

## Predator driven changes in prey size distribution stabilize secondary production in lacustrine food webs

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### Abstract

Data from 12 Colorado mountain lakes, some containing invertivorous fish and some without fish, show that fish suppressed biomass of benthic invertebrates and zooplankton and reduced their mean and maximum body size, but did not alter invertebrate production. Resilience of invertebrate production occurred because the smaller body size of invertebrates in lakes with fish raised the community P/B ratio and simultaneously caused an increase in abundance of small invertebrates (<10 mm benthic invertebrates; <1.5 mm zooplankton), probably by releasing small invertebrates from competition with large invertebrates. Together, these two changes in the invertebrate communities stabilized secondary production even though total invertebrate biomass was reduced. Compensatory stability of herbivore production in response to size selective predation by fish may be a common phenomenon in aquatic food webs. Because it involves both an increase in P/B ratio and an increase in biomass of invertebrates with high P/B ratio, compensation may to some degree explain the commonly observed failure of predation pressure by primary consumers to cause an increase in biomass of primary producers for trophic cascades with three levels, even when invertebrate biomass is reduced by predation. Addition of a fourth trophic level consisting of piscivorous fish would likely have less predictable effects because piscivores produce offspring that are invertivorous predators, thus potentially adding a qualitatively different compensatory mechanism to the trophic cascade.

Fish are an organizing feature of lake food webs (Brooks and Dodson 1965; Carpenter et al. 1985; Northcote 1988). The trophic cascade concept predicts that predators such as fish have alternating and opposite effects on the biomass of successively lower trophic levels down to primary producers ( Hairston et al. 1960; Paine 1980; Carpenter and Kitchell 1993; Terborgh and Estes 2010). Thus, if invertivorous fish are introduced in a fishless lake, invertebrate biomass and body size should decrease (Brooks and Dodson 1965) and algal biomass should increase (Carpenter and Kitchell 1993).

Some studies of trophic cascades show that fish substantially suppress biomass of invertebrate grazers and increase the abundance of primary producers (e.g., Carpenter et al. 1987; Leavitt et al. 1989; Jeppesen et al. 1999; Schindler and Vallentyne 2008), but other studies show that changes in primary producer biomass are weak or undetectable despite reductions in invertebrate biomass (e.g., Brett and Goldman 1996; Parker et al. 2001; Lake et al. 2011; Demi et al. 2012).

Trophic cascades appear to be strongest in nutrient poor environments, possibly because of increased abundance of unpalatable algae in nutrient enriched lakes (Sarnelle 1992; Jeppesen et al. 2003), and in ecosystems with low species diversity of primary consumers, for reasons not yet fully explained (Power 1990; Polis 1999). It is not clear why trophic cascades vary in strength when environmental conditions appear to be similar for lakes with and without fish, even if diversity of primary consumers is low. Explanations connected to trophic status or diversity could lie in seldom quantified effects of predation (e.g., varied size distributions of fish, DeLong et al. 2015; behaviorally mediated changes in predation, Schmitz et al. 1997; intraspecific competition of predators, Jones and Post 2013).

Rocky Mountain National Park (RMNP), the location of this study, is an ideal location for analysis of trophic cascades, as it offers a high density of lakes with and without fish. Furthermore, these lakes have been maintained with or without fish for several decades during which the food webs likely have reached equilibrium with respect to presence or absence of fish (Knapp et al. 2001; Schabetsberger et al. 2009). The purpose of the present study is to quantify the effect of fish on body size, biomass, and production of both benthic and planktonic invertebrates in physically similar lakes of RMNP.

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The fish of interest here are trout (*Oncorhynchus clarkii* and *Salvelinus fontinalis*); no other fish were present. Given that fish can suppress the mean size of invertebrates in lakes (Schielke et al. 2011; Jones and Post 2013; DeLong et al. 2015), one hypothesis is that fish cause reductions in mean body size and lower total biomass of invertebrates of the RMNP lakes. A corollary hypothesis, which is the main basis of this study, is that fish do not suppress invertebrate production in lakes to the extent that they suppress biomass. Differential response of invertebrate biomass and production may to some extent explain why suppression of invertivorous fish by piscivores does not consistently suppress biomass of primary producers in lakes.

**Methods**

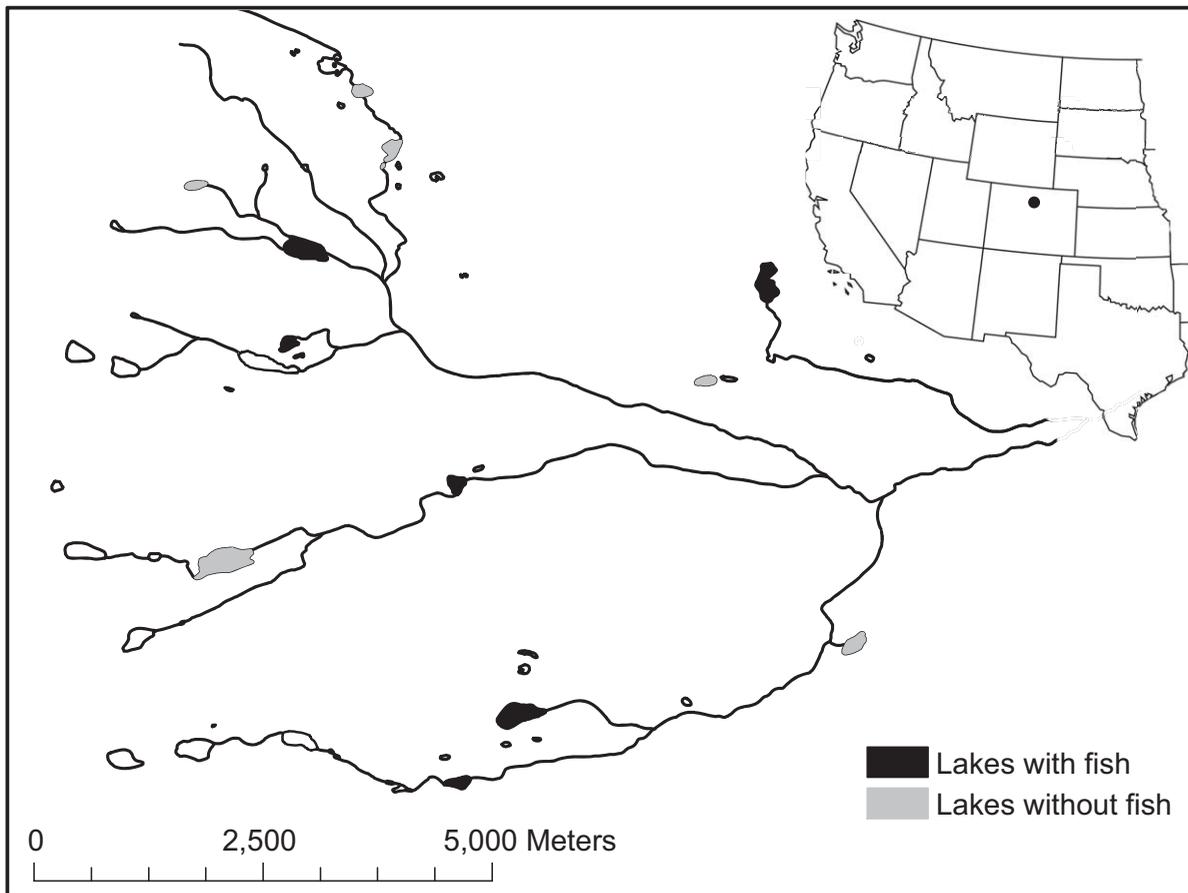
The study area is the headwaters of the North St. Vrain Creek (Wild Basin) of RMNP (Fig. 1). Lakes in the study vary in elevation, watershed area, and depth, but the two groups of lakes (six without fish, six with fish) did not differ significantly in any of these physical characteristics ( $p > 0.05$ ). Relevant

anthropogenic influence on the lakes is limited to nitrogen enrichment by atmospheric deposition (Lewis and Grant 1980; Baron et al. 2009) and introduction of fish to some lakes (Table 1).

Field studies were conducted on the 12 lakes during the 2009–2012 ice-free season (July–October). All lakes were sampled on multiple dates for at least 1 yr and five lakes were sampled multiple times in multiple years (Table 1). Samples were collected three or four times per year from the time of spring ice melt to onset of ice cover at intervals averaging 31 d ( $SE \pm 4.1$ ) and again the following spring after ice melt.

Records provided by the U.S. Fish and Wildlife Service indicate that of the six fishless lakes, two were never stocked and four were stocked but became fishless because of inadequate spawning habitat. The four lakes that were stocked but are now fishless have not contained fish for at least 30 yr and therefore likely show no residual effects of having been stocked (Knapp et al. 2005).

On each sampling date at each lake, temperature, Secchi depth, and outlet discharge were measured. Two liters of water were collected just below the surface, filtered through



**Fig. 1.** Study area and lake locations in Rocky Mountain National Park, Colorado. The bottom left corner of the map is 40.1696° latitude and -105.6658° longitude.

**Table 1.** Overview of lakes included in the study. NF = no fish; BT = brook trout; CT = cutthroat trout.

Lake	Fish Present	Elevation (m)	Lake area (ha)	Max. depth (m)	Mean depth (m)	Watershed area (ha)	Years Sampled
Bluebird	NF	3341	5.0	9.3	3.4	317	2010, 2012
Falcon	NF	3377	1.1	7.7	2.5	72	2011
Finch	NF	3021	2.6	2.6	1.3	27	2010
Lion Lake 1	NF	3373	1.8	2.8	0.6	325	2009
Lion Lake 2	NF	3469	1.5	12.8	4.3	230	2011, 2012
Twin	NF	2991	1.3	2.6	0.9	13	2009
Mean		3262 ± 83	2.2 ± 0.6	6.3 ± 1.8	2.2 ± 0.6	164 ± 59	
Box	BT	3266	1.6	9.3	3.9	28	2012
L. Hutcheson	CT	3304	1.7	7.6	2.9	396	2011
Ouzel	CT, BT	3052	2.0	2.7	0.7	1028	2009
Pear	CT	3225	6.0	16.8	6.2	182	2011, 2012
Sandbeach	CT	3135	4.8	7.9	2.4	67	2011, 2012
Thunder	CT	3225	5.9	12.9	4.3	321	2009, 2010
Mean		3201 ± 38	3.7 ± 0.9	9.5 ± 2.0	3.4 ± 0.8	337 ± 150	

a Whatman GF/C filter, and analyzed for dissolved organic carbon with a TOC analyzer (combustion with catalytic oxidation and nondispersive infrared CO<sub>2</sub> analysis), total dissolved nitrogen (Valderrama 1981; Davi 1993), total dissolved phosphorus (Murphy and Riley 1962; Valderrama 1981; Langner and Hendrix 1982), and chlorophyll *a* (Chl *a*) of phytoplankton (Marker et al. 1980; Nusch 1980). For each lake, periphyton was collected from four depths (15 cm, 30 cm, 45 cm, and 60 cm) at two or three arbitrarily selected locations for analysis of Chl *a*. At each lake for each of these depths, periphyton was scraped from a fixed area of the top surface of two rocks. Periphyton chlorophyll was analyzed by ethanol extraction with sonication, followed by spectrophotometric analysis (Lewis and McCutchan 2010).

Benthic invertebrates were sampled from the littoral zone, which is defined for this study as 0–3 m depth, rather than from the entire lake. Similarity among lakes in littoral benthic habitat favors inter-lake comparisons, whereas offshore habitat ranges considerably among lakes (e.g., maximum depth range is 3–17 m).

Large, motile epibenthic invertebrates (e.g., Ephemeroptera, Hirudinea, Odonata) were collected with a benthic sled similar to the one described by Hessler and Sanders (1967; mesh size = 250 μm; mouth = 20 cm). A piston corer (5.76 cm<sup>2</sup>) was used to collect infauna (e.g., *Pisidium* sp., Chironomidae, Oligochaeta; Gillespie et al. 1985). Both devices were used at 6–12 arbitrarily selected sites around each lake. At each site, three sled tows (3 m or more in length, 0.5 m s<sup>-1</sup>) were taken perpendicular to the shoreline, pooled, and stored in 70% ethanol and two sediment core samples were collected, pooled, and stored in a similar manner. All benthic invertebrate samples were taken at depths ≤ 3 m, within 7 m of shore, and at least 50 m from the inlet or outlet.

Benthic invertebrates were separated and identified to the lowest practicable taxonomic unit (typically genus or species; Thorp and Covich 1991; Merritt et al. 2008). For rare taxa, all individuals from each sample were measured with an optical micrometer. For abundant taxa, body lengths of at least 100 organisms were measured; appendages such as cerci and antennae were not included in the measurements. The relationship of length (*L*) to individual dry mass (*M*) was assumed to be  $M = aL^b$  where values of constants *a* and *b* were taken from Benke et al. (1999), Miserendino (2001), Baumgartner and Rothaupt (2003), and Johnston and Cunjak (1999).

Zooplankton were sampled from a raft with vertical tows of a conical zooplankton net (20 cm diameter, 53 μm mesh) from near the bottom to the surface at a rate of about 0.5 m s<sup>-1</sup>. Filtered volumes for zooplankton samples were assumed to reflect a filtration efficiency of 50% (Walters and Vincent 1973; Lewis 1979). One tow was taken at the deepest location in the lake and at least three other tows were taken at arbitrary locations at depths greater than one meter. Samples were fixed in 95% ethanol and transferred to 70% ethanol for storage (Black and Dodson 2003).

Zooplankton samples were concentrated and subsampled with a Hensen-Stempel pipette. Zooplankton were identified to genus or species according to Pennak (1989), Thorp and Covich (1991), and Stemberger (1979), and were enumerated in a 1 mL Sedgewick-Rafter cell or 20 mL modified Bogorov cell depending on the abundance of the taxon. Between 5% and 100% of each sample was evaluated, depending on abundance. Abundances were corrected for tow depth. For rare taxa, all individuals were measured for length; for abundant taxa at least 100 organisms of each taxon were measured for length. Dry mass (DM) was calculated from equations for crustaceans, rotifers and *Chaoborus trivittatus* (Dumont and Balvy 1979; EPA Great Lakes National Program Office 2003).

**Table 2.** Comparisons of mean annual species richness, Shannon diversity index, individual dry body mass, community biomass, and community production for lakes with and without fish. Individual dry body mass is shown in mg for benthic invertebrates and  $\mu\text{g}$  for zooplankton. Significant differences between categories are depicted with an asterisk ( $*p < 0.05$ ). Small taxa are those with a mean annual body size of  $< 1$  mg for benthic macroinvertebrates and  $< 1$   $\mu\text{g}$  for zooplankton.

Metric	Benthic invertebrates			Zooplankton		
	Lakes without fish Mean $\pm$ SE	Lakes with fish Mean $\pm$ SE	<i>p</i>	Lakes without fish Mean $\pm$ SE	Lakes with fish Mean $\pm$ SE	<i>p</i>
Species richness ( <i>n</i> )	18 $\pm$ 3	14 $\pm$ 1	0.17	15 $\pm$ 1	16 $\pm$ 2	0.34
Shannon diversity	1.49 $\pm$ 0.14	1.08 $\pm$ 0.18	0.09	1.53 $\pm$ 0.11	1.40 $\pm$ 0.16	0.52
Body size (mgDM, $\mu\text{g}$ )	0.19 $\pm$ 0.06	0.03 $\pm$ 0.01	<0.01*	2.67 $\pm$ 0.57	0.49 $\pm$ 0.47	0.03*
Biomass (mgDM $\text{m}^{-2}$ )	705 $\pm$ 72	364 $\pm$ 76	<0.01*	71 $\pm$ 14	41 $\pm$ 9	0.04*
Production (mgDM $\text{m}^{-2} \text{yr}^{-1}$ )	1871 $\pm$ 280	1544 $\pm$ 356	0.49	451 $\pm$ 103	308 $\pm$ 113	0.37
P/B	2.92 $\pm$ 0.20	4.54 $\pm$ 0.22	0.04*	7.10 $\pm$ 0.68	13.72 $\pm$ 2.02	0.02*
Small taxa biomass (mgDM $\text{m}^{-2}$ )	175 $\pm$ 32	353 $\pm$ 71	0.03*	4 $\pm$ 3	29.7 $\pm$ 12.3	0.02*
Small taxa production (mgDM $\text{m}^{-2} \text{yr}^{-1}$ )	812 $\pm$ 180	1447 $\pm$ 231	0.04*	75 $\pm$ 49	202 $\pm$ 65	0.03*
Small taxa P/B	4.87 $\pm$ 0.52	5.60 $\pm$ 0.56	0.66	25.44 $\pm$ 3.78	20.46 $\pm$ 4.70	0.45

For taxa with distinct cohorts that could be followed over time (e.g., *Siphonurus occidentalis*), production was estimated for each taxonomic group over each interval between sampling dates by the increment-summation method (Benke and Huryn 2006). The estimate over the interval between two sampling dates for a given taxon is  $P = (\bar{N} \Delta W) / t$  where  $P$  is daily production over an interval of  $t$  days,  $\bar{N}$  is the mean abundance between two dates spanning the interval, and  $\Delta W$  is the change in mean individual mass over the interval for a taxon. Annual production is the summation of  $P$  over all days of the year when growth occurs (growing season).

For taxa without distinct cohorts (e.g., Chironomidae), the instantaneous growth method was used to estimate production of benthic invertebrates (Benke and Huryn 2006). The estimate for a particular taxon over an interval of length  $t$  is  $P = g \bar{B}$  where  $P$  is daily production,  $g$  is daily instantaneous growth rate,  $\bar{B}$  is the mean interval biomass, and  $t$  is the length of the interval (days). Annual production is the sum of production for each taxon across all intervals in a growing season.

For benthic invertebrates, growth rates ( $g$ ) were estimated by use of a multiple regression equation that relates growth rate to body mass and temperature. The equation was calibrated with data from all sampling intervals for all taxa that could be followed as cohorts ( $N = 83$ ,  $p < 0.001$ ,  $R^2 = 0.28$ ; Huryn and Wallace 1986; Hauer and Benke 1987; McCutchan and Lewis 2002). The equation is  $\log g = -2.2 + 0.065 T - 0.19 \log m$  where  $g$  is growth rate per day,  $T$  is the mean temperature for the interval ( $^{\circ}\text{C}$ ), and  $m$  is mean dry mass for the interval in mg. For copepods, cladocera and rotifers, the model of Shuter and Ing (1997) was used:  $\log P = \alpha_{\text{taxon}} + \log(\bar{B}t) + 0.045 T_t + 0.6 \log(t)$  where  $P$  is production,  $\alpha_{\text{taxon}}$  is a taxon specific correction,  $\bar{B}_t$  is the mean growing season population biomass,  $T_t$  is the mean growing season temperature ( $^{\circ}\text{C}$ ) and  $t$  is the growing season length in days.

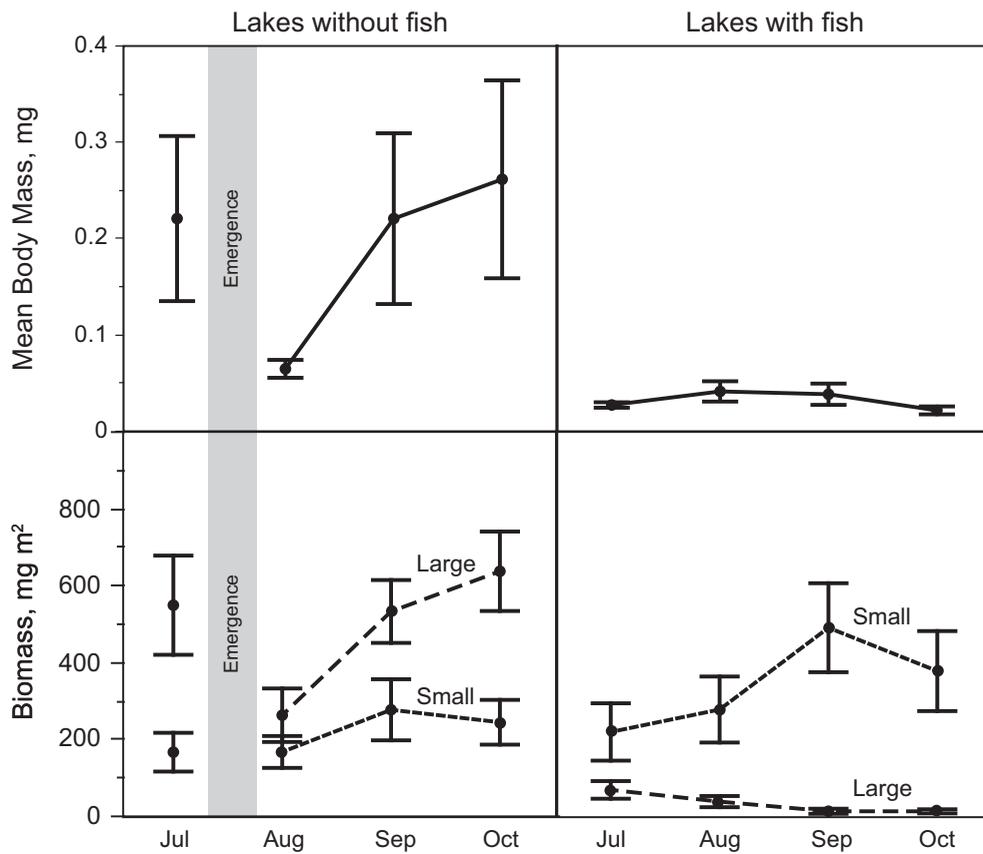
Quantification of  $P$  for individual invertebrate taxa based on field data and standardized equations as conducted for the present analysis is subject to a high degree of error variance. This defect in computation of  $P$  for individual taxa is offset to some degree for present purposes by pooling of  $P$  at the community level for comparisons of lake categories (fish, no fish), as shown in the results section. Also, the very large contrast in composition and size distribution of invertebrates across lake categories for this study greatly reduces the likelihood that general conclusions based on pooled  $P$  values are qualitatively incorrect.

When the water temperature is  $< 4^{\circ}\text{C}$  (November–June), the instantaneous growth rate of freshwater invertebrates is near zero and sampling for the purpose of measuring production is unnecessary (Pennak 1968; Makarewicz and Likens 1979; McCutchan and Lewis 2002). Growing season production for zooplankton is here assumed to equal annual zooplankton production (Pennak 1968; Shuter and Ing 1997).

For lakes that were sampled in more than 1 yr, body mass, biomass and production of invertebrates, chemical constituents, and concentrations of Chl *a* for phytoplankton and periphyton did not differ among years (ANOVA,  $p > 0.05$ ). Interannual averages were used for lakes that were sampled in multiple years.

Contrasts between lakes with and without fish for chemical constituents, concentrations of phytoplankton and periphyton, and invertebrate biomass were based on a repeated measures ANOVA test. Data were log transformed for analysis when data violated the assumption of equal variance, and the Greenhouse-Geisser correction was used when the assumption of sphericity was violated.

Data for the two groups of lakes also allow comparisons of community diversity. Diversity was contrasted between the two groups by mean taxonomic richness and Shannon Diversity Index (Shannon and Weaver 1948). Because the literature



**Fig. 2.** Mean dry body mass ( $\pm$  SE) of individual benthic invertebrates for lakes with and without fish (gray area indicates peak emergence of *S. occidentalis*). Mean ( $\pm$  SE) monthly benthic invertebrate dry biomass per unit area for lakes without and with fish (gray area indicates peak emergence of *S. occidentalis*).

shows varied responses of diversity to fish predation (e.g., Carlisle and Hawkins 1998; Knapp et al. 2001; Schilling et al. 2009), the basis for statistical testing is the null hypothesis, i.e., no effect of fish predation on diversity. Alpha diversity (diversity for individual lakes) was compared between lake categories with Student’s *t*-test. Beta diversity (diversity for all lakes of a given category) was quantified with the Sorensen Similarity Index (Sorensen 1948). Similarity values were averaged for each pairwise category (fishless-fishless, fishless-fish, and fish-fish) and groups were compared with a Tukey-Kramer HSD test.

A Student’s *t*-test was used to test the hypotheses that mean annual benthic invertebrate body mass, end of growing season biomass, and annual production were higher in the absence of fish because of predation. The same test was used for the hypothesis that production of small invertebrate taxa is greater in the presence of fish because elimination of large invertebrates by fish reduces competition (e.g., food availability) for small invertebrates. The Student’s *t*-test also was used to test similar hypotheses for zooplankton. For all contrasts, data were log transformed prior to analysis when variances for the groups were not equal.

**Results**

None of the abiotic measurements differed between lakes with and without fish over the growing season ( $p > 0.05$ ) and no interaction for time was found for any abiotic variables ( $p > 0.05$ ). Mean annual phytoplankton Chl *a* concentrations did not differ statistically between lakes with fish ( $2.6 \pm 0.8 \mu\text{g L}^{-1}$ ) and without fish ( $1.7 \pm 0.4 \mu\text{g L}^{-1}$ ) over the growing season (repeated measures ANOVA, data log transformed,  $F_{(1,10)} = 1.58, p = 0.24$ ). The quantity of periphyton Chl *a* also did not differ between lakes with ( $5.7 \pm 1.1 \mu\text{g cm}^{-2}$ ) and without fish ( $5.4 \pm 0.7 \mu\text{g cm}^{-2}$ ; repeated measures ANOVA,  $F_{(1,10)} = 0.08, p = 0.78$ ).

Forty-eight benthic invertebrate taxa and 36 zooplankton taxa were collected in the 12 lakes. Mean taxonomic richness (number of taxa) and Shannon Diversity Index were not significantly different for benthic invertebrates and zooplankton in the two lake categories (Table 2). Mean annual individual body mass and community biomass for benthic invertebrates and zooplankton were lower in lakes containing fish than in lakes without fish (Table 2). Despite significant differences in community biomass, production of benthic invertebrate and zooplankton did not differ between

**Table 3.** Annual mean dry body mass and population biomass in order of decreasing size for individuals of the most abundant benthic invertebrate taxa in lakes with and without fish (mean ± SE). Significant differences between lake categories for mean annual dry body mass are shown in the first column. In the last column, significance of biomass differences is shown for the end of the growing season (September and October pooled).

Taxonomic group	Mean body mass (mg individual <sup>-1</sup> )	Population biomass (mgDM m <sup>-2</sup> )				p
		July	August	September	October	
<i>Lakes without fish</i>						
<i>Limnephilus</i> <sup>1</sup>	8.98 ± 2.00	100 ± 47	89 ± 41	68 ± 27	80 ± 21	<0.01*
<i>Siphonurus occidentalis</i> <sup>2</sup>	7.13 ± 2.29*	282 ± 119	58 ± 26	202 ± 69	331 ± 105	<0.01*
<i>Ameletus velox</i> <sup>2</sup>	4.86 ± 0.51	6 ± 5	32 ± 22	75 ± 52	79 ± 56	0.04*
<i>Hesperophylax</i> sp. <sup>1</sup>	3.85 ± 0.80	117 ± 58	25 ± 25	3 ± 2	11 ± 11	0.72
<i>Psychoglypha subborealis</i> <sup>1</sup>	1.70 ± 0.52*	0 ± 0	0 ± 0	18 ± 13	37 ± 32	0.05*
<i>Amphiagrion abbreviatum</i> <sup>3</sup>	0.83 ± 0.24	7 ± 4	15 ± 9	53 ± 38	18 ± 13	0.12
<i>Callibaetis ferrugineus</i> <sup>2</sup>	0.54 ± 0.17	43 ± 29	26 ± 17	48 ± 32	37 ± 23	0.32
Chironomidae <sup>4</sup>	0.07 ± 0.02	120 ± 41	137 ± 43	218 ± 47	197 ± 40	0.25
Ostracoda	0.07 ± 0.02	21 ± 17	8 ± 5	20 ± 16	19 ± 15	0.71
<i>Pisidium</i> sp. <sup>5</sup>	0.02 ± 0.01	14 ± 6	10 ± 5	37 ± 28	26 ± 16	0.20
Oligochaeta	0.01 ± 0.01	16 ± 13	16 ± 7	21 ± 12	12 ± 4	0.13
<i>Lakes with fish</i>						
<i>Limnephilus</i> <sup>1</sup>	8.51 ± 4.04	8 ± 5	9 ± 9	6 ± 5	1 ± 1	
<i>Siphonurus occidentalis</i> <sup>2</sup>	1.08 ± 0.05	8 ± 6	0 ± 0	1 ± 1	0 ± 0	
<i>Ameletus velox</i> <sup>2</sup>	- ± -	0 ± 0	0 ± 0	0 ± 0	0 ± 0	
<i>Hesperophylax</i> sp. <sup>1</sup>	3.53 ± 1.08	24 ± 14	28 ± 16	4 ± 2	4 ± 2	
<i>Psychoglypha subborealis</i> <sup>1</sup>	0.85 ± 0.17	0 ± 0	1 ± 1	3 ± 2	4 ± 2	
<i>Amphiagrion abbreviatum</i> <sup>3</sup>	- ± -	0 ± 0	0 ± 0	0 ± 0	0 ± 0	
<i>Callibaetis ferrugineus</i> <sup>2</sup>	0.83 ± -	8 ± 8	7 ± 7	21 ± 21	17 ± 17	
Chironomidae <sup>4</sup>	0.05 ± 0.02	144 ± 46	206 ± 70	332 ± 92	237 ± 69	
Ostracoda	0.09 ± 0.02	26 ± 16	32 ± 19	52 ± 49	7 ± 5	
<i>Pisidium</i> sp. <sup>5</sup>	0.03 ± 0.01	24 ± 21	19 ± 11	59 ± 30	86 ± 55	
Oligochaeta	0.02 ± 0.01	21 ± 7	19 ± 12	43 ± 14	51 ± 23	

<sup>1</sup>Trichoptera <sup>2</sup>Ephemeroptera <sup>3</sup>Odonata <sup>4</sup>Diptera <sup>5</sup>Veneroida.  
\*p < 0.05.

lake categories because of (1) higher P/B ratio in lakes with fish than lakes without fish, and (2) higher biomass of small invertebrates in lakes with fish (Table 2).

**Benthic invertebrates**

Sorensen similarity was slightly but significantly lower among lakes without fish (0.54 ± 0.03) than among lakes with fish (0.67 ± 0.02; p < 0.01). Several taxa were present in all or nearly all lakes: Chironomids, Mollusca (*Pisidium* sp.), Hemiptera (*Corisella* sp.), oligochaetes, ostracods, trombidiforms, and Trichoptera (*Limnephilus*). Twenty-two taxa, including six odonate genera and four beetle genera, were present in fishless lakes and absent in lakes with fish, but most of these were present in only one or two lakes. All taxa in lakes with fish were also found in lakes without fish.

Mean benthic invertebrate body size was much lower in lakes with fish for the majority of the growing season (Fig. 2; July, September, and October, p < 0.05), but not so in August following emergence of *Siphonurus*. *Siphonurus* and

*Psychoglypha* were smaller in lakes with fish (Table 3) because of the low abundance of late instar individuals in lakes with fish.

Invertebrate biomass in lakes without fish reached a post emergence plateau in September–October similar to the pre-emergence plateau in July (Fig. 2). Invertebrate biomass in lakes containing fish increased slightly from July to September without any detectable emergence suppression, probably because of temporally dispersed emergence of dominant taxa and the near absence of *Siphonurus*.

Fish suppressed the biomass of caddisfly taxa over the growing season. One taxon (*Hesperophylax*), however, showed low suppression during the growing season but was greatly suppressed in lakes with fish just after ice out, when its mean body size was greatest.

Four of the five largest abundant benthic invertebrate taxa were greatly suppressed in biomass per unit area by fish (Table 3). No small taxa (taxa with a mean annual body size < 0.1 mg) differed significantly in biomass per unit area

**Table 4.** Annual production in decreasing order of body mass for dominant benthic invertebrate taxa in lakes with and without fish (mg DM m<sup>-2</sup> yr<sup>-1</sup>; mean ± SE; \*p < 0.05).

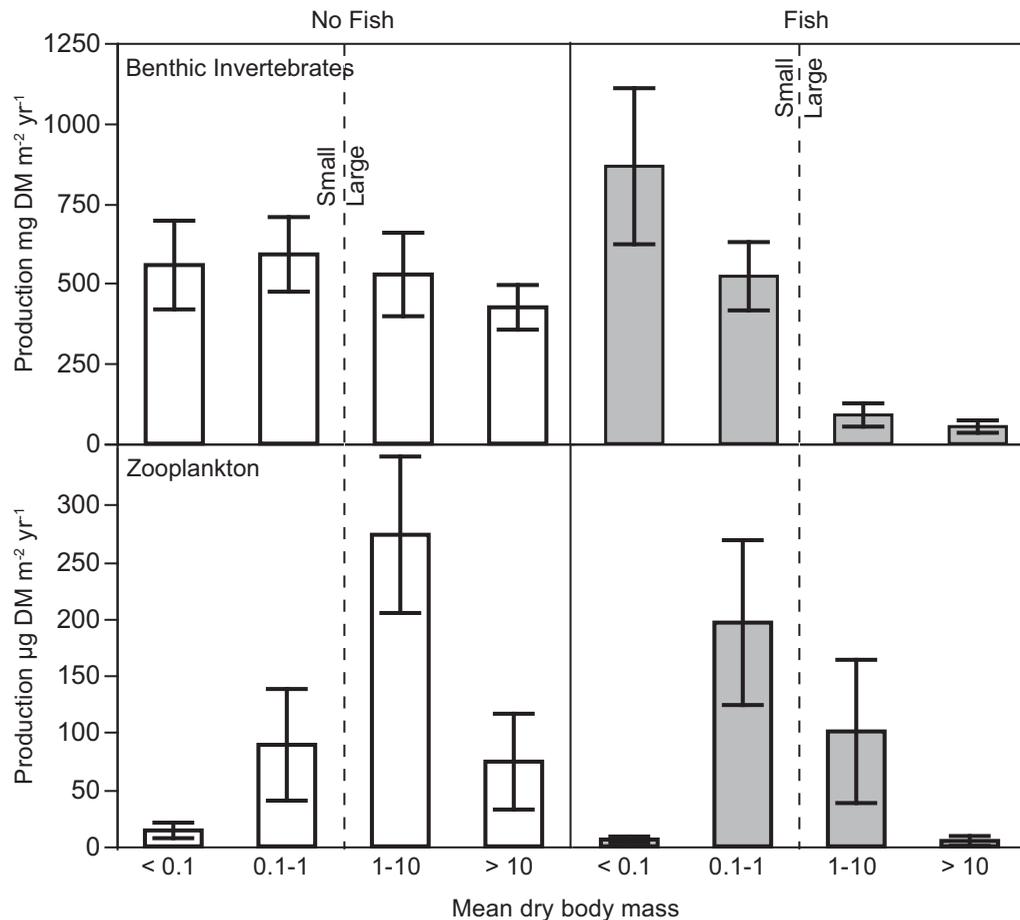
Taxonomic group	Lakes without fish	Lakes with fish	p
<i>Limnephilus</i>	159 ± 31	14 ± 13	<0.01*
<i>Siphonurus occidentalis</i>	249 ± 87	5 ± 3	0.04*
<i>Ameletus velox</i>	63 ± 40	0 ± 0	0.17
<i>Hesperophylax</i> sp.	73 ± 37	49 ± 18	0.58
<i>Psychoglypha subborealis</i>	18 ± 12	1 ± 1	0.22
<i>Amphiagrion abbreviatum</i>	56 ± 36	0 ± 0	0.18
<i>Callibaetis ferrugineus</i>	122 ± 78	45 ± 45	0.42
Chironomidae	754 ± 165	976 ± 277	0.51
Ostracoda	34 ± 19	88 ± 60	0.42
<i>Pisidium</i> sp.	96 ± 35	163 ± 72	0.44
Oligochaeta	100 ± 26	127 ± 38	0.57
Total production	1871 ± 280	1544 ± 356	0.49

\* p < 0.05.

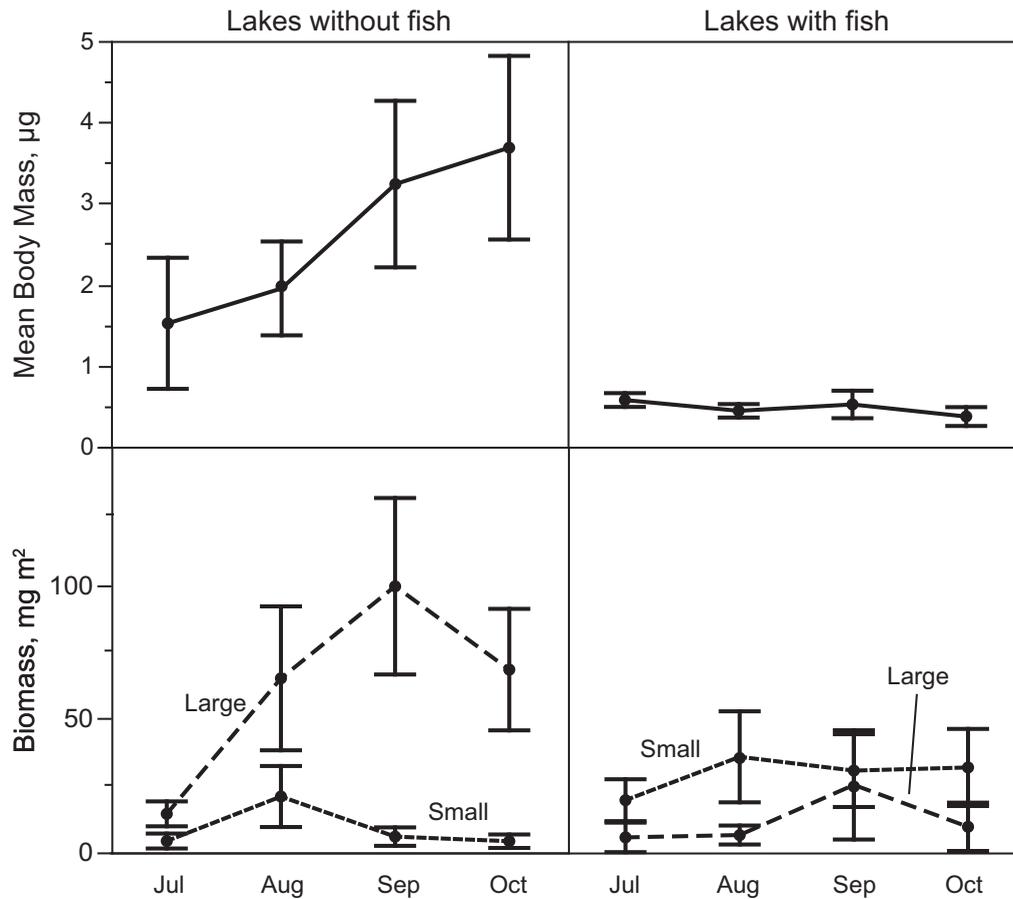
between lake categories. Collectively, however, the biomass of small taxa was more variable (Levene test, p = 0.04) and much greater in lakes with fish than lakes without fish (Table 2). *Siphonurus* had highest mean annual biomass in lakes without fish (Table 3; ~ 25% of mean annual benthic invertebrate biomass). Chironomids contributed proportionately more to the benthic invertebrate biomass of lakes with fish (58% ± 8%) than without fish (24% ± 5%; p < 0.01).

For the two largest abundant taxa, *S. occidentalis* and *Limnephilus*, lakes with fish had <10% of the production that occurred in lakes without fish (Table 4). Collectively, the production of small taxa was greater in lakes with fish than in lakes without fish (Table 2; p = 0.04) and contributed proportionately more to benthic invertebrate production of lakes with fish (84% ± 9%) than lakes without fish (49% ± 7%; p = 0.02).

Small benthic invertebrates (taxa with mean annual body size < 1 mg) accounted for a higher proportion of production in lakes with fish than in lakes without fish (Fig. 3A). In lakes with fish, because few large bodied taxa survived to late instars, production was skewed toward small organisms. In lakes without fish, production was more evenly distributed across size classes.



**Fig. 3.** Production for size classes of benthic invertebrates (mg) and zooplankton (µg) in lakes with and without fish.



**Fig. 4.** Mean dry body mass ( $\pm$  SE) of individual zooplankton for lakes with and without fish. Mean ( $\pm$  SE) monthly zooplankton dry biomass per unit area for lakes without and with fish.

**Zooplankton**

The Sorensen similarity index did not differ significantly between lakes without fish ( $0.62 \pm 0.05$ ) and with fish ( $0.54 \pm 0.03$ ). Several taxa were present in all or most of the lakes: *Diaptomus* sp., *Chydorus sphaericus*, *Conochilus* sp., *Diacyclops* sp., *Epischura* sp., and *Keratella cochlearis*. *C. trivittatus*, a large, predaceous dipteran, was present in two lakes without fish and in no lakes with fish. Although some taxa were found only in a single lake with fish, no taxa were present in two or more lakes with fish that were not also present in lakes without fish.

In lakes without fish, mean zooplankton body size increased during the growing season, but in lakes with fish it remained constant (Fig. 4). The body size of taxa did not differ between lakes with and without fish except for two of the largest taxa, *Diaptomus* sp. and *Daphnia middendorffiana* (Table 5). These species were smaller in lakes with fish, where large individuals were rare.

Lakes with and without fish had similarly low zooplankton biomass per unit area at the start of the growing season.

Zooplankton biomass per unit area increased in lakes without fish from July to September. In lakes with fish, zooplankton biomass per unit area also increased from July to September, but at a lower rate (Fig. 4).

Two of the three abundant large zooplankton, *Diaptomus* sp. and *D. middendorffiana*, were very abundant in lakes without fish but undetected or rare in lakes with fish (Table 5). *C. trivittatus* was moderately abundant in two lakes without fish but absent from all lakes with fish. *Diacyclops* sp., a small copepod, and the small *Daphnia rosea* had low abundance in lakes without fish but moderate abundance in lakes with fish. *Holopedium gibberum*, which showed similar abundance in lakes with and without fish, contributed a higher proportion of total biomass in lakes with fish. Small taxa ( $<1 \mu\text{g}$ ) were collectively much more abundant (nearly 7x) in lakes with fish than in lakes without fish (Table 2).

Although total zooplankton production did not differ between lakes with and without fish, the ratio of production by large zooplankton to production by small zooplankton did (Fig. 3B). The majority of zooplankton production occurred in

**Table 5.** Annual mean dry body mass and biomass in order of decreasing size for individuals of the most abundant zooplankton taxa in lakes with and without fish (mean ± SE). Significant differences between lake categories for mean annual dry body mass are shown in the first column. In the last column biomass differences are shown for the end of the growing season (September and October pooled).

	Mean body mass ( $\mu\text{g individual}^{-1}$ )	Population biomass ( $\text{mg m}^{-2}$ )				<i>p</i>
		July	August	September	October	
<i>Lakes without fish</i>						
<i>Daphnia middendorffiana</i>	10.40 ± 2.61*	2.7 ± 1.3	33.5 ± 30.3	26.5 ± 17.4	25.2 ± 18.1	0.03*
<i>Holopedium gibberum</i>	5.55 ± 0.61	1.0 ± 0.3	3.7 ± 3.7	10.4 ± 10.1	4.9 ± 4.9	0.44
<i>Diaptomus</i> sp.	5.05 ± 0.64*	9.5 ± 3.6	28.0 ± 8.9	67.0 ± 34.1	35.9 ± 15.8	0.01*
<i>Daphnia rosea</i>	1.15 ± 0.22	2.1 ± 1.5	3.6 ± 2.2	1.4 ± 0.5	1.2 ± 0.6	0.07
<i>Diacyclops</i> sp.	0.48 ± 0.12	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.0 ± 0.0	0.04*
<i>Epischura</i> sp.	0.35 ± 0.06	0.3 ± 0.2	0.5 ± 0.3	0.2 ± 0.1	0.1 ± 0.1	0.08
<i>Collotheca</i> sp.	0.21 ± 0.05	0.1 ± 0.1	12.6 ± 12.5	0.1 ± 0.0	0.0 ± 0.0	0.33
<i>Conochilus</i> sp.	0.07 ± 0.03	0.0 ± 0.0	0.4 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.09
<i>Lakes with fish</i>						
<i>Daphnia middendorffiana</i>	4.12 ± 0.20	5.4 ± 5.4	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	
<i>Holopedium gibberum</i>	7.46 ± 2.41	0.5 ± 0.4	5.8 ± 3.8	26.5 ± 21.4	8.6 ± 8.1	
<i>Diaptomus</i> sp.	2.82 ± 0.66	0.1 ± 0.1	1.1 ± 0.8	1.0 ± 1.0	1.5 ± 1.5	
<i>Daphnia rosea</i>	0.99 ± 0.10	5.9 ± 3.7	8.7 ± 7.7	14.5 ± 9.0	15.9 ± 10.8	
<i>Diacyclops</i> sp.	0.52 ± 0.19	6.4 ± 4.1	16.5 ± 10.5	2.4 ± 1.7	3.6 ± 2.7	
<i>Epischura</i> sp.	0.32 ± 0.08	1.0 ± 0.5	0.4 ± 0.2	7.9 ± 5.1	7.8 ± 4.8	
<i>Collotheca</i> sp.	0.18 ± 0.06	0.3 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	
<i>Conochilus</i> sp.	0.08 ± 0.03	0.0 ± 0.0	3.4 ± 3.4	5.9 ± 3.9	4.6 ± 3.3	

\*  $p < 0.05$ .

**Table 6.** Annual production of the most abundant zooplankton taxa for lakes without and with fish ( $\text{mg DM m}^{-2} \text{yr}^{-1}$ ; mean ± SE; \*  $p < 0.05$ ).

Taxonomic group	Lakes without fish	Lakes with fish	<i>p</i>
<i>Daphnia middendorffiana</i>	102 ± 42	2 ± 2	<0.01*
<i>Holopedium gibberum</i>	43 ± 43	97 ± 64	0.30
<i>Diaptomus</i> sp.	164 ± 42	7 ± 4	<0.01*
<i>Daphnia rosea</i>	21 ± 11	61 ± 35	0.29
<i>Diacyclops</i> sp.	2 ± 1	38 ± 15	0.01*
<i>Epischura</i> sp.	5 ± 2	16 ± 8	0.21
<i>Collotheca</i> sp.	46 ± 44	4 ± 3	0.39
<i>Conochilus</i> sp.	4 ± 2	32 ± 20	0.21
Total production	451 ± 103	308 ± 113	0.37

\*  $p < 0.05$ .

small zooplankton for lakes with fish and in large zooplankton for lakes without fish (Table 6).

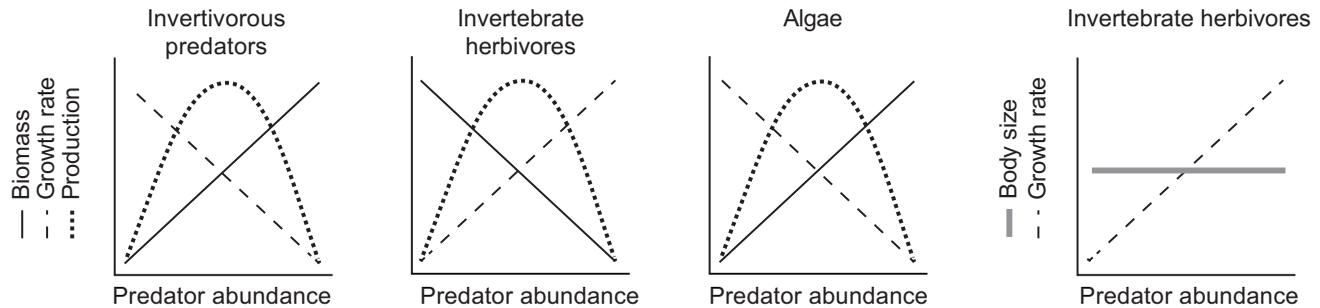
**Discussion**

The present study shows, as have other studies, that invertivorous fish change the composition and reduce the biomass of invertebrate communities in lakes through size

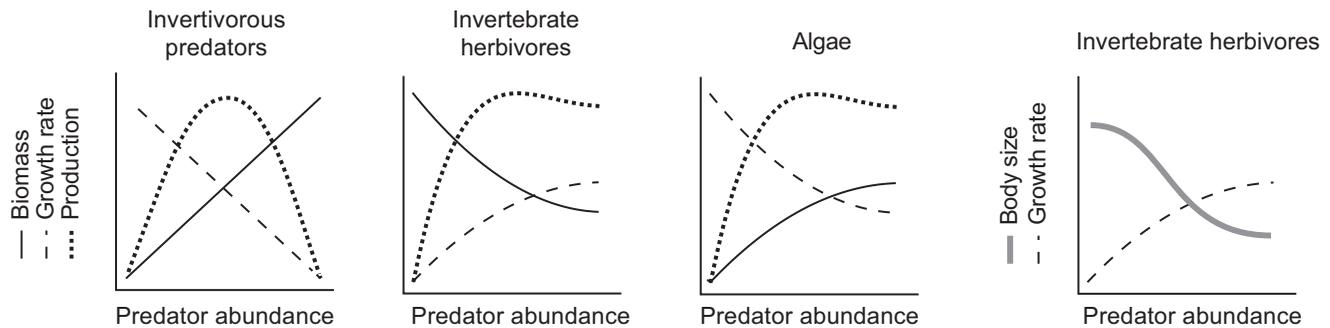
selective removal of large invertebrates (e.g., Carlisle and Hawkins 1998; Knapp et al. 2001; Parker and Schindler 2006; Schilling et al. 2009). The present study also shows, for two types of communities (benthos, zooplankton), that secondary production of invertebrates can remain constant even though invertebrate biomass is suppressed by the presence of fish. Homeostatic secondary production in trophic cascades also has been shown in one study of benthic invertebrates (Northington et al. 2010) and one study of zooplankton (Tronstad et al. 2011).

The mechanism for stability of invertebrate production in response to fish predation as documented here consists of two interacting factors. First, invertivorous fish feed selectively on large invertebrates, leading to dominance of small invertebrates. Second, small invertebrates become more abundant in the absence of large invertebrates, which suggests that they respond to release from competition when large invertebrates are removed (Figs. 2, 4). Greater abundance of small invertebrates in the absence of large invertebrates may be a general feature of foodwebs, as it is documented also for terrestrial vertebrates (e.g., Palmer et al. 2015). In lakes of RMNP, the increased dominance of small invertebrates causes a compensatory response of secondary production through an increase in community P/B ratio (Banse and Mosher 1980; Schwinghamer et al. 1986), and an increase in abundance of small invertebrates that augments

### Static Size Distribution Model



### Compensatory Size Distribution Model



**Fig. 5.** Comparison of a three-level trophic cascade based on a Static Size Distribution Model for invertebrate herbivores (redrawn from Carpenter et al. 1985) with a Compensatory Size Distribution Model that includes a shift toward smaller invertebrates and an increase in numeric abundance of invertebrates. All graphs show biomass ( $B$ ) and instantaneous growth rate ( $g$ ); production is calculated as  $P = Bg$ . Factors that would govern the abundance of invertivorous predators (variation along the  $x$  axis) are not specified but could include a fourth trophic level or other factors.

invertebrate production through partial restoration of biomass lost to selective predation loss of large invertebrates.

Evidence from RMNP lakes for compensatory response that suppresses the inverse cascade relationships of primary consumers and primary producers suggests that the cascade model proposed by Carpenter et al. (1985), here referred to as the Static Size Distribution (SSD) Model, would be enhanced by incorporation of changes in community P/B and increase in abundance of small invertebrates in response to removal of large invertebrates.

When applied to lakes with three trophic levels, the SSD Model, which does not take compensatory mechanisms into account, predicts that, at the lowest abundances for invertivorous fish, invertebrate biomass will be high and biomass of primary producers will be suppressed by invertebrate herbivores (Fig. 5). Increasing biomass of invertivorous fish, which causes increased predation on invertebrates, is matched in a uniform way by decreasing specific growth rate of invertivorous fish, reflecting suppression of invertebrate abundance

caused by predation. Production of the invertivorous fish population ( $P_f$ ) is calculated as the product of biomass and growth rate:  $P_f = B_f g_f$ . The calculation produces a yield (production) curve for  $P_f$  that shows initial increase in production leading to peak yield, followed by overharvesting, which suppresses invertebrate biomass and production. Depression of invertebrate biomass, through the cascade, causes an increase in algal biomass through reduced grazing intensity. Primary producers move toward a peak biomass that reflects limiting nutrient concentrations or reduced availability of PAR irradiance at high biomass. Net primary production progressively increases as removal of biomass by herbivores declines.

When modified by the inclusion of body size leading to compensatory change in community P/B and increase in abundance of small invertebrates when large invertebrates are removed, the SSD Model becomes a Compensatory Size Distribution Model (CSD Model, Fig. 5). As invertivorous fish become more abundant, increase in invertebrate P/B ratio

and increase in abundance of small invertebrates progressively compensate invertebrate production for reduction in total biomass of invertebrates caused by selective removal of large invertebrates. A decline in biomass occurs, however, even though biomass reduction through loss of large invertebrates is partially offset by increase in small invertebrates. These changes suppress the response of invertebrate production and biomass to increasing fish abundance. In addition, stable invertebrate production stabilizes production of algae by removal of algae biomass at a steady rate corresponding to invertebrate production. At the highest intensities of predation, however, efficiency of fish in consuming invertebrates is impaired because of constraints involving physical limitations of fish in consuming the smallest invertebrates (e.g., gillraker spacing, weak capacity for capture of infauna, etc.). Fish biomass remains high, but fish production (growth) declines. Invertebrate biomass persists in reduced amounts through increasing dominance of the smallest, least vulnerable taxa. Because grazers persist even at the highest levels of predation, grazing by invertebrates contributes to suppression of algal biomass even though abundance of invertebrate predators is high.

The CSD Model shows how compensation for predation by invertebrates can disrupt a trophic cascade through mechanisms that are documented for RMNP lakes. Degrees of disruption weaker than observed in RMNP may be possible, as may cascades that show negligible compensation, i.e., as predicted by the SSD Model. Whether most lakes show SSD cascades or CSD cascades is not clear, but some CSD compensation seems inevitable for three trophic levels in large lakes because invertivorous fish are size selective (Carpenter et al. 1985).

Cascades with four trophic levels also could be derived by addition of piscivores to SSD and CSD models with three trophic levels. In fact the SSD Model as presented by Carpenter et al. (1985) assumes linear suppression of invertivorous fish by hypothetically increasing biomass of piscivores, which reverses all of the cascade responses that would apply in the absence of piscivores. Figure 5 assumes no piscivory, reflecting conditions in RMNP lakes. Cascades involving piscivorous fish are qualitatively different than those involving only invertivorous fish, in that piscivores (level 4) continually reinforce the third trophic level through reproductive output of young fish, which are invertivorous (level 3) during early development. The extent to which invertivorous predation is compensated by this mechanism is not well documented, however. For example, Post et al. (1992) showed for Lake Mendota, MN, that invertivory was only modestly reinforced by offspring of piscivores, but they cite literature showing that the typical reinforcement effect is larger in most lakes than it was in Lake Mendota at the time of their study. The interpretation of piscivory through SSD and CSD Models is still unclear.

Further studies may focus more explicitly on compensatory mechanisms, which will clarify their overall significance. The potential for compensatory mechanisms does show, however,

that cascade structure is a weaker a priori predictor of cascade dynamics than it seemed to be originally (Carpenter et al. 1985). Compensatory mechanisms may also explain, along with other factors such as those modeled by DeLong et al. (2015, body size), or Gilbert et al. (2014, temperature), why empirical studies often fail to follow predictions of the SSD Model for trophic cascades (Brett and Goldman 1996).

While community characteristics dictate the significance of predation to invertebrate size distribution and abundance, a few species show anomalous responses to size selective predation. In the present study, *H. gibberum* did not respond to size selective predation (see also Carpenter and Kitchell 1993; Carlisle and Hawkins 1998; Drouin et al. 2009). The large, gelatinous mantle of this species (approximately 60% longer than the body length excluding the mantle) may reduce vulnerability of *Holopedium* to fish predation because the mantle is transparent; body length of *Holopedium* without the mantle (mantle length =  $0.88 \pm 0.03$  mm,  $n = 166$ ) is below the size range suppressed by fish in this study. The visible (non-gelatinous) portion of *Holopedium*, while below the consumption threshold for invertivorous fish, also would physically impede predation by smaller predators because of the large mantle (juvenile fish, invertebrate carnivores). *H. gibberum* also may be resistant to predation by fish because the gelatinous mantle is distasteful to fish (McNaught 1978; Balcer et al. 1984).

Developmental changes in body size also preclude binary classification of all taxa as either vulnerable or not vulnerable to fish predation. Small body size of *S. occidentalis* and *Psychoglypha* sp. in lakes with fish is explained by selective elimination of late instars. Among pelagic taxa, *D. middendorffiana* and *Diaptomus* sp. showed a pattern similar to that of *Siphonurus* and *Psychoglypha* in that small individuals are much less vulnerable to fish predation than large individuals.

## Conclusions

Because fish are size selective predators, invertebrate communities subject to increasing degrees of fish predation often will show a reduction in P/B ratio and increased abundance of small taxa, and thereby will have some degree of resilience in production in response to fish predation. This tendency can be reinforced by compensatory increase in abundance of small invertebrates when large invertebrates are removed by predation, as shown in both zooplankton and invertebrate communities of RMNP lakes. Changes in P/B ratio and abundance of small primary consumers are likely to affect trophic cascades generally and may explain, wholly or in part, why cascade responses to presence of invertivorous fish often are inconsistent with the SSD Model for trophic cascades. Because juvenile piscivores are likely to be invertivorous, yet another type of compensatory effect, caused by negative feedback affecting primary consumers,

may disrupt cascades that involve piscivorous fish. Recognition of compensatory effects in general will clarify the dynamics of trophic cascades.

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#### Conflict of Interest

None declared.

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