following the protocol of Miner et al. (2013; Fisher J, unpubl. data).

For the second zooplankton dataset, crustacean zooplankton were collected by whole water column vertical tows with a 35 cm diameter, 54 µm mesh Wisconsin net from 0.5 m off the bottom to the surface. Ideally the same net should have been used for both zooplankton datasets, but the long-term dataset (2014–2020) was part of another project. However, our findings for rotenone impacts on the density of sexually mature individuals of the 3 focal species of crustacean zooplankton were the same for both types of net. For the second zooplankton dataset, the zooplankton were sampled from 4 sampling stations along an open water transect across each lake, anesthetized with bromoseltzer, and then preserved with 95% ethanol. These 4 samples subsequently were pooled into a single sample per lake for enumeration of developmental stages in the focal species, using the taxonomic keys already described. The maturity of copepods was determined by the presence of eggs, or by using the fifth leg shape, as described by Wilson (1957) and Smith and Fernando (1978). The maturity of daphniids was determined by the presence of eggs or embryos, or by the examination of the abdominal processes according to Brooks (1957). Individuals were considered mature adults if the first process was longer than the second. Maturity rate was calculated as the ratio of mature individuals divided by the total density of each species (excluding nauplii) and represents the proportion of sexually mature adult individuals in the population. Rotifers were not quantified; although rotifers are important for freshwater food web ecology and ecosystem function (Porter 1995, Jürgens et al. 1999, Miracle et al. 2007),

they are not an important direct source of food for brook trout (Tiberti et al. 2014).

Macroinvertebrates

Nearshore littoral macroinvertebrate communities were collected semiquantitatively with a D-frame kick net at 8 sampling stations located around the lake. Sampling was performed by the Traveling-Kick-and-Sweep method with a 500 µm "D-net" as recommended by Jones et al. (2007) on a surface of approximatively 2 m^2. Samples were concentrated with a 500 µm sieve and preserved in 95% ethanol. Identification was done to the family level for insect larvae, at the subclass level for Collembola, and at the phylum level for Platyhelminthes and Mollusca with the exception of the Bivalvia class, which was counted separately. Identification was done using a 6.3–63 dissecting microscope and Merritt et al. (2008) and Moisan (2010). Subsamples were taken and counted until the 100th individual was reached. A ratio was calculated between the sample volume and the subsample volume to estimate the density of macroinvertebrates.

Statistical analyses

In all cases for crustacean zooplankton and for macroinvertebrates, statistical analyses were performed using R version 3.6.0 (R Core Team 2020).

Crustacean zooplankton

Time-series analyses are limited for datasets containing too few data points to properly calculate autocorrelation and satisfy independence assumptions. To address this problem in the long-term zooplankton dataset, we based our analysis on previously published work (Frost et al. 2006); we used the 10th and 90th percentiles of pre-rotenone historical density of the 3 focal species (2014–2018) to represent variability in Hidden Lake before the rotenone treatment. We inferred that a species was impacted by rotenone when the absolute density was outside of the bounds of the 10th and 90th percentiles for pre-rotenone density. Cohen's effect sizes were also calculated to compare pre- (2014–2018) and post- (2019–2020) rotenone densities for the 3 focal zooplankton species using the package effsize (Torchiano 2020).

Macroinvertebrates

To test the effects of rotenone on macroinvertebrate taxonomic community composition in relation to the 11 reference lakes in the region that did not receive rotenone treatment, linear mixed models using the package nlme (Pinheiro et al. 2020) were performed on the first 2 principal coordinates analysis (PCoA) ordination axes for each group with the package vegan (Oksanen et al. 2019). Hellinger dissimilarity was used as the distance metric for ordinations. The fixed effects of the linear models were as follows: elevation as continuous, season with 2 levels (summer and fall), and treatment with 5 levels: (1) reference lake communities that coexist with exotic brook trout, (2) reference lake communities that are fishless, (3) time of year before rotenone treatment (corresponding to 2 weeks before the rotenone application in Hidden Lake), (4) time of year immediately following the rotenone treatment (corresponding to 3 weeks following rotenone treatment in Hidden Lake), and (5) time of year in the season following rotenone treatment (corresponding to 11 months following rotenone treatment in Hidden Lake). Random effects were lake and sampling station nested in lake to account for within lake and temporal replication in the linear mixed model. When treatment effects were significant, pairwise post hoc contrasts were done on marginal means of the different treatments using the package emmeans (Lenth 2020). The 7 pairs compared were (1) Hidden Lake before rotenone – 3 weeks after, (2) Hidden Lake before rotenone – 11 months after, (3) Hidden Lake 3 weeks after – 11 months after, (4 and 5) Hidden Lake 3 weeks after rotenone–fish and fishless reference lakes, and (6 and 7) 11 months after rotenone–fish and fishless reference lakes. Benjamini and Hochberg corrections were applied to prevent type 1 error (Benjamini and Hochberg 1995).

To compare changes in density of macroinvertebrates in Hidden Lake, as a response to rotenone treatment in relation to the 11 reference lakes, the same mixed models as for community analyses were performed on (i) total macroinvertebrate density and (ii) density of taxonomic orders present in Hidden Lake that appeared to

have an important effect in the PCoA or that were gill-breathing (Amphipoda, Chironomidae, Trichoptera, Ephemeroptera, Plecoptera, Mollusca, Bivalvia, and Coleoptera). Densities were log10(x)-transformed to correspond to model assumptions. In cases where there was zero density of a particular taxon in a lake and this taxon was the dependent variable, the lake was removed from that particular test (e.g., Amphipoda in Helen Lake, Coleoptera in Mud Lake). If there were too many zero densities across sampling stations for a given taxon to respect the model's assumptions, a binominal mixed model was first performed (with the same fixed and random variables) to test whether there was an effect of rotenone on the presence and absence of that taxon, prior to conducting a linear mixed model only on sites that contained the taxon using the package lme4 (Bates et al. 2015). When the effect of the treatment was significant, a pairwise post hoc contrast was conducted to test the difference between marginal means as for the community analysis, with the Benjamini and Hochberg correction applied to correct for the number of tests (Benjamini and Hochberg 1995).

Results

Crustacean zooplankton

Considering the density of the 3 dominant crustacean zooplankton species in Hidden Lake over summers 2014 to 2020, zooplankton density was drastically reduced by rotenone treatment in 2019 and 2020 (Cohen's effect size, before rotenone vs. after rotenone; *A. vernalis*: $d = -2.57$, *L. tyrelli*: $d = -1.80$, *D. pulicaria*: $d = -1.62$). Close to zero densities were recorded for all 3 focal species (as well as other crustacean zooplankton species; Derry A, unpubl. data) on 6 August 2019, which was 11 months after the first rotenone application (Figure 1). In August 2019, *A. vernalis* was undetectable in the water column and the densities

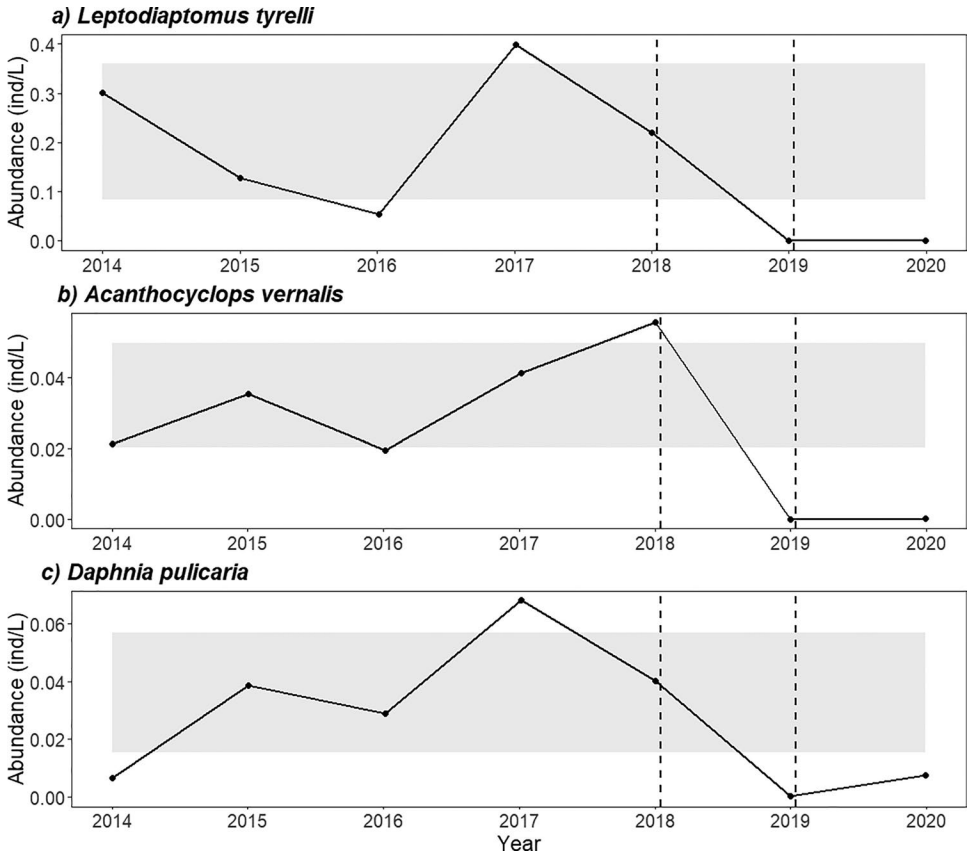

Figure 1. Changes in the summer density of 3 zooplankton focal species in Hidden Lake from 2014 to 2020: the cyclopoid *Acanthocyclops vernalis*, the calanoid *Leptodiaptomus tyrelli*, and the cladocera *Daphnia pulicaria*. The dotted lines represent the 2 dates of the rotenone application in each of 2018 and 2019. The 10th to 90th percentiles interval of pre-rotenone samples (2014–2018) is in the shaded area.

of *L. tyrelli* and *D. pulicaria* were reduced by approximately 100-fold compared to what they had been the previous year (Figure 1). Copepod density remained close to zero in August 2020, the summer following the second rotenone treatment (Figure 1: *A. vernalis* = 0.00024 ind/L, *L. tyrelli* = 0.0 ind/L). However, in August 2020, *D. pulicaria* density showed some recovery compared with the previous summer in August 2019, even though it remained under the 10th percentile of pre-rotenone density.

Five weeks before the first rotenone treatment, both copepod species had a relatively high density but a very low proportion of adults in each population compared to *D. pulicaria*, that had a lower density but a higher proportion of adults (Figure 2). Three weeks following the first rotenone treatment in 2018, *L. tyrelli* was undetectable from the water column and the *A. vernalis* population contained mature individuals but decreased in density by nearly 100-fold. By contrast with the copepods, the proportion of adult *D. pulicaria* at 3 weeks following rotenone treatment was lower, but their density remained at a level similar to that prior to the rotenone application (Figure 2). However, all 3 focal species were undetectable in the water column on 1 August 2019, in the following summer, 11 months after the first rotenone treatment. Rotifers were present in the water before, 3 weeks after and 11 months after the first rotenone application (Derry A, unpubl. data).

Macroinvertebrates

When compared with 11 regional lakes that did not receive rotenone, the macroinvertebrate community in Hidden Lake showed signals of responding to a combination of both direct non-target effects of rotenone and trophic interactions associated with the removal of brook trout 11 months after the rotenone treatment. The taxonomic composition of the macroinvertebrate community in Hidden Lake before the rotenone was similar to reference lakes with fish (early Aug 2018, square symbols; Figure 3). There were differences in taxonomic composition between Hidden Lake before the rotenone and 3 weeks

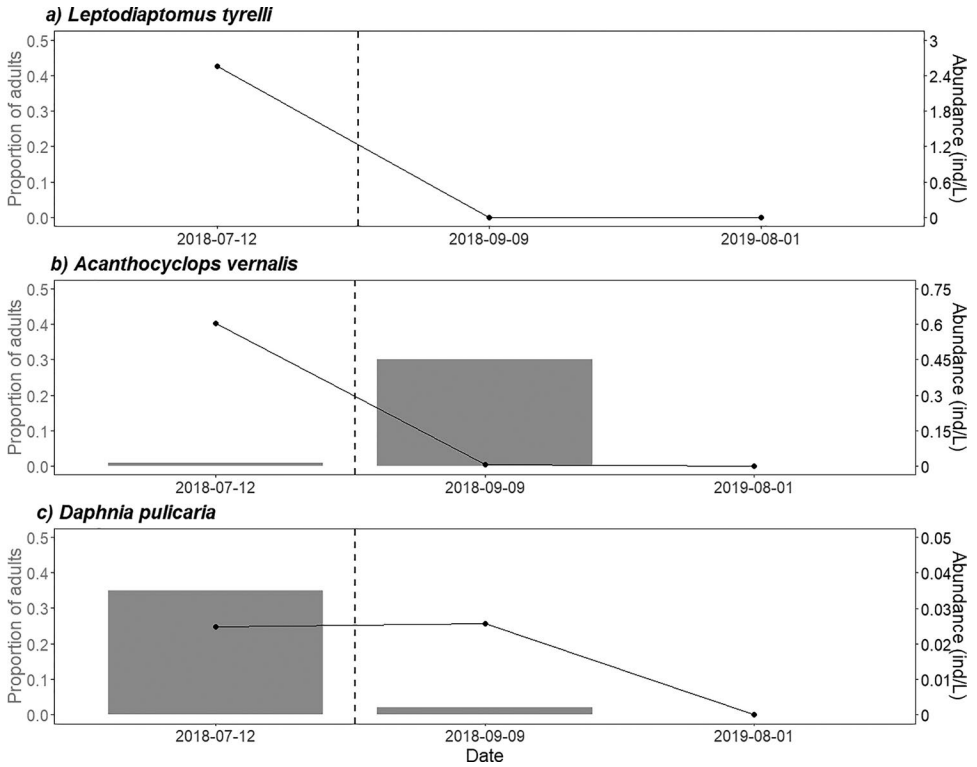

Figure 2. Proportion of adults (gray bars) and density (black dots with line connecting time points) of 3 focal crustacean zooplankton species at 5 weeks before, 3 weeks after, and 11 months after the first rotenone treatment (2018). The dotted line represents the date of the first rotenone application in 2018.

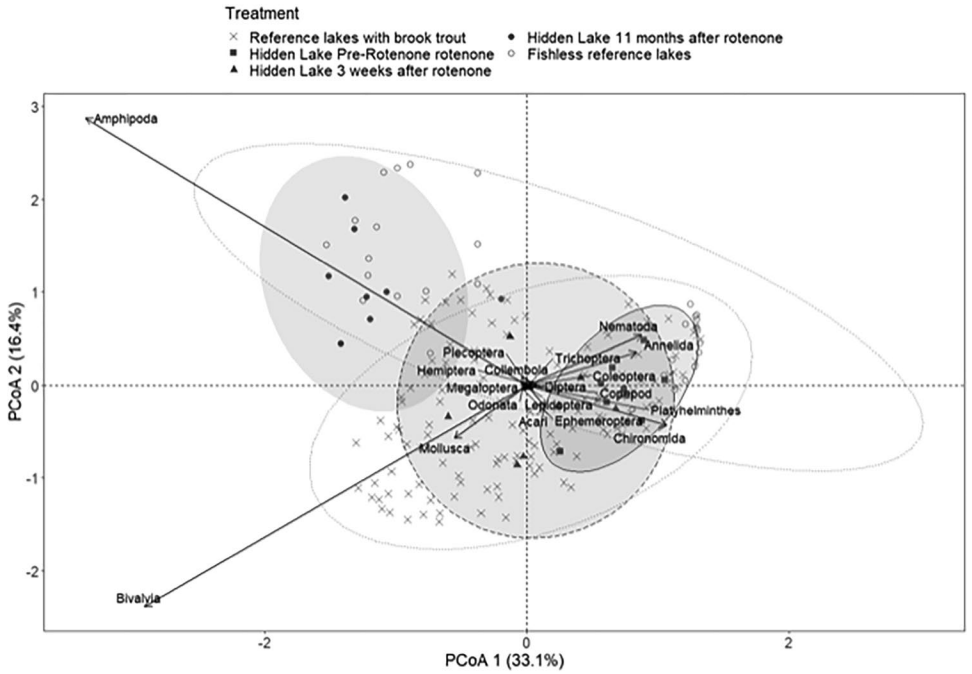

Figure 3. Principal coordinates analysis (PCoA) of the nearshore, littoral macroinvertebrate communities in reference lakes with brook trout (9 lakes; cross symbols, white ellipse, and dotted contour) and without fish (2 lakes; empty circles, white ellipse, and dotted contour) and in Hidden Lake (before rotenone treatment and with brook trout: gray ellipse with solid outline and squares symbols; 3 weeks after rotenone treatment: gray ellipse with dashed outline and triangle symbols; 11 months after rotenone treatment: gray ellipse with no outline and full circles symbols) situated along an elevation gradient (1185–2400 m). Eight samples per sampling season are plotted individually for each lake with 95% confidence interval of each treatment. Hellinger distance was used in the PCoA. Taxonomic group's position represents average coordinates of all families of that group present in our system. Percent variance explained by each axis is indicated on the figure axis labels.

after the rotenone (early Sep 2018, triangle symbols), but not when comparing Hidden Lake 3 weeks after rotenone to macroinvertebrate communities in reference lakes with brook trout (cross symbols) and that are fishless (open circles symbols; Table 2, Figure 3). At 11 months following the rotenone treatment (July 2019, full circle symbols), the Hidden Lake macroinvertebrate community became more similar to macroinvertebrate communities in the fishless reference lakes (open circle symbols) and differed from reference lakes with brook trout (cross symbols; Table 2, Figure 3).

Prior to rotenone treatment (early August 2018), the macroinvertebrate community of Hidden Lake included gill-breathing insect larvae (Figure 4). These were eliminated at 3 weeks following rotenone treatment (Plecoptera) and were replaced by a dominance of Chironomidae (even if less abundant than before rotenone; Table 3, Figure 4). In particular, Plecoptera showed a decreasing trend in density at 3 weeks after rotenone application, and this group did not return to pre-rotenone density at 11 months post treatment (Table 3, Figure 4). The density of Trichoptera showed a trend similar to that for Plecoptera, but their decline was not statistically detectable (Figure S1, Supplement). By contrast, in the summer following the 2018 rotenone application, there was a large increase in the total density of Amphipoda, at 10 times greater than before rotenone application (Tables 2 and 3; Figures 3 and 4). As a result, total macroinvertebrate density, albeit variable, remained within the range of total macroinvertebrate density observed among reference lakes both with brook trout and without fish (Table 3, Figure 4).

Discussion

We detected nontarget impacts of rotenone treatment on the crustacean zooplankton and macroinvertebrates in Hidden Lake, Banff National Park, Canada. The impacts on the crustacean zooplankton community were especially severe;

Table 2. Effect of treatment (reference with brook trout, before rotenone, 3 weeks after rotenone, 11 months after rotenone, and reference fishless) and comparisons between marginal means of ordination axis (PCoA) of nearshore littoral macroinvertebrate communities (Figure 2). The fixed effects of the model were treatment, elevation, and season. The random effects were lake with sample nested in lake. Benjamini and Hochberg (1995) correction was used to correct pairs' *P* values. Boldfaced *P* values are <0.05. *F* and *t* values are test statistics for the main effect of treatment and posteriori contrast, respectively.

Dependent variable	Subject	Df	Statistic	*P*	R^2 marg/ conditional
PCoA 1 (33.7% variance explained)	Effect of treatment	97	$F = 26.71$	**<0.0001**	0.54/0.81
	Before – 3 weeks after	99	$t = 3.64$	**0.001**	
	Before – 11 months after	99	$t = 9.94$	**<0.0001**	
	11 months after – 3 weeks after	99	$t = -5.87$	**<0.0001**	
	11 months after – Reference with brook trout	8	$t = -4.22$	**0.005**	
	11 months after – Reference fishless	8	$t = -3.18$	**0.018**	
	3 weeks after – Reference with brook trout	8	$t = -2.13$	0.08	
	3 weeks after – Reference fishless	8	$t = -1.15$	0.28	
PCoA 2 (16.6% variance explained)	Effect of treatment	97	$F = 9.96$	**<0.0001**	0.35/0.71
	Before – 3 weeks after	99	$t = 0.05$	**0.002**	
	Before – 11 months after	99	$t = -5.19$	**<0.0001**	
	11 months after – 3 weeks after	99	$t = 5.02$	**<0.0001**	
	11 months after – Reference with brook trout	8	$t = -1.45$	**0.009**	
	11 months after – Reference fishless	8	$t = 0.005$	**0.03**	
	3 weeks after – Reference with brook trout	8	$t = -0.38$	0.08	
	3 weeks after – Reference fishless	8	$t = -1.77$	0.28	

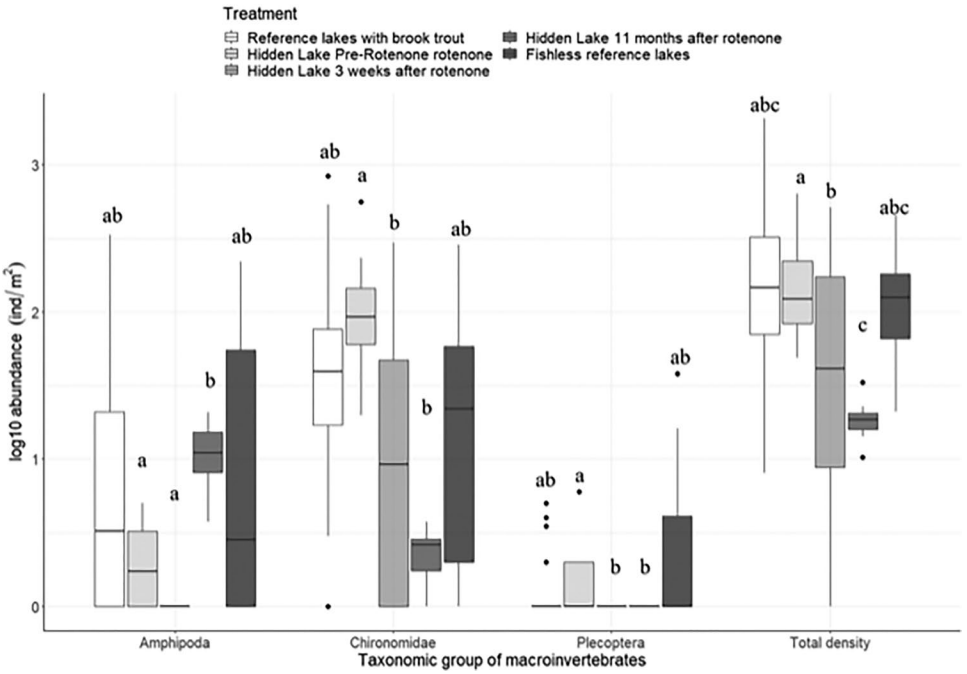

Figure 4. Density (number of individuals per m^2 littoral sediments) of macroinvertebrate taxa in reference lakes with brook trout (9 lakes) and without fish (2 lakes) and in Hidden Lake (before rotenone treatment and with brook trout, 3 weeks after rotenone treatment, and 11 months after rotenone treatment) situated along an elevation gradient (1185–2400 m). Significant differences ($P < 0.05$), mixed models, and post hoc contrasts are shown in Table 3 and significant pairwise differences ($P < 0.05$) are indicated by letters. The total density represents the sum of densities of each macroinvertebrate taxon present in samples collected from each category of lake. The middle line represents the median, the interquartile range represent the range between the 25th and 75th percentiles, the whiskers represent the 95% confidence interval, and the dots represent outliers (that were all kept in the analysis).

near zero crustacean zooplankton were found in the lake water column in 2019 and copepods remained near zero in 2020. The impacts on the macroinvertebrate communities were less severe; rotenone application to Hidden Lake caused macroinvertebrate community composition to shift from a preimpact taxon assemblage associated with fish coexistence (insect larva: loss of Plecoptera but resistance by Chironomidae to rotenone) to an Amphipoda-dominated assemblage that is often observed in fishless lakes (McNaught et al. 1999, Weidman et al. 2011).

Table 3. Effect of treatment (reference with brook trout, before rotenone, 3 weeks after rotenone, 11 months after rotenone, and reference fishless) and comparisons between marginal means of ordination axis (PCoA) of the nearshore littoral macroinvertebrate orders that were affected by rotenone treatment (Figure 3). Results of other taxa tested are available in the Supplement. The dependent variables were the $\log_{10}$ of the density of the taxon. The fixed effects of the model were treatment, elevation, and season. The random effects were lake with sample nested within lake. Benjamini and Hochberg (1995) correction was used to correct pairs' *P* values; boldfaced *P* values are <0.05.

Dependent variable	Subject	Df	Statistic	*P*	R^2 marg/ conditional
Log Amphipoda	Effect of treatment	35	$F = 6.50$	0.0002	0.44/0.67
	Before – 3 weeks after	77	$t = 0.65$	0.72	
	Before – 11 months after	77	$t = -3.32$	0.005	
	11 months after – 3 weeks after	77	$t = 3.78$	0.002	
	11 months after – Reference with brook trout	5	$t = 2.05$	0.22	
	11 months after – Reference fishless	5	$t = -1.17$	0.87	
	3 weeks after – Reference with brook trout	5	$t = 0.44$	0.79	
	3 weeks after – Reference fishless	5	$t = -1.71$	0.26	
Log Chironomida	Effect of treatment	44	$F = 11.98$	**<0.0001**	0.27/0.71
	Before – 3 weeks after	99	$t = 4.58$	**0.0004**	
	Before – 11 months after	99	$t = 46.61$	**<0.0001**	
	11 months after – 3 weeks after	99	$t = -1.75$	0.15	
	11 months after – Reference with brook trout	8	$t = -2.39$	0.10	
	11 months after – Reference fishless	8	$t = -1.57$	0.22	
	3 weeks after – Reference with brook trout	8	$t = -1.39$	0.24	
	3 weeks after – Reference fishless	8	$t = -0.60$	0.57	
Log Plecoptera	Effect of treatment	16	$F = 10.38$	**0.0002**	0.64/0.64
	Before – 3 weeks after	18	$t = 2.30$	**0.003**	
	Before – 11 months after	18	$t = 4.36$	0.08	
	11 months after – 3 weeks after	18	$t = 2.26$	0.08	
	11 months after – Reference with brook trout	1	$t = 2.32$	0.45	
	11 months after – Reference fishless	1	$t = 0.91$	0.55	
	3 weeks after – Reference with brook trout	1	$t = 0.85$	0.55	
	3 weeks after – Reference fishless	1	$t = -0.92$	0.55	
Presence Plecoptera (binominal model)	Effect of treatment	4	$Chi^2 = 16.5$	**0.002**	0.80/0.94
Log total density	Effect of treatment	97	$F = 5.92$	**<0.0003**	0.31/0.55
	Before – 3 weeks after	99	$t = 3.65$	**0.001**	
	Before – 11 months after	99	$t = 4.47$	**0.0001**	
	11 months after – 3 weeks after	99	$t = -0.63$	0.53	
	11 months after – Reference with brook trout	8	$t = -1.60$	0.26	
	11 months after – Reference fishless	8	$t = -1.86$	0.23	
	3 weeks after – Reference with brook trout	8	$t = -1.17$	0.32	
	3 weeks after – Reference fishless	8	$t = -1.44$	0.26	

However, macroinvertebrate total density was lower following rotenone treatment, even at 11 months following the application (Figure 4).

Our findings matched our predictions and are consistent with other literature on nontarget rotenone impacts on crustacean zooplankton (Kiser et al. 1963, Beal and Anderson 1993, Peterson et al. 2011, Dalu et al. 2015), especially in mountain ecozones (Anderson 1970, McGann 2018), and for macroinvertebrates (Dalu et al. 2015, Vinson et al. 2010). Crustacean zooplankton have generally been found to be absent from the water column of lakes from 1 to 6 months following rotenone application (Anderson 1970, Beal and Anderson 1993, Peterson et al. 2011, McGann 2018), or to have reduced densities (Melaas et al. 2001) before gradual recovery. Our findings offer 2 unique insights in relation to the other published rotenone studies: (1) The near absence of crustacean zooplankton after 11 months of rotenone treatment has not been reported previously, even for other mountain lakes (Anderson 1970), and (2) the community composition and total density of the macroinvertebrates shifted in response to the rotenone, and tracked ecological changes associated with the eradication of fish from the lake over the period of less than 1 yr.

Crustacean zooplankton

The 3 focal crustacean zooplankton species (cyclopoid copepod *Acanthocyclops vernalis*, cladoceran *Daphnia pulicaria*, and calanoid copepod *Leptodiaptomus tyrelli*) had different responses in density in the immediate 3 weeks following rotenone treatment of Hidden Lake. These divergent

short-term responses to rotenone may be explained by differences in reproductive life history and in the timing of rotenone application. The calanoid copepod *Leptodiaptomus tyrelli* disappeared in the 3 weeks following rotenone treatment of Hidden Lake (Figure 2a). This species was likely highly vulnerable to the rotenone because it reproduces once a year during winter in high-elevation lakes and has a long development time (Anderson 1971). Indeed, 5 weeks prior to the first rotenone treatment in 2018, the *L. tyrelli* population was entirely dominated by immature individuals that would have emerged seasonally from the egg bank in spring (Figure 2a). By contrast, at 3 weeks following rotenone application, the cyclopoid copepod *Acanthocyclops vernalis* persisted at low densities with mature individuals (Figure 2b) and the density of the cladoceran *Daphnia pulicaria* was unaffected (Figure 2c). *Acanthocyclops vernalis* and *D. pulicaria* reproduce continuously during the summer, with a peak in July or August, and have a generation time of approximatively 2 weeks (*A. vernalis*: Anderson 1971, Abdullahi 1990; *D. pulicaria*: Gulbrandsen and Johnsen 1990). Five weeks before the rotenone application to Hidden Lake, *A. vernalis* had a high density but a low proportion of adults (1%) while *D. pulicaria* had more adults (35%; Figure 2), suggesting they both could have had a reproduction peak prior to the rotenone application. Given the high toxicity of rotenone for crustacean zooplankton (Anderson 1970, Beal and Anderson 1993, Peterson et al. 2011, McGann 2018), the survivors at 3 weeks following the application were probably eggs when rotenone was applied and hatched thereafter. Recent studies have suggested that crustacean dormant eggs in sediments are not completely resistant to rotenone and that rotenone exposure could prevent emergence (brine shrimp, *Artemia franciscana*: Covi et al. 2016; calanoid copepods: Reed et al. 2018). However, it is likely that diapausing and subitaneous eggs could have provided some protection from rotenone. Although we did not quantitatively evaluate the rotifer community, we noted that while crustacean zooplankton were absent, rotifers were present in the water column 11 months after the rotenone application, suggesting a potential compensatory response.

The temporary short-term resistance of *Daphnia pulicaria* and *Acanthocyclops vernalis* in our study in the several weeks following rotenone treatment could potentially be explained by fortuitous timing of the rotenone treatment relative to reproduction. The resistance of *D. pulicaria* to rotenone at 3 weeks following treatment was high compared to other studies in mountain lakes (Anderson 1970, McGann 2018: in each of these 2 other studies, *D. pulicaria* were absent at 9 months and at 3 months following rotenone treatment, respectively). The resistance of *A. vernalis* at 3 weeks was also high compared to Anderson (1970), but a trend similar to our study was found in some lakes in McGann (2018). If the rotenone treatment occurred following the reproductive peak for *A. vernalis* and *D. pulicaria*, such that these species were able to produce at least partially resistant eggs early enough in the summer, this may have enabled subsequent emergence of these species from eggs in late summer. In high-elevation lakes, *D. pulicaria* have been found to hatch from resting eggs in the first 3 weeks following the thaw, and they produce most diapausing eggs in the fall (Pérez-Martínez et al. 2007, 2013). The individuals of *D. pulicaria* that we detected 3 weeks after the rotenone treatment in early September 2018 therefore likely emerged from subitaneous eggs. This assumes that *Daphnia* sp. embryos can develop inside the mother even after the mother is dead, in which case, the mother would act as a protective shield for the subitaneous eggs. However, this possibility remains unverified. By contrast, *A. vernalis* emerge later in the summer (Hairston et al. 2000) and may have emerged from both diapausing and subitaneous eggs in early September 2018, following the first rotenone application. However, crustacean zooplankton were almost undetectable in the water column of Hidden Lake in the following summer after the first rotenone application (Figures 1 and 2).

In our study, all 3 species failed to become reestablished in the water column the following spring. By contrast, other studies have reported

that crustacean zooplankton are usually partially or totally recovered in density and community composition after 1 yr (Anderson 1970, Beal and Anderson 1993, Melaas et al. 2001, Peterson et al. 2011, McGann 2018). Any immigration from upstream or overland dispersal was likely limited in this isolated, headwater alpine lake, and this process likely occurs over longer time periods than the 2 yr span covered in our study. In a similar ecozone, the reestablishment of zooplankton following their eradication by exotic trout predators, which were subsequently removed by nonchemical methods, took 4 yr for the cladoceran *Daphnia melanica* and 6 yr for the calanoids *Hesperodiaptomus shoshone* (Sarnelle and Knapp 2004, Knapp and Sarnelle 2008). Any zooplankton reestablishment in Hidden Lake in the spring following rotenone treatment would therefore have come from resting egg banks in lake sediments.

Reestablishment of zooplankton in the water column from sedimentary resting egg banks following their near eradication from a lake can be limited by many factors. Copepods are obligate sexual reproducers, and they can be susceptible to Allee effects via mate limitation if their population densities do not reach a critical threshold (Sarnelle and Knapp 2004, Kramer et al. 2008). This threshold is thought to be around 0.003 mature individuals/L for copepods (Kramer et al. 2008). This density is higher than the density of mature individuals observed in Hidden Lake 3 weeks after rotenone application (*A. vernalis*: 0.0024 mature individuals/L and *L. tyrelli*: 0.0 mature individuals/L), 11 months after the first rotenone treatment (Aug 2019), as well as 11 months after the second rotenone treatment (Aug 2020). By contrast, *D. pulicaria* can reproduce both sexually and asexually and therefore are less likely to be subject to Allee effects at low population densities (Gulbrandsen and Johnsen 1990, Knapp and Sarnelle 2008). This difference in reproductive strategy could possibly explain the partial recovery of *D. pulicaria* 11 months following the second rotenone treatment, while copepod density remained close to zero, but not the quasi-absence of *D. pulicaria* 11 months after the first rotenone treatment (Figure 1). The important decrease in the number of mature individuals (and effective population size) caused by rotenone in September 2018 (Figure 2), which likely occurred before the opportunity for sexual production and diapausing egg production (Pérez-Martínez et al. 2007, 2013), could partly explain the quasi-absence of *D. pulicaria* in the following summer of 2019 (Figures 1 and 2). That said, the sediments likely contained some ephippia. We speculate that an additional factor that possibly slowed zooplankton reestablishment in Hidden Lake from the sedimentary resting egg bank following the fish removal was resting egg bank depletion through predation by amphipods. Amphipods in mountain lakes feed on zooplankton eggs and juveniles, especially in fishless lakes, which could have delayed crustacean zooplankton recolonization (Parker et al. 1996, Sarnelle and Knapp 2004). In Hidden Lake, amphipods increased in density between fall 2018 and summer 2019 to attain a density that was 10-fold higher than pre-rotenone density (Figure 4). Moreover, the presence of fish for a long period in Hidden Lake suggests that the egg bank was already small before rotenone application (Sarnelle and Knapp 2004). Our study is the only one, to our knowledge, to report such an extreme impact of rotenone on the crustacean zooplankton community, even for mountain lakes, in the year following rotenone application.

Macroinvertebrates

Most other studies have found little or no initial impact of rotenone on macroinvertebrate communities, and they usually recover within 1 yr (Vinson et al. 2010). We found that the macroinvertebrate community was still impacted in the summer following rotenone treatment of Hidden Lake because total macroinvertebrate density was lower than pretreatment total density. Our study design does not allow us to consider interannual variation for macroinvertebrates, and it is impossible to say whether this reduction in density was related to environmental conditions in 2019 or to the rotenone treatment. However, this reduction in total macroinvertebrate density was related to a reduction in Plecoptera and Chironomidae densities (Figure 3). Plecoptera larvae are

gill-breathing and are particularly vulnerable to rotenone (Vinson et al. 2010, Booth et al. 2015, Dalu et al. 2015); this taxon did not recover after 11 months following the first rotenone treatment. Chironomidae density decreased slightly in the first 3 weeks after rotenone treatment, but it continued to decrease between fall 2018 and summer 2019. We speculate that this delayed response could be related, in part, to predation of Chironomidae by the amphipod *Gammarus lacustris*, which can adjust their trophic position and feeding behavior when fish predators are absent from mountain lakes (McNaught et al. 1999, Weidman et al. 2011). Notably, and consistent with this explanation, Amphipoda density increased 10-fold above pretreatment densities in the absence of brook trout in Hidden Lake by summer 2019 (Figure 4). There was, therefore, a considerable shift in the macroinvertebrate community composition because of the combined effects of rotenone treatment and brook trout removal from the lake. Insect larvae that had coexisted with the brook trout were particularly susceptible to rotenone toxicity, and following rotenone treatment of Hidden Lake, the macroinvertebrate community shifted to an Amphipoda-dominated assemblage that was more similar to what we observed in the fishless reference lakes. However, it is possible that the transition toward fishless macroinvertebrate assemblages had begun before the fish eradication by rotenone in Hidden Lake because of previous attempts to eradicate brook trout with nonchemical methods (2011–2017; Parks Canada 2020).

Implications for lake and reservoir management

The timing of rotenone treatment of lakes in relation to reproductive peaks and the abundance of "resistant" life stages (resting eggs) in crustacean zooplankton have often been used to explain interspecies and interstudy variation in zooplankton resistance to rotenone and recovery time (Anderson 1970, Beal and Anderson 1993, Melaas et al. 2001, Peterson et al. 2011, McGann 2018). Late fall rotenone application is thought to favor long-term recovery by allowing larger late-season egg banks to develop before rotenone treatment occurs (Anderson 1970, Melaas et al. 2001, McGann 2018), especially in mountain lakes where the ice-free period is short. The rotenone application in Hidden Lake occurred in late summer, rather than in fall as has been done for other mountain lakes (Anderson 1970, McGann 2018), and our study is the only one that we are aware of to report the close to zero density of crustacean zooplankton after 11 months following rotenone application. The rotenone was applied in late summer in Hidden Lake to avoid logistic complications with freezing temperature and ensure warmer lake temperature to minimize the degradation time of rotenone (Humphries SH, Parks Canada, Mar 2021, pers. comm.). Given that rotenone can block development and emergence of crustaceans from dormant eggs (brine shrimp: Covi et al. 2016; calanoid copepods: Reed et al. 2018), more studies are needed to understand how the timing of rotenone application can influence the viability of resting egg banks in lake sediments and the subsequent reestablishment of crustacean zooplankton in the following season.

This study showed that rotenone can eliminate crustacean zooplankton from the water column of mountain lakes. We suggest that more research is required to understand the long-term consequences of rotenone application for crustacean zooplankton community reestablishment in mountain lakes over the long term. For example, the combined effects of rotenone treatment and fish eradication may have promoted the surge of amphipod density and dominance in the macroinvertebrate community in Hidden Lake. This could have changed the predator–prey dynamics of the lake, and it may have contributed to the suppression or delay in zooplankton community reestablishment that has been observed in other mountain lakes (Parker et al. 1996). Amphipoda can provide an abundant and nutritious food resource to native fishes (Schindler and Parker 2002), and therefore may facilitate the reestablishment of native fishes if and when native fishes are reintroduced to lakes following eradication of exotic fish by rotenone. Therefore, for the goal of native fish restoration, the rotenone-mediated shift in macroinvertebrate community dominance toward amphipods may be considered an asset for native fish introduction. However, zooplankton can be an important resource for young-of-year fish in lakes (Sánchez-Hernández et al. 2019). Lake

managers could consider delaying native fish reintroductions to allow for at least partial recovery of the zooplankton community before adding an additional trophic impact to the food web, especially if zooplankton restoration is also a conservation objective. However, assisted recolonization of native fishes to lakes that received rotenone treatment may alleviate Amphipoda predation effects that delay zooplankton community reestablishment, furthering both fish and zooplankton restoration. Further scientific investigation is needed to address the unknown ecological interactions and trophic cascades associated with the assisted restoration of aquatic food webs following exotic fish eradication by rotenone.

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Data Availability

The data are available in the repository of the Environmental Data Initiative (EDI).
Zooplankton: https://doi.org/10.6073/pasta/b27053aaabbff61248819a7396b9dad2
Macroinvertebrates: https://doi.org/10.6073/pasta/3bc27eeccd0f943fe7d19678bd67a6ad

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