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**Limited effects of non-native trout on microcrustacean zooplankton in boreal foothills
lakes: comparisons of stocked, unstocked, and fishless lakes**

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Abstract

Stocking lakes with trout can have strong effects on native communities, however, the nature of impacts is not universal across receiving ecosystems. To assess effects of non-native trout, relative to native small-bodied fish, on microcrustacean zooplankton we compared stocked, unstocked (but fish-bearing), and fishless lakes in the boreal foothills of Alberta, Canada. Relative to unstocked lakes, stocked lakes had greater richness, but otherwise showed few additional effects on microcrustacean communities. In contrast, fishless lakes supported lower abundances of Cladocera, Calanoida, and Cyclopoida, but were dominated by larger cladoceran and calanoid taxa, compared to fish-bearing lakes (stocked and unstocked). Vertical distributions also differed significantly between lake types; microcrustaceans had far higher relative abundances at 1 m than at 2 m in fishless lakes compared to fish-bearing lakes (distributions in stocked and unstocked lakes were similar). Microcrustacean communities in fishless lakes were likely shaped by the invertebrate planktivore, *Chaoborus*, which was abundant in these systems, whereas native fishes likely structured microcrustacean communities prior to trout introductions, with planktivory by trout causing few additional effects.

Introduction

Sport fish stocking is employed throughout North America to create and/or enhance angling opportunities. Many species used for this purpose belong to the family Salmonidae, such as Rainbow Trout (*Oncorhynchus mykiss*), Brown Trout (*Salmo trutta*), and Brook Trout (*Salvelinus fontinalis*). The introduction of non-native trout, however, can alter populations of a variety of native taxa, including native small-bodied fish (e.g., Townsend 1996; Jellyman and McIntosh 2010), macroinvertebrates (e.g., Bradford *et al.* 1998; Herbst *et al.* 2009; Martinez-Sanz *et al.* 2010), and amphibians (e.g., Bradford *et al.* 1998; Mathews *et al.* 2001; Welsh *et al.* 2006). Trout can have especially strong effects on microcrustacean communities (Bradford *et al.* 1998; Budy *et al.* 2005). Stocking mountain lakes in North America and elsewhere with Rainbow, Brown, and/or Brook trout has decreased the abundance and mean body size of microcrustacean taxa (Jeppesen *et al.* 1997, 2000; Parker *et al.* 2001; Tiberti *et al.* 2014). In many cases, common large-bodied species become rare or absent in stocked lakes (Bradford *et al.* 1998). Stocked trout have also been found to influence the distribution of zooplankton in a manner similar to other visually foraging vertebrate planktivores (Hembre and Megard 2003).

The most pronounced effects of trout stocking have been documented in unproductive and naturally fishless mountain lakes, where native communities evolved in the absence of fish (reviewed by Dunham *et al.* 2004). Many stocked lakes, however, are located in more productive, lower elevation ecoregions and in systems with native fish populations, but these remain relatively understudied. Potential effects of trout in such systems can be difficult to predict due to the varying responses of different local taxa and differences in habitat characteristics across ecosystems (Dunham *et al.* 2004; Amsinck *et al.* 2006; Schank *et al.* 2011). Freshwater systems in these areas often have higher productivity, limited water clarity, and greater species diversity than mountain systems and their (often more dense) populations of native taxa may respond to stocked trout differently (Wissinger *et al.* 2006; Pink *et al.* 2007; Schilling *et al.* 2009a).

For microcrustacean communities, the presence of native fish could also limit impacts of trout, as planktivory by native fishes can be similarly size- and taxa-selective (Naud and Magnan 1988; Laurich *et al.* 2003), so few additional effects might be expected after stocking trout in naturally fish-bearing systems. At lower elevations, shared characteristics of microcrustacean communities in stocked and unstocked lakes containing native planktivorous fishes are expected to contrast with characteristics of communities in naturally fishless lakes, where high densities of macroinvertebrate predators may have different effects on zooplankton communities than fish (Von Ende 1979; Elser *et al.* 1990). In addition, a competitive dominance of large taxa can shape microcrustacean communities in the absence of fish.

Relative to neighboring Canadian provinces, Alberta has a paucity of lakes supporting game fish; combined with a large population of anglers, this translates into more than two orders of magnitude more anglers per fishing lake (Sullivan 2003). This high angling pressure has contributed to the decline of many native gamefish populations (Post *et al.* 2002) and consequently, an active fish-stocking program. Although a majority of the gamefish raised in Alberta fish hatcheries are native species, ca. 300 non-alpine lakes and ponds are stocked annually or biennially (some since the 1950s) with non-native trout to create additional angling opportunities that can help alleviate angling pressure on native populations (ASRD 2010, Zwickel 2012). These stocked lakes lack native gamefish, but many contain native non-game species. Only recently have studies started to examine effects of stocked trout in these systems.

Initial studies compared stocked with unstocked lakes, detecting weak effects of trout on density of native fish (Nasmith *et al.* 2010), composition and size structure of macroinvertebrates (Nasmith *et al.* 2012; Hanisch *et al.* 2013), and amphibian abundance (Schank *et al.* 2011). The latter two results were attributed, in part, to the presence of native fishes in the stocked lakes, which likely “pre-structured” resident populations prior to trout introductions. These resident vertebrates and invertebrates are primarily littoral, and may also have benefitted from the

presence of dense macrophyte beds than can serve as refuge habitat. Does “pre-structuring” by native fishes also limit the impacts of stocked trout on zooplankton offshore in more open-water habitats?

To examine effects that introduced trout may have on microcrustacean zooplankton, relative to those of native fishes, in lakes of the boreal foothills region of Alberta, we compared communities in a set of stocked and unstocked (but fish-bearing) lakes; to put any similarities or differences into a broader ecological context, we also characterized the microcrustacean zooplankton in a smaller set of nearby fishless lakes. Given that similar selectivity for larger and/or slower zooplankton by trout and native fishes is frequently observed (Hambright and Hall, 1992; Laurich et al., 2003; Budy et al., 2005), we expected generally similar communities (taxa, body sizes) in both stocked and unstocked lakes but relatively different microcrustacean communities in fishless systems. We also predicted that differences between fishless and fish-bearing (native and/or stocked) systems (i.e., fewer, but larger zooplankton in fishless vs. fish-bearing lakes) would increase as the summer progressed, after trout are stocked, young-of-year native fish begin foraging, and predation by late-instar *Chaoborus* in fishless systems increases (von Ende 1982). As well, because large-bodied microcrustacea can outcompete smaller taxa in the absence of size-selective vertebrate predators (Brooks and Dodson 1965), fish may mediate the coexistence of species (Paine 1966), resulting in greater species richness in fish-bearing compared to fishless lakes. We also predicted that the epilimnetic vertical distribution of zooplankton in fishless ecosystems would contrast with the pattern seen in fish-bearing lakes, but distributions in both stocked and unstocked (but fish-bearing) lakes would be similar. Finally, as study lakes were broadly comparable limnologically, we expected that the presence or absence of fish (stocked and native) would be more important in structuring microcrustacean communities than would environmental variables.

Methods

Study Area and Study Lakes

Study lakes (n=14) in the boreal foothills near Rocky Mountain House (52°22'39''N and 114°54'37''W) and Caroline (52° 5'36''N and 114°45'28''W), Alberta were sampled monthly (May- August 2009). Lakes were relatively small (1-31 ha) and shallow (2-13 m), and typically surrounded by forest. Many shorelines supported thick patches of *Typha latifolia*, while littoral zones were generally characterized by dense macrophytes (*Potamogeton* spp., *Sparganium angustifolium*, and *Nuphar variegatum*; Nasmith *et al.* 2010).

Lakes were either fishless (n=3), unstocked (n=5) or stocked with trout (n=6; primarily Rainbow, > 245 mm fork length; Table 1). Stocking typically occurs in spring and is repeated annually or biannually, as trout do not reproduce in these lakes (S. Herman and R. Konynenbelt, Alberta Fish and Wildlife, personal communication). Stocked and unstocked lakes both supported populations of native small-bodied fishes (Table 1). Although unstocked lakes were chosen from a list of regional lakes under consideration for future stocking by Alberta Fish and Wildlife, and preliminary visits to the lakes confirmed their general similarity to stocked lakes (C. Paszkowski, G. Scrimgeour, and W. Tonn, personal observations), fish managers do not select lakes randomly for stocking; stocked lakes tend to be somewhat larger, deeper, and less productive to reduce potential for winterkill (see also Pope 2008).

Epilimnetic water samples were collected at the deepest location within each lake. Using standard methods, samples were analysed for total nitrogen (TN), total dissolved nitrogen (TDN), total phosphorous (TP), total dissolved phosphorous (TDP), and chlorophyll-a (Chl-a) at the University of Alberta's Biogeochemical Analytical Laboratory (Edmonton, Alberta). Full temperature and dissolved oxygen (DO) profiles were also taken at the end of each month (May-August) at 1 m intervals, in addition to Secchi transparency and epilimnetic measures of pH and conductivity.

Microcrustacean Collection and Laboratory Processing

Pelagic microcrustaceans were collected in daylight during 5-d periods in each month (May- August 2009). Samples were collected at 1-m intervals from the deepest location in each

lake using a 30-L, 63- μ m mesh Schindler-Patalas trap and preserved in 80% ethanol until laboratory processing. For May, June, and August, samples from each metre were combined to produce a single composite sample for each lake, whereas samples from each depth were processed separately for July to examine vertical distribution (Holmes 2012).

Microcrustaceans were counted and identified to the lowest feasible taxonomic level (LFTL; generally species, however, family was used for Chydoridae); identifications were based on Edmondson (1959). In the case of damaged individuals, only fragments with a head were counted. Samples were sub-sampled using a 1 mL Hensen-Stempel pipette until at least 250 individuals were counted, with a maximum of 50 individual from each LFTL contributing to the total (see Christensen et al. 2006). Larvae of *Chaoborus*, the only macroinvertebrate caught consistently in the plankton trap, were also counted and identified to species for July.

For each LFTL from each sample, a subset ($n=15$ if possible, intact individuals only) was measured using a calibrated ocular micrometer. Measurements were dorsal lengths, excluding appendages/projections, on straightened individuals. With these measurements, we calculated “taxon length” for Calanoida, Cyclopoida, and Cladocera for each sample by determining the mean length of each LFTL within an order and then taking the average of those mean lengths. Lengths of each LFTL were also used to convert abundances into biomass (McCauley 1984; Culver *et al.* (1985).

Statistical Analyses

Univariate analyses were conducted using SPSS for Mac OS X (Rel. 19.0.0 2010). A Komolgorov-Smirnov test assessed normality for each data set and Levene’s test assessed the homogeneity of variance. Data that were not normally distributed were $\log_{10}(x+1)$ transformed. Results were considered significant if $p<0.05$, and marginally significant if $0.05<p<0.1$.

Linear Mixed Models (LMM) assessed differences in abundance, biomass, and mean taxon length of Cladocera, Calanoida, and Cyclopoida, and total taxon richness among the three lake types and the four sampling periods, using lake type, month, and their interaction as fixed

variables and lake as a random variable (SPSS Inc. 2010). Juvenile cladocerans and copepod copepodites were grouped with adults, but because copepod nauplii could not be classified, they were removed from LMMs. Due to insufficient sample sizes (<15 lengths/lake/sample period), length analyses excluded cladocerans in May, and calanoids and cyclopoids in May and June. For these and all other LMMs, if the interaction term was not significant ($p>0.05$), it was subsequently removed from the analysis. After lake type was found to have a significant effect on taxonomic richness, we examined richness – lake area and richness – depth relations using linear regression to assess the potential for increases in richness with greater morphometric complexity (Tessier and Welser 1991). We also assessed differences in *Chaoborus* abundance among lake types in July using a one-way Analysis of Variance (ANOVA).

To compare patterns of microcrustacean community composition among the three lake types, we applied Nonmetric Multidimensional Scaling (NMS) ordinations using Sorensen (Bray-Curtis) distance measure to LFTL presence/absence data. Ordinations were conducted separately for each sampling period, and for all lake-months combined; for the latter analysis, lake type-month centroids were plotted to illustrate the succession of microcrustacean communities through time. Ordinations were performed using the “slow and thorough” method of PC-ORD version 6.0 (McCune and Mefford 2011). Rare taxa (occurring in < 3 lakes) were deleted or merged to form a larger taxonomic group. When three or more axes were recommended, the two axes that represented the most variation were plotted for visual assessment. Biplots of important taxa ($r^2 > 0.5$) and environmental variables ($r^2 > 0.3$) were plotted to examine relationships with the ordination axes.

To test for compositional differences among the three lake types, we performed Multiple Response Permutation Procedures (MRPP; McCune and Grace 2002) on LFTL presence/absence data. MRPPs were also performed on environmental data. Area and depth, selected to be greater by fish managers for stocked lakes, were removed from the final analyses to see if environments differed among lake types based on the remaining variables. All MRPPs were done separately for each month.

Mantel tests were performed on microcrustacean LFTL and fish taxa presence/absence to compare similarities between the two matrices. Fish taxa included were “trout”, Fathead Minnow, Brook Stickleback, dace species complex, and a “fishless” category. Mantel Tests were also performed on microcrustacean and environmental data. Area and maximum depth were again removed from the analysis to assess relationships with the remaining environmental variables. All Mantel tests were done separately for each sampling period.

A two-way Variance Partitioning Analysis (VPA; Borcard *et al.* 1992; Hall *et al.* 1999) was used to assess the proportion of variance in the composition of microcrustacean communities that could be explained by the environmental variables and the fish assemblage type (stocked, unstocked, and fishless). Analyses were conducted using CANOCO for windows, version 4.5 (ter Braak and Smilauer 2006) for June, July, and August. Based on the length of the dominant axis from a preliminary Detrended Correspondence Analysis (DCA), a linear model (using Redundancy Analysis – RDA) was deemed appropriate (ter Braak and Smilauer 2006). To reduce the number of environmental variables entering the analyses, CANOCO ranks and chooses the variables by their importance for the microcrustacean data via forward stepwise selection ($p < 0.09$; ter Braak and Smilauer 2006).

Study lakes displayed a variety of maximum depths, water clarities (Table 1), and both extent and depth of temperature-based stratification (Holmes 2012), which precluded the application of many vertical-distribution contrasts across all lakes, e.g., epi- versus hypolimnion, photic versus aphotic zone, shallow versus deep. Minimum Secchi depths across the three lake types were 1.3–2.7 m, suggesting some impairment of the ability of visual fish predators to detect zooplankton prey occurred in lakes of each type at depths of 2 m. Despite warmer temperatures within the 2-m depth zone, both stocked trout and small-bodied native fishes were regularly captured there (Nasmith *et al.*, 2010) and mesocosm experiments held trout successfully within the 1 m depth zone (Hanisch *et al.*, 2012). For these reasons, we limited our vertical distribution contrasts across all lakes to 1 m versus 2 m, i.e., within the epilimnion of all study lakes.

For the major taxonomic groups (Cladocera, Calanoida, and Cyclopoida), we determined the mean relative abundance (% of individuals) at 1 and 2 m for each lake; these values were then used to determine means ($\pm$ SE) for each lake type (stocked, unstocked, and fishless). Juvenile *Daphnia* and copepod copepodites were included with adults in these analysis. Mean relative abundances (arcsine square root transformed) were analyzed using LMMs, with treatment (lake type) and depth as fixed factors, and lake as a random factor.

Results

Limnology

Although the three lake types overlapped in limnological characteristics, as expected, stocked lakes were a bit larger and deeper than unstocked lakes, which were, in turn, a bit deeper and larger than fishless lakes, although there was considerable overlap among lake types (Table 1). Nutrients indicated that stocked lakes were mesotrophic, while unstocked and fishless lakes were meso-eutrophic (Table 1; Carlson 1977). Lakes were stratified to various degrees by the end of July (Holmes 2012). Thermal stratification often resulted in reduced oxygen concentrations in the lower half of the water column, regardless of lake depth (Table 1).

Microcrustacean Abundance, Biomass, and Length

In total, 143,194 microcrustaceans were counted and 13,709 were measured from the 130 samples collected. Across the 14 study lakes and four sampling periods we identified 13 cladoceran, three cyclopoid and three calanoid taxa (Appendix A).

Cladoceran abundance differed marginally among lake types ($p=0.061$) and significantly among months ($p<0.001$, LMM). Cladoceran abundance, lowest in May and highest in July, was greater in stocked compared to fishless lakes ($p=0.022$), with unstocked lakes intermediate (Table 2). Calanoid abundance differed among lake types ($p=0.029$) and months ($p<0.001$), with a significant interaction ($p=0.042$). Abundance was lowest in fishless lakes ($p<0.03$), but similar between stocked and unstocked lakes ($p>0.10$). Abundance in fish-bearing lakes increased

dramatically after May, but remained relatively low in fishless lakes (Table 2). Cyclopoid abundance differed among lake types ($p=0.012$) but not months. Abundance was lowest in fishless lakes ($p<0.032$), but did not differ between stocked and unstocked lakes (Table 2).

Cladoceran taxa were largest in fishless lakes ($p<0.006$), but mean taxon length did not differ between stocked and unstocked lakes, nor among months (Table 2). Calanoid taxon length differed among lake types ($p=0.034$), but not months. Fishless lakes supported larger ($p=0.011$) and marginally larger ($p=0.056$) calanoid taxa than stocked and unstocked lakes, respectively; the two fish-bearing lake types did not differ (Table 2). In contrast, mean lengths of cyclopoid taxa did not differ among lake types or months (Table 2).

Integrating patterns of abundance and size, cladoceran and calanoid biomass both differed among months ($p<0.001$) but not lake types ($p>0.159$). Cladoceran biomass was lowest in May ($p<0.001$) and marginally highest in July ($p<0.089$; Table 2). Calanoid biomass was also lowest in May ($p<0.001$) and highest in July and August, which did not differ from each other ($p=0.976$, Table 2). In contrast, cyclopoid biomass differed among lake types ($p=0.002$) but not among months ($p=0.296$). Cyclopoid biomass was lowest in fishless lakes ($p<0.015$) and marginally lower in unstocked than in stocked lakes ($p=0.066$, Table 2).

Microcrustacean Community Composition

Crustacean richness differed among lake types ($p<0.05$) and months ($p<0.01$, LMM). Richness was greater in stocked compared to unstocked and fishless lakes ($p<0.05$); the latter lake types did not differ ($p>0.10$; Table 2). Richness increased from May through July and then dropped in August. Only in May and July was lake area correlated with richness ($p<0.05$); correlations with depth were never significant.

No useful ordination (*sensu* McCune and Mefford 2011) of microcrustacean communities was created for May, most likely due to the absence of many crustacean taxa as identifiable adults. Ordination analyses of microcrustacean communities throughout the summer (June–August) were similar (Holmes 2012) and best illustrated by the August ordination, which

represented 92% of variance in the data set (17 taxa), at a stress level of 8.4 (Monte Carlo test, $p=0.003$). Community composition differed among lake types (MRPP; $p=0.004$), with fishless lake communities differing from both stocked ($p=0.003$) and unstocked lakes ($p=0.008$); composition in the latter two lake types differed marginally ($p=0.078$) (Fig. 1). Microcrustacean taxa that were strongly correlated with the two axes ($r^2>0.5$) included *Diaptomus leptopus*, *Daphnia middendorffiana*, and *Daphnia schodleri* (associated with fishless lakes), whereas *Skistodiaptomus oregonensis*, *Mesocyclops edax*, and *Diaphanosoma* were associated with fish-bearing lakes. In contrast, there was no difference in environmental factors (excluding area and maximum depth) among the three lake types (MRPP; $p>0.10$), and no environmental variables were strongly correlated with the two axes ($r^2>0.3$). Microcrustacean and fish communities showed significant correspondence (Mantel Test; $p=0.002$), whereas the microcrustacean and environmental matrices were not related (Mantel Test; $p=0.365$).

The ordination of all lake-months represented 84% of variance in the data set (18 taxa), at a stress level of 13.6 (Monte Carlo, $p=0.003$; Fig. 2). Successional vectors for stocked and unstocked lakes moved in a similar upward direction from May through August, suggesting increased importance of *Skistodiaptomus oregonensis* and *Diaphanosoma*, whereas vectors for fishless lakes followed a perpendicular leftward trajectory through time, consistent with increasing importance of *Diaptomus leptopus* and *Daphnia middendorffiana*. No environmental variables were correlated ($r^2>0.3$) with the ordination axes.

Environmental variables chosen for Variance Partitioning Analysis were surface temperature (June), TDP (July), depth (July, August), and area and dissolved oxygen (August). These variables explained 11- 21% of the variance in microcrustacean communities, compared to 16- 21% explained by the fish assemblage, and 15-16% by the interaction of environment and fish assemblage (Fig. 3).

Vertical Distribution

Significant ($p < 0.05$) lake type *depth interactions were detected for relative abundances of Cladocera, Calanoida, and Cyclopoida (Fig. 4). In both stocked and unstocked lakes, these taxa had either a similar or somewhat higher mean relative abundance at 2 m compared to 1 m; in contrast, abundances in fishless lakes were much higher at 1 m (Fig. 4). The same pattern was observed for biomass of all three taxa (Holmes 2012).

Chaoborus Abundance and Composition

We identified four species of *Chaoborus* from the study lakes (Table 1). *C. americanus* was exclusive to fishless lakes, *C. punctipennis* was exclusive to fish-bearing lakes (stocked and unstocked), *C. trivittatus* was found in unstocked and fishless lakes, whereas *C. flavicans* was common to all lake types. *Chaoborus* densities differed among lake types ($p < 0.05$); densities were three and 14 times higher in fishless compared to unstocked and stocked lakes, respectively (Table 1).

Discussion

Overall, our comparative “natural experiment” investigating lakes in the boreal foothills of Alberta found statistically significant differences in zooplankton abundance, size, richness, community composition, and vertical distribution, and a more limited difference in biomass, among the three lake types (unstocked lakes, with native, small-bodied fish, stocked lakes, with native fishes and non-native trout, and fishless lakes). Our samples size, 56 lake-month samples across 14 lakes, was similar to other studies of fish effects on zooplankton (e.g., Donald et al. 2001, Schabetsberger and Luger 2009, Schilling et al. 2009a). Indeed, in contrast to studies based on single site-visits, our repeated-sampling design allowed us to incorporate seasonal variation in zooplankton communities (Sommer 1989).

Overall effects of lake-type, however, masked a more nuanced pattern. With the exception of taxon richness, most zooplankton metrics showed no or limited differences between stocked and unstocked lakes. In contrast, these fish-bearing lakes differed significantly from

fishless systems in most respects, thus revealing a general fish effect, not specifically a stocked trout effect. Stable isotope signatures of dace (*Chrosomus* spp.), Fathead Minnow, and Brook Stickleback in our stocked and unstocked lakes indicated that zooplankton were an important dietary component (Hanisch 2016), consistent with studies on these and related species elsewhere (e.g., Naud and Magnan 1988; Hambright and Hall 1992; Laurich *et al.* 2003). Similarly, the positions of trout in stable isotope biplots were also consistent with a diet for which zooplankton is an important component (Hanisch 2016). Indeed, Hanisch (2016) identified microcrustaceans, especially cladocerans, as frequent and important components in the diets of trout in these systems, based on stomach-content analyses. Across 18 lake-years, representing 1055 total fish, frequency of occurrence of cladocerans averaged 52.5% (± 5.2 SE), while copepods averaged 9.0% (± 2.1 SE). Cladocerans were consistently among the top two prey items numerically and, along with chironomids, comprised collectively 20-50% of trout diets based on relative importance. The frequency and importance of planktivory was largely independent of trout size (J. Hanisch, University of Alberta, *pers. comm.*).

Despite the largely dichotomous pattern between microcrustacean communities (fish-bearing vs. fishless lakes), limnological characteristics of lakes tended to form gradients, from stocked, to unstocked to fishless lakes (albeit with considerable overlap). The dichotomous nature of the microcrustacean communities was thus fully consistent with the well-documented effects of fish planktivory (and limited differences between predation by native fishes versus trout), but less consistent with variation in environmental factors.

Microcrustacean Abundance, Biomass, and Length

Cladocerans and calanoid copepods had greater abundances, but smaller lengths, in fish-bearing compared to fishless lakes, resulting in comparable biomass among lake types. The combined planktivory of stocked trout and native fishes in stocked lakes failed to translate into additional effects on the abundance and size of major microcrustacean taxa beyond those observed in unstocked lakes generated by native fishes alone. The pattern of increased

abundance but decreased size that we documented, although consistent with the outcome of trout introductions into mountain lakes lacking fish (Carlisle and Hawkins 1998), indicate that it is the presence of (zooplankton-consuming) fish, not of non-native trout per se, that are behind these community shifts. Indeed, following Hrbáček et al. (1961) and Brooks and Dodson (1965), many studies have found small microcrustaceans dominating communities in (native and/or non-native) fish-bearing lakes, whereas various invertebrate predators (e.g., *Chaoborus*) and large microcrustaceans, e.g., certain *Daphnia* species, dominate fishless systems. Both trout and the native fishes feed selectively on large microcrustacea (Naud and Magnan 1988; Lynott et al. 1995; Laurich et al. 2003). Trout and the native fishes also feed on macroinvertebrate predators (Cochran et al. 1988; Lynott et al. 1995); in our lakes, an average of 21.1% of trout stomachs examined contained *Chaoborus* (J. Hanisch, unpublished data). Both of these foraging preferences should contribute to the dominance of smaller cladocerans and calanoids in fish-bearing lakes (Dodson 1974; Carlisle and Hawkins 1998; Schilling et al. 2009a). In contrast, invertebrate planktivores and/or the competitive superiority of large grazing microcrustaceans can reduce or exclude smaller species in fishless systems (Brooks and Dodson 1965; Gliwicz et al. 2010).

In contrast to cladocerans and calanoids, cyclopoid copepods displayed greater mean abundance but no difference in mean length between fish-bearing (stocked and unstocked) and fishless lakes, resulting in greater cyclopoid biomass in the fish-bearing lakes. Unlike the cladoceran and calanoid species found in our study lakes, the cyclopoids (*Mesocyclops edax/leukarti* and *Cyclops bicuspidatus thomasi*) are relatively small as adults, which should reduce predation by fish (Kerfoot 1980; Ha and Hanazato 2009). In addition, cyclopoids are strong swimmers compared to cladocerans and calanoids, and thus more efficient at evading fish predation (Thorp and Covich 1991).

Beyond the lack of a size effect, fish (native or stocked) could increase cyclopoid abundance by (i) reducing the abundance of their macroinvertebrate predators, (ii) decreasing competition between cyclopoids and predatory macroinvertebrates (Liljendahl-Nurminen et al.

2003), and (iii) shifting the size structure of cladocerans towards a dominance of small taxa, e.g., *Bosmina*, which are common prey of cyclopoids (Kerfoot 1980; Ha and Hanazato 2009). An abundance of smaller cladocerans in fish-bearing lakes should increase survival and reproduction of adult cyclopoids (Williamson and Butler 1986; Hansen and Santer 1995; Hopp *et al.* 1997) and developmental rates and survival of their nauplii and copepodites (Hopp and Maier 2005).

Microcrustacean Communities

Stocked lakes had richer microcrustacean communities compared to unstocked and fishless lakes. Although the larger and deeper stocked lakes might provide increased habitat heterogeneity (Tessier and Welser 1991), richness was unrelated to lake depth and only marginally correlated with area, suggesting that lake morphometry contribute minimally to richness patterns across lake types. richness differences among lake types. We suggest that the greater diversity of fish predators (trout plus native fishes) in stocked lakes played a more important role.

The presence of fish could lead to greater richness through predator-mediated coexistence of species (Hairston *et al.* 1960). Fish feed selectively on large, often competitively superior zooplankton, which could facilitate the coexistence of competitively inferior taxa. Fish can also impact the composition and density of invertebrate predators that are capable of excluding small zooplankton (Dodson 1974). Donald *et al.* (2001) documented a similar increase in microcrustacean richness in lakes with both stocked trout and native fish, compared to lakes with only stocked trout and fishless lakes, suggesting that a diversity of fish species, sizes, and feeding strategies reduces dominance more effectively and allows the establishment of additional zooplankton taxa. Relative to fishless and unstocked lakes, stocked lakes also had lower densities and richness of *Chaoborus*, perhaps allowing some smaller, more susceptible taxa to persist (Chess *et al.* 1993; Schabetsberger and Luger 2009). For example, *Daphnia galeata mendotae* and *Daphnia parvula* were found mostly in stocked lakes, and another small cladoceran species (*Ceriodaphnia lacustris*) was restricted to a single stocked lake.

The microcrustacean and fish community matrices were significantly related during summer months, as fishless and fish-bearing lakes harbored distinct microcrustacean communities, consistent with a strong fish effect in the latter (Sosnovsky and Quiros 2009; Schabetsberger et al. 2009). The contrasting composition and densities of invertebrate predators, including the absence of *Chaoborus americanus* in fish-bearing lakes, could also have contributed to the dichotomy (Mackay *et al.* 1990). Microcrustacean communities in stocked and unstocked lakes, however, differed only marginally. Although the two largest cladoceran species (*Daphnia middendorffiana* and *D. pulex*) showed a strong affinity for fishless lakes, there was no evidence that large cladocerans were completely extirpated after trout were introduced to naturally fish-bearing lakes, suggesting reduced effects of stocking in Alberta's boreal foothills relative to lakes at higher elevations (e.g., Schindler 2000). In addition, the largest calanoid species (*Diaptomus leptopus*) was exclusive to fishless lakes, while the smallest calanoid species (*Skistodiaptomus oregonensis*) showed a strong affinity for fish-bearing lakes (see also Donald *et al.* 2001).

Because of the strong relationships between fish and zooplankton, Jeppesen et al. (2011) suggested several plankton-related trophic ratios as indices of predation pressure on zooplankton. Interestingly, neither zooplankton biomass : Chl-a, Chl-a : TP nor Chl-a : TN differed among our three lake types (ANOVAs, $P > 0.10$; Holmes 2012 and unpublished).

Seasonal Effects on Microcrustaceans

The NMS ordinations and corresponding MRPP tests revealed similar microcrustacean communities among lake types in May, but an increasing difference between fish-bearing and fishless lakes as communities developed through the summer. Indeed, differences in microcrustacean community composition (MRPP) among lake types and a relationship between fish and microcrustacean community matrices (Mantel test) were not detected in May, and the percentage of variance explained by fish increased throughout the summer from June to August (VPA). These results suggest that the ecological processes causing divergence among microcrustacean communities in the different lake types were weak or absent in spring but strong

throughout the summer. Trout are stocked in the spring and early summer (May and June), and all the native fishes in our lakes reproduce in spring, with young hatching by the end of June, to begin feeding on zooplankton (Abrahams 1996). Likewise, *Chaoborus americanus* and *C. flavicans*, two of the three species found in fishless lakes, pupate early in spring (von Ende 1982), suggesting that during our sampling in May, populations were dominated by early instars. In contrast, densities of instar IV, to which zooplankton prey are most sensitive (Neill and Peacock 1980; Elser et al. 1987), should increase over the course of the summer (von Ende 1982). Thus, while lake depths and areas did not change between spring (May) and summer (June-August), increased planktivory by fish and *Chaoborus* (in fishless lakes) in June-August likely contributed to the increasing community differences between fish-bearing and fishless lakes seen during the summer. In contrast, the ordination trajectories of stocked and unstocked lakes were essentially parallel in June, with relatively minor changes in July-August.

Vertical Distribution

Fish-bearing lakes had similar or slightly higher relative abundance and biomass of Cladocera, Calanoida, and Cyclopoida at 2 m vs. 1 m, whereas fishless lakes had much greater amounts at 1 m vs. 2 m. This pattern suggests that cladocerans (e.g., Dini and Carpenter 1992) and copepods (Gliwicz and Pijanowska 1988; Doulka and Kehayias 2011) (i) occupied deeper waters during the day in response to predation by fish, and/or (ii) occupied surface waters in the absence of fish, potentially in response to high densities of *Chaoborus* and/or other environmental factors (Lampert et al. 2003). In contrast, it is difficult to explain differences in vertical distribution between fishless and fish-bearing lakes on the basis of depth-related differences in abiotic factors.

In the absence of fish, zooplankton should occupy habitat based on factors such as temperature (Gliwicz and Pijanowska 1988) and availability of phytoplankton resources (Johnsen and Jakobsen 1987; Leibold 1990; Dini and Carpenter 1992). We lack data on the vertical distribution of phytoplankton in our lakes, but in other moderately productive lakes, phytoplankton are often abundant in warm shallow waters (Dawidowicz and Loose 1992),

responding to greater available light (Wang et al. 2011). In addition, zooplankton growth and development benefit from higher temperatures. With a mean temperatures of 22.4 ± 0.4 °C at 1 m and 20.7 ± 0.5 °C at 2 m during our study, zooplankton would have benefitted from the warmer temperature at 1 m (Orcutt and Porter 1983).

Chaoborus is the dominant planktivore in the pelagic zone of our fishless lakes. Several species of this non-visual predator migrate vertically to deeper waters during the day and then ascend at night in both fish-bearing (Stahl 1966; Halat and Lehman 1996) and fishless lakes (Xie et al. 1988). In fishless lakes containing migratory *Chaoborus*, including *C. flavicans*, deeper waters will not protect zooplankton from predation; as a result, zooplankton should preferentially occupy shallow waters with their warmer temperatures and higher food availability (Dodson 1988; Gonzalez 1998). Occupying shallow water in fish-bearing lakes, however, can increase susceptibility of zooplankton to predation by trout (Budy et al. 2005) and native fish (Naud and Magnan 1988; Laurich et al. 2003). Indeed, daytime distributions of zooplankton can be shaped by fish in lakes as shallow as 1.6 m (Castro et al. 2007). Thus, the lack of difference between stocked and unstocked lakes further supports our hypothesis that native fish “pre-structure” microcrustacean communities prior to trout stocking.

Fish, *Chaoborus*, and Microcrustacean Communities

Frequency of occurrence, density, and species composition of *Chaoborus* all differed between fishless and fish-bearing lakes, with *C. americanus* exclusive to the former and *C. punctipennis* exclusive to the latter, as reported for other systems (e.g., Von Ende 1979, 1982; Yan et al. 1985; Schilling et al. 2009b). Given that *Chaoborus*, particularly *C. americanus*, can strongly affect zooplankton communities through selective feeding (Luecke and Litt 1987; Mackay et al. 1990; Liljendahl- Nurminen et al. 2003), these results reflect strong indirect impacts of fish predation. We did observe some density and minor compositional differences in *Chaoborus* between stocked and unstocked lakes, suggesting some additional effects of trout

beyond those of native small-bodied fish, likely reflecting the increased diversity of fish in stocked lakes, as discussed above (Donald et al. 2001).

Fish versus Environmental Differences

In contrast to the dichotomous nature of microcrustacean communities, with highly significant differences between fishless and fish-bearing lakes, but little or no difference between stocked and unstocked lakes, environmental factors differed only marginally and followed a continuous gradient across the three lake types, and overlap among lake types was extensive. The fish-bearing vs. fishless dichotomy in microcrustacean communities developed strongly only after May, consistent with the timing of trout stocking and the phenology of reproduction among native fishes. Fish also accounted for a slightly but consistently larger portion of explained variance than did the environment (VPA). Given the well-established mechanisms by which fish can affect microcrustaceans, we propose that fish were more important in structuring microcrustacean communities than environmental conditions. Similarly, Carlisle and Hawkins (1998) found that differences in environmental variables did not mediate the overriding effects of fish presence in mountain lakes in Utah.

Comparisons with Fishless Lakes

Numerous studies have demonstrated that stocking non-native salmonids into alpine and other fishless lakes can have serious negative effects on native zooplankton, as well as other taxa (e.g., Knapp et al. 2001; Dunham et al. 2004; Eby et al. 2006). Consequently, many aquatic scientists view them as “a dangerous biological pollutant” (e.g., Schabetsberger et al. 2009). Specifically with respect to native microcrustaceans, trout stocked into fishless lakes decrease abundance and mean size, and alter the taxonomic composition and vertical distribution of the community, as common, large-bodied taxa displaying at most subdued vertical migration become rare or absent, and smaller taxa (either existing minor members of the community or new colonists) become dominant, occupying deeper refuge layers during daytime.

Comparing the microcrustacea in our stocked boreal foothills lakes to those in the fishless lakes, we saw the same patterns found in alpine lakes. However, these patterns were also documented for unstocked lakes containing native small-bodied fishes; indeed, for nearly all of the variables we measured, there was no difference between stocked and unstocked lakes, clearly indicating that a generic fish effect, not specifically a stocked trout effect, is largely behind the patterns observed. Our data thus add to a growing body of evidence of relatively minor effects of trout stocking on native biological communities in boreal foothills lakes (Nasmith *et al.* 2010, 2012; Schank *et al.* 2011, Hanisch *et al.* 2012, 2013). Relative to alpine lakes, lakes within Alberta's boreal foothills may be partly buffered against trout impacts on zooplankton due to greater lake productivity, extensive macrophyte cover, and more complex native zooplankton communities. We suggest, however, that the most important factor is that boreal foothills lakes contain native small-bodied fishes, along with more complex invertebrate communities. Native fish shape the ecology and life history of invertebrate prey prior to trout introduction, resulting in communities that are not naïve to predation by fish (Jeppesen *et al.* 2000; Aguilera *et al.* 2006; Schilling *et al.* 2009b).

Understanding how stocking non-native trout influences lake ecosystems is essential for the conservation of native communities. Resource managers and aquatic scientists should not assume that trout introduction will (or will not) automatically result in strong negative effects on native biological communities (Schabetsberger *et al.* 2009). If stocking can be justified on broader resource management grounds, isolated lakes in Alberta's boreal foothills lacking sport fish but with native small-bodied fish can provide good candidates for trout stocking.

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Table 1. Summary of the fish and *Chaoborus* populations, as well as limnological characteristics of the 14 study lakes located in the boreal foothills of Alberta, categorized by lake type. Shown are means $\pm$ SE (range).

Lake characteristics	Stocked (n = 6)	Lake type	
		Unstocked (n = 5)	Fishless (n = 3)
Fish populations			
Trout species (no. of lakes)	RN(5), BN(1), BK(1)	-	-
Trout stocking density (fish/ha)	357±140 (76-790)	-	-
Mean Trout total length (mm) ^a	333±30 (248-452)	-	-
Native fish species (no. of lakes)	DA (6), FM (3), BS (4)	DA (5), FM (5), BS (5)	-
Native fish densities (fish/ha) ^b	5115 (1288-17,766)	5292 (592-12,767)	-
<i>Chaoborus</i> populations			
<i>Chaoborus</i> species (no. of lakes)	CF (4), CP (2)	CF (3), CP (2), CT (2)	CF (3), CT (3), CA (3)
<i>Chaoborus</i> density (individuals/L)	1.7±1.4 (0.0-8.7)	7.3±4.2 (0.0-22.6)	24.5±4.6 (15.6-31.1)
Lake Characteristics			
Area (ha)	17.1± 4.4 (3.3-31.2)	11.1± 2.5 (5.9-17.5)	4.7±2.7 (1.0-10.0)
Maximum depth (m)	9.7± 1.1 (6.6-13.0)	7.1± 1.8 (3.9-13.4)	4.8±1.2 (2.5-6.0)
Surface temperature (°C)	17.8±0.3 (17.1-18.7)	18.6±0.2 (17.9-19.2)	19.9±0.1 (19.7-20.1)
Minimum dissolved oxygen (mg/L)	3.6±0.9 (1.4-6.9)	2.6±0.8 (0.5-4.8)	2.9±0.8 (1.7-4.5)
Total nitrogen (µg/L)	660±53 (495-850)	910±55 (722-1018)	887±159 (699-1203)
Total phosphorus (µg/L)	17±4 (9-34)	26±4 (14-39)	37±12 (16-55)
Chlorophyll-a (µg/L)	1.5±0.3 (0.2-2.4)	3.7±0.8 (1.9-6.3)	4.1±2.1 (0.6-7.9)
Conductivity (µS/cm)	157±32 (50-265)	151±32 (70-230)	124±75 (38-272)
pH	7.6±0.2 (6.8-7.9)	7.6±0.1 (7.2-7.8)	7.8±0.3 (7.3-8.4)
Secchi depth (m)	4.0±0.4 (2.7-5.9)	2.6±0.3 (1.7-3.7)	2.4±0.8 (1.4-4.0)

Note: RN, Rainbow Trout, *Oncorhynchus mykiss*; BN, Brown Trout, *Salmo trutta*; BK, Brook Trout, *Salvelinus fontinalis*; DA, dace, including Pearl Dace *Margariscus nachtriebi*, and a species complex consisting of Northern Redbelly Dace, *Chrosomus eos*, Finescale Dace, *Chrosomus neogaeus*, and their parthenogenic hybrid; FM, Fathead Minnow, *Pimephales promelas*; BS, Brook Stickleback, *Culaea inconstans*; CF, *Chaoborus flavican*; CP, *C. punctipennis*; CT, *C. trivittatus*; CA, *C. americanus*.

^aData from 2009 (J. Hanisch, University of Alberta, personal communication).

^bDA and FM only (Nasmith et al. 2010, 2012).

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Table 2 Mean ($\pm$ SE) abundance (individuals·L⁻¹), taxon length (mm), and biomass (mg·L⁻¹) of major taxa and LFTL richness in each month in 2009 for each lake type: stocked lakes (S; n= 6), unstocked lakes (U; n=5), and fishless lakes (F; n= 3). Also presented are results from Linear Mixed Models for each taxa with lake type (LT), month (M), and their interaction (I) as main effects, and lake as a random effect. If the interaction was not significant based on preliminary analysis ($p>0.05$), it was removed from the model.

*0.1> p >0.05, ** p <0.05

Taxa	Lake Type	May	June	July	August	Mean of Months	Main Effect	F-statistic
Abundance								
Cladocera	S	3.7 $\pm$ 1.8	25.3 $\pm$ 10.7	63.1 $\pm$ 10.3	49.0 $\pm$ 8.0	35.3 $\pm$ 6.2	LT	F _{2,11} =3.6*
	U	4.8 $\pm$ 3.0	22.2 $\pm$ 5.7	35.9 $\pm$ 13.7	22.2 $\pm$ 12.9	21.3 $\pm$ 5.2	M	F _{3,38} =23.7**
	F	0.4 $\pm$ 0.3	6.7 $\pm$ 2.2	22.6 $\pm$ 2.2	9.1 $\pm$ 3.0	10.5 $\pm$ 2.7	I	Removed
Calanoida	S	1.4 $\pm$ 0.8	10.5 $\pm$ 3.1	29.4 $\pm$ 6.2	22.6 $\pm$ 6.0	16.0 $\pm$ 3.1	LT	F _{2,11} =4.9*
	U	0.4 $\pm$ 0.2	18.8 $\pm$ 8.0	18.7 $\pm$ 4.7	35.5 $\pm$ 13.7	18.3 $\pm$ 4.8	M	F _{3,32} =33.0**
	F	0.1 $\pm$ 0.0	1.5 $\pm$ 1.3	9.7 $\pm$ 4.4	1.9 $\pm$ 0.5	3.6 $\pm$ 1.6	I	F _{6,32} =2.5**
Cyclopoida	S	20.7 $\pm$ 9.2	16.9 $\pm$ 5.6	27.5 $\pm$ 7.1	20.5 $\pm$ 2.5	21.4 $\pm$ 3.2	LT	F _{2,11} =6.6**
	U	41.0 $\pm$ 17.6	14.4 $\pm$ 9.0	13.0 $\pm$ 5.5	10.3 $\pm$ 3.3	19.7 $\pm$ 5.6	M	F _{3,38} =1.2
	F	3.7 $\pm$ 3.6	0.3 $\pm$ 0.2	3.9 $\pm$ 1.6	2.4 $\pm$ 1.4	2.5 $\pm$ 0.8	I	Removed
Length								
Cladocera	S	n/a	0.82 $\pm$ 0.05	0.87 $\pm$ 0.03	0.88 $\pm$ 0.06	0.85 $\pm$ 0.03	LT	F _{2,11} =9.5**
	U	n/a	0.76 $\pm$ 0.17	0.77 $\pm$ 0.14	0.68 $\pm$ 0.11	0.74 $\pm$ 0.08	M	F _{2,26} =0.0
	F	n/a	1.25 $\pm$ 0.04	1.16 $\pm$ 0.18	1.24 $\pm$ 0.14	1.22 $\pm$ 0.07	I	Removed
Calanoida	S	n/a	n/a	1.05 $\pm$ 0.05	1.05 $\pm$ 0.02	1.05 $\pm$ 0.02	LT	F _{2,11} =4.7**
	U	n/a	n/a	1.09 $\pm$ 0.08	1.14 $\pm$ 0.06	1.12 $\pm$ 0.05	M	F _{1,13} =2.8
	F	n/a	n/a	1.24 $\pm$ 0.06	1.34 $\pm$ 0.02	1.29 $\pm$ 0.04	I	Removed
Cyclopoida	S	n/a	n/a	0.88 $\pm$ 0.03	0.83 $\pm$ 0.01	0.85 $\pm$ 0.01	LT	F _{2,11} =2.2
	U	n/a	n/a	0.74 $\pm$ 0.09	0.80 $\pm$ 0.04	0.77 $\pm$ 0.05	M	F _{1,13} =0.8
	F	n/a	n/a	0.53 $\pm$ 0.11	0.81 $\pm$ 0.26	0.67 $\pm$ 0.14	I	Removed

Biomass								
Cladocera	S	12.8±7.4	96.2±47.9	359.5±67.7	286.0±51.8	188.6±37.0	LT	F _{2,11} =1.5
	U	19.4±11.6	121.8±42.1	200.4±111.2	80.5±45.3	105.5±33.0	M	F _{3,38} =28.7**
	F	0.7±0.5	45.9±20.6	132.0±49.6	78.6±7.9	70.1±19.3	I	Removed
Calanoida	S	9.4±4.4	47.9±15.9	151.1±34.5	120.9±36.0	82.3±17.0	LT	F _{2,11} =2.2
	U	0.6±0.3	73.0±31.5	97.3±18.7	197.7±79.9	92.1±25.8	M	F _{3,38} =47.4**
	F	0.2±0.1	25.3±22.1	107.4±81.1	32.0±7.1	45.0±23.4	I	Removed
Cyclopoida	S	46.8±21.4	33.8±8.6	86.7±24.2	69.5±14.6	59.2±9.5	LT	F _{2,11} =11.1**
	U	42.3±17.6	35.7±18.7	34.9±20.4	28.8±16.4	35.4±8.5	M	F _{3,38} =1.3
	F	3.7±3.1	0.4±0.2	3.3±1.6	3.4±1.6	2.6±0.8	I	Removed
Richness								
	S	6.0±0.3	7.2±0.5	9.0±0.9	6.3±0.6	7.1±0.4	LT	F _{2,11} =10.8**
	U	4.8±0.4	6.2±1.0	5.8±0.4	4.4±0.2	5.3±0.3	M	F _{3,38} =8.1**
	F	3.5±0.5	4.3±0.3	5.7±0.3	5.0±1.0	4.7±0.4	I	Removed

Figure legends

Fig. 1. Non-metric Multidimensional Scaling (NMS) joint plot of pelagic microcrustacean communities and key taxa in study lakes in August 2009. Vectors point in the direction of increased presence of key microcrustacea taxa ($r^2 > 0.5$) and the length of vectors indicate the strength of the relationship with the ordination axes. Black triangles: stocked lakes ($n=6$), dark grey squares: unstocked lakes ($n=5$), light grey circles: fishless lakes ($n=3$). None of the environmental variables examined (Table 1) were correlated ($r^2 > 0.3$) with the axes.

Fig. 2. Non-metric Multidimensional Scaling (NMS) ordinations of pelagic microcrustacean communities in study lakes during the four monthly sampling periods (May-August) in 2009. (A) Successional vectors follow monthly centroids of each lake type through time. (B) Joint plot vectors point in the direction of increased presence of microcrustacea taxa ($r^2 > 0.5$); the length of vectors indicate the strength of the relationship with the ordination axes. None of the environmental variables examined (Table 1) were strongly correlated with the axes ($r^2 > 0.3$). Symbols in (B) are individual lake-months: black symbols: stocked lakes; dark grey symbols: unstocked lakes; light grey symbols: fishless lakes; circles: May, squares: June, triangles: July, diamonds: August; “plus” signs: monthly centroids.

Fig. 3. Results from a two-way Variance Partitioning Analysis of effects environmental variables and fish taxa on the composition of microcrustacean communities in June, July and August, 2009. Values represent the percentage of variance in the composition of microcrustacean communities explained independently by environmental variables and fish taxa, the percentage shared by environment and fish, and the unexplained variation.

Fig. 4. Mean ($\pm$ SE) relative abundance of Cladocera, Calanoida, and Cyclopoida at 1 m (vs. 2 m) within stocked ($n=6$), unstocked ($n=4$), and fishless ($n=2$) lakes. Interactions between depth and lake type were significant ($p < 0.05$) for all three taxa, based on Linear Mixed-Model analyses.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Appendix A.

Table A1. Taxa of pelagic microcrustaceans identified in the study lakes during 2009. Species listed together could not always be differentiated. Mean lengths $\pm$ SE (n) are from all individuals measured across all lakes and months. The % Occurrence in each lake type is based on all lake-months (May-August, except one fishless lake that was not sampled in May). S: stocked (n=24), U: unstocked (n=20), F: fishless (n=11).

Order	Family	Genus	Species	Mean Length	% Occurrence		
				$\pm$ SE (n)	S	U	F
Cladocera	Bosminidae	Bosmina	longirostris	0.27 $\pm$ 0.00 (786)	92	70	36
	Chydoridae	-	-	0.26 $\pm$ 0.00 (220)	42	55	27
	Daphniidae	Ceriodaphnia	lacustris	0.73 $\pm$ 0.05 (7)	8	0	0
			catawba	1.20 $\pm$ 0.01 (377)	42	35	18
		Daphnia	galeata mendotae	1.33 $\pm$ 0.01 (666)	79	5	9
			middendorffiana	2.36 $\pm$ 0.05 (121)	4	15	45
			parvula	0.96 $\pm$ 0.01 (118)	33	15	0
			pulex	1.69 $\pm$ 0.02 (604)	42	40	64
			rosea	1.46 $\pm$ 0.01 (317)	38	10	45
			schodleri	1.23 $\pm$ 0.01 (212)	4	10	45
	Sididae	Diaphanosoma	brachyurum/	0.63 $\pm$ 0.01 (1077)	67	65	18
			leuchtenbergianum				
Calanoida	Diaptomidae	Acanthodiaptomus	denticornis	1.68 $\pm$ 0.01 (283)	13	30	18

		<i>Diaptomus</i>	<i>leptopus</i>	1.95 ± 0.03 (134)	0	0	82
		<i>Skistodiaptomus</i>	<i>oregonensis</i>	1.25 ± 0.00 (981)	92	65	9
<i>Cyclopoida</i>	<i>Cyclopidae</i>	<i>Cyclops</i>	<i>bicuspidatus thomasi</i>	0.98 ± 0.00 (565)	79	35	18
		<i>Mesocyclops</i>	<i>edax/leukarti</i>	1.16 ± 0.01 (877)	83	85	55

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