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Predatory impact of non-native rainbow trout on endemic fish populations in headwater streams in the Cape Floristic Region of South Africa

Jeremy M. Shelton · Michael J. Samways · Jenny A. Day

Abstract Non-native rainbow trout *Oncorhynchus mykiss* have been widely introduced in the Cape Floristic Region (CFR) at the south-western tip of Africa and may pose a serious threat to endemic freshwater fishes in the region. Quantitative information about trout impacts in the CFR is scarce but is urgently needed to guide legislation and management efforts. We used a combination of comparative and experimental approaches to evaluate impacts of introduced trout on native fish populations in headwater streams draining the upper Breede River catchment in the CFR. Fish populations were surveyed, and 19 environmental variables measured, in 24 minimally-disturbed streams, half of which had been invaded by trout. The mean densities of native Breede River redfin *Pseudobarbus burchelli*, Cape kurper *Sandelia capensis* and Cape galaxias *Galaxias zebratus*, were 89–97 % lower in invaded streams than in streams without trout. Furthermore, while native fish were present at all 12 sites without trout, they were not recorded at seven of the 12 invaded sites. None of the measured environmental variables differed significantly between sites with and without trout, and distance-based linear models identified trout density as the best predictor of redfin and kurper density, while galaxias density was best predicted by other environmental variables (riparian vegetation, canopy cover, substrate length, site slope). Native fish ≤40 mm in length were largely absent from invaded streams, but generally abundant in streams without trout, and a field experiment confirmed that trout selectively consume small redfin. Taken together, these findings constitute evidence that trout have depleted the abundance of CFR-endemic fishes through size-selective predation. It is recommended that managers aim to prevent new trout introductions and consider eradicating trout populations where they pose a threat to highly threatened native species.

Keywords Invasive · *Oncorhynchus mykiss* · Predation · Threatened native fish

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Introduction

The rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) is among the most widely introduced fish in the

world (Fausch 2007). From its native range in Pacific North America and eastern Russia, it has been introduced to at least 97 countries, and to every continent except Antarctica (Crawford and Muir 2008). Rainbow trout are gape-limited predators (Lescak and von Hippel 2011), and while as juveniles they feed mostly on small invertebrates, they can consume increasingly larger prey, such as amphibians and fish, as they grow (Raleigh et al. 1984). In many cases, introduced rainbow trout have established self-sustaining populations (Fausch 2007) and negative impacts on native fish populations, largely as a result of predation, have been reported from across the globe [e.g. New Zealand (McDowall 2006), Australia (Crowl et al. 1992; Lintermans 2000; McDowall 2006), South America (Young et al. 2010; Habit et al. 2010), North America (Dunham et al. 2004) and in Japan (Kitano 2004)]. Because of their widespread and severe impacts, rainbow trout have been listed by the World Conservation Union Global Invasive Species Programme (GISP) as one of the World's 100 Worst Alien Invasive Species (Lowe et al. 2000). Although the consequences of rainbow trout introductions have received detailed study in many areas, impacts in other locations, such as South Africa, remain largely unknown.

Rainbow trout (henceforth "trout") were introduced to South Africa in 1897 for angling purposes (de Moor and Bruton 1988), and widespread stocking of the country's rivers ensued (Hey 1926). Today trout occur in ∼75 % of South Africa's major river systems, and while self-sustaining populations are generally limited to the cooler headwater reaches of streams, many other populations are sustained through continual stocking (van Rensburg et al. 2011). Beginning in the 1960s, conservation organizations gradually became aware that trout appeared to be having a negative impact on native aquatic species, particularly fishes (de Moor and Bruton 1988). Despite the fact that negative impacts of trout in South Africa have long been suspected, evidence is mostly circumstantial and anecdotal (de Moor and Bruton 1988; Cambray 2003). Quantitative information on trout impacts in South Africa is urgently needed to guide legislation and management efforts (Cambray 2003).

The Cape Floristic Region (CFR) at the south-western tip of South Africa is a hotspot for freshwater fish endemism (Linder et al. 2010; de Moor and Day 2013). Of the 20 species that have been described, 17 are

endemic to the region (Skelton 2001; Chakona and Swartz 2013), but nearly all of these endemic species appear in the categories vulnerable, endangered and critically endangered of the IUCN Red List (IUCN 2013). Threats include habitat loss and fragmentation, hydrological alteration, climate change, overfishing and pollution, but the greatest threat is that posed by introduced predatory fish (Tweddle et al. 2009; Chakona and Swartz 2012). To date, 16 species of non-native freshwater fish have established self-sustaining populations in the CFR (Marr 2012), and several of these species have been linked to declines in native fish populations (de Moor and Bruton 1988; Tweddle et al. 2009).

Interactions with non-native fish, combined with the effects of habitat degradation, have led to the disappearance of native fish from the middle and lower sections of many rivers in the CFR (Tweddle et al. 2009; de Moor and Day 2013; Weyl et al. 2013). Consequently, the region's native fish populations have become highly fragmented, and many species are now largely restricted to headwater reaches of streams (Swartz et al. 2004; Tweddle et al. 2009; Chakona and Swartz 2012). Headwater streams have generally been less severely impacted by human-related activities than lower-lying reaches because they are situated in mountainous areas that are difficult to access and unsuitable for agriculture, human settlements and reservoirs (Swartz et al. 2004; Tweddle et al. 2009; de Moor and Day 2013). Consequently, the headwater reaches of streams function as native fish refugia within the region's highly degraded riverscapes, and are thus critical habitats from a conservation perspective. Trout are well adapted to environmental conditions in these headwater streams (Raleigh et al. 1984) and may pose a serious threat to remaining native fish populations in the CFR (Cambray 2003).

To our knowledge, there has only been one previous assessment of trout impacts on native fish in the CFR; that of Woodford and Impson (2004), who studied interactions between trout and three species of native fish and found some evidence for spatial segregation between trout and native fish and predation by trout on one native species, the Cape galaxias *Galaxias zebratus* (Castelnau 1861). Although their study was confined to five pools within a single stream (the upper Berg River), their findings are consistent with the view that trout may have a negative predatory impact on native fish populations in CFR streams. The aim of the present study was to expand on their preliminary work by
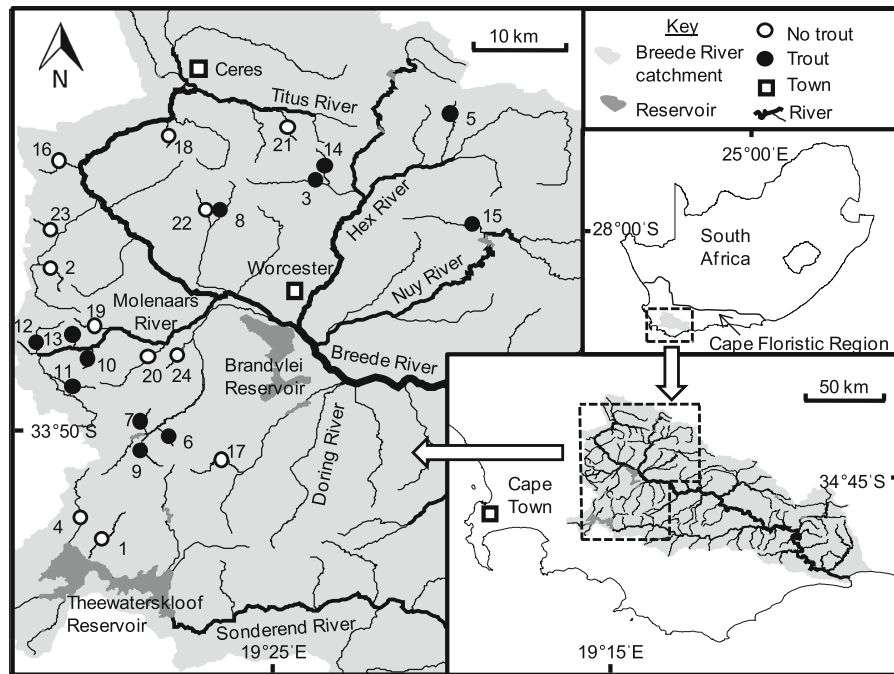
Fig. 1 Location of sampling sites in the upper Breede River catchment in the CFR of South Africa. *White circles* represent sampling sites without trout, and *black circles* represent sites with trout. The numbers of the sampling sites correspond to the numbers in Supplementary Material 1. Names of towns, as well as major rivers and reservoirs, are shown

evaluating the predatory impact of introduced trout on CFR-endemic fishes through a combination of comparative and experimental approaches. We surveyed fish populations, and measured environmental variables, at sites on 24 headwater streams in a catchment partially invaded by trout to assess their impacts on native fish abundance and size distribution at a broad spatial scale. In addition, we conducted a small-scale field experiment to examine size-selective predation by rainbow trout on one of the native fish species.

Methods

Study area

The Breede River Catchment is the fourth largest in the CFR, draining an area of ±12,600 km². From its source in the Skurweberg Mountains, it flows in a south-easterly direction for 322 km before opening into the Indian Ocean (Steynor et al. 2009). The present study was conducted in the mountainous upper catchment which includes the tributary systems that join the main river upstream of the Doring River, as well as the upper

tributaries of the Sonderend River upstream of Thee-waterskloof Reservoir (Fig. 1). The area experiences a Mediterranean climate (Cowling and Holmes 1992) and has a mean annual rainfall of ~800 mm (Steynor et al. 2009). Natural vegetation is predominantly Sandstone Fynbos (Rebelo et al. 2006), and riparian vegetation generally consists of broad-leaved woody species (Cowling and Holmes 1992). The geology is dominated by hard, quartzitic sandstones of the Table Mountain group (Tankard et al. 1982), and the streams flowing over this stratum are acidic, oligotrophic and low in dissolved solids (de Moor and Day 2013). The middle and lower reaches of many streams in the upper catchment have been degraded by human-related activities, while headwater reaches are generally in a near-natural state (RHP 2011). Five native species of primary freshwater fish (all of which are CFR endemics), namely the Breede River redfin *Pseudobarbus burchelli* (Smith 1841)[1], the giant redfin *P. skeltoni* Chakona and Swartz

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[1] In this study "*Pseudobarbus burchelli*" refers to a lineage currently known as *Pseudobarbus* sp. "burchelli Breede" which is regarded as Near Threatened (Tweddle et al. 2009), but is still awaiting formal taxonomic description (IUCN 2013).

2013, the Cape kurper *S. capensis* (Cuvier 1831), the Cape galaxias *G. zebratus* and the Berg-Breede River whitefish *Barbus andrewi* Barnard 1937, occur in streams in the upper Breede River catchment. Whitefish, which are listed as Endangered in the IUCN Red List (IUCN 2013), have disappeared from nearly all of their native range (Impson 2001), and were not recorded in the present study. The recently-described giant redfin is known from only two localities and is considered to be highly threatened (Chakona and Swartz 2013). The Cape kurper and Cape galaxias are listed as data-deficient in the IUCN Red List (IUCN 2013). Trout were initially stocked into many of the larger streams that drain the upper Breede River catchment and have subsequently spread into many of the smaller headwater tributaries that feed into these larger streams (de Moor and Bruton 1988).

Field survey

While many of the headwater tributaries draining the upper Breede River catchment have been invaded by trout, a considerable number still remain trout-free. Several factors could potentially influence whether trout are able to invade and establish in a tributary, including the physico-chemical characteristics of the stream, anthropogenic disturbances and stocking history. In many cases, the presence of physical dispersal barriers such as waterfalls, wiers and dry/braided reaches of stream appear to have prevented trout from colonizing tributaries. This situation presented a valuable opportunity to investigate trout impacts on native fish populations by means of a broad-scale correlative field survey. Variation in biotic and abiotic conditions among streams is intrinsically high, and it was therefore important to account for factors other than trout that may influence native fish populations. We attempted to account for such factors in two ways. First, we selected sites with and without trout that were as similar to one another as possible, and second, we measured a set of physical and chemical variables (described in detail below) that could potentially influence stream fish populations, and assessed their influence on native fish abundance.

Site selection

Because stream fish assemblages can be affected by 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. To select our study sites, we first visited 64 potentially suitable streams identified using topographic maps and the opinion of local freshwater biology experts. From this set, we identified 24 minimally-disturbed 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 was determined by extensive underwater observations (1–2 h). One 50 m long site was arbitrarily selected on each of the 24 headwater streams. This site length was chosen based on the recommendation of Bovee (1982) that a stream segment of 7–10 times the stream width is generally sufficient to capture the physical heterogeneity of that stream reach; wetted channel width at our study sites was usually about 3–4 m. We conducted extensive underwater observations (1–2 h) in the reaches upstream and downstream of the site to confirm that it was representative of the fish assemblage present in that stream. All sites fell within the mountain stream geomorphological zone (as defined by Rowntree and Wadeson 1999), had predominantly open canopies (<50 % canopy cover) and were not dominated by bedrock substrate (<50 % stream bed cover). We surveyed fish populations and environmental conditions at all sites during summer (16 February–19 March 2010) when water clarity was high and flows were low. One site was sampled per day and sites were sampled in a random order.

Fish density and size distributions

Electrofishing is the standard technique for estimating the abundance of stream fishes (Hardie et al. 2006), but this method was not effective at our study sites because of the low conductivity of the water (range across all sites: 8.15–28.55 $\mu S\ cm^{-1}$). Visual methods have been demonstrated to provide reliable estimates of fish abundance in small, clear streams in the CFR (Ellender et al. 2012; Weyl et al. 2013) and snorkel surveys were used to estimate fish densities and population size structures at out study sites. Snorkel surveys have the advantages of requiring minimal equipment and time (our sampling sites were situated in rugged terrain and were difficult to access), but have potential bias against certain size classes and behaviours (Hankin and Reeves 1988; Hardie et al. 2006),

and in this study, we made the assumptions that the detection probability for each species was the same, and that the presence of trout did not affect detection probability for the native species. We used the multiple-pass snorkel survey method described by Thurow (1994) to estimate the mean abundance of each fish species at each site. A single diver (J. M. Shelton) did the surveys because the entire channel width could be seen, and same diver conducted all snorkel censuses so that sampling effort among sites was constant (Hankin and Reeves 1988). The diver began at the downstream end of each 50 m site and proceeded upstream in a zigzag pattern (Hankin and Reeves 1988; Mullner et al. 1998) recording the species and length (total length, TL; accuracy 10 mm) of all fish encountered. Three passes were conducted so that the mean and variance of fish numbers per size class per site could be estimated. Passes were conducted 10–15 min apart to allow fish to recover from the disturbance caused by the snorkeler during the previous pass. Snorkelling was conducted between 11 h30 and 13 h30, when the sun was directly overhead, so as to maximize the accuracy of fish abundance estimates (Thurow 1994).

Environmental variables

We measured 19 physico-chemical variables at each site following completion of the fish surveys. We measured wetted channel width (cm) at 5-m intervals along the length of the site, giving a total of ten width measurements. We then measured water depth (cm), substrate (mm), flow (m s^{-1}), canopy cover, submerged macrophytes and woody debris at three equidistant points along the 10 width transects. Depth was measured with a calibrated rod placed vertically on the streambed, and substrate length (maximum particle diameter) measured using callipers or a tape measure, at each point. Average flow of the water column was measured at each point with a digital flow meter. Canopy cover was estimated by recording whether canopy was present or absent directly above each point along each transect, and the presence or absence of riparian vegetation and undercut banks on either end of each transect was noted. We recorded temperature (°C), dissolved oxygen (% saturation), pH, conductivity (μS cm^{-1}) and turbidity (NTU) at three randomly-selected points within each site. Three 500 mL water samples were collected at randomly-

selected locations at each site, thoroughly homogenized, and a 200 mL sub-sample was taken for analysis of nutrient levels in the laboratory (protocol detailed below). Nutrient samples were held on ice in the field and frozen in the dark within 12 h of collection. We recorded latitude and longitude at each site, and measured elevation and site slope on digitized 1:250,000 topographic maps.

Laboratory protocols

We estimated $NO_3^-+NO_2^-$–N, PO_4^{3+}–P and NH_4^+–N concentrations using a Lachat Flow Injection Analyser, as follows: NO_3^- and NO_2^- were estimated using Lachat's QuikChem$^®$ Method 31-107-04-1-E, in which NO_3^- is converted to NO_2^- and diazotized with sulfanilamide to form an azo dye; PO_4^{3+} was measured by forming an antimony-phospho-molybdate complex using QuikChem$^®$ Method 31-115-01-1; 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: for NO_3^- and NO_2^- 2.5 μg L^{-1} N; for PO_4^{3+} 15 μg L^{-1} P; and for NH_4^+ 5 μg L^{-1} N. These variables are herein referred to in the text as "phosphates", "nitrates + nitrites" and "ammonium" respectively.

Predation experiment

We conducted a predation experiment in Morainekloof Stream (site 14, Fig. 1) to measure consumption of three size classes of native Breede River redfin by two size classes of trout. The Breede River redfin (henceforth "redfin") was chosen for this experiment because it was the numerically dominant member of the native fish assemblage. The fish were held in 12 rectangular, plastic tanks (90 × 45 × 40 cm; 162 L volume) which had windows cut from the front and back ends of tanks (30 × 20 cm) and from the top (60 × 20 cm), and were lined with 2 mm plastic mesh. Windows at the front and back ends allowed water flow through the tanks, and windows on the tops of tanks allowed sunlight to penetrate. Tank bottoms were lined with six small cobbles (80–120 mm) and six large cobbles (180–220 mm) collected from the stream using a 30 × 30 cm diameter hand net with 250 μm mesh. Cobbles were lifted from the streambed into the net and then placed in a tank, so that the invertebrates on the cobble, as well as those dislodged

when the cobble was lifted, were transferred to the tank. The cobbles were used to anchor tanks to the streambed and to provide shelter for the native fish, while the invertebrates provided a source of food.

The design of the experiment was based on that conducted by McIntosh (2000). We established three predator treatments, namely small trout (one individual <150 mm), large trout (one individual >150 mm) and no trout (which acted as a control treatment), and each treatment was replicated four times in a randomized complete block design. Blocks were placed in runs, and each block was separated from the other blocks by at least 10 m of pool habitat. Three size classes of redfin were used, <30 mm (small), 30–60 mm (medium) and >60 mm (large), and three individuals in each size class were stocked in each tank. Redfin for the tanks were captured using seine, fyke and hand nets in Morainekloof Stream over the 2 days preceding the experiment. Trout were caught using fyke nets set in Morainekloof stream the night before the experiment begun. All fish were held in aerated plastic buckets containing stream water, cobbles and invertebrates for food, for 18–48 h before being placed into the experimental tanks. Redfin were stocked into the tanks between 11 h00 and 12 h00 on March 11, and trout were stocked approximately 1 h later to allow redfin time to acclimate to conditions in the tanks. The experiment ran for 48 h and was terminated at 13 h00 on March 13. At the end of the experiment we removed all cobbles from the tanks and counted and measured the remaining redfin.

Statistical analyses

We used univariate analyses to compare native fish densities and size distributions, and the 19 physico-chemical variables, between sites with and without trout, as well as the survival of redfin between treatments in the predation experiment. Mean density of each native fish species at each site was estimated by dividing the average of the three snorkel passes by an estimate of the stream area sampled. Stream area was estimated by multiplying site length by the mean of the ten width measurements taken at each site. Densities of each native fish species were compared between sites with and without trout using Mann–Whitney U tests, since data did not meet assumptions of parametric tests, even after transformation (Zar 1999). Environmental variables were compared

between the two groups of sites using independent sample t tests. Percentage oxygen saturation, riparian vegetation and canopy cover were arcsin square root transformed, while turbidity, flow velocity and elevation were $\ln(x + 1)$ transformed to meet the assumptions of the analysis. Differences in the length frequency distribution of each native fish species between sites with and without trout were evaluated using Kolmogorov–Smirnov goodness-of-fit tests for discrete data since the number of observations in certain size categories was small (Zar 1999). We used a mixed model ANOVA, with block as a random factor and treatment as a fixed factor, to test for differences in the number of redfin surviving among treatments in the predation experiment (Quinn and Keough 2002). Tukey's HSD tests were used to determine which treatments differed significantly from one another.

We used distance-based linear models (DISTLM, Anderson et al. 2008), a non-parametric, permutation-based multiple regression technique, to explore relationships between native fish densities and a set of predictor variables including environmental factors, as well as trout density. We used a varimax-rotated PCA to reduce the 19 physico-chemical variables to a limited number of independent, uncorrelated factors (Quinn and Keough 2002) which could then be used, along with trout density, as predictors in DISTLM models. 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 even out their skewed distributions. Principal components (PCs) with eigenvalues >1 were retained and variables with loadings >0.7 were considered important and were used to interpret individual components (Quinn and Keough 2002). Predictor variables were checked for multicollinearity, but no variables were dropped from the analysis since the correlation coefficient r never exceeded 0.7 (Anderson et al. 2008). Resemblance matrices were calculated using Euclidian distance, which is appropriate for models with a univariate response (Anderson et al. 2008). The density of each species was $\ln(x + 1)$ transformed prior to analysis to improve normality. We employed a step-wise procedure using Akaike's information criterion (AIC) adjusted for small sample sizes (AIC$_c$; Burnham and Anderson 2002) to identify the best (most parsimonious) model for each native fish

species. We also considered all competing models within 2 AIC_c units of the best model to be potentially important (Burnham and Anderson 2002) and identified all predictor variables that featured in this "best set" of models. All univariate analyses were carried out with SPSS 20.0 (SPSS 2011) and multivariate analyses were performed using PRIMER-E (Clarke and Gorley 2006) with the add-on package PERMANOVA+ (Anderson et al. 2008).

Results

Differences in native fish densities and size distributions between sites with and without trout

Three species of native fish were recorded at the sampling sites, namely the redfin, the Cape kurper (henceforth "kurper") and the Cape galaxias (henceforth "galaxias"). Native fish were present at all 12 sites without trout, but only five of the 12 sites invaded by trout, and were generally far more abundant where trout were absent than where they were present (Fig. 2; Supplementary Material 1). Redfin was the most abundant native species at the majority of sites, on average comprising 64.37 and 76.23 % of the native fish assemblage by number at sites with and without trout respectively. Redfin were recorded at all 12 sites without trout, but at only four of the 12 invaded sites. The mean density of redfin at invaded sites was significantly lower ($\sim$97 %) than that at sites without trout ($U_{22} = 8.00$, $p < 0.001$; Fig. 2a). Kurper were recorded at seven of the 12 sites without trout, but at only three of the 12 sites with trout. The

mean density of kurper at sites invaded by trout was also significantly lower ($\sim$89 %) than that at sites invaded by trout ($U_{22} = 38.50$, $p = 0.028$; Fig. 2b). Galaxias were only present at seven of the 24 sites; six without trout and one with trout. The density of galaxias at the site invaded by trout was $\sim$97 % lower than the mean density of galaxias at sites without trout (Fig. 2c), but this difference was not statistically significant ($U_{22} = 42.00$, $p = 0.172$). The length frequency distribution of each native species at sites without trout differed significantly from its distribution at invaded sites (Kolmogorov–Smirnov goodness-of-fit tests; redfin: $d_{max} = 36.67$, $p < 0.001$; kurper: $d_{max} = 41.21$, $p < 0.001$; galaxias: $d_{max} = 72.56$, $p < 0.001$). For all three species, small individuals ($\leq$40 mm) were relatively abundant at sites without trout, but all but absent at sites where trout occurred (Fig. 3).

Differences in environmental conditions between sites with and without trout

Independent-sample t tests revealed that none of the measured environmental variables differed significantly between sites with and without trout (Table 1), indicating that there were no consistent differences in environmental conditions between these two groups of sites.

Influence of environmental variables and trout on native fish density

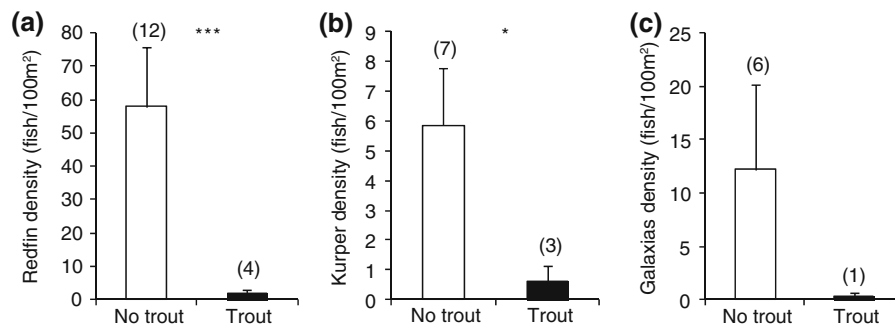The PCA produced seven principal components with eigenvalues >1, which together accounted for

Fig. 2 Mean + SE density of **a** redfin, **b** kurper and **c** galaxias at sites with and without trout. Numbers in parentheses above *bars* indicate the number of sites were the species was present.

An *asterisk* indicates a significant difference based on the results of Mann–Whitney U tests (* = < 0.05, ** = < 0.01, *** = < 0.001)
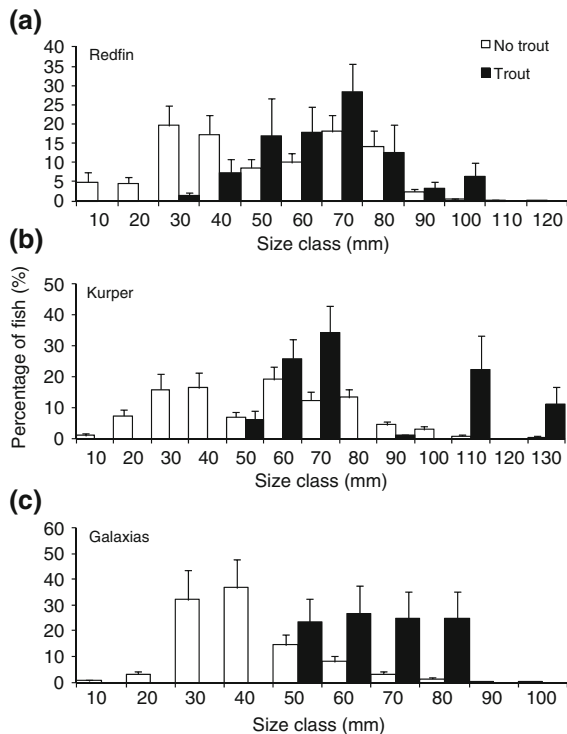
(a)

(b)

(c)

Fig. 3 Length frequency distributions for **a** redfin, **b** kurper and **c** galaxias at sites with (*black bars*) and without (*white bars*) trout. *Bars* show the mean + SE percentage of fish in each size class

74.10 % of the variation in environmental conditions among sites (Supplementary Material 2). These seven components were therefore used, alongside trout density, as predictors in DISTLM models. Table 2 summarizes the results of the step-wise DISTLM used to investigate the relative influence of trout density and other environmental factors on variation in redfin, kurper and galaxias density among the 24 sampling sites. The best model for redfin contained just two predictors, namely trout density and PC 5 ($R^2 = 0.50$; Table 2). Trout density was identified as the best predictor of redfin density, and was the only predictor that explained a significant proportion of the overall variation ($F_{1,22} = 15.58$, $p < 0.001$; 41.45 % variation explained). Redfin density was negatively related to trout density in that redfin were absent from sites where trout density was relatively high (>3 fish/ 100 m^2), but persisted at a relatively low density at some of the sites where trout density was relatively low (<3 fish/100 m^2) (Fig. 4a). PC 5 represented gradients in % canopy cover and % riparian

vegetation, but this predictor explained only 9.28 % of the variation beyond that already explained by trout density, and did not emerge as statistically significant in the final model. Seven competing models fell within 2 AIC$_c$ units of the best model (Supplementary Material 3). Trout density was fitted first in all of these models, reaffirming that it was the best predictor of redfin density. Other predictors contained in the set of best models included PC 7, PC 4, PC 2 and PC 1, indicating that several aspects of the stream environment (including % canopy cover, % riparian vegetation, site slope, substrate length, oxygen saturation, ammonium concentration, pH and elevation) explain small proportions of the variation in redfin density beyond that accounted for by trout density.

The best model for kurper contained four predictors, namely trout density, PC 7, PC 1 and PC 2 ($R^2 = 0.52$; Table 2). Trout density was identified as the best predictor of kurper density and explained a significant proportion of the variation in kurper density among sites ($F_{1,22} = 6.17$, $p = 0.024$; 21.91 % variation explained). As was the case with redfin, kurper density was negatively related to trout density in that redfin were absent from sites where trout density was relatively high (>3 fish/100 m^2), but persisted at a relatively low density at some of the sites where trout density was relatively low (<3 fish/100 m^2) (Fig. 4b). The next best predictor was PC 7 which explained a further 16.61 % of the variation, beyond that already accounted for by trout density, and the proportion of variation explained was statistically significant ($F_{1,22} = 5.67$, $p = 0.025$). PC 7 represented gradients in site slope and substrate length, and kurper density was generally higher at sites with a relatively gentle gradient and a fine mean substrate length (Fig. 4c). PC 1 represented gradients in phosphate concentration and water temperature, while PC 2 largely represented gradients in ammonium concentration, and although not significant, these two predictors explained 7.38 and 6.81 % of the variation captured by the final model respectively. Trout density was fitted first in all three competing models, and PCs 1, 2 and 7 were also contained in the set of best models (Supplementary Material 3).

The best model for galaxias density contained three predictors, namely PC 7, PC 5 and PC 3 ($R^2 = 0.43$; Table 2). PC 5 ($F_{1,22} = 3.94$, $p = 0.046$; 15.19 % variation explained) and PC 7 ($F_{1,22} = 3.94$, $p = 0.046$, 15.19 % variation explained) both explained significant proportions of the overall variation in galaxias

Table 1 Mean ± SE values of each environmental variable at sites with and without trout

Variable	No trout		Trout		t test	
	Mean	SE	Mean	SE	t_{22}	p
$NO_3 + NO_2$ (mg L^{-1})[a]	6.21	1.88	9.52	2.06	−0.99	0.335
NH_4 (mg L^{-1})[a]	24.97	1.94	33.09	7.02	−0.68	0.504
PO_4 (mg L^{-1})	17.69	3.13	16.68	3.4	0.22	0.831
pH	4.9	0.16	5.3	0.15	−1.88	0.074
Temperature (°C)	22.39	0.69	21.07	0.53	1.52	0.144
Conductivity (µS cm^{-1})	16.3	1.46	15.38	1.64	0.42	0.677
Oxygen saturation (%)[b]	92.13	1.97	90.51	1.92	0.79	0.441
Turbidity (NTU)[a]	0.67	0.08	0.58	0.11	0.84	0.411
Width (cm)	389.75	13.76	384.58	17.51	0.23	0.819
Depth (cm)	25.16	1.03	24.09	1.23	0.66	0.515
Substrate length (mm)	295.3	16.68	291.26	16.25	0.17	0.864
Flow velocity (m s^{-1})[a]	0.2	0.02	0.18	0.02	0.49	0.628
Riparian vegetation (%)[b]	65.83	5.14	62.08	6.56	0.55	0.586
Canopy cover (%)[b]	19.44	1.92	28.33	4.09	−1.08	0.102
Elevation (m)[a]	419.17	35.94	473.83	25.05	−1.62	0.121
Site slope (%)	6.71	0.52	6.72	0.86	0.46	0.651
Submerged macrophytes (%)[b]	16.39	5.82	4.44	1.38	1.96	0.063
Undercut bank (%)[b]	3.33	1.36	3.06	1.04	0.19	0.848
Woody debris (%)[b]	5.28	0.96	8.06	3.03	−0.18	0.859

Results for independent-sample t tests for each variable are shown

[a] Variable was ln(x + 1) transformed

[b] Variable was arcsin square root transformed

density among sites. PC 5 was fitted first and represented gradients in riparian vegetation and canopy cover, and galaxias density was generally higher at sites where the cover of riparian vegetation and canopy were high (Fig. 4d). PC 7, fitted next, represented gradients in site slope and substrate length, and galaxias density was generally higher at sites where site slope and mean substrate length were greater (Fig. 4e). PC 3, representing gradients in pH and elevation did not explain a significant proportion of the variation in galaxias density beyond that explained by PCs 5 and 7. No competing model fell within 2 AIC_c units of the best model for galaxias.

Experimental verification of trout predation on redfin

All medium- and large-sized redfin survived in all tanks, indicating that predation by trout on these size classes did not occur during the experiment (Fig. 5). At the end of the experiment, two of the 12 small-sized redfin were not present in the tanks with small trout, and seven of the 12 small-sized redfin were not present in the tanks with large trout. Survival of redfin in control tanks was 100 % and the fish absent from the trout treatments at the end of the experiment were therefore assumed to have been consumed by trout. The number of small redfin surviving differed significantly among treatments (mixed model ANOVA; $F_{2,9} = 13.00$, $p = 0.007$), with survival in treatments with large trout being significantly less than in treatments with small trout (Tukey post hoc test; $p = 0.028$) or no trout (Tukey post hoc test; $p = 0.006$). The number of small redfin surviving in the small trout treatment was not significantly different from that in the treatment with no trout (Tukey post hoc test; $p = 0.155$).

Table 2 Test statistics for distance-based linear model (DIST-LM) analysis investigating relationships between native fish densities and a set of predictor variables including seven principal components that represent major axes in variation in environmental conditions, as well as trout density

Variable	AIC_c	SS	F	p	Variation (%)	Cumulative variation (%)	Residual (df)
Redfin							
Trout density	20.99	33.69	15.58	0.001**	41.45	41.45	22
PC 5	19.49	7.54	3.96	0.061	9.28	50.73	21
Kurper							
Trout density	−1.29	5.87	6.17	0.035*	21.91	21.91	22
PC 7	−1.82	4.45	5.67	0.025*	16.61	38.52	21
PC 1	−1.98	1.98	2.73	0.120	7.38	45.90	20
PC 2	−1.99	1.83	2.74	0.129	6.81	52.71	19
Galaxias							
PC 5	9.51	5.28	3.94	0.046*	15.19	15.19	22
PC 7	7.77	4.91	4.19	0.048*	14.11	29.29	21
PC 3	5.41	4.84	4.91	0.057	13.93	43.23	20

Sequential tests were used to identify the most parsimonious model for each native fish species using a step-wise selection procedure, and the selection criterion adjusted AIC_c

Asterisks indicate predictors explaining a significant proportion of variation in the response variable (* = < 0.05, ** = < 0.01, *** = < 0.001)

Discussion

Understanding impacts of invasive predators on native prey populations is vital from a biodiversity management perspective. Native fish populations in the CFR of South Africa are highly fragmented, with many species now largely confined to the headwater reaches of rivers. Despite the fact that introduced trout may pose a serious threat to remaining populations, quantitative studies of trout impacts in the CFR are scarce. In this study we used a combination of comparative and experimental approaches to investigate impacts of trout on native fish populations in headwater streams draining the upper Breede River catchment in the CFR, South Africa.

Influence of trout and other environmental factors on native fish densities

Since our analyses of environmental conditions revealed no consistent differences between sites with and without trout, the absence, or relatively low abundance (89–97 % lower than at trout-free sites), of native fish at invaded sites is therefore best explained by the presence of trout. Moreover, the finding that, while present at all 12 sites without trout, native fish were absent from seven of the 12 sites with trout implies that in addition to reducing their density, trout may be capable of completely eliminating native fish populations from CFR headwater streams. Distance-based linear models identified trout density as the best predictor of both redfin and kurper density at our study sites, adding further support to the view that trout, rather than some other variable, is primarily responsible for the differences in redfin and kurper abundance between the two groups of sites. These results are consistent with records of declines in abundance of other small cyprinid species (Hey 1926; Harrison 1950a; de Moor and Bruton 1988; Tweddle et al. 2009), and kurper populations (Hey 1926; Skelton 1987), following the introduction of trout into South African streams. Site slope and substrate length also emerged as important predictors of kurper density, and the finding that kurper were generally more abundant at sites with finer mean substrate particle size and lower gradient is consistent with their known preference for relatively slow-flowing, quiet stream habitats (Chakona and Swartz 2012). Although most available evidence points towards negative impacts of trout on redfin and kurper abundance, Woodford and Impson (2004) found that kurper and the Berg River redfin *P. burgi* (Boulenger 1911) were relatively abundant in
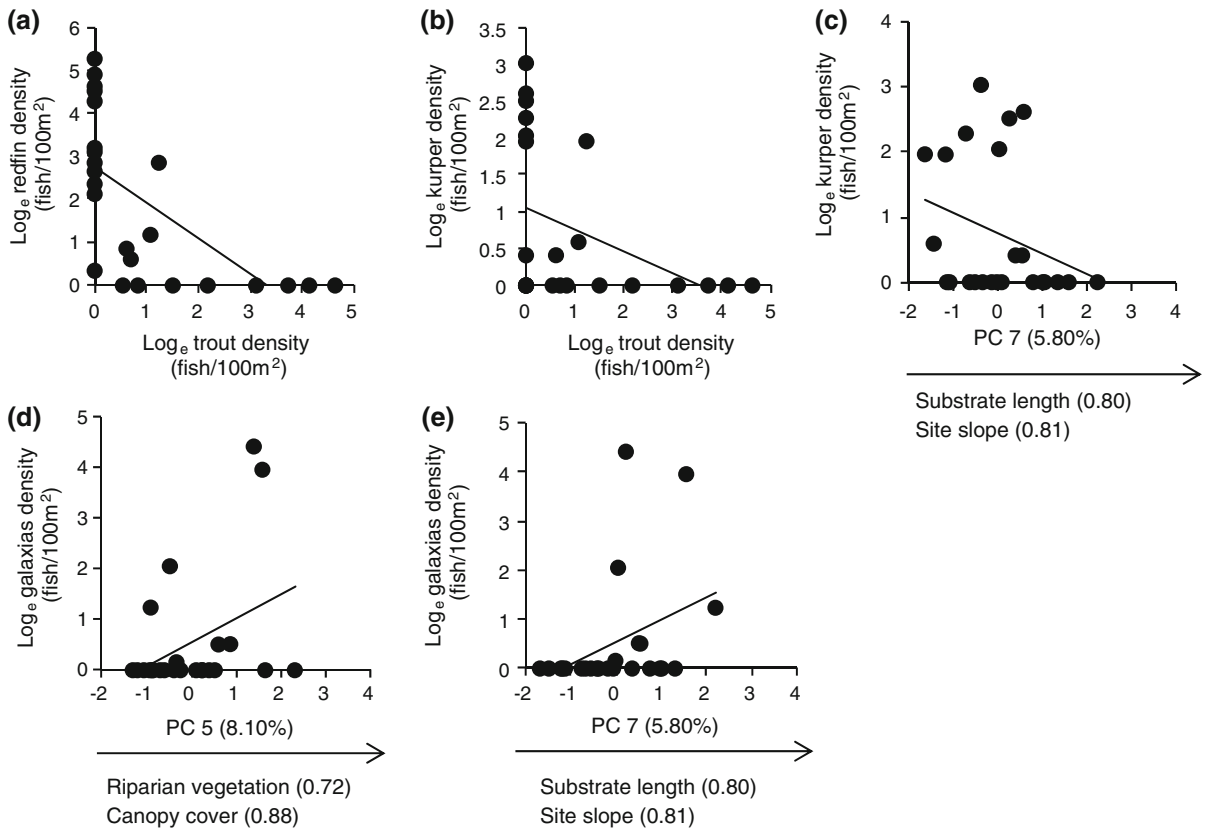
Fig. 4 Linear relationships between the density of each native fish species and predictor variable(s) that emerged as significant in the final model for that species. Trout density was the only significant predictor of redfin density (**a**), significant predictors of kurper density included trout density (**b**) and PC 7 (**c**), and significant predictors of galaxias density included (**d**) PC 5 and (**e**) PC 7. The percentage of variation explained by each PC is shown, as well as that explained by variables with loadings >0.7, are shown
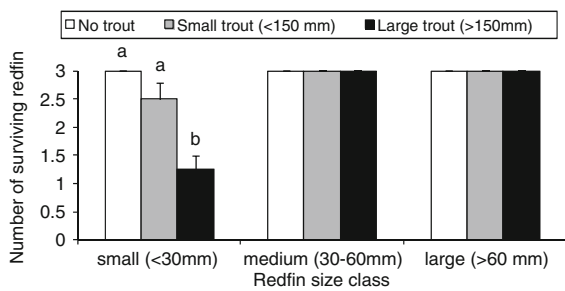
Fig. 5 Mean + SE number of small, medium and large-sized redfin surviving in tanks with no trout (n = 4), small trout (n = 4) and large trout (n = 4). *Different letters* indicate a significant difference in redfin survival as detected by mixed model ANOVA and Tukey post hoc tests (α = 0.05)

pools inhabited by trout in the upper Berg River suggesting that trout impacts on CFR-endemic fish are not always severe. The authors speculated that impacts

in that system may be influenced by trout density, and the results from the present study support this view.

The inverse relationships between trout density and the densities of both redfin and kurper imply that the strength of trout impacts on the abundance of these species is density-dependent. Specifically, the finding that the native species co-occurred with trout at some of the sites where trout densities were relatively low (<3 fish/100 m^2), but none of the sites where trout densities were relatively high (>3 fish/100 m^2), indicates that impacts were weaker at sites with low trout densities, and stronger at sites with high trout densities. Similar density-dependent impacts of non-native trout on populations of native, small-bodied, stream-dwelling fish have also been documented in New Zealand (McIntosh et al. 2010) and North America (Peterson et al. 2004). The density-dependent nature of trout impacts on native fish species' in the CFR

could have important conservation implications, in that sites supporting low-density trout populations may be of greater conservation value than sites supporting high-density trout populations.

In contrast, galaxias density at the study sites was best explained by environmental predictors, rather than trout density, and galaxias density was generally highest at sites with the steepest gradient, where the mean substrate size was large, and where the cover of riparian vegetation and canopy were high. Despite the fact that DISTLM is flexible with respect to the distribution of the response variable, the large number of zero data points (galaxias was absent from 17 of the 24 sampling sites, and present at only one site with trout) meant that the effective sample size for galaxias was relatively small, and the linear models constructed for galaxias should therefore be treated with some caution. Interestingly, the only site where trout and galaxias co-occurred had the lowest density of trout measured in our study (Kaaimansgat Stream, 0.72 trout/100 m^2) suggesting that galaxias populations may be able to persist if trout density is relatively low. Further survey work is needed to increase the sample size of galaxias-containing sites in order to confirm the impact of trout on galaxias populations in the CFR. However, the fact that galaxias were present at six of the sites without trout, but only one of the sites with trout, suggests that galaxias are vulnerable to predation by trout. Records of trout impacts on galaxias populations elsewhere in South Africa suggest that impacts may indeed be severe (McVeigh 1977; Cambray 2003; Woodford and Impson 2004), while there is little doubt that non-native salmonids, particularly brown *Salmo trutta* Linnaeus 1758 and rainbow trout, have caused severe declines in populations of native galaxiids in other parts of the world including New Zealand (McDowall 2006), Australia and Tasmania (Cadwallader 1996), Chile (Young et al. 2010; Habit et al. 2010), Patagonia (Garcia de Leaniz et al. 2010), Argentina (Macchi et al. 1999) and the Falkland Islands (McDowall et al. 2001).

In this study we made the assumptions that detection probability for each native species was the same, and that detection probability was unaffected by trout presence, but this may not have been the case. Galaxias is a relatively small and cryptic species, while kurper are known to occupy complex benthic habitats (Woodford and Impson 2004), and thus our detection probability may have been lower for these

species than for redfin which are more conspicuous. Furthermore, our visual surveys may have been less effective at detecting native fish at sites with trout than at uninvaded sites because fish can display less conspicuous behaviours (Cadwallader 1996; McDowall 2006; Januchowski-Hartley et al. 2013), or exhibit subdued morphological traits (Reznick and Endler 1982; Reznick et al. 1996), in the presence of introduced predators. Despite these potential biases, we believe that our sampling method provided reasonable estimates of the relative abundance of native fish at sites both with and without trout for two reasons. First, underwater observations at invaded and uninvaded sites suggest that the native fishes have not radically changed their behaviours in the presence of trout. Second, recent studies undertaken in streams elsewhere in the CFR have shown that visual methods provide reliable estimates of native fish abundance at sites both with and without introduced predatory fish (Ellender et al. 2012; Weyl et al. 2013). Finally, it is noted that other studies (e.g. White and Harvey 2001; Woodford et al. 2005) have also used underwater observations to infer invader impacts of native fish abundance.

Size-selective predation

The absence of native fish shorter than 40 mm in length at sites with trout implies that trout prey selectively on small size classes of native fish. Alternatively, the truncated native fish length frequency distributions (Fig. 3) could also potentially be a consequence of size-dependent predator-induced behavioural changes, whereby small individuals seeking shelter from trout become less easily detectable by the observer. Indeed, Woodford and Impson (2004) observed that juvenile, but not adult, *P. burgi* were spatially segregated from trout in pools in the upper Berg River, suggesting a predator-induced behavioural response. Investigation of behavioural changes in CFR native fish in response to trout would be an interesting avenue for future research.

Our predation experiment confirmed that both small (<150 mm) and large (>150 mm) trout were capable of consuming small (<30 mm) redfin, implying that size-selective predation is likely an important mechanism underlying the observed patterns in native fish size distributions. It may be that, in streams supporting relatively high trout densities, native fish

were unable to recruit successfully because of high predation pressure on juveniles, leading to their disappearance once the adult fish present at the time of the invasion eventually died. On the other hand, in streams where trout density is relatively low, some of the recruitment might make it through the "predation window" (i.e. survive to a size of 40 mm), and thereby allow populations to continue to persist. Taken together, our survey and experimental results indicate that predation by trout on small size classes of native fish is the best explanation for the observed differences in native fish size distribution and density between sites with and without trout. This conclusion is lent support from records in South Africa documenting the presence of native fish in the stomachs of trout in the CFR (Harrison 1950b, 1952; Woodford and Impson 2004). Considering that the native species in our study area evolved in systems naturally largely devoid of large predatory species functionally similar to trout (Swartz et al. 2004; Tweddle et al. 2009), it is perhaps not surprising that they will be especially vulnerable to predation by introduced trout (Cox and Lima 2006).

Our predation experiment suffered from several limitations, and the results should therefore be treated with some caution. Fish were confined to a relatively small area and substrate complexity was probably lower than that in natural streams, potentially increasing the vulnerability of redfin to predation by trout. Also, the relatively short duration of the experiment (48 h) may have influenced predation dynamics in the tanks. However, despite its shortcomings this experiment does demonstrate that trout selectively consume small-sized redfin. Further experimental work is needed to confirm size-selective predation on kurper and galaxias, although the presence of young galaxias in trout stomachs in the upper Berg River (Woodford and Impson 2004) shows that trout are certainly capable of feeding on galaxias. Additionally, experimental work conducted in New Zealand has demonstrated size-selective predation by brown trout on the native galaxiids (Fletcher 1979; McIntosh 2000; Woodford 2009). Finally, although selective predation by trout on small size classes of native fish appears to be the main process responsible for the relatively low abundance (or absence) of native fish at the invaded sites, competition for food and space may also have played a role, and this could be also be examined in future studies.

Conclusions and conservation implications

Our results indicate that, in headwater streams draining the upper Breede River catchment in the CFR, (1) native fishes appear to have been eliminated from sites with high-density trout populations; (2) native fish may be able to persist at relatively low abundance at sites with low-density trout populations; (3) where native fish do co-occur with trout, small-sized individuals of native fish (<40 mm) tend to be absent; and (4) predation on small size classes of native fish appears to be an important mechanism driving the observed patterns in native fish density and size distribution. Our comparisons of environmental variables suggest that if introduced into headwater streams that are presently trout-free, trout will establish self-sustaining populations with negative consequences for the native fish that inhabit these streams. The role of headwater streams as refugia for native fish populations in the CFR may therefore depend on preventing trout introductions into these streams. Finally, the eradication of trout from headwater streams where their impacts are unacceptably high, for example where trout populations directly threaten distinct native taxonomic lineages of native biota, should also be considered.

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