

# Non-native rainbow trout change the structure of benthic communities in headwater streams of the Cape Floristic Region, South Africa

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**Abstract** Introduced rainbow trout *Oncorhynchus mykiss* have invaded many headwater streams in the Cape Floristic Region (CFR) and depleted, or eliminated, native fish populations. However, the question of whether trout invasions also have consequences for lower trophic levels in these systems has not been addressed. We used a broad-scale comparative study in the upper Breede River catchment (CFR) to evaluate differences in benthic community structure between sites on headwater streams with and without trout, and thereby infer community-level impacts of trout. There were differences in invertebrate abundance and assemblage composition, and algal biomass, between sites with and without trout. Specifically, the abundance of

certain herbivorous invertebrate taxa was higher, and the biomass of benthic algae lower, at sites invaded by trout. This pattern implies that trout have induced a trophic cascade by releasing herbivorous invertebrates from predation, leading to an increase in grazing pressure and a consequent indirect decrease in the biomass of benthic algae; a pattern that contrasts with the majority of studies investigating community-level impacts of introduced trout elsewhere. These findings, together with comparisons of environmental conditions between invaded and uninvaded sites, indicate that trout invasions have changed the structure and function of benthic communities in these streams.

**Keywords** Algae · Particulate organic matter · Invasive predatory fish · Invertebrates · Native fish · Trophic cascade

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## Introduction

Predators are functionally important components in biological systems. From the top of the trophic web they can regulate the structure and function of biological communities beneath them through a combination of direct and indirect interactions (Estes et al., 2011). Directly, they regulate prey populations by reducing their abundance, or by restricting their movements, which can then translate into indirect effects on other components of the food web to which the prey are linked (Simon & Townsend, 2003;

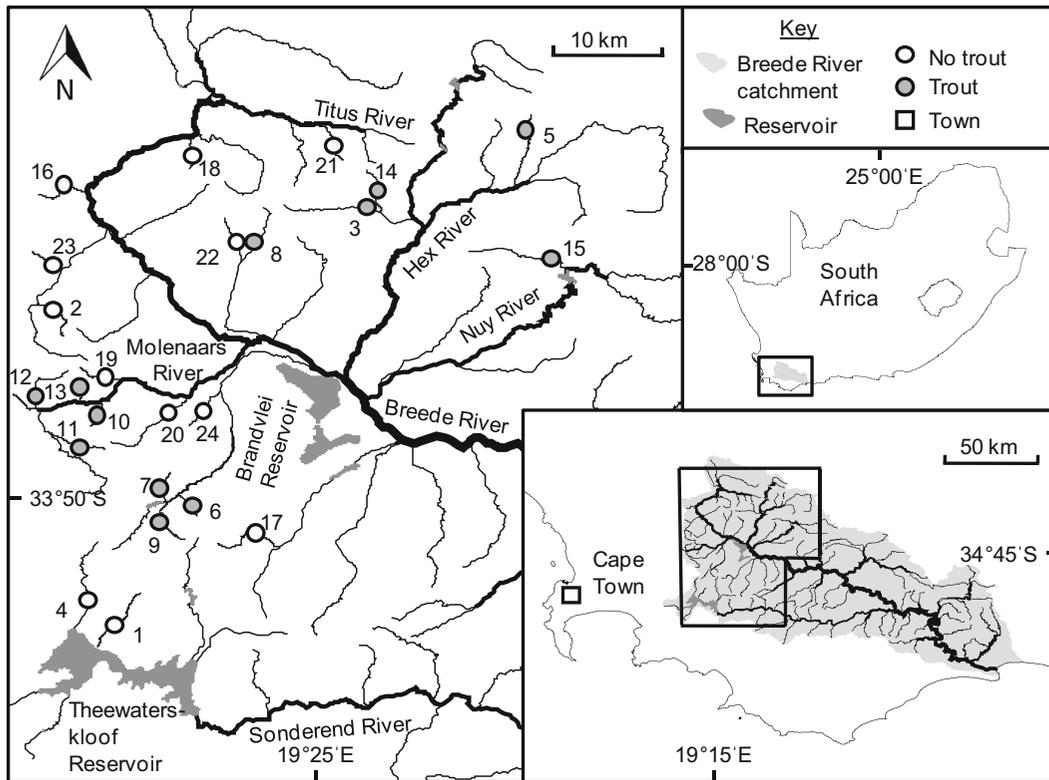
Townsend, 2003). The introduction of new predators can therefore result in the restructuring of entire communities if there are direct effects on adjacent trophic levels that then cascade down to non-adjacent trophic levels (Pace et al., 1999; Eby et al., 2006).

The consequences of predator introductions for recipient communities are difficult to predict and can be influenced by multiple biotic and abiotic factors (Lodge, 1993; Biggs et al., 2000; Sih et al., 2010). In general, impacts of introduced predators are influenced by how the introduced predator changes the predation regime (Schmitz & Suttle, 2001; Schmitz, 2008). Introduced predators sometimes prey on native predators and thereby effectively add an extra trophic level to the community (Eby et al., 2006). In such cases, a reduction in native predator abundance may then result in relaxation of predation pressure on herbivores, causing an increase in herbivory, and decrease in plant biomass at the base of the food web (Power, 1990). In situations where introduced predators eliminate native predators (or severely reduce their abundance), the degree to which the rest of the community is affected may then depend on how closely the functional role performed by the introduced predator matches that previously performed by the native predator(s) (Chalcraft & Reserits, 2003). If they consume similar types and amounts of prey to the native predators, then impacts on lower trophic levels may be minimal. On the other hand, if prey selectivity or consumption rates differ from the native predator(s), then it is likely that prey assemblages will be altered, with potential indirect effects on lower trophic levels (Benjamin et al., 2011; Lepori et al., 2012).

The human-assisted spread of predatory fish around the world for angling and aquaculture has led to a disproportionately large number of predator introductions in freshwater systems relative to terrestrial and marine systems (Ricciardi & MacIsaac, 2011). In many cases, introduced predatory fish have had strong effects on native biotas and community structure (Simon & Townsend, 2003; Eby et al., 2006). Non-native piscivorous fish have been widely introduced for angling purposes in the Cape Floristic Region (CFR) of South Africa, a global hotspot for biological diversity (de Moor & Bruton, 1988). In many CFR streams these non-native species appear to have largely eliminated small-bodied native fishes (de Moor & Bruton, 1988; Cambray, 2003a; Tweddle et al. 2009)

that are the dominant invertivores in these systems. In particular, invasive bass (*Micropterus* spp.) have eradicated native fish populations from the downstream reaches of rivers (de Moor & Bruton, 1988; Woodford et al., 2005; Weyl et al., 2010; Ellender et al., 2011), whereas rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) have severely depleted (or eliminated) native fish populations upstream in the headwater reaches of many streams (Shelton et al., 2014). Our understanding of whether these perturbations at the level of the fish assemblage have cascaded down the food web to lower trophic levels is inadequate (de Moor & Bruton, 1988; Cambray, 2003b; Lowe et al., 2008), but such information is needed if we are to appreciate the full extent of the non-native fish impacts in CFR streams. The results from two recent studies conducted in the CFR (Lowe et al., 2008; Weyl et al., 2010) suggest that the impact of invasive bass may indeed extend beyond the elimination of native fish populations, in that the composition of aquatic invertebrate assemblages was found to differ between sections of streams with and without bass. On the other hand, the question of whether rainbow trout introductions have influenced lower trophic levels in CFR streams has not yet been addressed, and forms the focus of this study.

Rainbow trout are aggressive, opportunistic predators that feed primarily on drifting aquatic and terrestrial invertebrates, but become increasingly piscivorous as they grow (Mittelbach & Persson, 1998; Arismendi et al., 2012). They are one of the most widely introduced fish in the world (Fausch, 2007), and are known to have altered the structure and function of benthic communities in invaded streams elsewhere (e.g. Herbst et al., 2009; Buria et al., 2010). In many cases, introduced trout have been shown to deplete populations of small-bodied native fish through predation and/or competition for space and resources (Cambray, 2003b). In general, this then leads to a decrease in invertebrate abundance and corresponding increase in the biomass of resources at the base of the food web (Simon & Townsend, 2003); presumably, because trout exert stronger predation pressure on benthic invertebrates than do the native fish species that they deplete (Biggs et al., 2000; Townsend, 2003). Based on this general pattern, we hypothesized that CFR streams with rainbow trout would have a lower abundance of benthic invertebrates and a higher biomass of benthic algae and/or particulate organic matter, than would streams without trout. To evaluate



**Fig. 1** Location of sampling sites in the upper Breede River catchment in the CFR of South Africa. White circles represent sampling sites without trout, and grey circles represent sites with

trout. The numbers of the sampling sites correspond to the numbers in Appendix 1 in Supplementary Material. Names of major rivers and reservoirs are shown

these hypotheses, we sampled benthic invertebrate assemblages, and estimated the biomass of benthic algae and particulate organic matter, at sites on 24 headwater streams, half of which had been invaded by rainbow trout, and none of which had any other non-native fish species present. We used differences in benthic community structure between invaded and uninvaded sites to infer trout impacts, and we measured a set of environmental variables to assess the potential confounding influence of variation in environmental conditions on our comparisons of community structure.

## Methods

### Study area

This study was conducted in headwater streams in the mountainous upper Breede River catchment in the

CFR (Fig. 1). These streams are generally narrow (<4 m wide), shallow (<0.50 m deep) and clear, dominated by cobble and boulder substrates and comprise alternating sections of erosional (riffles and runs) and depositional (pools) habitats. The area experiences a Mediterranean climate, with warm, dry summers and cool, wet winters, and the mean annual rainfall is ~800 mm, of which 80% falls between the months of April and September (Steynor et al., 2009). Natural vegetation covering the mountains is predominantly Sandstone Fynbos, a diverse assemblage of low-growing, fine-leaved, sclerophyllous shrubs. Riparian vegetation is largely composed of broad-leaved woody species including perennial shrubs and small trees, but also characteristic fynbos elements such as species of Restionaceae and Ericaceae (Cowling & Holmes, 1992). The mountains generally comprise hard, quartzitic sandstones of the Table Mountain group (Tankard et al., 1982), and the

streams flowing over this stratum are acidic, oligotrophic, low in dissolved solids, and support short and simple food webs (de Moor & Day, 2013).

Two distinct trophic pathways operate in these streams: an autotrophic pathway that is based on benthic algae, and a heterotrophic pathway that is based on detritus inputs from the adjacent riparian zone. Algae and detritus are fed upon by non-predatory benthic invertebrates, which in turn are fed upon by predatory invertebrates and fish, although fish may also feed on predatory invertebrates. Having trophic links to both algae- and detritus-eating invertebrates, fish can potentially influence the structure of both autotrophic and heterotrophic pathways in these systems. Four species of primary (salt intolerant) freshwater fish occur in headwater streams in the upper Breede River catchment: the Breede River redbfin *Pseudobarbus burchelli* (Smith 1841), the giant redbfin *P. Skeltoni* Chakona and Swartz 2013, the Cape kurper *Sandelia capensis* (Cuvier 1831) and the Cape galaxias *Galaxias zebratus* (Castelnau 1861). Although still abundant in some areas, native species abundance has been strongly depressed by piscivory from non-native trout in many headwater streams (Shelton et al., 2014). Non-native rainbow trout (henceforth “trout”) were introduced to the region in 1897 for angling and are now present in all major catchments in the CFR (Scott et al., 2006). Trout were initially stocked into many of the larger streams that drain the upper Breede River catchment and have since spread into smaller headwater tributaries (Tweddle et al., 2009). However, many tributaries still remain trout-free due to the presence of physical dispersal barriers such as waterfalls and weirs, providing an opportunity to study top-down effects of trout by comparing the structure of benthic communities between invaded and uninvaded headwater streams.

#### Site selection

Because stream communities are highly sensitive to human-related disturbances, we sought to select sites on headwater streams with and without trout that were not influenced by human activities and had no other non-native fish species present. We first surveyed 64 potentially suitable streams identified using topographic maps and the opinion of local freshwater biology experts. From these surveys, we identified 24

minimally disturbed (no evidence of human-related disturbance upstream) headwater streams, 12 of which had been invaded by trout and 12 of which had not. These streams were shallow and clear, and the presence/absence of trout, and other non-native fish species, was determined by extensive underwater observations. One 50-m-long site was arbitrarily selected on each of the 24 headwater streams, and this site length was chosen based on the recommendation of Bovee (1982) that a stream segment of 7–10 times the stream width is sufficient to capture the physical heterogeneity of that stream reach (wetted channel width at our study sites was usually about 3–4 m). All sites fell within the mountain stream geomorphological zone, had predominantly open canopies (<50% canopy cover), were not dominated by bedrock substrate (<50% stream bed cover) and had no other non-native fish species present.

#### Field sampling

We surveyed benthic communities and environmental conditions at all sites during summer (16 February–19 March 2010) when water clarity was high, and flows low. One site was sampled per day and sites were sampled in a random order. Snorkel surveys provide reliable estimates of fish abundance in small, clear streams in the CFR (Ellender et al., 2012; Weyl et al., 2013), and we used three-pass snorkel surveys (Thurrow, 1994) to estimate fish densities and population size structures at each site (see Shelton et al., 2014 for further details). The same diver conducted all snorkel censuses so that sampling effort among sites was constant (Hankin & Reeves, 1988). Each pass began at the downstream end of the 50-m site moving upstream in a zigzag pattern (Hankin & Reeves, 1988; Mullner et al., 1998), and the species and length (total length, TL; precision  $\pm 10$  mm) of all fish encountered were recorded. Passes were conducted 10–15 min apart to allow fish to recover from the disturbance caused by the snorkeler during the previous pass. Trout and native fish were collected from a subset of the 24 sites using a 3-m seine net and measurements of weight (to the nearest 0.01 g) and total length (TL, mm) were taken so that species-specific length-weight regressions could be constructed. Native fish were collected from sites 19, 20 and 22, and trout were collected from sites 5, 10 and 11. After processing, fish were released back to the stream unharmed.

Benthic communities were sampled in both erosional (including runs and riffles) and depositional (pools) habitats at each site. Sampling followed a stratified random design, with samples of invertebrates, algae and organic matter collected from each of five randomly selected erosional and depositional habitat patches at each site. Areas of stream where the water surface was broken or rippled (depth < 0.5 m) were erosional habitats, whereas areas with a smooth surface and minimal visibly detectable flow (depth > 0.5 m) were depositional habitats.

Samples of benthic invertebrates and organic matter were collected with a box sampler (basal area 0.09 m<sup>2</sup>, 250 µm mesh). At each sampling point, the box sampler was placed on the stream bed with the net extending downstream, and the area of stream bed falling within the net was disturbed by hand for 1 min, ensuring that all movable substrate particles were turned over and rubbed to dislodge invertebrates and other organic matter. The contents of each box sample were preserved in 70% ethanol. Five fist-sized stones were randomly collected from both erosional and depositional habitats at each site for assessment of algal biomass. Each stone was scrubbed in 500 ml stream water for 2 min with a toothbrush, after which the resulting slurry was homogenized and a 200 ml sub-sample collected, held on ice in the field, and frozen in the dark within 3 h of collection. The *x*, *y* and *z* dimensions of each stone were measured using plastic callipers (mm) so that the stone surface area available to algae could be estimated and linked to chlorophyll *a* measurements (Biggs & Kilroy, 2000).

The following 21 physico-chemical variables were measured to characterize and compare environmental conditions between sites with and without trout (see Shelton et al., 2014 for details of sampling protocols): erosional habitat (%), depositional habitat (%), wetted channel width (cm), water depth (cm), substrate length (mm), flow velocity (m s<sup>-1</sup>), canopy cover (%), riparian vegetation (%), submerged macrophytes (%), undercut banks (%), woody debris (%), water temperature (°C), dissolved oxygen (% saturation), pH, conductivity (µS cm<sup>-1</sup>), turbidity (NTU), elevation (m), site slope and the concentrations (mg l<sup>-1</sup>) of nitrates (NO<sub>3</sub><sup>-</sup>) plus nitrites (NO<sub>2</sub><sup>-</sup>), phosphates (PO<sub>4</sub><sup>3+</sup>) and ammonium (NH<sub>4</sub><sup>+</sup>). Habitat type was recorded at three equidistant points along ten width transects at each site.

## Laboratory protocols

All invertebrates were removed from each sample, and remaining material set aside for analysis of particulate organic matter (see below). Invertebrates were identified to the lowest possible taxonomic level using available keys (Day et al., 2001, 2003; Day & de Moor, 2002a, b; de Moor & Scott, 2003; de Moor et al., 2003; Stals & de Moor, Stals & de 2007; Cummins et al., 2008) and expert knowledge, and counted. Invertebrate taxa were assigned to functional feeding groups (FFGs) including collector-gatherers, grazer-scrappers, filter-feeders, shredders, macropredators and micropredators based on the above-listed references and the densities (number m<sup>-2</sup>) of each invertebrate taxon and FFG estimated.

The material remaining after invertebrates had been removed was used to estimate levels of fine (FPOM) and coarse (CPOM) particulate organic matter in each sample. Samples were elutriated to remove sand and gravel, and the remaining material was passed through a 1-mm sieve to separate organic matter into FPOM (250–1,000 µm) and CPOM (>1,000 µm). The ash-free dry mass (AFDM) of organic matter samples was obtained by drying samples at 60°C for 24 h in a drying oven, and then combusting the samples at 500°C for 1 h. The mass of the ashed sample was subtracted from that of the oven-dried sample and converted to AFDM m<sup>-2</sup> using the area of streambed incorporated in each box sample.

Algal samples were defrosted, homogenized and passed through Whatman GF/F 0.7-µm glass fibre filter papers, and the volume (usually approximately 150 ml) of filtered sample recorded. Chlorophyll *a* was extracted from filter papers using 90% ethanol and concentrations were measured using the spectrophotometric method described by Biggs & Kilroy (2000). Absorbance (665 and 750 nm) was measured using a Merck Spectroquant Pharo 100 spectrophotometer. The *x*, *y* and *z* dimensions of each stone were used to estimate area of exposed surface available for algae (estimated at ~65% of the total surface area; method described in Biggs & Kilroy, 2000) and algal biomass (as mg chlorophyll *a* m<sup>-2</sup>).

We estimated NO<sub>3</sub><sup>-</sup> + NO<sub>2</sub><sup>-</sup>-N, PO<sub>4</sub><sup>3+</sup>-P and NH<sub>4</sub><sup>+</sup>-N concentrations using a Lachat Flow Injection Analyser, as follows: NO<sub>3</sub><sup>-</sup> and NO<sub>2</sub><sup>-</sup> were estimated using Lachat's QuikChem<sup>®</sup> Method 31-107-04-1-E, in which NO<sub>3</sub><sup>-</sup> is converted to NO<sub>2</sub><sup>-</sup> and diazotized with

sulphanilamide to form an azo dye;  $\text{PO}_4^{3+}$  was measured by forming an antimony–phospho–molybdate complex using QuikChem® Method 31-115-01-1;  $\text{NH}_4^+$ -N was measured using Lachat's QuikChem® Method 31-107-06-1, based on the Berthelot reaction in which indophenol blue is generated. Approximate detection limits are as follows: for  $\text{NO}_3^-$  and  $\text{NO}_2^-$   $2.5 \mu\text{g l}^{-1}$  N; for  $\text{PO}_4^{3+}$   $15 \mu\text{g l}^{-1}$  P; and for  $\text{NH}_4^+$   $5 \mu\text{g l}^{-1}$  N.

### Data analyses

Length–weight regressions were constructed for each fish species based on  $\ln(x + 1)$  transformed length (mm) and weight (mg) measurements (see Appendix 2 in Supplementary Material for sample sizes, regression equations and regression plots). The mean total density and biomass of fish (i.e. native plus non-native species) was estimated for sites with and without trout, and compared using independent sample *t* tests on  $\ln(x + 1)$  transformed data. Rainbow trout in CFR streams appear to undergo an ontogenetic diet shift from invertivory to piscivory at a length of  $\sim 160$  mm (Woodford & Impson, 2004), although size at onset of piscivory may be strongly dependent on environmental context and the availability of different food sources (Mittelbach & Persson, 1998). A length frequency distribution was constructed for trout based on all individuals recorded at all sites to ascertain what proportion of individuals were likely piscivorous.

The mean density (number  $\text{m}^{-2}$ ) of each invertebrate taxon was estimated for erosional and depositional habitats from the five samples collected in each habitat type at each site. Site-level density estimates for each taxon and FFG were obtained by weighting the mean density in each habitat by the proportional cover of erosional and depositional habitat at each site. Multivariate analysis was used to assess differences in the taxonomic composition of invertebrate assemblages between sites with and without trout. Invertebrate abundance data were  $\ln(x + 1)$  transformed prior to analysis to down-weight the influence of the most abundant taxa, and converted to a resemblance matrix using Bray–Curtis similarity. Non-metric multidimensional scaling (nMDS) ordination was used to visualize differences in assemblage composition between sites with and without trout. PERMANOVA (one-way test using Bray–Curtis similarity and 9,999 permutations), a semi-parametric, permutation-based analogue of traditional ANOVA/MANOVA was then used to test for

significant differences in assemblage composition between sites with and without trout. The assumption of no significant difference in dispersion between the groups being compared was evaluated using permutational analysis of multivariate dispersion (PERMDISP). Analysis of similarity percentages (SIMPER) was then used to identify the taxa contributing most to the overall dissimilarity in assemblage composition between the sites with and without trout. An nMDS bubble plot with bubbles scaled to taxon abundance was generated for the taxon identified by SIMPER as contributing the most to the overall dissimilarity between the two groups of sites. Total invertebrate density, the densities of the top ten taxa identified by SIMPER analysis and the density of each FFG, were compared between the two groups of sites using independent sample *t* tests on  $\ln(x + 1)$  transformed data.

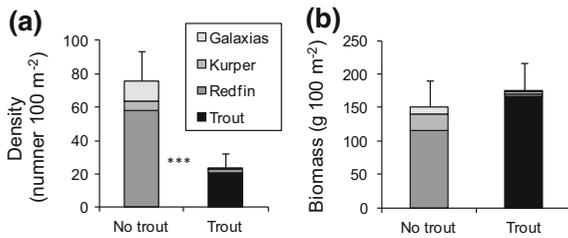
The mean biomass of benthic algae (as mg chlorophyll *a*  $\text{m}^{-2}$ ) and mean AFDM ( $\text{g m}^{-2}$ ) of FPOM and CPOM were estimated for both erosional and depositional habitats at each site by averaging the five samples collected from each habitat. Site-level estimates for these three metrics were then calculated using the estimates of the proportional cover of each habitat type at each site. Mean chlorophyll *a* concentration and levels of FPOM and CPOM, were  $\ln(x + 1)$  transformed to improve normality and homogeneity of variances, and compared between sites with and without trout using independent sample *t* tests.

Each environmental variable was compared between sites with and without trout using an independent sample *t* test. Percentage oxygen saturation, riparian vegetation and canopy cover were arcsin square root transformed, while turbidity, flow velocity and elevation were  $\ln(x + 1)$  transformed prior to analysis to improve normality and meet the assumptions of the analysis. All univariate analyses were carried out with SPSS 20.0 (SPSS, 2011), and multivariate analyses were performed using PRIMER-E (Clarke & Gorley, 2006) with the add-on package PERMANOVA+ (Anderson et al., 2008).

## Results

### Fish

The Breede River redbfin dominated the native fish assemblage at uninvaded sites, comprising  $>75\%$  of



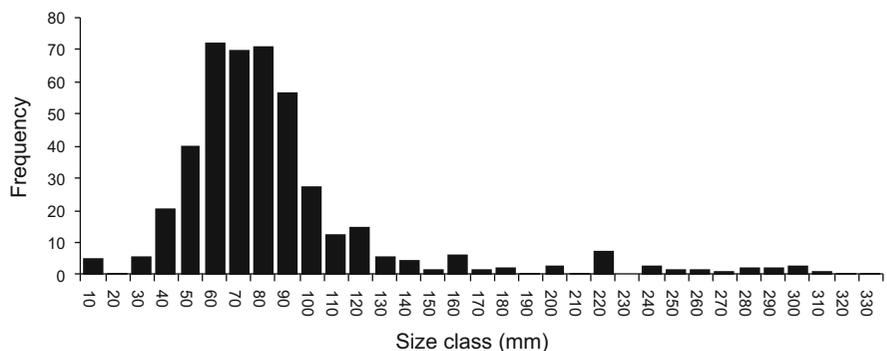
**Fig. 2** Mean  $\pm$  SE of **a** total density and **b** total biomass of fish at sites with and without trout. “Galaxias” *Galaxias zebratus*, “Kurper” *Sandelia capensis*, “Redfin” *Pseudobarbus burchelli* and “Trout” *Oncorhynchus mykiss*. Asterisks indicate significant differences based on *t* tests (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ )

the assemblage on average both by number (Fig. 2a, Appendix 1 in Supplementary Material) and biomass (Fig. 2b). In contrast, rainbow trout was the dominant species at invaded sites, making up >85% of the fish assemblage by both number and weight, and was the only fish species present at 7/12 of the invaded sites. Thus, fish assemblages at our sites were dominated either by Breede River redbfin or trout. When all fish species were combined, the mean total density of fish at sites without trout was significantly greater than that at invaded sites ( $t_{1,22} = 3.23$ ,  $P < 0.001$ ), whereas no significant difference in mean total fish biomass was detected ( $t_{1,22} = -0.37$ ,  $P = 0.712$ ). The length frequency distribution of trout at our study sites was skewed to the right with the vast majority (>90%) of individuals falling between lengths of 0–160 mm (Fig. 3).

### Invertebrates

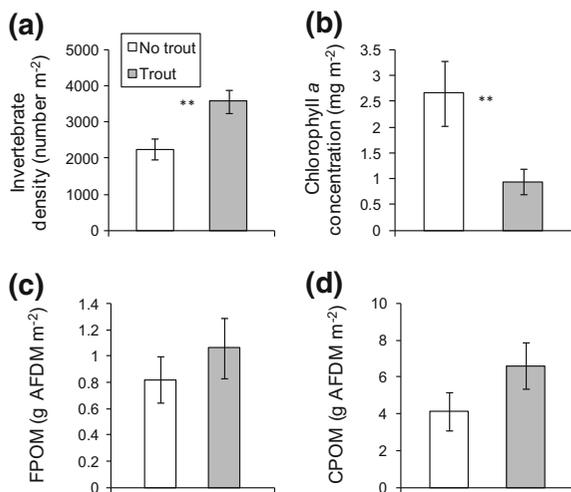
The mean density ( $\pm$ SE) of invertebrates at sites with trout ( $3,568 \pm 315 \text{ m}^{-2}$ ) was significantly higher than

**Fig. 3** Length frequency distribution for rainbow trout ( $n = 447$ ) based on snorkel-survey estimates of fish populations at the 12 study sites where trout were present



that at sites without trout ( $2,238 \pm 291 \text{ m}^{-2}$ ;  $t_{1,22} = -2.90$ ,  $P = 0.005$ , Fig. 4a). The nMDS ordination revealed that the composition of invertebrate assemblages at sites with trout differed consistently from that at sites without trout (Fig. 5a;  $F_{1,22} = 3.01$ ,  $P = 0.002$ ). The average dissimilarity between sites with and without trout was 59.06%, and the ten taxa most important in discriminating between these groups of sites accounted for 63.10% of that dissimilarity. *Baetis* (Ephemeroptera) contributed most to the overall dissimilarity and the bubble plot shows that it was generally more abundant at sites with trout than at sites without trout (Fig. 5b). The mean density of *Baetis* mayflies at sites with trout ( $648 \pm 143 \text{ m}^{-2}$ ) was significantly higher than at sites without trout ( $165 \pm 77 \text{ m}^{-2}$ ;  $t_{1,22} = -3.96$ ,  $P = 0.001$ ). Other taxa contributing strongly to the dissimilarity included the ephemeropterans *Lestagella penicillata*, *Demoreptus capensis* and *Pseudocloeon*, the coleopteran Elmidae, the dipterans *Simulium*, Orthocladiinae and Chironominae, the plecopteran *Aphanicercella* and the trichopteran *Athripsodes*, which collectively contributed a further 44.64% of the overall dissimilarity between the two groups of sites (Fig. 6). With the exception of *Athripsodes* and *Pseudocloeon*, the densities of these taxa were higher at sites with trout, and differences in the mean densities of *L. penicillata* ( $t_{1,22} = -3.03$ ,  $P = 0.004$ ), *D. capensis* ( $t_{1,22} = -3.03$ ,  $P = 0.006$ ) and *Simulium* ( $t_{1,22} = -2.270$ ,  $P = 0.033$ ) between the two groups of sites were significant.

The crab *Potamonautes*, which is an omnivore and chironomids that could not be identified to subfamily, could not be confidently assigned to specific FFGs and were therefore excluded from the FFG analysis. Collector-gatherers were notably more abundant than

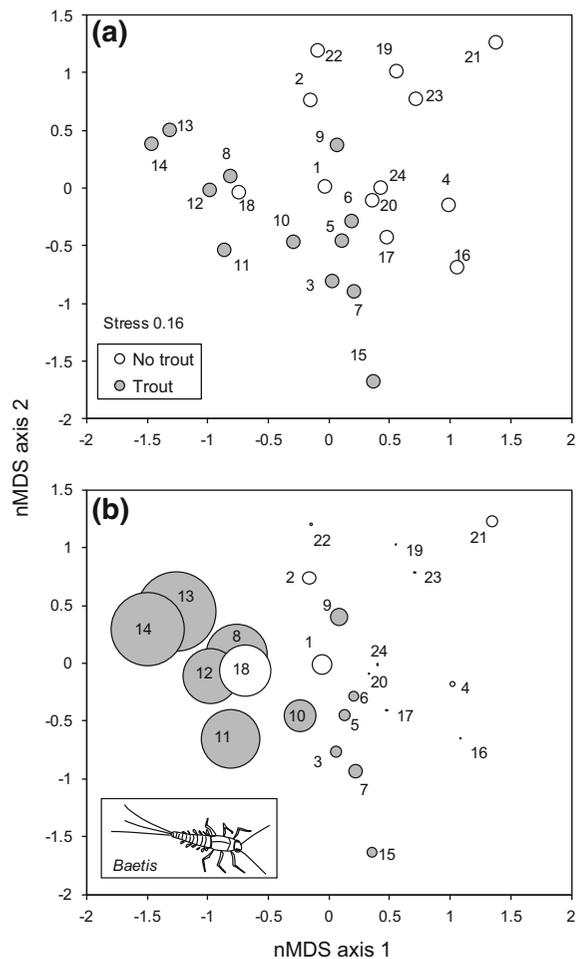


**Fig. 4** Mean  $\pm$  SE of **a** total invertebrate density, **b** algal biomass (measured as chlorophyll *a* concentration), **c** the AFDM of FPOM and **d** the AFDM of CPOM at sites without (*white bar*) and with (*grey bar*) trout. Asterisks indicate significant differences based on *t* tests on  $\ln(x + 1)$  transformed data (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ )

any of the other FFGs at our sampling sites, comprising >65% of the invertebrate assemblage at both sites with and without trout (Fig. 7). The mean density of collector-gatherers at sites with trout ( $2379.23 \pm 169.14 \text{ m}^{-2}$ ) was significantly higher than that at sites without trout ( $1518.34 \pm 197.36 \text{ m}^{-2}$ ;  $t_{1,22} = 3.30$ ,  $P = 0.003$ ). On the other hand, although somewhat more abundant at sites with trout, the densities of grazer-scrappers ( $t_{1,22} = 1.84$ ,  $P = 0.079$ ), shredders ( $t_{1,22} = 1.38$ ,  $P = 0.182$ ) and filter-feeders ( $t_{1,22} = 1.53$ ,  $P = 0.141$ ) did not differ significantly between the two groups of sites. Similarly, no significant difference in macropredator ( $t_{1,22} = 0.17$ ,  $P = 0.870$ ) or micropredator ( $t_{1,22} = 1.71$ ,  $P = 0.102$ ) densities were detected between sites with and without trout.

#### Lower trophic levels

The mean algal biomass (measured as chlorophyll *a* concentration) at sites with trout ( $0.94 \pm 0.24 \text{ mg m}^{-2}$ ) was significantly lower than that at sites without trout ( $2.65 \pm 0.63 \text{ mg m}^{-2}$ ;  $t_{1,22} = 2.77$ ,  $P = 0.011$ , Fig. 4b). Levels of both FPOM and CPOM were somewhat higher at sites with trout relative to sites without trout (Fig. 4c, d), but these differences were not statistically significant (FPOM,  $t_{1,22} = 0.85$ ,  $P = 0.417$ ; CPOM,  $t_{1,22} = 0.17$ ,  $P = 0.089$ ).



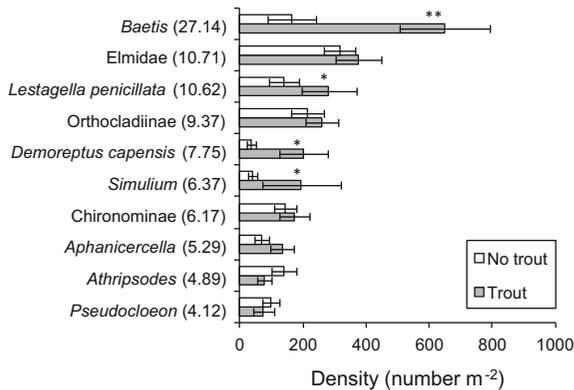
**Fig. 5** nMDS ordination plots of the composition of invertebrate assemblages at the 24 study sites (numbers correspond to site numbers in Fig. 1). Panel **(a)** indicates sites without (*white circles*) and with (*grey circles*) trout, and panel **(b)** is a bubble plot on the same ordination indicating the density of *Baetis* mayflies at each study site (bubble size is scaled to *Baetis* density)

#### Environmental conditions

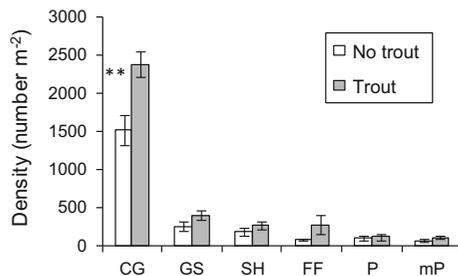
None of the 21 measured physico-chemical variables differed significantly between the sites with and without trout (Table 1), indicating a lack of consistent difference in environmental conditions between the two groups of sites.

#### Discussion

Non-native rainbow trout have invaded many head-water streams in the CFR and appear to have severely



**Fig. 6** Mean  $\pm$  SE of the density of the ten taxa identified by SIMPER analysis as contributing the most to the dissimilarity in taxonomic assemblage composition between sites with and without trout. The average dissimilarity between sites with and without trout was 59.06% and values in parentheses indicate the percentage contribution of each taxon to this dissimilarity. Asterisks indicate significant differences based on  $t$  tests on  $\ln(x + 1)$  transformed data (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ )



**Fig. 7** Mean  $\pm$  SE of the density of each invertebrate functional feeding group. CG collector-gatherers, GS grazer-scrappers, SH shredders, FF filter-feeders, P macropredators and mP micropredators. Asterisks indicate significant differences based on  $t$  tests on  $\ln(x + 1)$  transformed data (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ )

depleted, or eliminated, native fish populations in these systems (Shelton et al., 2014). In this study, we investigated whether trout impacts extended beyond native fish, down to lower trophic levels. We found consistent differences in benthic invertebrate density and assemblage composition, as well as algal biomass (measured as chlorophyll *a* concentration), but not levels of particulate organic matter, between sites with and without trout. There were no consistent differences in measured environmental variables between these two groups of sites, implicating the presence of trout as the factor primarily responsible for the observed differences in benthic community structure.

The significantly higher density of benthic invertebrates at invaded sites suggests that trout have reduced predation pressure on benthic invertebrates. The taxa driving differences in invertebrate assemblage composition fell almost exclusively within the collector-gatherer, grazer-scraper and filter-feeder FFGs, and in general these taxa had higher densities at invaded sites than at sites without trout. Taxa within these FFGs feed, to varying degrees, on algae and detritus on the surfaces of stones or on food particles suspended in the water column (Cummins et al., 2008), and these feeding behaviours likely render them vulnerable to insectivorous fish (Meissner & Muotka, 2006), and thus sensitive to changes in fish assemblages. *Baetis* mayflies, in addition to being the most abundant taxon when taxon density was averaged across all sites ( $14.01 \text{ m}^{-2}$ , Appendix 3 in Supplementary Material), contributed strongly to the overall dissimilarity in assemblage composition between sites with and without trout. *Baetis* abundance has been shown to be strongly influenced by top-down effects of insectivorous fish elsewhere (Bechara et al., 1992; Rosenfeld, 2000; McIntosh et al., 2004; Ruetz et al., 2004), and *Baetis* mayflies often form an important trophic link between insectivorous fish and algae and organic matter at the base of the food web (Barber-James & Lugo-Oritz, 2003). The higher abundance of some taxa at uninvaded sites could be a result of adaptations that offer protection from fish predation and because the higher biomass of benthic algae may have increased food availability. For example, the caddisfly *Athripsodes*, which was more abundant at the uninvaded sites, may be relatively invulnerable to fish because of its hard sand grain case as has been documented for cased caddisflies elsewhere (e.g. Bechara et al., 1992; Nyström et al., 2003).

The lower mean chlorophyll *a* concentration (which provides a measure of benthic algal biomass) at invaded sites relative to uninvaded sites implies that by releasing herbivorous invertebrates from predation, trout have indirectly increased the grazing pressure on benthic algae. This pattern is comparable to that documented in other CFR streams where non-native bass *Micropterus* spp. have depleted native fish abundance; where bass have invaded, algal biomass is lower than that at similar sites where bass are absent and healthy native fish populations persist, apparently as a consequence of a higher abundance of certain herbivorous taxa (e.g. Baetidae, Simuliidae,

**Table 1** Mean  $\pm$  SE for each of the 21 physico-chemical variables measured at sites with ( $n = 12$ ) and without ( $n = 12$ ) trout

Variable	No trout	Trout	$t_{1,22}$	$P$
Erosional habitat (%)	70.28 $\pm$ 3.96	68.06 $\pm$ 3.08	0.44	0.663
Depositional habitat (%)	29.72 $\pm$ 3.96	31.94 $\pm$ 3.08	0.44	0.663
Width (cm)	389.75 $\pm$ 13.76	384.58 $\pm$ 17.51	0.23	0.819
Depth (cm)	25.16 $\pm$ 1.03	24.09 $\pm$ 1.23	0.66	0.515
Substrate length (mm)	295.3 $\pm$ 16.68	291.26 $\pm$ 16.25	0.17	0.864
Flow velocity ( $\text{m s}^{-1}$ ) <sup>a</sup>	0.2 $\pm$ 0.02	0.18 $\pm$ 0.02	0.49	0.628
Canopy cover (%) <sup>b</sup>	19.44 $\pm$ 1.92	28.33 $\pm$ 4.09	-1.08	0.102
Riparian vegetation (%) <sup>b</sup>	65.83 $\pm$ 5.14	62.08 $\pm$ 6.56	0.55	0.586
Submerged macrophytes (%) <sup>b</sup>	16.39 $\pm$ 5.82	4.44 $\pm$ 1.38	1.96	0.063
Undercut bank (%) <sup>b</sup>	3.33 $\pm$ 1.36	3.06 $\pm$ 1.04	0.19	0.848
Woody debris (%) <sup>b</sup>	5.28 $\pm$ 0.96	8.06 $\pm$ 3.03	-0.18	0.859
Temperature ( $^{\circ}\text{C}$ )	22.39 $\pm$ 0.69	21.07 $\pm$ 0.53	1.52	0.144
Oxygen saturation (%) <sup>b</sup>	92.13 $\pm$ 1.97	90.51 $\pm$ 1.92	0.79	0.441
pH	4.9 $\pm$ 0.16	5.3 $\pm$ 0.15	-1.88	0.074
Conductivity ( $\mu\text{S cm}^{-1}$ )	16.3 $\pm$ 1.46	15.38 $\pm$ 1.64	0.42	0.677
Turbidity (NTU) <sup>a</sup>	0.67 $\pm$ 0.08	0.58 $\pm$ 0.11	0.84	0.411
Elevation (m) <sup>a</sup>	419.17 $\pm$ 35.94	473.83 $\pm$ 25.05	-1.62	0.121
Site slope (%)	6.71 $\pm$ 0.52	6.72 $\pm$ 0.86	0.46	0.651
$\text{NO}_3 + \text{NO}_2$ ( $\text{mg l}^{-1}$ ) <sup>a</sup>	6.21 $\pm$ 1.88	9.52 $\pm$ 2.06	-0.99	0.335
$\text{NH}_4$ ( $\text{mg l}^{-1}$ ) <sup>a</sup>	24.97 $\pm$ 1.94	33.09 $\pm$ 7.02	-0.68	0.504
$\text{PO}_4$ ( $\text{mg l}^{-1}$ )	17.69 $\pm$ 3.13	16.68 $\pm$ 3.4	0.22	0.831

<sup>a</sup> Variable was  $\ln(x + 1)$  transformed

<sup>b</sup> Variable was arcsin square root transformed

Leptophlebiidae) at invaded sites (Lowe et al., 2008, Lowe, pers. comm. 2010).

The pattern documented here contrasts with most studies on multi-trophic level impacts of non-native trout elsewhere in the world. In general, the abundance of herbivorous invertebrates is lower, and the biomass of algae higher, where trout have been added to stream communities (see reviews by Simon & Townsend, 2003; Townsend, 2003). Discrepancy between our results and others may be because most studies of community-level trout impacts have been conducted either in three trophic level systems that lack native vertebrate predator assemblages (e.g. Herbst et al., 2009; Buria et al., 2010) or in four trophic level streams where trout have depleted native predators that exert relatively weak predation pressure on herbivorous invertebrates (e.g. Flecker & Townsend, 1994; McIntosh & Townsend, 1996; Biggs et al., 2000; Nyström et al., 2003). In both situations, the resulting predation pressure on invertebrates where trout occur is higher than that where they do not, leading to a decrease in the abundance of herbivorous invertebrates and corresponding increase algal

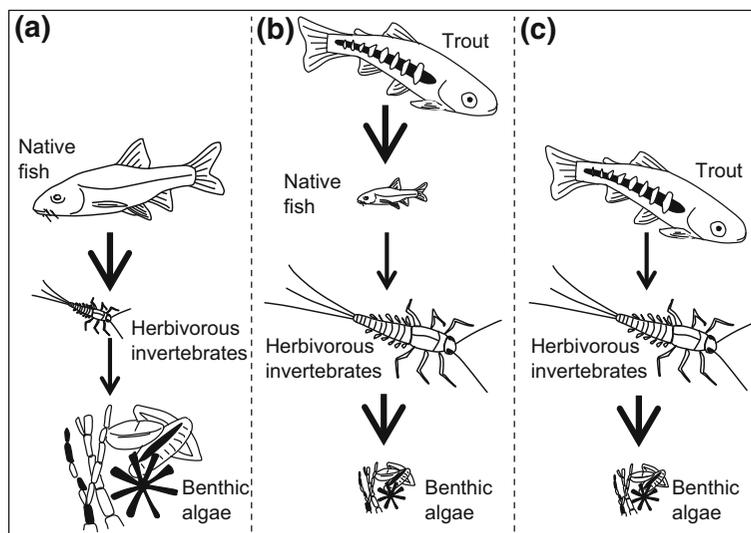
biomass. In contrast, the systems sampled in our study supported abundant native invertivorous fish populations that may exert relatively strong top-down control over benthic invertebrate abundance and provide forage for large piscivorous trout. Differences in the size structure of trout populations between systems may also influence predation dynamics in that populations dominated by small-sized individuals may be expected to exert stronger control over benthic invertebrates than populations dominated by large-sized trout. However, the majority (>90%) of the individuals recorded at our study sites were <160 mm in length suggesting that these populations were likely dominated by invertivores, not piscivores, and would therefore be expected to be relatively strong regulators of benthic invertebrate abundance.

We are aware of just two studies that have examined community impacts of trout in southern Africa, neither of which was conducted in the CFR. Rivers-Moore et al. (2013) found differences in invertebrate assemblage composition between sites above and below waterfalls that act as dispersal barriers to rainbow and brown (*Salmo trutta* Linnaeus, 1758) trout in

headwater streams in KwaZulu-Natal (South Africa), but could not attribute the observed differences to the presence of trout. On the other hand, Kadye et al., (2013) found that rainbow trout tended to deplete benthic invertebrate abundance more strongly than did the benthic-feeding native mountain catfish *Amphilius uranoscopus* (Pfeffer, 1889) in headwater streams in the Nyanga Mountains (Zimbabwe). These results contrast with the relatively weak suppression of benthic invertebrates by trout observed in our study but are in line with the view that introduced trout generally elevate predation pressure on benthic invertebrates (Simon & Townsend, 2003; Townsend, 2003).

Whether or not a community operates primarily as a three or four trophic level system will depend on the relative strengths of the different interaction pathways, particularly where the top predator (in this case trout) consumes both mesopredators (small fish, predatory invertebrates) and primary consumers (herbivorous/detritivorous invertebrates). In streams in the CFR, the introduction of trout may have added a trophic level, changing the community from a three to a four trophic level system (Fig. 8a, b). Trout may then have induced

a trophic cascade by suppressing the abundance of native insectivorous fish (and potentially also predatory invertebrates, although we found no evidence for this in our study) through predation, which would relax predation pressure on herbivorous invertebrates and allow them to proliferate on the stream bed. The relatively high abundance of herbivorous invertebrates at invaded sites may then result in strong down grazing on benthic algae *sensu* Power (1990). Although this mechanism may be in operation at sites where native fish co-occur with trout, trout was the only fish species recorded at most (7/12) of our invaded sites (Appendix 1 in Supplementary Material). At these sites, there was only one trophic level of fish, and food webs would therefore have only three trophic levels. Even though the sites where trout and native fish co-occurred may technically have four trophic levels, they probably also function as three trophic level systems, because trout likely feed directly on benthic invertebrates, given the scarcity of native fish as prey. Indeed, cascading effects of predators on plant biomass are predicted in systems with three (or some other odd number of) trophic levels (Oksanen et al., 1981). In this view, instead of adding a trophic level, trout replace native



**Fig. 8** Conceptual diagram showing proposed mechanisms of community-level trout impacts. The size of each community component represents its relative density or biomass, and the thickness of the arrows represents the strength of the effect exerted by each community component on the one below it (i.e. *thick arrow* strong effect). At uninvaded sites, native fish are the dominant top predators and control herbivorous invertebrate

abundance, allowing algae to proliferate on the stream bed (a); at invaded sites, trout add a trophic level to the community (b); and may ultimately replace native fish as the dominant invertebrates (c). Both b and c lead to a relaxation of predation pressure on herbivorous invertebrates and a corresponding down grazing of benthic algae

fish as the dominant tertiary consumers after depressing native fish abundance and possibly extirpating them through piscivory. The relatively high density of herbivorous invertebrates at invaded sites where native fish are extirpated therefore implies that trout are weaker regulators of benthic invertebrate abundance than are the native fish (Fig. 8c).

The lower predation pressure on herbivorous invertebrates at invaded sites could potentially be a consequence of the lower overall fish density at these sites. However, the mean total biomass of fish at invaded and uninvaded sites was similar (Fig. 2b). It may be that the native fish species have a higher per unit body mass energy demand because they are generally smaller than trout (Shelton, unpubl. data). Tertiary production at uninvaded sites would therefore be relatively high and translate into a greater impact on invertebrates than at sites dominated by trout. Alternatively, differences in foraging behaviour and prey selectivity between trout and the native fish could potentially explain differences in predation pressure on benthic invertebrates between the invaded and uninvaded sites (Parker et al., 1999; Schmitz, 2007, 2008). Although rainbow trout is a drift-feeder (Nakano et al., 1999), the Breede River redfin and Cape kurper are primarily benthic foragers (de Wet, 1990; Shelton, unpubl. data) which could account for the relatively low-predation pressure on benthic invertebrates at invaded sites (Dahl & Greenberg, 1996). Our data do not enable us to distinguish between these different hypotheses, and studies comparing energetic demands (e.g. Huryn, 1998) and foraging behaviours between trout and native fish in CFR streams would be important steps towards resolving differences in top-down effects between trout and the native species and identifying the mechanism(s) underlying their differential impacts.

The lack of overall difference in predatory invertebrate density between sites with and without trout is surprising given the wealth of studies that report strong effects of trout on predatory invertebrate abundance (Meissner & Muotka, 2006). The reason for this general pattern is that visual predatory fish like trout are known to favour large-bodied, conspicuous prey and many predatory invertebrates fit these criteria. It is perhaps not surprising then that we found no difference in micropredator abundance between sites with and without trout since these taxa are neither large-bodied nor conspicuous. Samways (1994) noted

that in South Africa, the distribution of the synlestid dragonfly *Ecchlorolestes peringueyi* appeared to be negatively affected by trout presence, but here the abundance of the synlestid *Chlorolestes* was not significantly influenced by trout presence (Appendix 3 in Supplementary Material). However, some of the larger, more conspicuous predatory taxa, including the coleopteran Gyrinidae and the dragonflies *Ceratogomphus* and *Notogomphus*, were indeed less abundant at sites with trout, but their generally low overall abundance likely reduced our ability to detect significant differences in their densities. Although the abundances of most large predatory taxa were generally low, the body sizes of these taxa are large compared to other invertebrates, and differences in the predator component of the assemblage between sites with and without trout may therefore have been underestimated by our density-based comparisons. Future studies of this kind should therefore look to should employ a sampling technique that provides better density estimates of large, rare predatory invertebrates and incorporate biomass-based estimates of assemblage composition.

That particulate organic matter on the stream bed did not differ significantly between sites with and without trout is consistent with other studies (Reice, 1991; Rosenfeld, 2000; Rosemond et al., 2001; Herbst et al., 2009; Buria et al., 2010). In general, cascading effects in detritus-based trophic pathways appear to be less common than in algae-based trophic pathways (Rosenfeld, 2000). This phenomenon has been attributed to the fact that herbivorous invertebrates, which feed on exposed rock surfaces where algae grow, are more vulnerable to fish predation than are detritus-feeders that forage on leaf accumulations in interstices in the stream bed, where they are relatively concealed from fish (Rosenfeld, 2000; Herbst et al., 2009; Buria et al., 2010). Indeed, here shredder density did not differ between sites with and without trout, implying that fish were not effective at exploiting shredders as a food source, consistent with the lack of significant difference in CPOM levels between the two groups of sites. In contrast, the higher abundance of collector-gatherers at invaded sites may have been expected to have depleted FPOM relative to that at uninvaded sites, but this was not the case. FPOM levels in these streams may therefore be regulated by factors other than consumer abundance. Indeed, detritus-based food chains are donor-controlled systems driven by leaf-

litter inputs from the adjacent riparian ecosystem (Polis & Strong, 1996), and although detritivorous invertebrates have the potential to reduce the biomass of detritus (Ruetz et al., 2002; Nyström et al., 2003; Greig & McIntosh, 2006), they have no control over the amount of detritus entering the stream (Rosenfeld, 2000).

In summary, our results suggest that trout have induced a trophic cascade, where a reduction in native fish abundance appears to have released certain taxa of herbivorous invertebrates from predation, leading to an increase in grazing pressure and consequent indirect decrease in the biomass of benthic algae. Furthermore, our results suggest that trout are relatively weak regulators of benthic invertebrate abundance and do not compensate for the absence/depleted abundance of native fish at the invaded sites. The patterns documented in our study contrast with the majority of studies investigating community-level impacts of trout elsewhere, but are similar to patterns documented where bass have invaded CFR streams. Finally, our results show that the influence of trout can indeed extend beyond negative impacts on native fish populations down to lower trophic levels, and biodiversity managers should weigh multi-trophic level impacts of trout into decisions regarding the conservation of headwater stream communities in the CFR.

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