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Experimental evidence that predator range expansion modifies alpine stream community structure

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Abstract: Climate change is projected to facilitate altitudinal range expansions of 'lowland' taxa, creating novel species interactions. However, how range shifts will alter biotic interactions and community structure in alpine streams is not well understood. In the Pyrénées, climate-induced physicochemcial habitat change is hypothesized to facilitate the colonization of high-altitude streams by Perla grandis, a carnivorous stonefly. A field-based experiment was done in mesocosm channels beside a hillslope spring (2000 m asl) in the Taillon-Gabiétous catchment, French Pyrénées. The influence of P. grandis predation on community structure, feeding trait composition, body-size spectrum, and algal chlorophyll a concentration was examined. Gut contents were analyzed and used to identify consumed prey. Total invertebrate density was not significantly reduced by P. grandis, but Baetis spp. densities were depressed in the treatment channels through a combination of direct consumption and predator avoidance (emigration/drift). However, despite fewer grazers in the predator treatment channels, the magnitude of the trophic cascade effect on basal resources (measured as chlorophyll a density) was comparable between treatment and control channels. The results of this experiment suggest that size/species specific predation, intraguild predation, and interference competition are the likely mechanisms that altered the body-size spectrum in treatment channels. In synergy with climate-driven physicochemical habitat change, the extinction risk of some range-restricted taxa (prey and other predators) could be increased where P. grandis colonization occurs. Hence, conservation efforts are required to ensure that additional anthropogenic stressors (e.g., nutrient enrichment, cattle trampling, hydropower development, ski runs, and tourism) are limited to minimize further pressures on these unique and sensitive habitats.

Key words: climate change, mesocosm, intraguild predation, Perla grandis, Pyrénées, food web, body size, enemy release

Future climate warming will alter ecosystem processes, biotic patterns, and interactions across a range of spatial and temporal scales (Parmesan 2006, Bellard et al. 2012), which in turn, will influence a wide variety of habitat types and taxonomic groups (Dirzo and Raven 2003, Thomas et al. 2004, Xenopoulos et al. 2005, Engler et al. 2011, Sauer et al. 2011). Mountain environments support unique biota (Brown et al. 2009, Engler et al. 2011) that are often at their range limits. These taxa are particularly vulnerable to warming because current and predicted warming rates in high-altitude environments are typically higher than the global mean (Beniston 2012). Altitudinal range shifts or expansions, although less well documented than latitudinal expansions (Parmesan 2006), have been observed for a variety of species (Pauli et al. 2007, Chen et al. 2011). However, in freshwater ecosystems, the spatial and temporal variability in trophic interactions make predictions about range shifts based on species–environment relationships potentially problematic (Woodward et al. 2010).

The sensitivity of alpine benthic stream ecosystems to climate change and range expansions has been highlighted increasingly in recent years (Muhlfeld et al. 2011, Sauer et al. 2011, Jacobsen et al. 2012, Khamis et al. 2014). Many range-restricted benthic organisms will be the ‘losers’ of future climate change (Somero 2010) because they will be unable to respond spatially or physiologically to water temperature increase (Bellard et al. 2012). Synergistic effects of climate/hydrological change and altered biotic interactions are likely to promote extinctions in pristine alpine river habitats (Tierno de Fueroa et al. 2010). Warming will cause changes in meltwater dynamics, and thus, stream discharge (magnitude and variability), water temperature, and stream channel stability will be altered (Brown et al. 2007a, Jacobsen et al. 2012) making habitats more favorable to some species, e.g., upstream colonization by more downstream or ‘lowland’ taxa (Brown et al. 2007a).

The type and strength of interactions between ‘invaders’ and ‘native’ taxa can have important implications for both biotic interactions and foodweb properties (Woodward et al.

2005). Woodward and Hildrew (2001) presented one of the few examples of (invertebrate) predator invasion effects on a low-order stream system and showed an increase in biotic interactions and foodweb trophic height after the invasion of a large-bodied dragonfly (Woodward and Hildrew 2001). In the context of low-order alpine streams, perturbations caused by predator invasion are likely to have significant effects because these food webs are characterized by high levels of omnivory and dietary overlap (Zah et al. 2001), with relatively high connectance and short food-chain lengths (Clitherow et al. 2013). Hence, factors affecting one node may propagate quickly through the network, with potential for cascading effects (Shurin et al. 2002). Therefore, in light of the rapid rate of environmental change predicted for alpine river ecosystems, the potential implications of predator range expansion on biotic interactions in these systems needs to be quantified (Milner et al. 2009).

Perla grandis (Plecoptera:Perlidae), a rheophilous mesothermal predatory stonefly, is widely distributed across the mountain ranges of southern and central Europe (Fenoglio et al. 2008) and is common throughout mid-altitude Pyrenean streams where it is the top invertebrate predator (Lavandier and Decamps 1984, Vincon 1987). In the alpine zone, its distribution appears to be limited by stream water-source contribution and altitude because higher-altitude streams, fed predominantly by melting snow or ice in spring, have a habitat template that is unsuitable (i.e., low water temperature, unstable beds, and high turbidity; Brown et al. 2007b). Sparse data exist regarding the feeding habits and ecology of P. grandis nymphs. The only study is from a mid-elevation stream (800 m asl) in the Appenines, northwestern Italy. Fenoglio et al. (2007) reported that the principal prey were chironomids, Baetis spp., and other Ephemeroptera. However, work on a similar species (Dinocras cephalotes:Perlidae) identified other large-bodied, predatory invertebrates as a dietary component (Bo et al. 2008). As glacier and snow packs recede, P. grandis is expected to expand its range upwards into lower-order, higher-altitude streams (Brown et al. 2007a).

However, brown trout (Salmo trutta), a potential competitor/predator of P. grandis, will be unable to track such range expansion because of migratory barriers, such as waterfalls. Hence, the likely decoupling of this historical trophic interaction suggests that P. grandis will experience ‘enemy release’, with significant effects on prey and predators/competitors in the invaded community (Gilman et al. 2010, Sih et al. 2010).

A field-based experimental approach was taken to assess potential effects of climate-driven range expansion (i.e., change in river water-source dynamics) of the stonefly P. grandis on stream benthic communities. Artificial through-flow mesocosm channels fed by a 1st-order stream were used to test 4 complementary hypotheses:

H_1: The abundance of key prey taxa will be reduced in P. grandis-invaded systems through either direct consumption or nonconsumptive effects (e.g., increased drift).

H_2: Community feeding-guild structure will be altered by P. grandis invasion through prey selection of active grazing taxa and interference competition with other large bodied predators.

H_3: Perla grandis immigration will alter population and community body size distributions through increased predation pressure and competition with resident predators.

H_4: Perla grandis will increase the magnitude of the trophic cascade by decreasing prey abundance (H_1), particularly active grazing taxa (H_2).

METHODS

Study site, experimental channels, and experimental organisms

Our study was conducted in the Taillon-Gabiétous catchment, Cirque de Gavarnie, French Pyrénées (lat 43°6′N, long 0°10′W) between 4 July and 27 July 2011. A detailed description of the study basin was provided by Hannah et al. (2007). Briefly, the catchment lies above the tree line (i.e., alpine zone), and has steep slopes (30–70°) and a sedimentary geology. On south-facing slopes a number of groundwater-fed streams are sourced from hillslope, alluvial aquifers. Here, allochthonous inputs are limited to grasses and sedges. Thus, the basal resources in these systems consist of primarily diatoms and benthic algae. Perla grandis is currently absent from streams >1900 m asl.

To emulate groundwater-fed stream habitat, experimental channels were situated beside a 1st-order stream, ~2000 m asl (Fig. 1A, B), where P. grandis was absent. Water was diverted from the stream via a feeder pipe (diameter = 10 cm) into 2 plastic header tanks (0.6 m × 0.4 m × 0.3 m). Each tank fed a block of 4 channels directly through equally spaced gate valves. Channels were made from rectangular plastic gutter (1 m × 0.13 m × 0.17 m) with a 0.05-m-diameter outflow pipe (Fig. 1A) through which water flowed into a drainage pipe that returned water to the main stream channel. Drift nets (250-µm mesh) attached to the outflow pipes captured emigrating P. grandis, which were then returned to the channels, and other emigrating taxa. Gravel (5–25 mm) and pebbles (25–45 mm) were collected from the feeder stream, elutriated thoroughly to ensure attached organisms and eggs were removed, and then used to fill the channels to a depth of 5 cm. Five cobbles (intermediate axis > 100 mm) were then placed in each channel, and the attached biofilm was inspected, and macroinvertebrates removed with forceps.

Flow velocity was recorded on 5 occasions in the center of each channel (0.6 depth from the water surface) using a Sensa RC2 electro-magnetic flow meter (Sensa, Aqua Data Services, Calne, UK). The velocity across all channels and dates was similar (mean ± SE, 0.13 ± 0.03 m/s, n = 40). Flow velocity was low, but the channels represented riffled habitat because at the low water depth and water volume in channel, broken water was observed over the substrate. Electrical conductivity (EC) and pH (measured using a Hanna HI 98129 handheld probe; Hanna Instruments, Woonsocket, USA), was also recorded on 5 dates. Both

EC (177 ± 2 µS/cm, n = 40) and pH (8.62 ± 0.3, n = 40) were similar between channels and dates. Water temperature was recorded continuously (15-min intervals for the duration of the experiment) in 1 channel from each block using a Gemini Tinytag Plus (instrument error ± 0.2°C; Gemini, Chichester, UK). Mean water temperature was comparable (10.2°C ± 0.9, n = 2208) between blocks and was lower than the Tourettes stream (11.4°C ± 2.7, n = 2208; KK, unpublished data) where the experimental P. grandis were collected. Water depth was similar throughout all channels and ranged from 6 cm above fine gravel to 2 cm above cobbles. Before initiating the experiment, flow in the channels was established for 3 d with the inflow pipe covered by 100-µm mesh, to inhibit colonization by drifting invertebrates while allowing algal colonization (Ledger et al. 2006).

Perla grandis (n = 33) were collected from the nearby Tourettes stream (1800 m asl; Fig. 1B) from which 8 well developed nymphs of equal body length (mean ± SE, 22.05 ± 0.66 mm) were selected for the experiment. The remaining nymphs (n = 25) were retained for gut-content analysis and stored in 70% ethanol.

Experimental design

The experiment followed a systematically balanced design with 2 treatments replicated 4 times: 1) a predator-free control, and 2) a P. grandis treatment (2 individuals [ind]/channel), corresponding to a density of 15 ind/m^2. The ambient density of P. grandis in the Tourettes stream was between 10 and 30 ind/m^2. All P. grandis nymphs were placed in the treatment channels on 4 July 2011, and the mesh was removed from the inlet pipe to enable colonization from the proximal stream species pool. Drift nets attached to the outflow pipes were inspected at least every 48 h for P. grandis. Invertebrate emigration via drift was sampled on 3 occasions (10–11, 18–19 and 26–27 July) for 24-h periods. Drift nets (250-µm mesh) were emptied into Whirlpak$^{\circledR}$ bags and stored in 70% ethanol. The experiment was terminated after 23 d on 27 July 2011.

At the end of the experiment, 3 cobbles were selected from each channel for chlorophyll a (chl a) analysis, and all attached invertebrates were removed with forceps. Epilithon was removed from the surface of cobbles in the laboratory with a stiff toothbrush in 50 mL of deionized water. The resultant slurry was drawn through a Whatman GF/F filter paper (0.7 µm; Whatman, Maidstone, UK) and frozen immediately. Samples were analyzed for chl a with the trichromatic spectroscopy method outlined in ASTM D3731 (ASTM 2004). Pigment extractions were made in 90% acetone. Periphyton concentrations were converted to mass per unit area (mg/m^2) as

$$Chl\ a = \frac{CaE}{A} \qquad \text{(Eq. 1)}$$

where Ca = concentration of chlorophyll a in the extract (mg/L), E = extract volume (L), and A = substrate area sampled (m^2).

All substrate from each experimental channel was transferred into a bucket, sieved, and the remaining organic material and invertebrates transported to the laboratory where macroinvertebrates were sorted from gravel under a bench lamp and stored in 70% industrial methylated spirit (IMS). Individuals from both the drift and end-point community were identified to the lowest practical taxonomic level (i.e., 60% of all individuals were identified to genus level or below) with the aid of a selection of taxonomic keys (Müller-Liebenau 1969, Tachet et al. 2000, Zwick 2004) and assigned to functional feeding groups following Moog (1995). For the most abundant taxa (>15 ind/m^2) and larger bodied predators, body length (mm) of all individuals in each taxon was measured on a dissecting microscope at 6.5 to 75× magnification (Stemi 2000-C; Ziess, Oberkochen, Germany) fitted with an eye-piece graticule. Gut contents of the mesocosm P. grandis (n = 8) and the individuals collected from the Tourettes stream (n = 25) were assessed. The entire gut was dissected and placed on a slide, and the contents were dispersed and identified on a dissecting microscope (6.5–75×) or a stage microscope at 100 to 1000× magnification (Optiphot-2; Nikon, Tokyo, Japan) as necessary. Partial specimens of consumed prey were counted only if the head was attached to the thorax.

Data analysis

All abundance data were standardized before statistical analysis to ind/m^2 and the relative abundance (%) of functional feeding groups was calculated. Taxonomic richness (i.e., number of taxa) and community dominance (Berger–Parker dominance index) were calculated for each channel using nontransformed abundance data. Drift propensity was calculated for the final sampling date (24–25 July) by dividing the number of drifting individuals of a given taxon by the total number of individuals of that taxon recorded in the channels.

Chl a, macroinvertebrate abundance, drift propensity, and functional feeding group data were tested for normality using a combination of QQ plots and the Shapiro–Wilk test. Variances were tested for homogeneity with Levene’s test (Zuur et al. 2010). Subsequently, Chl a and abundance data were $\sqrt{(x + 0.5)}$-transformed, relative abundance data were $\arcsin\sqrt{(x)}$-transformed, and drift propensity data were $\log_{10}(x + 1)$-transformed to meet assumptions of parametric analysis.

Because of the large number of statistical tests reported herein, null hypothesis testing was complimented by the calculation of standardized effect size (SES; McCabe et al. 2012). Unlike the application of stringent Bonferroni corrections, which reduce power and increase type II errors to unacceptable levels (Nakagawa 2004), calculation of SES enables biological importance and significance to be assessed simultaneously and reduces publication bias of selective reporting of results (Garamszegi 2006). Cohen’s d (SES) for each test was calculated as:

$$d = \frac{\bar{X}_1 - \bar{X}_2}{S^2} \qquad \text{(Eq. 2)}$$

where $\bar{X}_1$is the mean of the control, $\bar{X}_2$ is the mean of the treatment, and S^2 is the pooled standard deviation (SD) calculated as:

$$S^2 = \frac{(n_1 - 1)S_1^2 + (n_2 - 1)S_2^2}{n_1 + n_2} \qquad \text{(Eq. 3)}$$

where $S_i^2$is the SD of the of the ith group, and n_i is the sample size. Confidence intervals (95%) were calculated for d in the R environment (version 2.14.1; R Project for Statistical Computing, Vienna, Austria) using script created by Smithson (2011) that are freely available for download (http://psychology3.anu.edu.au/people/smithson/details/CIstuff/CI.html).

To test H_1 (the abundance of key prey taxa will be reduced in P. grandis-invaded systems through either direct consumption or nonconsumptive effects), prey selection was estimated using the raw abundance data from the treatment channels. The Log of the Odds Ratio (LOR) was calculated following Broduer (1998) as

$$LOR = ln\frac{g_i(100 - g_i)}{c_i(100 - c_i)} \qquad \text{(Eq. 4)}$$

where g_i is the relative abundance of taxon i found in the gut of P. grandis and c_i s the relative abundance of taxon i found in the treatment channels. This ratio varies from –∞ to +∞, and positive values represent preference.

The most abundant prey items (Fig. 2) were identified based on gut contents from our study (Table 1) and other relevant studies (Fenoglio et al. 2007, Bo et al. 2008). One-way analysis of variance (ANOVA), with block included as an additive variable (c.f. model 2; Newman et al. 1997), was used to identify treatment effect on the density of the most abundant potential prey taxa and the drift propensity. Hence, the error term for treatment effect in both these tests was the residual mean square (Newman et al. 1997).

Nonmetric dimensional scaling (NMDS), based on Bray–Curtis dissimilarity, was used to assess the effect of treatment on prey community structure. Analysis of similarity

(ANOSIM) was adopted to test whether the 2 treatments had different taxonomic compositions (i.e., dissimilarities between treatments greater than within treatment).

To explore $H_{2,}$ 1-way ANOVA (with block as an additive effect) was carried out to identify treatment effects on functional feeding group density and functional feeding group relative abundance. Predatory taxa that colonized the channels were split into 2 groups. Individuals >10 mm body length were classified as large-bodied predators and those <10 mm as small bodied (c.f. Ilg and Castella 2006).

To explore the first component of H_3 (P. grandis would alter population-level body-size distributions) Student's t-tests were used to test for treatment effect on mean body length of the most abundant prey taxa (Baetis gemellus, Baetis muticus, Simulium sp., and Orthocladiinae). Raw body-size data were used for statistical analysis because they were normally distributed and displayed homogeneity of variance. Violin plots (a combined box plot and kernel density plot) were used to assess body length differences between treatments because they display more information on data spread than box plots alone. The probability density function of the data at different values is shown, much like a histogram, but each block is centerd at each data point rather than fixed in the form of class bins (Hintze and Nelson 1998).

To test the 2nd component of H_3 (P. grandis would alter community-level body-size distributions), body mass (ash free dry mass [AFDM], mg) was calculated for the measured taxa using published length–mass regressions (Table S1). The body mass data for all taxa were then pooled and $\log_{10}(x)$-transformed to explore the effect of treatment on community-level body-size distribution (Brown et al. 2011). Transformed biomass data were sorted into 5 size classes (<–1.3, –1.3 to –0.7, –0.7 to –0.1, –0.1 to 0.5, > 0.5 mg). Treatment response was calculated as the % difference between treatment and control for each size class. Pairwise comparisons were used to calculate the mean difference and standard error (SE) for each size class. Each treatment channel was compared to all control channels, hence n = 16 for the mean and SE calculations. A Kruskal–Wallis test was used to test for treatment effect on the number of individuals in each body-mass class.

To test H_4, 1-way ANOVA (with block as an additive effect) was carried out to identify treatment effect on Chl a density. All tests were considered significant at $p < 0.05$. All plots, t-tests, ANOVA, and multivariate analyses were made using the base and vegan (Oksanen et al. 2012) packages in R (version 2.14.1).

RESULTS

Taxonomic composition and community structure of the mesocosm channels

Perla grandis individuals acclimatized rapidly to the channels, and only 2 individuals were returned from the drift nets to the channels (i.e., no mortality recorded). A total of 33 aquatic invertebrate taxa (excluding Collembola) colonized the experimental channels (Table S2). These taxa were representative of the source stream community (KK, unpublished data), and included predominantly several Diptera, Ephemeroptera, and Coleoptera (larvae and adults). Trichoptera were more abundant in the control than in the treatment channels, and Plecoptera taxa were rare in both treatment and control channels. Oligochaeta and the triclad, Polycelis sp., were the only noninsect taxa to colonize the channels.

Baetis gemellus was the most abundant taxon in control channels, whereas Orthocladiinae dominated in treatment channels (Table S2). Eight insect taxa (B. gemellus, B. muticus, Baetis alpinus, Simulium sp., Elmis sp., Orthocladiinae, Diamesinae, and Tanypodinae) were recorded at mean densities >10 ind/m^2 (Table S2), whereas other taxa were recorded in low densities (<10 ind/m^2). Large-bodied species, other than P. grandis, were rare and consisted of 5 taxa: 2 dipteran taxa (Tipulidae and Rhagionidae, <1 ind/m^2, across all channels) and 3 predatory trichopterans, Rhyacophila spp., Rhyacophila intermedia, and Plectrocnemia sp. Rhyacophila spp. were found exclusively in the treatment channels (mean ± SE, 2 ± 2 ind/m^2), whereas R. intermedia and Plectrocnemia sp. were recorded in higher densities (14 ± 5 ind/m^2 and 8 ± 3 ind/m^2, respectively) but exclusively in the control channels. The body sizes of R. intermedia (12.87 ± 0.75 mm) and Plectrocnemia sp. (11.21 ± 0.67 mm) were markedly smaller than P. grandis (22.05 ± 0.66 mm).

Total macroinvertebrate density was greater on average in control (1043 ± 65 ind/m^2) than in treatment channels (812 ± 73 ind/m^2). The treatment effect, though marginally nonsignificant (ANOVA, $F_{1,5} = 5.44$, $p = 0.058$) was large ($d = -1.56$, CI = –3.18–0.001). Mean species richness of the treatment and control channels was comparable (15.25 ± 0.75 and 14.75 ± 0.68, respectively). Community dominance was lower in treatment (0.29 ± 0.01) than control channels (0.39 ± 0.01). This effect was large ($d = -4.7$, CI = –7.4 to –2.0) and significant (ANOVA, $F_{1,5} = 34.38$, $p = 0.0006$).

H_1: The effect of P. grandis on invertebrate prey abundance and drift

The average number of prey/P. grandis gut was similar in the experimental channels (3.6 ± 0.5) and the Tourettes stream (3.4 ± 0.4), and the diet was entirely carnivorous. All prey items were insects, and Baetis spp. and Orthocladiinae were the most frequent. However, Baetis spp. were proportionally more abundant in the guts of P. grandis in the experimental channels (Table 1). Large-bodied prey items also were recorded, and entire Rhyacophila spp. and Limnephilidae larvae were found in the foreguts of P. grandis from the Tourettes stream. Perla grandis had a positive LOR and selectivity for Protonemura spp. in the channels (+2.85) and the Tourettes stream (+1.62), Baetis spp. (+0.26) in the experimental channels, and Orthocladiinae (+1.35) in the Tourettes stream (Table 1). High positive LOR values also were apparent for Rhyacophila spp (+1.37) and Limnephilidae (+1.13) in the Tourettes stream. Perla grandis displayed no selectivity (negative LOR values) for Simuliidae in either the experimental channels or Tourettes stream (Table 1).

The abundances of the mayflies, B. gemellus and B. muticus, were significantly lower in the treatment than in the control channels (Table 2) and the effect size was large (Fig. 2). Abundance of B. alpinus was significantly greater in the treatment than in the control channels (Table 2, Fig. 2). Other common prey taxa (i.e., Orthocladiinae and Diamesinae) showed no significant response to the treatment (Table 2, Fig. 2). The most stable solution (stress = 0.04) of the NMDS analysis of the abundant prey taxa (>15 ind/m^2) consisted of 2 dimensions. The treatment and control channels were divided along axis 1 (Fig. 3), and the stress plot indicated the loss of a negligible amount of the variation in the original data set (R^2 = 0.99). Treatment significantly affected prey community structure (ANOSIM, R = 0.47, p = 0.02). Control channels were characterized by greater abundance of B. gemellus, B. muticus, and Elmis sp. (Fig. 3).

Baetis alpinus and Protonemura spp. were the most abundant taxa in the drift compared to their channel densities (Fig. 4). Drift propensity rates for all other key prey taxa (Orthocladiinae, B. gemellus and B. muticus) were low (<1) (Fig. 4). A positive treatment effect was recorded for the drift propensity rate of B. gemellus, and a negative treatment effect was recorded for B. alpinus (Table 3). No significant treatment effect was detected for B. muticus and Protonemura spp. (Table 3).

H_2: Effects of P. grandis on invertebrate feeding guild structure

Grazers were the most abundant feeding guild and large predators were the least abundant in control and treatment channels (Table 4). Filter feeders (predominantly Simulium spp.) were numerically and relatively more abundant in treatment channels, as were predators (predominantly Tanypodinae). The density and relative abundance of grazers was significantly lower in treatment than in control channels (Table 4, Fig. 5). Shredder and collector abundances were similar between treatment and control channels (Fig. 5). When predators (excluding P. grandis) were divided into small- (5–10 mm) and large-bodied (>10 mm) classes, a significant negative effect of treatment was observed for the large-bodied predators (Table 4, Fig. 5). The most common of these large-bodied predators, R. intermedia, was more abundant in control (13 ± 5 ind/m^2) than in treatment channels (2 ± 2 ind/m^2), but this effect was not significant (ANOVA, $F_{1,5} = 3.89$, $p = 0.096$).

H$_3$: Effects of P. grandis on body-size spectrum

The predator treatment had no significant effect on the body size of Orthocladiinae or Simulium spp. individuals (Table 5). Mean body lengths of B. muticus and B. gemellus were 0.15 mm and 0.25 mm smaller in treatment than in control channels, respectively (Table 5). However, effect sizes were smaller for both taxa ($d < 0.5$, $p < 0.1$; Table 5). Violin plots of B. gemellus body lengths revealed an asymmetric density distribution, with fewer 5- to 6-mm individuals and smaller median body size in the predator treatment channels (Fig. 6).

The body mass distributions for the control and treatment (including P. grandis) channels were broadly similar but displayed some important differences: 1) distributions in the treatment channels displayed strong right skew because P. grandis individuals were considerably larger than any other taxa; and 2) there were fewer taxa between 1–10 mg in the treatment than in the control channels (Fig. 7). When all taxa (excluding P. grandis) were pooled and allocated to body-mass size classes, a significant negative treatment response was observed for the largest class (>5 mg; Fig. 7).

H$_4$: Cascading effects of P. grandis

Chl a content of the cobble biofilm was lower in the control (4.81 ± 0.86 mg/m^2) than in the treatment channels (7.13 ± 2.16 mg/m^2), but the effect size was small ($d = 0.63$, CI =

0.15–0.95) and not significant (ANOVA, $F_{1,5} = 4.03$, $p = 0.092$).

DISCUSSION

Predation is a key biotic process in aquatic systems that can drive physiological and behavioral responses of prey taxa (Peckarsky 1982) and alter community structure and functioning (Jefferies and Lawton 1984, Sih et al. 1998). Our study identified a number of community- and population-level responses to the experimental simulation of P. grandis range expansion. The density of conspicuous grazing taxa (Baetis spp.) was depressed through direct consumption and prey-avoidance mechanisms (Lancaster 1990). However, the magnitude of the trophic cascade (basal resources estimated as Chl a) did not change, probably because predators were present in the control (i.e., R. intermedia and Plectrocnemia sp.). A negative shift in mean body size was apparent in the presence of P. grandis at the population (B. gemellus) and community levels (avoidance by potential competitors).

Effects of P. grandis on prey abundance and drift

The finding that Baetis spp. and chironomid larvae (Orthocladiinae) were the most abundant prey items in the guts of P. grandis was similar to findings in other studies on a range of predatory stoneflies from Europe and North America (Allan 1982, Peckarsky 1985, Elliott 2003, Céréghino 2006, Bo et al. 2008). In our study, P. grandis displayed a preference for Baetis spp. in the experimental channels but not in the Tourettes stream and for orthoclads in the Tourettes stream but not in the experimental channels. The differences in preference between the Tourettes stream and experimental channels might be a consequence of the different proportions of Baetis species in the 2 environments. Baetis alpinus made up >90% of the Baetidae in the Tourettes stream, whereas B. gemellus made up >70% in the experimental channel. These 2 species appear to display different antipredator behaviors.

Baetis alpinus was a more mobile, stronger swimmer than B. gemellus (KK, personal observation) and tended to drift more frequently, a common response to plecopteran predation pressure (Kratz 1996). Calotriton asper, the top predator in many alpine springs, typically selects for more mobile prey (Montori 1992). Hence, the more sedentary behavior of B. gemellus when compared to B. alpinus may reflect adaption to C. asper predation pressure, but a degree of prey naivety in the presence of P. grandis (Cox and Lima 2006). On the other hand, the difference may have been an artefact of the small size of the experimental channels, which would have reduced in-channel predation refugia when compared to the Tourettes stream (Bechara et al. 1993).

Intraguild predation occurred in the benthic community of the Tourettes stream. Large Rhyacophila spp. were found in the guts of P. grandis. However, further work is needed to ascertain the symmetry of this relationship, i.e., to learn whether P. grandis is always the predator of Rhyacophila or whether the roles change depending on body size or life-cycle stage (Polis et al. 1989). Both these taxa share chironomid prey (Lavandier and Céréghino 1995, KK, unpublished data), thus some degree of interference competition can be inferred. Bo et al. (2008) also found Rhyacophila and other caseless caddisfly larvae in the guts of stoneflies, results suggesting that intraguild predation may be a common feature in low-order streams. Hence, the range expansion of P. grandis is likely to intensify biotic interactions by increasing the number of foodweb links with only a slight increase in the number of species (Woodward and Hildrew 2001). This shift will in turn reduce niche space, particularly among predators which, because of dietary overlap with P. grandis, will increase competition for prey items (Wissinger and Mcgrady 1993, Woodward and Hildrew 2002a).

Despite a large effect size, the reduction in total invertebrate abundance was not significant, probably because of high prey turnover rates, i.e., immigration replaced consumed or emigrated individuals (Lancaster 1990), or the small number of replicates (low statistical power). However, densities of 2 Baetis spp., which are typically important components of carnivorous stonefly diets (Peckarsky 1985, Céréghino 2006), were significantly reduced in our study. This finding supported H_1 (P. grandis would reduce prey abundance) and suggests that predatory stoneflies are more efficient at catching Baetis nymphs than other, more sedentary organisms, such as chironomids (Peckarsky and Cowan 1995, Elliott 2003). This greater success is primarily a result of the conspicuous swimming behavior of Baetis, which acts as a predator stimulus (Peckarsky and Penton 1989).

In contrast to our results, stonefly predation reduced chironomid densities in other laboratory and field experiments (Peckarsky 1985, Lancaster 1990, Elliott 2003). These investigators used ‘predation arenas’ (Allan et al. 1987, Elliott 2003), with the abundance and diversity of prey and predatory taxa strictly controlled, or field-based mesocosms where colonization by other, nontarget, large-bodied invertebrates was limited (e.g., Woodward and Hildrew 2002b). In our experiment, predators other than P. grandis were free to colonize all channels. The most abundant other predators were Rhyacophila spp. (mainly R. intermedia) and Tanypodinae, both of which feed predominantly on chironomids (Lavandier and Céréghino 1995, Woodward and Hildrew 2002b). These predators were relatively abundant in the control channels, so predation of orthoclad larvae probably occurred in treatment and control channels, but by different taxa, i.e., P. grandis consumed both Baetis and chironomids in the treatment channels, whereas R. intermedia and tanypods consumed chironomids in the control channel.

The increased drift rate by B. gemellus and B. muticus observed in the P. grandis treatment is a common behavioral response among Baetidae (Wooster and Sih 1995, Peckarsky et al. 2008). This response enables increased resource acquisition when mortality (predation) risk is high (Peckarsky 1996). However, B. alpinus exhibited a per capita drift rate far greater than that of the other Baetis spp., most likely because its co-evolution with P.

grandis amplified this behavioral trait (McPeek 1990). These findings further support H_1 (P. grandis would reduce prey abundance) because the key prey found in the guts (Baetis spp.) also were more abundant in the drift from P. grandis channels. Baetis alpinus drift was significantly greater from the control than from treatment channels, possibly because of apparent and exploitative competitive interactions among the Baetis spp. (Holt and Lawton 1994), with B. gemellus and B. muticus primarily predator (P. grandis) limited and B. alpinus primarily resource limited (Chase et al. 2002). Prey with superior resource acquisition capabilities, in this case, B. gemellus and B. muticus, also are the most vulnerable to predation (Holt and Lawton 1994).

Macroinvertebrate feeding guild structure

Distinct changes in functional feeding guild structure were observed in our study. These changes appeared to support H_2 (P. grandis would alter community feeding guild structure through selective predation and competition). The density of grazing taxa was lower in treatment than in control channels, probably because Baetis spp., the most abundant grazers recorded during the experiment, were more prone than other taxa to stonefly predation (Peckarsky and Penton 1989, Elliott 2003). The significantly lower relative abundance of large-bodied predators in the P. grandis channels probably was the result of intraguild predation/interference competition (Polis et al. 1989). However, all P. grandis nymphs used in our experiment were fully developed and the experiment ran for a relatively short time interval, so ontogenetic shifts in feeding habits of P. grandis and other predatory taxa were not incorporated into the study design (Lavandier and Céréghino 1995, Woodward and Hildrew 2001, Céréghino 2006). Nevertheless, these findings suggest the potential for future predator replacement as the physicochemical habitat template of low-order alpine streams changes under a warmer climate (Khamis et al. 2013).

Body-size spectrum

The smaller individuals of B. gemellus in the treatment channels (highlighted by the skewed violin plots) may a consequence of size-selective predation by P. grandis, with a preference for larger individuals as prey. Few investigators have studied size-selective predation in Plecoptera, but both Allan et al. (1987) and Peckarsky (1985) found experimentally that developed stonefly nymphs (>25 mg) preferred medium-sized prey (>0.2 mg). A 2nd explanation for the B. gemellus body-size distribution would agree with the findings of Lancaster (1990), who found that larger Baetis nymphs drifted more frequently than small nymphs from channels in the presence of a predatory stonefly.

When body size was considered at the community level (individual based rather than taxon averaged) individuals in the larger body-size classes were less abundant in the treatment than in the control channels, supporting H_3. This difference probably was a result of intraguild predation/interference competition, as evidenced by the presence of Rhyacophila spp. in the diet of P. grandis and associated positive LOR scores. This result suggests significant niche overlap between Rhyacophila spp. and P. grandis resulting from shared common prey (Lavandier and Céréghino 1995). Hence, the pattern of reduced body size in the treatment channels was caused by consumption of other large-bodied invertebrate predators by P. grandis or by avoidance of P. grandis by other large-bodied predators (Woodward and Hildrew 2002a, Vanak and Gompper 2010). This result has important implications for foodweb stability and structure because changes in the body-size spectrum (see Fig. 7), particularly an increase in size of the apex predator, can reduce refugia associated with gape-limited predation (Woodward et al. 2005). However, predicting how such changes will propagate through the food web in alpine systems is difficult because changes in interaction strength and omnivory can destabilize and stabilize food webs, respectively (Borrvall et al. 2000).

Cascading effects of P. grandis

Top-down, predation-driven, trophic cascades are more prevalent and often more pronounced in aquatic systems than terrestrial settings, primarily because of larger consumer to producer biomass ratios (Shurin et al. 2002). However, our study did not reveal any significant change in the magnitude of the trophic cascade caused by the presence of P. grandis (H_4 not supported). This lack of support may have been a result of a number of factors. First, the reduction in grazer densities observed in the treatment channels was relatively small (Table 4). Second, the high feeding plasticity of macroinvertebrates in alpine streams (Zah et al. 2001, Füreder et al. 2003, Clitherow et al. 2013) may increase ecological redundancy among feeding guilds (i.e., detritivores/predators also consume algae), thus dampening the trophic cascade (Polis et al. 2000). Third, the presence of other large-bodied predatory taxa (e.g., Rhyacophila spp.) probably would have affected grazing taxa in the control channels, potentially reducing grazing efficiency (Wooster and Sih 1995).

Conclusions and implications

As physicochemical habitat characteristics of alpine streams become more benign because of climate warming/river water-source changes, upstream migration of P. grandis is likely to increase the trophic height of invaded communities as current invertebrate predators (e.g., Rhyacophila spp.) become prey. Our study highlighted interference competition and interguild predation as important structuring mechanisms with the potential to alter the body-size spectrum and foodweb interactions in P. grandis-invaded systems (Woodward and Hildrew 2002b). Therefore, the predicted range expansion is likely to intensify biotic interactions, reduce niche breadth, and increase competition among predators). Furthermore, certain grazing taxa, primarily B. gemellus and B. muticus, are likely to be selectively predated, which could alter community structure and, potentially, its ecological functioning.

Our study has further emphasised the need to consider biotic interactions in species-abundance models (Araújo and Luoto 2007) because both community structure and body-size structure were altered under experimental predator range expansion. These findings have important implications for ecosystem stability because predator and prey body-size ratios control trophic interaction strengths (Emmerson and Raffaelli 2004, Woodward et al. 2005). Thus, ignoring or treating biotic interactions as constant is likely to cause erroneous predictions regarding future distributions and extinction vulnerability. This increased extinction vulnerability is particularly poignant in alpine river networks because, despite having low α diversity, 1st-order streams are important sites for regional biodiversity (Finn et al. 2011). Upstream movement by predatory taxa will create synergistic feedbacks among biotic interactions and climate-driven physicochemical habitat change, which are likely to increase the risk of species extinctions to the detriment of both β and γ diversity (Brown et al. 2007a). Therefore, work is urgently needed to ensure that additional anthropogenic pressures (e.g., water abstraction, hydropower schemes, nutrient enrichment, and cattle trampling) are limited to prevent more pressure on this unique and fragile habitat (Hannah et al. 2007, Khamis et al. 2013).

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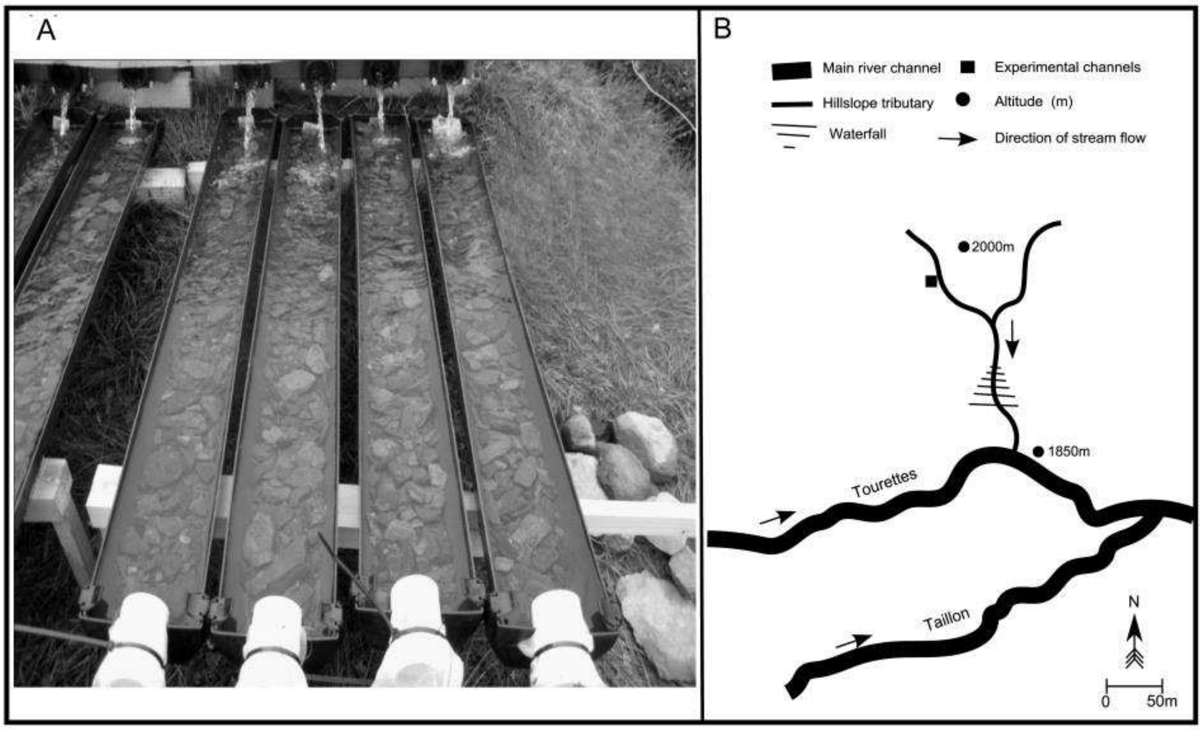

Fig. 1. Experimental channels (A) and a map of the study area showing the field site and location of experimental channels (B).

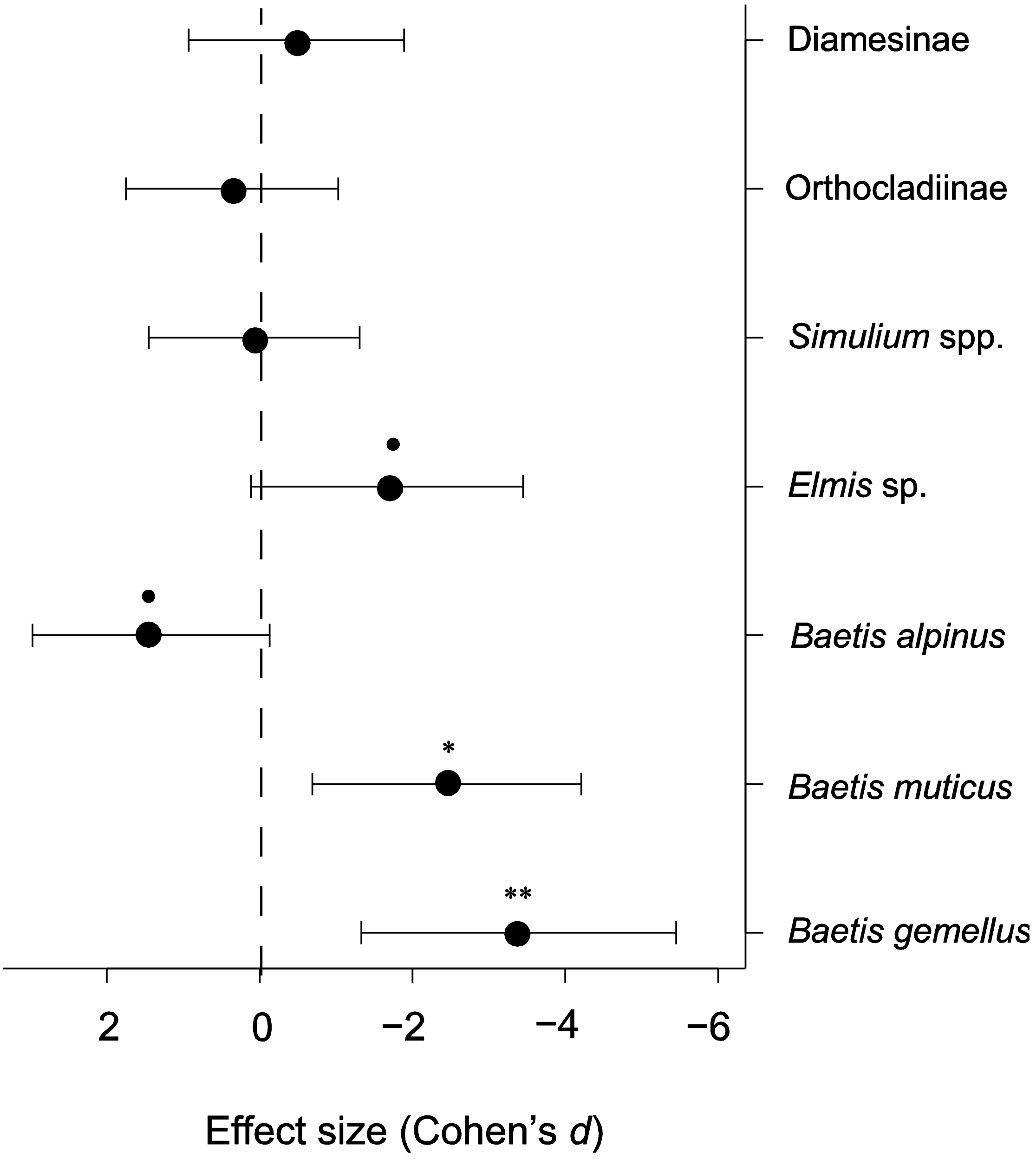

Fig. 2. Standardized effect size (Cohen's d) for the difference between treatment and control channels for prey density (individuals/m^2). Whiskers represent the 95% confidence intervals, and significant 1-way analysis of variance tests are indicated by ** = $p < 0.01$, * = $p < 0.05$, $^{\bullet}$ = $p < 0.1$.

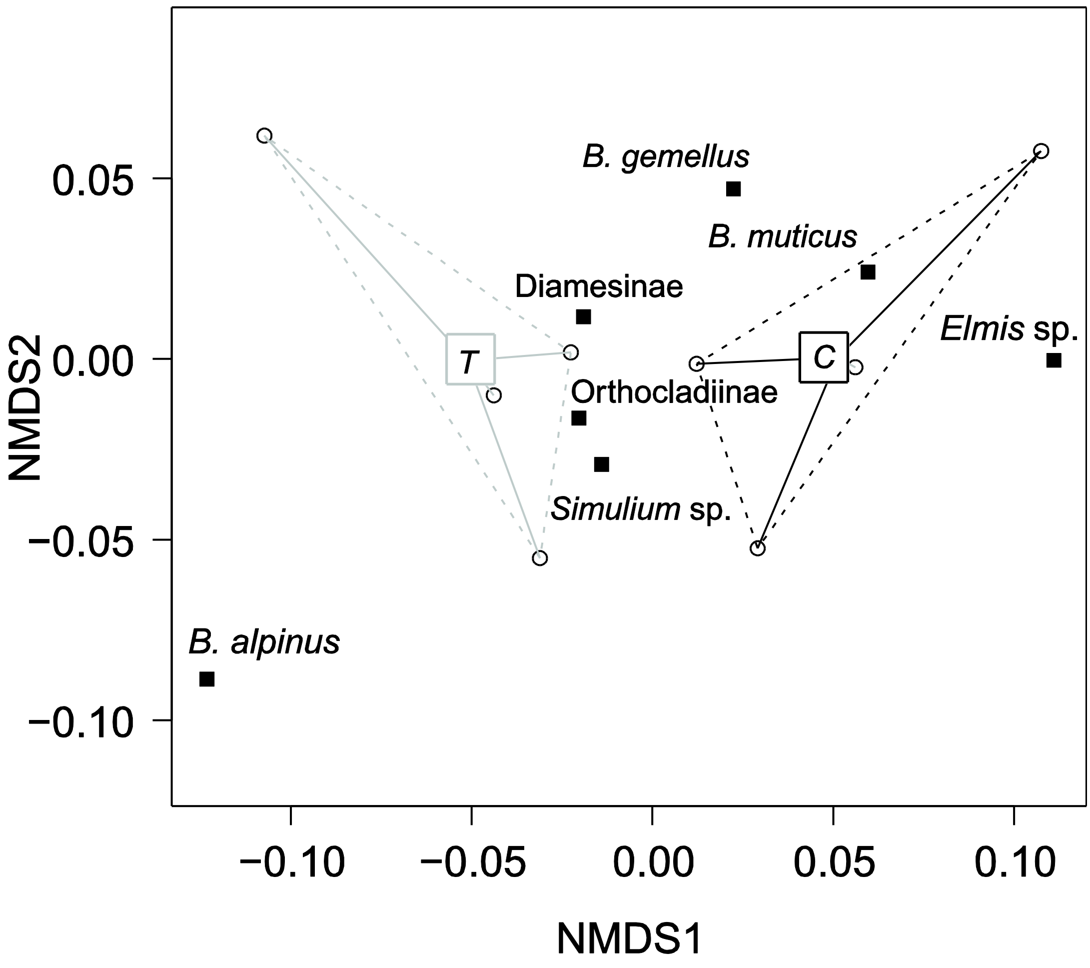

Fig. 3. Nonmetric dimensional scaling (NMDS) ordination of abundant taxa (B. = Baetis) in experimental channels. Numbers denote channels (treatment: 1–4, control: 5–8). Dashed line shows the convex hull for treatment (black) and control channels (gray).

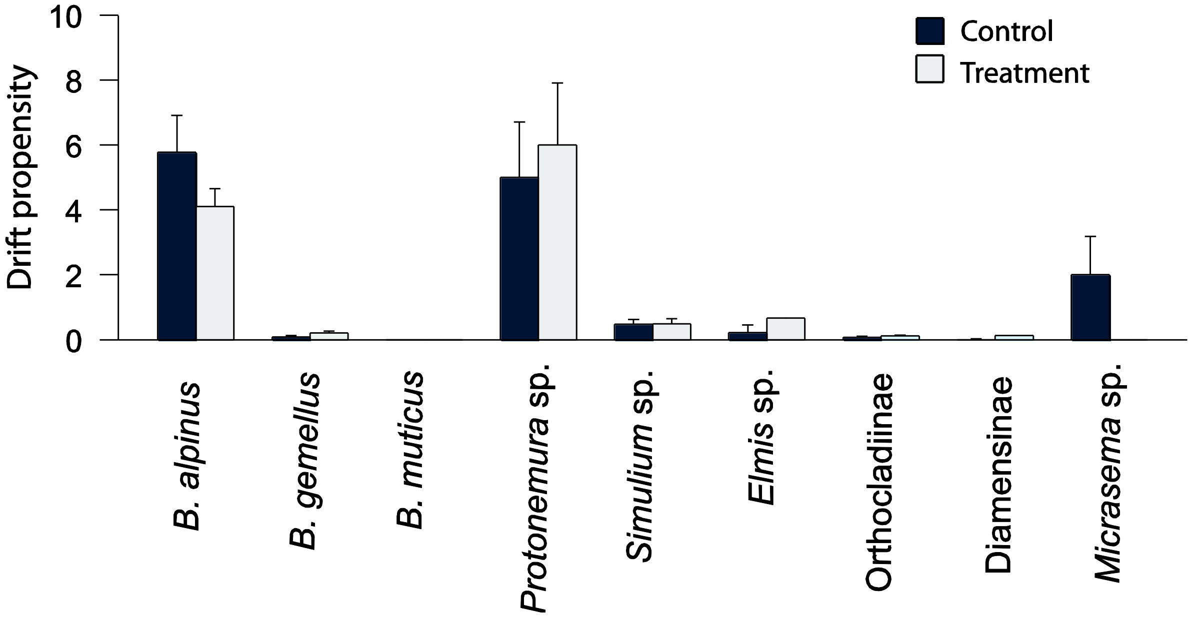

Fig. 4. Drift propensity (emigration/benthic density) of the most abundant taxa recorded from the mesocosm channels, 26–27 July. B. = Baetis.

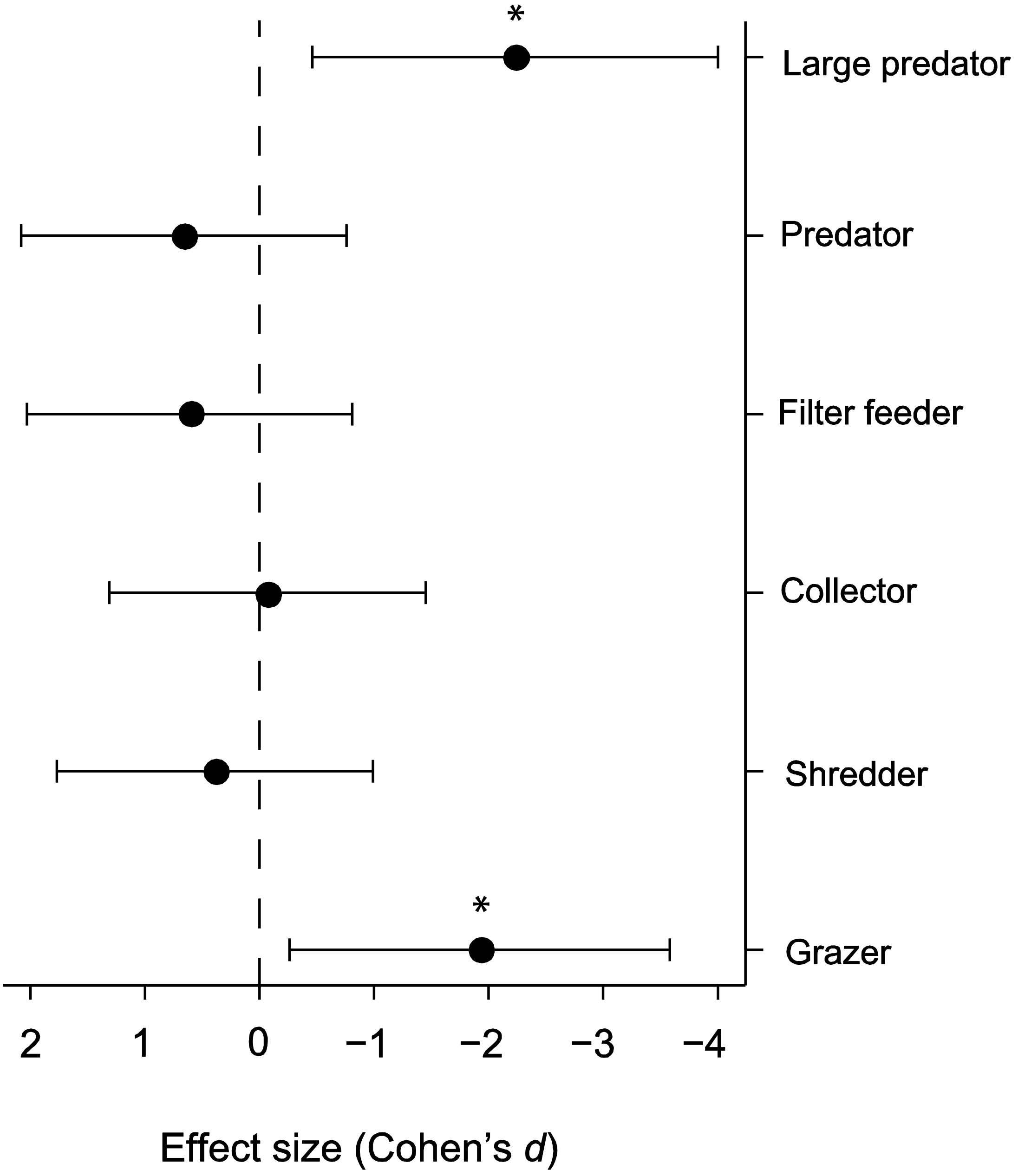

Fig. 5. Standardized effect size (Cohen's d) for the difference between treatment and control channels for functional feeding group relative abundance. Whiskers represent the 95% confidence intervals and significant 1-way analysis of variance tests are highlighted by $^{*} = p < 0.05$, $^{\bullet} = p < 0.1$.

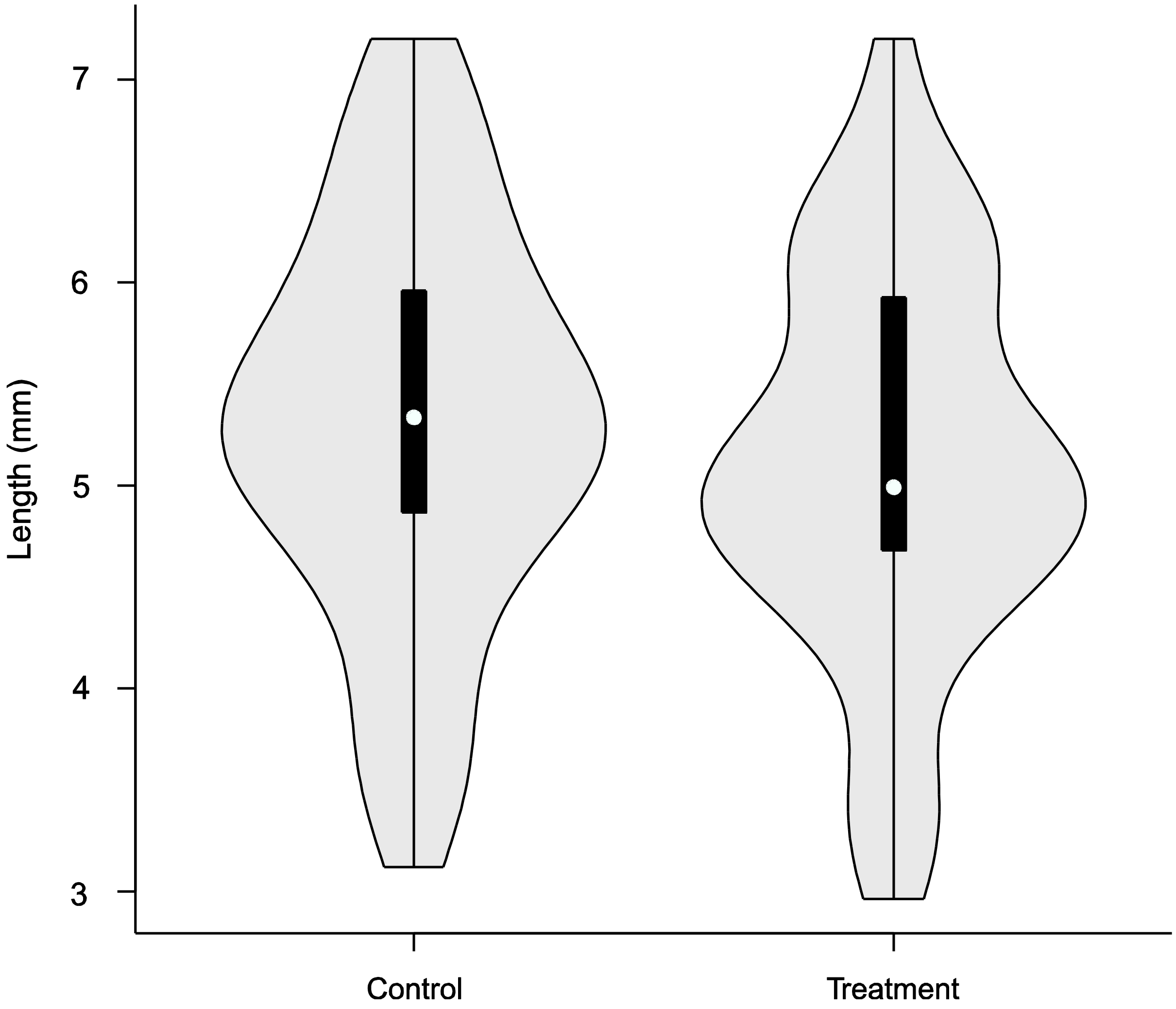

Fig. 6. Violin plots for the length (mm) of Baetis gemellus recorded in the mesocosm channels. The light grey area represents a kernel density function. The black box and line represent a traditional box plot where, box ends are quartiles, whiskers are 1.5 multiplied by the inter-quartile range (1st and 3rd quartiles), and the white dot represents the median.

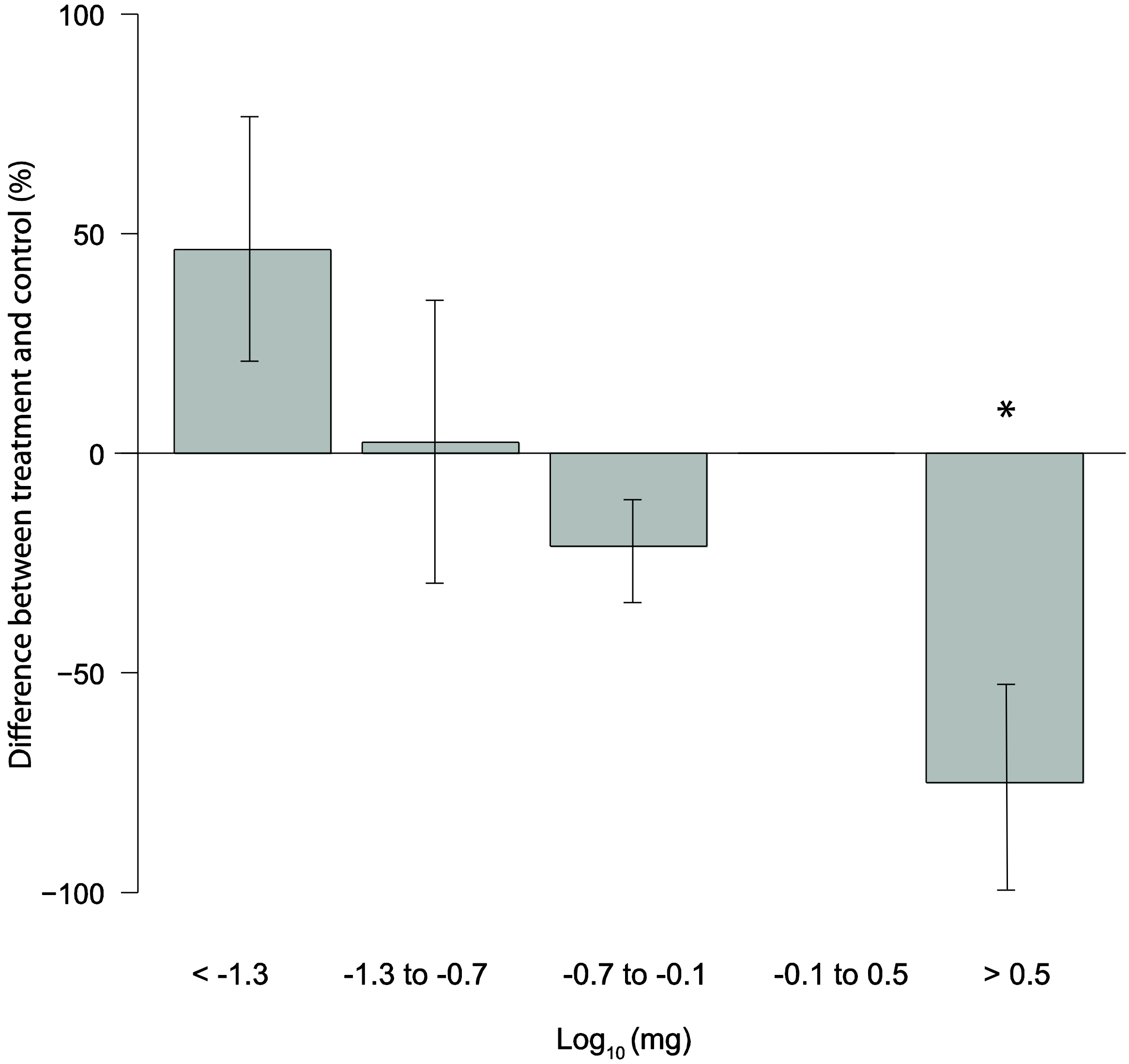

Fig. 7. Mean (±1 SE) % difference between treatment (not including Perla grandis) and control for the number of individuals in each of the 5 log$_{10}$(body mass) size classes. Mean and SE were calculated from all possible pairwise comparisons of individual treatment and control channels (for each size class, n = 16). * denotes significant Kruskal–Wallis test (H = 3.94, $p < 0.05$).

Table 1. Diet of Perla grandis nymphs in the Tourettes stream (n = 25) and mesocosm channels (n = 8).

Location	Prey taxon	% in gut	% in substrate	LOR	Mean (SE) prey items/gut

Tourettes Stream	Baetis spp.	37.6	57.1	-0.04	3.4 (0.2)
	Orthocladiinae	34.1	6.2	1.35	
	Protonemura spp.	11.8	2.1	1.62	
	Rhithrogena sp.	4.7	21.2	-1.32	
	Simulium spp.	3.5	4.9	-0.31	
	Unidentified arthropod	3.5	NA	NA	
	Limnephilidae	2.4	0.74	1.13	
	Chloroperla sp.	1.2	1.6	-0.32	
	Rhyacophila sp.	1.2	0.27	1.37	
Experimental channels	Baetis spp.	48.3	37.4	0.26	3.6 (0.3)
	Orthocladiinae	27.6	28.4	-0.01	
	Unidentified Plecoptera	10.3	NA	NA	
	Unidentified arthropod	6.9	NA	NA	
	Protonemura spp.	3.4	0.2	2.85	
	Simulium spp.	3.4	9.1	-0.96	

Table 2. Mean (SE) abundance (individuals/m^2) of the abundant prey taxa in control and treatment channels. Results of the one-way analysis of variance examining the effect of Perla grandis (treatment) on prey abundance are also displayed

	Abundance		ANOVA		
Taxa	Control	Treatment	Source	$F_{1,5}$	p
Baetis. gemellus	366 (23)	233 (19)	Treatment	18.89	0.007
			Block	0.01	0.94
Baetis muticus	106 (9)	50 (12)	Treatment	10.77	0.02
			Block	0.362	0.57
Baetis alpinus	19 (2)	36 (8)	Treatment	4.57	0.08
			Block	2.28	0.19
Elmis sp.	17 (4)	6 (2)	Treatment	6.84	0.04
			Block	1.39	0.29
Simulium spp.	64 (12)	36 (35)	Treatment	0.01	0.91
			Block	1.57	0.27
Orthocladiinae	283 (70)	235 (24)	Treatment	0.41	0.55
			Block	1.61	0.24
Diamesinae	21 (6)	15 (3)	Treatment	0.98	0.37
			Block	7.52	0.04

Table 3. One-way analysis of variance for the effects of predator treatment on drift propensity (per capita 24-h drift rate) for date 23–24 July. The standardized effect size (Cohen’s d) is presented with associated 95% confidence intervals. No block effect was identified.

Taxon	$F_{1,5}$	p	d (95 % CI)
Baetis muticus	2.82	0.23	0.94 (0.42–1.48)
Baetis gemellus	36.54	0.05	3.41 (2.53–4.31)
Protonemura spp.	0.02	0.90	0.07 (–1.31–1.46)
Baetis alpinus	28.07	0.05	–2.98 (–3.81 to –2.18)

Table 4. Mean (SE) abundance (individuals/m^2) and relative abundance (%) of functional feeding groups in control and treatment channels and results of 1-way analysis of variance results. Significant block effects are indicated as * = $p < 0.05$.

Functional feeding group	Relative abundance		Abundance		Relative abundance		Abundance	
	Control	Treatment	Control	Treatment	$F_{1,5}$	P	$F_{1,5}$	P
Grazer	77.0 (7.1)	69.3 (5.9)	804 (40)	564 (40)	7.29	0.04	7.77	0.03
Shredder	2.1 (0.7)	2.6 (1.0)	21 (1)	21 (1)	0.30	0.60	0.00	0.97
Collector	3.6 (1.0)	3.5 (0.8)	37 (3)	27 (1)	0.01	0.93	0.83	0.40
Filter feeder	5.6 (1.5)	9.2 (3.6)	60 (5)	75 (6.1)	0.74	0.42	0.17	0.69
Predator	11.7 (2.5)	15.4 (3.3)	121 (7)	125 (9)	0.88	0.38^*	0.31	0.60^*
Large predator	0.02 (0.05)	0.01 (0.04)	25 (4)	6 (1)	10.0	0.01	4.66	0.07

Table 5. Mean (SE) length of the 4 most abundant taxa recorded in the end-point community. Results from Student’s t-test are complimented by standardized effect sizes (unbiased estimate of Cohen’s d) and 95% confidence interval (CI).

	Body length (mm)					
Taxon	Treatment	Control	n	t	p	d (95% CI)
Baetis gemellus	5.06 (0.09)	5.31 (0.09)	120	2.29	0.02	–0.42 (–0.78 to –0.05)
Baetis muticus	5.99 (0.06)	6.14 (0.06)	80	1.79	0.09	–0.36 (–0.84–0.04)
Orthocladiinae	4.06 (0.16)	4.10 (0.15)	50	0.03	0.85	0.01 (–0.13–0.14)
Simulium spp.	4.25 (0.13)	4.13 (0.15)	50	0.33	0.57	0.07 (–0.07–0.21)