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PRIMARY RESEARCH PAPER

Response of benthic macroinvertebrates to whole-lake, non-native fish treatments in mid-elevation lakes of the Trinity Alps, California

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Abstract Introduced fish reduce the abundance and diversity of native aquatic fauna, but the effect can be reduced in complex habitats. We manipulated fish populations in forested mountain lakes to determine whether or not fish affected benthic macroinvertebrate composition across lakes with differing habitat complexity. We compared abundance, biomass, body-length, and community structure of benthic macroinvertebrates from 16 lakes with three treatments (fish stocked, suspended stocking, fish removed) and unstocked fishless "controls". Over 4 years, we assessed the relative importance of fish and environmental variables influencing the composition of benthic macroinvertebrates. Control lakes had the greatest overall abundance of macroinvertebrates when chironomid midges were excluded. Abundances of insects in the clinger/swimmer functional group and caddisflies were greatest in the control lakes but were primarily influenced by habitat variables including the availability of aquatic vegetation and wood. Total biomass and mean body length of macroinvertebrates were not affected by treatment. Taxon richness of macroinvertebrates was about 40% greater in the control lakes compared to the treatment lakes but did not differ among treatments. Our results suggest that fish reduce susceptible macroinvertebrate richness and abundances, but that changes associated with alterations of fish composition are confounded by other factors in complex lake habitats.

Keywords Aquatic insects · Introduced trout · Habitat complexity · Libellula · Chironomidae · Klamath Mountains

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Introduction

Macroinvertebrate assemblages in lakes are determined by both abiotic and biotic factors and the regional pool of colonizing species. Abiotic conditions such as temperature and pH set habitat parameters that limit the potential macroinvertebrate assemblage, and then biological interactions such as competition and predation determine the composition of a given community (Wellborn et al., 1996; de Mendoza et al., 2012). The constantly changing interactions between abiotic and biotic factors within lakes create distinct macroinvertebrate assemblages (McPeek, 1998; Blumenshine et al., 2000).

While each lake supports a unique biota, lakes are susceptible to widespread influences that may be strong enough to cause similar responses in community

structure across landscapes. For instance, large-scale introductions of predatory fishes into naturally fishless lakes have had some significant and characteristic effects on aquatic invertebrate populations over wide geographic areas (Carlisle & Hawkins, 1998; McNaught et al., 1999; Knapp et al., 2001; Nystrom et al., 2001; Resetarits, 2001; Angelon & Petranka 2002; Knapp et al., 2005). Fish are visual predators that reduce nektonic, large-bodied, or otherwise conspicuous aquatic insects, especially predators (Carlisle & Hawkins, 1998; Blumenshine et al., 2000; Reshetnikov, 2003; Glaz et al., 2012). Benthivorous fishes are assumed to have stronger predatory effect on benthic macroinvertebrates than salmonids, though as generalist feeders, salmonid species also have strong negative effects on benthic taxa (Carlisle & Hawkins, 1998). For example, Glaz et al. (2012) used stable isotopes to determine that brook trout (*Salvelinus fontinalis*) derived 60–90% of its carbon from benthic predatory macroinvertebrates. In some cases, introductions of predatory fish have been shown to change food webs and induce trophic cascades (Schindler et al., 2001; Simon & Townsend, 2003; Baxter et al., 2004; Knight et al., 2005). For example, Knight et al. (2005) found that fish predation on dragonfly larvae indirectly facilitates near-shore terrestrial vegetation reproduction via an increase in insect pollinators released from the predation pressure of adult dragonflies.

However, the physical characteristics of a lake can affect the resilience of its food web to the introduction of a predator. Simple systems, such as alpine lakes have low primary productivity, little heterogeneity in substrate, and minimal aquatic vegetation or woody debris, and therefore, the effects of fish predation on aquatic invertebrates can be substantial (Gilinsky, 1984; Diehl, 1992; Wellborn et al., 1996; Carlisle & Hawkins, 1998; Knapp et al., 2001; Epanchin et al., 2010). More complex systems, such as lakes within forested landscapes have higher primary productivity, more substrate heterogeneity, and increased presence of aquatic macrophytes and terrestrially derived woody debris (Horne & Goldman, 1994; Knapp et al., 2005). Littoral zone structure reduces the foraging efficiency of visually feeding fishes, which puts differential predator pressure on different taxa depending on their niche, life history or behavioral responses to fish presence (Crowder & Cooper, 1982; Gilinsky, 1984; Diehl, 1992; Fisher et al., 2012). For example, Gilinsky (1984) found that artificial macrophytes provided refugia for benthic macroinvertebrates so that fish were unable to effectively prey upon them.

Most field studies assessing the impacts of nonnative trout on invertebrates have focused on alpine habitats and have not used lake-scale experimental manipulations. We implemented a 4-year, whole-lake manipulative experiment in a subalpine-mixed conifer zone of the Klamath Mountains in northern California to determine whether or not fish affected benthic macroinvertebrate composition in complex montane lake habitats. The Klamath Mountains reach 2,751 m elevation and are known for their high levels of biotic diversity and endemism (Coleman & Kruckeberg, 1999; DellaSala et al., 1999). Similar to lakes in much of the mountainous western U.S., lakes in the Klamath Mountains were formed when large glaciers retreated during the Pleistocene epoch and scoured the landscape, leaving behind numerous large bodies of freshwater, which were isolated from lower elevation fish-bearing waters by steep cascades. The majority of these historically fishless lakes have been stocked with salmonids, primarily brook trout (*S. fontinalis*) and rainbow trout (*Oncorhynchus mykiss*). Introduced trout are found in approximately 85% of the lakes deeper than 2 m in the Klamath Mountains (Welsh et al., 2006).

We previously assessed the effects of 3 fish treatments (fish stocked, temporarily suspended fish stocking, fish removed) on a range of aquatic fauna including amphibians, garter snakes (*Thamnophis atratus* and *T. sirtalis*), and emerging aquatic insects. We found significant differences in the fish-containing lakes compared to lakes where we removed fish and naturally fishless lakes in terms of abundance and survival of Cascades frogs (*Rana cascadae*) (Pope, 2008), composition of aquatic garter snakes (Pope et al., 2008), and abundance and composition of emerging aquatic insects (Pope et al., 2009). The assessment of the responses of aquatic insects to fish treatments focused on adult phases as they emerged from the water, but also included a gross assessment of large-bodied (>4 mm) benthic taxa collected in 2006. For the analyses of benthic insects, Pope et al. (2009) grouped the insects into four categories: trichopterans, ephemeropterans, dipterans, and large predators (Odonata, Megaloptera, Coleoptera).

Here we take a more detailed look at the benthic invertebrate composition and structure at a higher

taxonomic resolution over the 4-year study to specifically examine effects on benthic community structure across treatments and habitat characteristics. We expected to see a difference in the benthic insect community in the treatment lakes compared to the fish-free control lakes but that the effect would decrease in lakes with increasing aquatic habitat complexity. We tested for differences in macroinvertebrate abundance, body-length, biomass, and community structure in relation to treatment and habitat, and tested whether the response variables changed over 3 years in the fish removal lakes. In addition, we compared responses of specific taxa that were found a posteriori to differ in abundance in the presence or absence of predatory fish.

Methods

Study area

We selected 16 headwater lakes that ranged from 1,896 to 2,210 m in elevation and 2.4–11.3 m in maximum depth (Table 1) in the eastern portion of the Trinity Alps Wilderness in the Klamath Mountains, CA, USA (41.0160°N, 123.0900°W). Over the past several decades, the California Department of Fish and Wildlife (CDFW) has stocked the majority of large lakes in the wilderness to provide a recreational fishery. Prior to the experiment, 12 lakes supported fish and four were fishless. Lakes were grouped into four blocks of four lakes, following an approximate latitudinal gradient, with one historically fishless (control) lake included in each block. The other three lakes in each block were randomly selected as fish removal lakes, lakes in which fish stocking was suspended between 2002 and 2006, or fish stocked lakes in which CDFW stocked annually. We tried to match the physical parameters of the fish-containing and fishless lakes, but due to prior stocking of nearly all larger lakes, the fishless sites were smaller (mean = 0.6 ha, SE = 0.2) and shallower (mean = 2.7 m, SE = 0.2) than the fish treatment lakes (mean = 1.2 ha, SE = 0.2 and mean = 5.0 m, SE = 0.3, respectively) (Pope et al., 2009).

Fish treatment and sampling

Removal of fish at the fish-removal lakes began in the fall of 2003 following the summer pre-treatment surveys. Fish were removed by setting numerous gill nets repeatedly in the lakes throughout the fall following methods described in Knapp and Matthews (1998). Eight nets were left in each lake through the winter and netting continued in the spring of 2004. In 2005, we noticed a fish in one of the removal lakes (Echo Lake). While trout did recover in the lake in the following years, we include the lake in the removal treatment because we believe the fish population was reduced enough to be effectively treated during the study period. The other three removal lakes remained fish-free throughout the study. We determined fish density in the stocked and stocking suspended lakes by setting gill nets in the beginning of each field season and recording catch-per-unit-effort. Trout densities showed an increasing trend at the stocked lakes and a decreasing trend at the stocking suspension lakes from 2003 to 2006, although densities were not significantly different between treatments across years ($F_3 = 1.31$, $P = 0.32$) (Pope, 2008). The stocked lakes averaged 5.77 fish per hour (SE = 0.37) and the stocking suspended lakes averaged 3.22 fish per hour (SE = 0.33).

Invertebrate sampling

We sampled benthic macroinvertebrates at all 16 lakes during two 7-day periods in July and August each year from 2003 (pre-treatment) to 2006. Benthic sweeps were performed in the littoral zone of the west side of each lake by taking three 1-m passes with a standard aquatic "D" net, similar to the hand-net sweep sampling technique assessed by García-Criado & Trigal (2005). Samples were collected from three substrate categories: emergent vegetation, organic/silt substrate, and rock. Samples were cleaned of debris and stored in 70% ethanol. A total of 96 samples were collected each year for a total of 384 samples. A few samples from 2003 were lost in the field or otherwise destroyed but all lakes were represented during each sampling period. Samples from the three post-treatment years were complete. In the laboratory, specimens were sorted to family for the dipterans and genus for other taxa. Within each taxon, we sorted specimens by instar then measured the body lengths of 5–15 randomly selected individuals of each instar from each sample. We used the mean length of each group to estimate biomass using length-weight regressions calculated based on Sabo et al. (2002). We added the

Table 1 Characteristics of lakes in the fishless controls and three fish treatment categories

Variable	Lake Category			
	Fishless	Remove trout	Suspend stocking	Stocked
Elevation (m)	2,006 (1,922–2,087)	2,120 (1,895–2,212)	2,120 (2,049–2,179)	2,085 (1,950–2,179)
Surface area (ha)	0.64 (0.3–1.1)[a]	1.07 (0.7–1.3)[b]	1.14 (0.7–1.5)[b]	1.26 (0.2–2.0)[b]
Maximum depth (m)	2.67 (2.4–3.1)[a]	4.86 (3.7–5.3)[b]	4.91 (3.9–7.3)[b]	5.11 (4.1–6.7)[b]
Fine sediment (%)	87 (77–93)[a]	67 (56–87)[ab]	59 (39–87)[b]	82 (79–85)[ab]
Large wood (%)	5 (0–15)[a]	9 (0–19)[a]	12 (3–28)[a]	17 (1–29)[b]
Aquatic vegetation (%)	46 (40–60)	48 (27–68)	49 (31–65)	46 (10–74)
Littoral zone slope	0.28 (0.16–0.54)	0.39 (0.24–0.47)	0.37 (0.22–0.65)	0.29 (0.22–0.65)

The range for each lake category is provided in parentheses

[ab] Letters indicate the statistical significance of differences between lake categories. Categories with different letters are significantly different at the $P < 0.05$ level (ANOVA followed by Tukey's HSD)

total biomass per instar to get a total biomass per taxon.

Environmental variables

We recorded water temperature at each study lake every 2 h at depths of 0.5 and 1.25 m throughout the survey season using Onset® temperature loggers and computed the sum of the average of the daily temperatures for each lake. We recorded the pH of each lake using handheld pH meters during each sampling session and used the mean in analyses. We sampled littoral zone features (depth, substrate, aquatic macrophytes and woody debris) at three distances from shore (0.1, 0.5, 1.0 m) from approximately 25 evenly spaced transects around each lake. We used the depth-by-distance measurements to estimate a mean littoral zone slope and we calculated the percentage of points per lake with aquatic vegetation and wood (>10 cm diameter) (Table 1). Lake elevation, maximum depth, and area had been previously collected (Welsh et al., 2006) or were obtained from GIS maps.

Analytical methods

We compared abundances, biomass, and lengths of benthic insects among the four lake categories with analysis of variance. We first compared the lakes in the three fish treatment categories (stock, stocking suspension, and fish removal) in 2003 to ensure there were no differences prior to initiation of the experiment. Based on previous findings (Nystrom et al., 2001) and our previous study (Pope et al., 2009), we hypothesized that fish would have no effect on, or would indirectly increase, the abundance of small-bodied benthic insects. The latter can occur if the fish directly affect invertebrate predator composition. The chironomid family includes many larval midges with respiration adaptations (Armitage et al., 1995) that allow them to hide in the sediment where they are primarily unavailable to trout. We, therefore, excluded chironomids from some of the analyses to account for this expected effect. Although we did not sample the water column, taxa in the clinger/swimmer functional group such as adult dytiscid beetles like *Celina* spp., *Dytiscus* spp., and *Hygrotus* spp. (Coleoptera: Dytiscidae), and backswimmers (*Notonecta* spp.), were collected in the benthic samples and included in the analyses, as these organisms have been found to be sensitive to introduced fish in other studies (e.g., Knapp et al., 2001).

We ran five repeated measures ANCOVAs on the data collected between 2004 and 2006 with the response variables being annual averages of abundances of insects with and without chironomids, biomass of all insects, mean annual abundance of insects in the clinger/swimmer functional group (Merritt et al., 2008), mean annual abundance of caddisflies (order Trichoptera), and body length of insects (excluding chironomids), and the predictor variables being treatment and year. We also included lake area as a covariate in all analyses since the control lakes were significantly smaller than the treatment lakes. After log-transforming abundances, all met normality assumptions. We followed significant ANCOVAs with Tukey–Kramer multiple comparison

tests to determine which treatment categories were responsible for significant results. We also ran post hoc ANOVAs on specific taxa such as baetid mayflies and libellulid dragonflies because we saw clear patterns of differences among treatment categories during the analysis process. Additional repeated measures ANOVAs were run to test for differences among years in the fish removal lakes for the five response variables.

We used generalized linear mixed models and multi-model inference based on information-theoretic approaches (Anderson, 2008) to assess the effect of various physical and habitat predictor variables relative to the effect of fish on the same biomass, abundances, and body length response variables used in the ANCOVAs. We used mean values from the three benthic samples collected twice per year from 2004 through 2006 at each lake as dependent variables and included physical, habitat, and fish variables as fixed predictors (Table 2). In all models, we included lake and year as random factors to account for the lack of independence of samples collected from the same lake and within the same year. We developed a global physical and a global habitat model then conducted a variable reduction exercise using Akaike's Information Criterion with a second-order bias correction (AICc) to remove unimportant predictor variables from each global model (Anderson, 2008). We dropped each variable from the model, and if AICc scores were improved (reduced), we eliminated the variable from the model. We then combined the reduced physical and habitat models and conducted another variable reduction exercise to obtain the most adequate model or models (if within two AICc units of the lowest scoring model) for each response variable. We ran a null model (intercept only) with each response variable as a reference for assessing model importance (Anderson, 2008). AICc-based model probabilities, or "Akaike weights", were calculated for every model in the final candidate set (Anderson, 2008). Model-averaged parameter estimates were obtained from the weighted average of parameter estimates from each of the candidate models, with a value of zero assigned for models in which the parameter being estimated does not appear (Anderson, 2008; Lukacs et al., 2010). Approximate 95% confidence intervals (CI) for each parameter were calculated as the model-averaged mean ± two times the model-averaged standard errors (Anderson, 2008; Lukacs et al., 2010). *Z* values and *P* values were also estimated for each parameter in the final model candidate set for ease of interpretation. Analyses were conducted in R (R Development Core Team, 2012). Mixed models were fit using the 'glmer' function in the 'lme4' package (Bates & Maechler, 2010). Post-hoc comparisons were performed using the 'glht' function in the 'multcomp' package (Hothorn et al., 2008).

To assess the community level effects of fish in context with habitat characteristics, we used a multi-response permutation procedure (MRPP) using Bray–Curtis ecological distance between samples to explore any differences in macroinvertebrate composition. We also compared taxon richness and assemblage evenness between the treatments using the Camargo evenness coefficient (Camargo, 1995). We used mean abundances of invertebrates per lake as the response variable. The MRPP analyses were performed with PCord 4.0 (MjM Software Design, Gleneden Beach, OR, USA)

Table 2 Variable descriptions for linear mixed models

Model	Variable short name	Variable description
Habitat	Depth	Mean water depth (cm) of the 3 sweep net samples.
	CPUE	Number of fish captured per unit effort (h)
	AquaticVeg	Percent of littoral zone with aquatic vegetation
	Wood	Percent of littoral zone transects with submerged wood
	FineSubstrate	Percent of littoral zone transects on silt or sand substrates
Physical	Elev	Elevation of the lake (m above sea level)
	LakeDepth	Maximum depth of the lake (m)
	Area	Estimate of the lake surface area (m^2)
	pH	Mean recorded pH of surface water
	LakeTemp	Sum of summer daily average water temperature

Results

A total of 38 genera from 24 families and 8 orders were identified from all samples combined (Table 3). More than 78% of all macroinvertebrates sampled were chironomids. While there was no significant difference in abundances among lake categories ($F_3 = 1.12$, $P = 0.27$), chironomids were especially abundant in the treatment lakes: they made up 91% (SE = 2; range: 89–97%) of the invertebrates sampled from the stocked lakes, 88% (SE = 2; range: 83–92%) of the samples from the fish removed lakes, and 84% (SE = 7; range: 63–97%) of the samples from the stocking suspended lakes. On the other hand, the mean percentage of chironomids in the control lakes was 60% (SE = 10; range: 35–84%).

Lake category had a significant effect on three of the six response variables tested using ANCOVA: abundances of non-chironomid benthic insects, abundances of insects in the clinger/swimmer functional group, and caddisflies (Fig. 1). The treatment-by-year effect was not significant in any of the models (Table 4). The covariate lake area was marginally important ($P = 0.07$) for predicting insect body length (greater length in smaller lakes) but was not significant in any other models (Table 4). Tukey–Kramer multiple comparisons showed the control lakes had greater abundances of invertebrates excluding chironomids, more clinger/swimmers, and more caddisflies than the fish removal lakes ($P < 0.05$), stocked lakes ($P < 0.01$), and stocking suspension lakes ($P < 0.08$), but that there were no differences among the three treatment categories in any of the groups (Fig. 1).

When physical and habitat variables were included in the analyses, fish density (CPUE) was only important for predicting abundances of clinger/swimmers (Table 5), with higher CPUE resulting in lower abundances of the insect group (Table 6). For total macroinvertebrate biomass, models with lake temperature alone (AICc weight = 0.71) and lake temperature and aquatic vegetation (AICc weight = 0.27) were the most adequate, with greater biomass found in warmer lakes with more aquatic vegetation. Depth of sample, aquatic vegetation, and wood were in both best models predicting abundances of invertebrates with and without chironomids, whereas lake temperature was included only in the total abundance model, and fine substrate and lake depth were included only in

Table 3 Macroinvertebrate taxa recovered from each lake treatment category

Taxa	Lake category			
	Fishless	Remove trout	Suspend stocking	Stocked
Diptera	1,914	12	70	19
Ceratopogonidae	817	98	1,893	220
Chironomidae	13,511	11,207	18,988	12,166
Chaoboridae	138	2	1	–
Dixidae	–	–	4	–
Stratiomyidae	1	–	0	–
Tabanidae	2	–	2	–
Tipulidae	20	18	834	56
Coleoptera	0	1	0	1
Dytiscidae	23	5	11	5
Acilius	–	–	–	–
Agabus	3	–	–	–
Celina	16	1	–	1
Copelatus	–	–	2	–
Coptotomus	1	–	–	–
Dytiscus	6	1	1	–
Hydroporus	–	6	–	–
Hydrovatus	3	–	–	–
Hygrotus	4	–	1	–
Laccophilus	1	–	–	–
Liodessus	1	–	–	–
Oreodytes	22	33	–	11
Rhantus	2	–	–	–
Uvarus	11	13	–	1
Hydrophilidae	3	–	–	–
Tropisternus	1	–	–	–
Sphaeridiinae	1	–	1	–
Gyrinidae	6	–	–	–
Zygoptera	207	124	130	33
Lestidae	31	–	–	–
Archilestis	71	–	–	–
Lestes	9	2	16	–
Coenagrionidae	335	13	79	39
Enallagma	5	28	7	15
Zoniagrion	39	15	10	17
Anisoptera	127	116	59	216
Libellulidae	49	8	70	16
Libellula	73	35	33	115
Aeshnidae	27	14	5	39
Aeshna	39	13	23	26
Anax	11	4	2	3

Table 3 continued

Taxa	Lake category			
	Fishless	Remove trout	Suspend stocking	Stocked
Ephemeroptera	676	35	22	8
Baetidae	853	267	27	45
Centroptilum	1,018	231	7	22
Caenidae	–	–	–	–
Caenis	–	–	–	2
Trichoptera	99	86	95	28
Limnephilinae	142	12	–	–
Ecclisomyia	50	–	2	–
Halesochila	191	15	3	5
Hesperophylax	–	2	–	–
Gumaga	413	73	4	47
Lenarchus	6	1	–	–
Limnephilus	1	–	–	–
Leptoceridae	12	1	13	–
Oecetis	549	5	49	42
Hemiptera	–	0	–	–
Gerridae	3	4	4	5
Trepobates	–	–	–	5
Limnoporus	9	11	85	1
Notonectidae	18	4	1	1
Notonecta	33	6	5	5
Corixidae	5	17	3	–
Corisella	2	–	–	4
Belostomatidae	–	–	–	–
Belostoma	1	–	–	–
Lethocerus	1	–	–	–
Megaloptera	4	1	–	–
Sialidae	–	–	–	–
Sialis	156	84	75	27

Values represent the total number of animals at the finest taxonomic resolution identified

the abundance without chironomids model (Table 5). Elevation and wood (AICc weight = 0.70) were the most adequate predictors of caddisfly abundance with greater numbers of caddisflies found in lakes at lower elevations but with less wood (Table 6). With habitat and physical variables included, density of fish did not prove important in the parameter estimate analysis for caddisflies (Table 6). None of the variables included in the models were important for predicting mean body length of invertebrates (Table 5). In a post hoc analysis, however, we found that invertebrates were larger in samples collected from aquatic vegetation compared to samples taken from silt or rock ($F_{2,9} = 12.33$, $P < 0.001$), regardless of the lake sampled.

Taxon richness was consistently higher in the control lakes compared to the treatment lakes ($F_{3,9} = 24.2$, $P < 0.001$, Fig. 2). Nineteen taxa were unique to the control lakes, 18 of which were predators including10 beetles (Coleoptera), four damselflies or dragonflies, and one caddisfly (Table 3). Overall macroinvertebrate structure, however, was not significantly different among lakes within the different treatment categories or controls (MRPP: $T = 0.66$, $P = 0.35$). In the post hoc analyses, we captured more mayflies (Ephemeroptera: Baetidae: *Centroptilum*; $F_{3,9} = 9.79$, $P < 0.01$), coenagrionid damselflies (Odonata: Coenagrionidae; $F_{3,9} = 2.74$, $P = 0.04$), and specific caddisflies: *Oecetis* spp. ($F_{3,9} = 5.07$, $P < 0.01$), *Halesochila* spp. ($F_{3,9} = 3.28$, $P = 0.02$), and *Gumaga* spp. ($F_{3,9} = 2.56$, $P = 0.05$) in the control lakes compared to the treatment lakes. In contrast, the predaceous dragonfly, *Libellula* spp. (Odonata: Libellulidae), one of the most prevalent predatory insects sampled in this study, was most abundant and in greater proportion relative to all other invertebrate predators (for example, Megaloptera: *Sialis*, Trichoptera: *Oecetis*, Anisoptera: *Aeshna*, and zygopterans) in the fish stocked lakes compared to the control, fish removal and suspend stocking lakes ($F_{3,9} = 4.11$, $P = 0.007$). In addition, there was a decrease in abundance of libellulid dragonflies following fish removals (2003 > 2004 and 2005; $F_{1,3} = 4.15$, $P = 0.04$, $F_{1,3} = 3.41$, $P = 0.06$, respectively). The trend held in 2006 but was not significant ($F_{1,3} = 2.13$, $P = 0.16$).

We found no significant difference for any of the response variables in the fish removal lakes among years following fish removals ($F_{2,9} < 1.6$, $P > 0.20$, Fig. 3). We did, however, note an increase in the number of taxa from 15 in 2003 to 26 in 2006. Specifically, all caddisflies, except for a few early instars, were absent in 2003, but were represented by 2 genera, *Gumaga* and *Halesochila*, in 2004 and 5 genera in 2006, *Gumaga*, *Halesochila*, *Hesperophylax*, *Lenarchus*, and *Oecetis*. Similarly, true bugs of the order Hemiptera were also absent in 2003, but in 2006 *Notonecta* (Hemiptera: Notonectidae), *Limnoporus* (Hemiptera: Gerridae), and members of Corixidae were recovered from the samples.

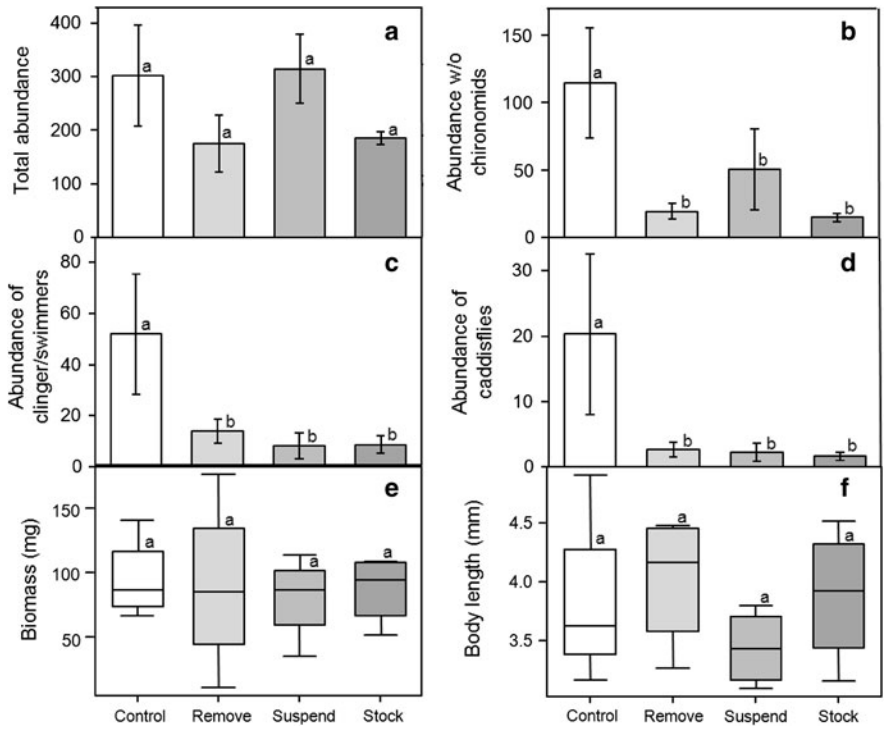

Fig. 1 The average benthic macroinvertebrate **a** total abundance, **b** abundance without chironomids, **c** abundance of taxa in the clinger/swimmer functional group (Merritt et al., 2008), **d** abundance of caddisflies, **e** total macroinvertebrate biomass, and **f** body length for the fishless control lakes (*white bars*) and lakes in the three treatment categories (*light grey* fish removal, *medium grey* suspended stocking, *dark grey* stock). Four study lakes are included in each lake category and values for each are averages of the three post-treatment years (2004–2006). For the abundance graphs, *bars* represent the average number of macroinvertebrates sampled and *lines* indicate SE. For biomass and body length, the *solid line* within each *box* represents the median, the bottom and top borders indicate the 25th and 75th percentiles, and the *whiskers* below and *above* each *box* mark the 10th and 90th percentiles. *Different letters* above each *box* indicate statistically significant differences among lake categories at the $P < 0.05$ level

Discussion

Habitat variables proved more important than fish densities for predicting benthic macroinvertebrate abundances and biomass. In addition, we did not observe an increase in abundance, biomass or body size of macroinvertebrates in fish removal lakes following removals. These findings contrast studies conducted in higher elevation lake habitats where fish have strong top-down effects (Carlisle & Hawkins, 1998; Knapp et al., 2001; de Mendoza et al., 2012). Important variables in our models included water temperature of the lake over the course of the summer and the percent aquatic vegetation and wood in the littoral zone. In mountain climates, warm lakes tend to be more productive than cold lakes and, thus, have the capacity to affect the distribution, richness and community composition of invertebrates (de Mendoza & Catalan, 2010). Beresford & Jones (2010) found that lake nutrients positively influenced the biomass and abundance of macroinvertebrates, and reduced the effect of fish on macroinvertebrates. In addition, macrophytes and wood provide both surface area and refuge habitat so are positively associated with invertebrate biomass and abundance (Boll et al., 2012). While coarse, our lake-level estimates of aquatic vegetation and wood did seem to represent habitat complexity for aquatic invertebrates in the littoral zone that allowed for comparisons among lakes. Overall, in our mid-elevation study lakes with warm temperatures and habitat complexity, the density-dependent relationship between predatory fish and invertebrate prey may be weak and, therefore, overwhelmed by other environmental variables.

Table 4 Analysis of covariance results assessing the effects of the fish treatment and year on total macroinvertebrate abundance, abundance of macroinvertebrates excluding chironomid midges, total macroinvertebrate biomass, abundance of insects in the clinger/swimmer functional group, abundance of caddisflies (order Trichoptera), and mean body length

Source	df	SS[a]	MSE[b]	F	*P*
Abundance w/chironomids					
Treatment (T)	3	2.74	0.91	1.57	0.21
Year (Y)	2	7.08	3.54	6.06	0.01*
Area	1	0.69	0.69	1.19	0.28
T × Y	6	2.05	0.34	0.59	0.74
Abundance w/o chironomids					
Treatment (T)	3	22.46	7.49	9.5	<0.001**
Year (Y)	2	5.03	2.52	3.2	0.05*
Area	1	0.01	0.01	0.01	0.94
T × Y	6	2.63	0.44	0.56	0.76
Biomass					
Treatment (T)	3	7.11	2.37	1.79	0.17
Year (Y)	2	4.22	2.11	1.59	0.22
Area	1	1.57	1.57	1.18	0.28
T × Y	6	3.81	0.64	0.48	0.82
Abundance Clinger/Swimmer					
Treatment (T)	3	28.2	9.4	11	<0.001**
Year (Y)	2	2.08	1.04	1.22	0.31
Area	1	0.02	0.02	0.02	0.88
T × Y	6	2.08	0.35	0.41	0.87
Abundance Caddisflies					
Treatment (T)	3	17.72	5.9	6.05	0.002*
Year (Y)	2	1.78	0.89	0.91	0.41
Area	1	0.18	0.18	0.18	0.67
T × Y	6	2.66	0.44	0.45	0.84
Length					
Treatment (T)	3	0.06	0.02	0.75	0.53
Year (Y)	2	0.24	0.12	4.28	0.02*
Area	1	0.1	0.1	3.4	0.07
T × Y	6	0.09	0.01	0.51	0.79

Treatments include fish-removal, stocked annually, stocking-suspension and were compared to fish-free reference lakes

[a] Sum of squares, [b] mean square error

* $P \leq 0.05$,** $P < 0.01$

We did find that the fishless control lakes supported about 40% higher taxon richness and 33% greater non-chironomid benthic macroinvertebrate abundances than all treatment lakes over the 4 years of the study. This finding is supported in the literature (e.g., Macan, 1977; Knapp et al., 2005) and has both direct and indirect causes. Even in complex habitats, trout prey upon vulnerable taxa and may indirectly affect the habitat selection of some insects to make them less common in lakes with fish (Cooper, 1984; Pierce, 1988; Stoks et al., 2003). For example, some adult insects have been found to selectively oviposit in lakes without fish (Pierce, 1988; Resetarits, 2001; Angelon & Petranka, 2002). In a controlled experiment, *Tropisternus* (Coleoptera: Hydrophylidae) selectively avoided colonizing pools containing insectivorous fish and oviposited more frequently in fish-free ponds (Resetarits, 2001). The few individuals that did occupy the less preferred fish-containing habitat drastically reduced their activity and even left the water to climb up the sides of the holding tanks. *Tropisternus* was able to detect fish even when fish were restricted in enclosures and there was no predatory interaction (Resetarits, 2001). In our study, *Tropisternus* was found only in the control lakes.

The differences in richness and abundances did not translate to overall differences in biomass of macroinvertebrates, likely because of the positive relationship between introduced fish and chironomids. Chironomids represent the vast majority of aquatic macroinvertebrates from all lentic ecosystems (Horne & Goldman, 1994; Carlisle & Hawkins, 1998) and were by far the most abundant insect family collected in our benthic samples from all lakes. However, the samples from the treatment lakes were comprised of a much greater proportion of chironomids than those from the control lakes. Chironomidae is a diverse family whose members belong to various functional feeding groups and as a result, the direct and indirect effects of fish may vary among species (e.g., Gilinsky, 1984; Hershey, 1985). However, our results are not surprising because, in general, most chironomids are sedentary benthic-dwelling, deposit feeders and tend to show minimal negative responses to fish predation (Herbst et al., 2009; Kadye & Booth, 2012). Kadye & Booth (2012) found that chironomids were more abundant in experimental reaches of rivers with predatory catfish compared to reaches without catfish and, similarly to Knapp et al. (2001), conclude that fish likely confer indirect positive effects through elimination of invertebrate predation pressure.

We did not find increases in biomass, macroinvertebrate abundance or significant changes in community structure in the fish removal lakes, even 3 years after removing fish. The recovery of the

Table 5 Final linear mixed-effects models after removing parameters that do not improve AICc values by at least two AICc units and combining the best scoring (lowest AICc) physical and habitat models for each response variable. Model deviances (Dev.), number of parameters in the models (k), change in AICc scores from the most adequate model (ΔAICc), and AICc weights (W_i) are provided

Response	Model	Dev.	k	ΔAICc	W_i
Biomass	LakeTemp	1087.8	5	0.00	0.71
	LakeTemp + AquaticVeg	1087.5	6	1.98	0.27
	Null	1096.9	4	6.91	0.02
Abundance[a]	Depth + LakeTemp + AquaticVeg + Wood	253.1	8	0.00	0.32
	Depth + LakeTemp + AquaticVeg + Wood + FineSubstrate	251.4	9	0.67	0.23
	Depth + LakeTemp + Wood	256.2	7	0.70	0.23
	Null	275.8	4	13.46	0.00
Abundance w/o chiro.[a]	Depth + AquaticVeg + FineSubstrate + Wood + LakeDepth	238.6	9	0.00	0.44
	AquaticVeg + Wood + FineSubstrate + LakeDepth	267.1	8	0.34	0.38
	Null	302.2	4	32.54	0.00
Clinger-swimmer[a]	Depth + CPUE + AquaticVeg + Wood + FineSubstrate + LakeTemp + LakeDepth	255.9	11	0.00	0.21
	AquaticVeg + Wood + LakeTemp + LakeDepth + CPUE	263.9	9	0.68	0.15
	Depth + AquaticVeg + Wood + LakeTemp + LakeDepth + CPUE	261.8	10	0.72	0.14
	AquaticVeg + Wood + LakeTemp + LakeDepth	261.8	8	0.75	0.14
	AquaticVeg + FineSubstrate + Wood + LakeTemp + LakeDepth + CPUE	259.4	10	0.81	0.14
	Null	302.2	4	49.34	0.00
Caddis[a]	Elev + Wood	262.6	6	0.00	0.70
	Elev + Wood + CPUE	261.9	7	1.69	0.30
	Null	285.0	4	19.96	0.00
Length w/o chiro.	Null	315.7	4	0.00	1.00

[a] Natural log transformed

macroinvertebrate community after fish removals depends on the dispersal capabilities of the adults and the proximity of source populations (Caudill, 2003) and may take longer than 3 years and probably as many as 11 years (Knapp et al., 2001; Boll et al., 2012). In addition, invertebrate communities can become unstable following predation-related disturbances (Angeler & Moreno, 2007). Macrophyte growth and nutrient distributions change following fish removals (Schindler et al., 2001) and can lead to unpredictable changes in macroinvertebrate responses (Boll et al., 2012). Alternatively, with only four lakes per treatment and fairly high variability among lakes and years, we may not have had sufficient power to detect significant changes that may have occurred. We did recover more taxa from the removal lakes each year following fish removals, and invertebrate diversity was lowest in 2003 when fish were still present in the lakes. For example, caddisflies were absent in the samples collected from the fish removal lakes prior to fish removal in 2003, but 5 genera were recovered from the lakes in 2006. Despite their protective cases, caddisflies are selectively consumed by trout (Carlisle & Hawkins, 1998; Knapp et al., 2001). We also did not see an effect of suspending fish stocking on benthic invertebrate abundance or community structure. These results can most likely be attributed to a relatively consistent fish density in this treatment group throughout the study (Pope et al., 2009).

Because fish preferentially prey on large insects, we expected, but did not find, the mean macroinvertebrate total biomass and body-length to be greatest in samples from the fish-free control lakes. Other studies have found that fish cohabitate with large insects in lakes with dense aquatic vegetation where the insects can take refuge (Macan, 1977; Morin, 1984; Chivers

Table 6 Parameter estimates and approximate 95% confidence intervals from candidate linear mixed effects models within 2 AICc units of the most adequate model

Response	Parameter	Estimate	95% CIs		Z value	P value
			Lower	Upper		
Biomass	LakeTemp	0.155	0.044	0.265	2.752	0.0060**
	AquaticVeg	36.083	−92.784	164.949	0.549	0.5831
Abundance	Depth	0.018	0.003	0.032	2.398	0.0165*
	LakeTemp	0.003	0.001	0.005	3.407	0.0007**
	AquaticVeg	2.123	−0.060	4.305	1.906	0.0567
	Wood	−3.328	−6.368	−0.288	2.146	0.0319*
	FineSubstrate	−0.908	−2.226	0.411	1.350	0.1772
Abundance w/o chironomids	Depth	0.012	−0.002	0.027	1.686	0.0918
	AquaticVeg	5.953	3.972	7.935	5.889	<0.0001**
	FineSubstrate	−1.890	−3.233	−0.547	2.759	0.0058**
	Wood	−5.935	−8.944	−2.926	3.866	0.0001**
	LakeDepth	−0.412	−0.542	−0.281	6.188	<0.0001**
Clinger/swimmer	Depth	0.012	−0.001	0.025	1.738	0.0823
	CPUE	−0.058	−0.124	0.007	1.740	0.0819
	AquaticVeg	3.044	0.847	5.241	2.716	0.0066**
	Wood	−4.580	−7.371	−1.788	3.215	0.0013**
	FineSubstrate	−1.103	−2.373	0.168	1.702	0.0888
	LakeTemp	0.004	0.002	0.006	4.143	<0.0001**
	LakeDepth	−0.325	−0.477	−0.174	4.214	<0.0001**
Caddisflies	Elev	−0.006	−0.008	−0.003	4.449	<0.0001**
	Wood	−5.722	−8.287	−3.157	4.372	<0.0001**
	CPUE	−0.030	−0.102	0.043	0.800	0.4240

Parameter Z and P values provided for reference

* $P < 0.05$,** $P < 0.01$

et al., 1996; McPeek, 1998; Caudill & Peckarsky, 2003; Caudill, 2005; Fisher et al., 2012). In our study, all lakes had habitats with emergent vegetation and most large insects were sampled from these protected areas regardless of fish presence. This corroborates the findings from Diehl (1992) and Pope et al. (2009), in which habitat attributes influenced the distribution of large-bodied predators more than the presence of fish. Whereas our results did not find a size difference of benthic insects in lakes with or without fish, in the same experimental system Pope et al. (2009) did find fewer large-bodied emerging predaceous insects in lakes containing fish compared to lakes without fish. It appears that the insects are relatively safe in the benthos, but become vulnerable to predation as they emerge through the water column. Trout, then, may have a greater effect on the abundances of the terrestrial stages of aquatically derived insects

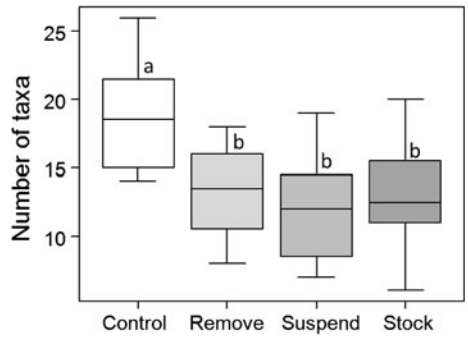

Fig. 2 Mean annual richness of benthic macroinvertebrate taxa in the fishless control lakes (*white bars*) and lakes in the three treatment categories (*light grey* fish removal, *medium grey* suspended stocking, *dark grey* stock). The *solid line* within each *box* represents the median, the bottom and top borders indicate the 25th and 75th percentiles, and the *whiskers* below and above each *box* mark the 10th and 90th percentiles. *Different letters* above each *box* indicate statistically significant differences among lake categories at the $P < 0.05$ level

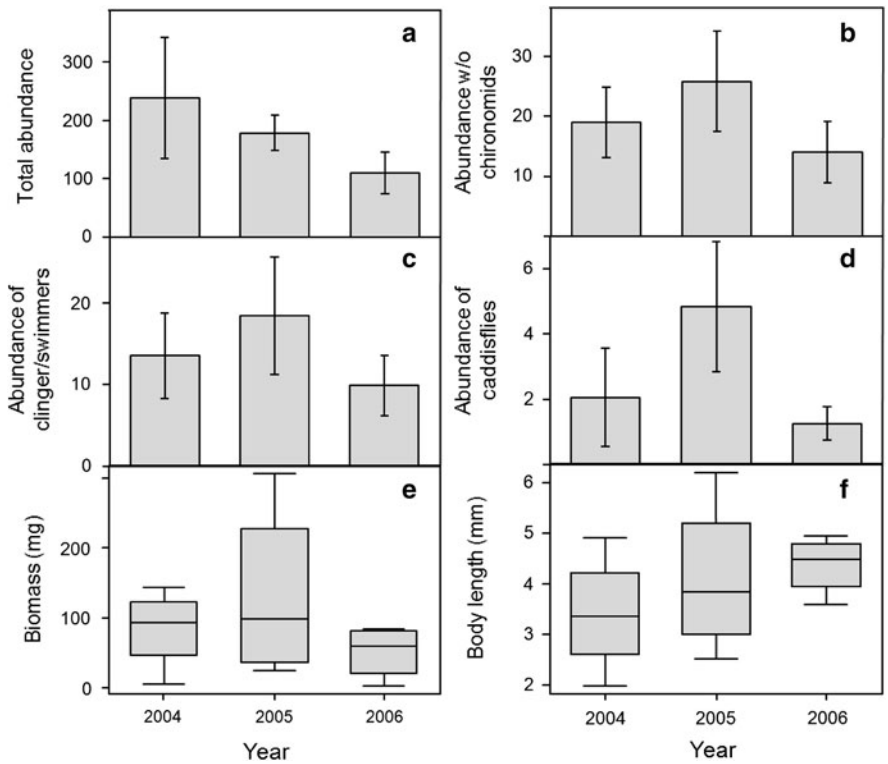

Fig. 3 For the fish removal lakes post fish removal (2004–2006), mean benthic macroinvertebrate **a** total abundance, **b** abundance without chironomids, **c** abundance of taxa in the clinger/swimmer functional group, **d** abundance of caddisflies, **e** total macroinvertebrate biomass, and **f** body-length. For the mean abundance graph, bars represent the average number of non-chironomid macroinvertebrates sampled from four fish removal lakes per year and lines indicate SE. For the biomass and body length graphs, the *solid line* within each *box* represents the median, the bottom and top borders indicate the 25th and 75th percentiles, the *whiskers* below and above each *box* mark the 10th and 90th percentiles, and *dots* indicate points outside the 10th and 90th percentiles. None of the categories are significantly different from each other among years (ANOVA, $P > 0.05$)

compared to the aquatic stages, which may have ramifications for near-shore terrestrial ecosystems (e.g., Knight et al., 2005) even when no effect is noted in the aquatic system.

Interestingly, *Libellula*, a large, stout-bodied, predaceous dragonfly, was most abundant and in greater proportion relative to other invertebrate predators in the lakes annually stocked with trout. Additionally, the abundance and proportion of *Libellula* to other insect predators decreased dramatically in the fish-removal lakes in 1 year following treatments. Their life history, behavior, and morphology may give them an advantage over other invertebrate predators in lakes with fish (Sih, 1986). Adults do not possess an ovipositor, but can lay eggs directly on the surface of the water, and the larvae are sprawlers with small, dorsally positioned eyes, allowing them to remain concealed from fish while still foraging as sit-and-wait predators (Merritt et al., 2008). In addition, Wohlfahrt et al. (2006) observed species-specific anti-predatory behavior by *Libellula depressa* that increased survival when combined with the predatory fish, gudgeon (*Gobio gobio*). If fish consume other predaceous invertebrate competitors, *Libellula* may indirectly benefit from fish presence. In the fish removal lakes, predaceous alderflies (Megaloptera: Sialidae) were only found in samples collected after fish removals when *Libellula* abundances decreased. Unfortunately, we did not sample sufficient numbers of individuals of *Libellula* or *Sialis* to quantify this correlation.

This research improves our understanding of the interplay between natural abiotic and biotic conditions and non-native predators in driving benthic insect community dynamics in montane lake environments.

Introduced trout clearly reduce richness and abundances of taxa susceptible to predation by a visual predator, but these and other effects on overall biomass and body length of benthic macroinvertebrates are muted when near-shore habitats are complex. Regardless, over large landscapes such as the Trinity Alps Wilderness, high densities of stocked trout in the majority of large lakes alter the relative composition of benthic insects resulting in fewer active, large-bodied insect groups such as predators, caddisflies and clinger/swimmers and more chironomid midges. This change in the benthos has ramifications for near-shore terrestrial communities because the majority of the benthic insects have terrestrial adult stages that are preyed upon by a range of predators including amphibians and birds (Epanchin et al., 2010; Joseph et al., 2010). Therefore, high densities and diversities of emerging aquatic insects are important for sustaining high densities and diversities of the native terrestrial fauna of montane lake basins. We conclude that a reduction in the number of lakes with fish and densities of fish may not result in short-term recovery of most benthic insects, but will likely result in a long-term recovery.

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