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ORIGINAL PAPER

Detecting impacts of invasive non-native sharptooth catfish, *Clarias gariepinus*, within invaded and non-invaded rivers

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Abstract In aquatic ecosystems, impacts by invasive introduced fish can be likened to press disturbances that persistently influence communities. This study examined invasion disturbances by determining the relationship between non-native sharptooth catfish *Clarias gariepinus* and aquatic macroinvertebrates in the Eastern Cape, South Africa. A Multiple Before–After Control–Impact (MBACI) experimental design was used to examine macroinvertebrate communities within two rivers: one with catfish and another one without catfish. Within the invaded river, macroinvertebrates showed little response to catfish presence, whereas predator exclusion appeared to benefit community structure. This suggests that the macroinvertebrate community within the invaded river was adapted to predation impact because of the dominance of resilient taxa, such as Hirudinea, Oligochaeta and Chironomidae that were abundant in the Impact treatment relative to the Control treatment. High macroinvertebrate diversity and richness that was observed in the Control treatment, which excluded the predator, relative to the Impact treatment suggests predator avoidance behaviour within the invaded river. By comparison, within the uninvaded river, catfish introduction into the Impact treatment plots indicated negative effects on macroinvertebrate community that was reflected by decrease in diversity, richness and biomass. A community-level impact was also reflected in the multivariate analysis that indicated more variation in macroinvertebrate composition within the Impact treatment relative to the Control in the uninvaded river. Catfish impact within the uninvaded river suggests the dominance of vulnerable taxa, such as odonates that were less abundant in the Impact treatment plots after catfish introduction. From a disturbance perspective, this study revealed different macroinvertebrate responses to catfish impact, and suggests that within invaded habitats, macroinvertebrates were less responsive to catfish presence, whereas catfish introduction within uninvaded habitats demonstrated invasion impact that was shown by a decrease in the abundance of vulnerable taxa. The occurrence of non-native sharptooth catfish within many Eastern Cape rivers is a concern because of its predation impact and potential to influence

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trophic interrelationships, and efforts should be taken to protect uninvaded rivers, and, where possible, eradicate the invader.

Keywords Benthic macroinvertebrates · Invasions · MBACI design · Multivariate ordination · Disturbances

Introduction

The response of biological communities to impacts can be categorised as either pulse disturbance, which indicates short-term and often unpredictable changes, press disturbance, which shows long-term changes that increase initially before reaching constant levels, or ramp disturbance that represent accumulation of impacts over time (Underwood 1991, 1992; Lake 2000; Parkyn and Collier 2004; Harper and Peckarsky 2005). In aquatic ecosystems, disturbances from biological invasions are widely recognised as determinants of community patterns and threats to biodiversity (Johnson et al. 2009). Detecting these invasive impacts can unfortunately be confounded by other forms of environmental change that preclude the identification of the invader's role (Underwood 1994, 1997). In particular, stochastic variability in animal abundance over long temporal scales and their lack of concordance at different localities often result in interactions in trends of abundance over space and time (Grossman et al. 1990; Beugly and Pyron 2010). The underlying principle within an impact study is to be able to distinguish between these natural and stochastic changes from the perceived impact.

Benthic aquatic macroinvertebrates are widely used as indicators in environmental impact studies. Their ubiquity and differential response to different categories of disturbances makes them excellent candidates (Rosenberg and Resh 1993). In predation impact studies, especially by non-native invasive fish, aquatic macroinvertebrates are highly susceptible and can exhibit responses ranging from simple interactions such as reduction or local extinction of populations, to complex interactions such as trophic cascading (Flecker and Townsend 1994; Nyström and McIntosh 2003; Williams and Taylor 2003). Experimental studies indicate that when invasive predators become established, they tend to remove the most vulnerable macroinvertebrate taxa, and the resultant community either shows little response to predation-related disturbances (Meissner and Moutka 2006), or it becomes highly unstable and stochastic (Angeler and Moreno 2007). Community instabilities in predator-mediated communities are a consequence of a transition to a new alternative stable state during both the disturbance and post-disturbance periods (Suding et al. 2004). Such communities are often dominated by macroinvertebrate taxa that can either seek alternative refuge and quickly recolonise from adjacent habitats (Miller and Crowl 2006), or are not preferred by the predator (Meissner and Moutka 2006; Effenberger et al. 2008). Therefore, the presence of invasive non-native predators can be likened to press disturbances that persistently influence community structure and function. Press disturbances represent environmental perturbations caused by a sustained impact that continuously disrupts community structure and composition (Underwood 1992; Lake 2000; Parkyn and Collier 2004).

Green's (1979) BACI (Before–After Control–Impact) experimental approach has been widely used in impact studies. This experimental design is based on the basic principle of collecting samples Before and After the perceived impact at both Control and Impact locations, and was designed to draw inference on ecological impacts based on field experiments. The BACI rubric has been modified at various levels to address concerns related to experimental design, such as pseudo-replication (Hurlbert 1984) and the confounding effects of spatial and temporal variation (Stewart-Oaten et al. 1986; Underwood 1994; Keough and Mapstone 1997; Stewart-Oaten and Bence 2001). Although BACI designs are important in many habitat impact-based studies, they are rarely used in predation impact studies. This study used the BACI design to examine the impact of invasive non-native African sharptooth catfish *Clarias gariepinus* on patterns of benthic macroinvertebrate communities in the Eastern Cape Province, South Africa. The catfish was first introduced in 1976 into the Great Fish River through an 82.8 km tunnel of the Orange River–Fish River inter-basin water transfer (IBWT) scheme from its native range in the Orange River (Cambray and Jubb 1977; Laurenson and Hocutt 1986). The catfish has since expanded its distribution range and now occurs in many rivers and dams throughout the region. Due to its possession of an arborescent organ, the catfish has remarkable capabilities to live in a wide range of habitats including rivers, swamps, natural lakes and man-made reservoirs (Teugels 1986; De Graaf and Janssen 1996) and adapts easily to new environments (Bruton 1988). The catfish is a highly mobile omnivorous predator that feeds on a wide range of prey, including fish, macroinvertebrates, plant material, plankton, reptiles, and amphibians (Bruton 1979; Merron 1993; Winemiller and Kelso-Winemiller 1996; Yalçin et al. 2001). Several studies indicate that in addition to its aggressive predatory behaviour, the catfish is highly competitive and has the ability to alter food webs and poses a threat to native biota in areas outside its native range (Lal et al. 2003; Khan and Panikkar 2009). In the Eastern Cape, South Africa, there is concern over the dispersion of the catfish into rivers with endemic native fish and macroinvertebrates, which have disappeared at most localities where the catfish has established (de Moor and Bruton 1988). The importance of IBWT schemes for facilitating its invasion have been noted, with dietary studies indicating that it poses a potential negative impact on aquatic macroinvertebrates (Kadye and Booth 2012).

This study describes a comparison of benthic macroinvertebrate community response using short-term enclosure/exclosure experiments between two rivers: one with a high catfish density and another one without catfish. By comparing community responses in ecosystems with and without catfish, this study provides insights into detecting impacts from an invader. By excluding catfish, macroinvertebrates communities should be subjected to minimum predation disturbance and therefore reveal responses to short-term temporal change to other environmental factors. Within the enclosure/exclosures, the macroinvertebrate communities should reveal more variation when catfish are present.

Materials and methods

Sampling localities

The study was conducted in the Koonap River and Brak River, two tributaries of the Great Fish River. These tributaries were selected because they were variably impacted by catfish. The Koonap River had high ambient densities of the catfish that co-occurred with other fish species that include longfin eel (*Anguilla mossambica*), moggel (*Labeo umbratus*) and smallmouth yellowfish (*Labeobarbus aeneus*), whereas the Brak River has no catfish. The two rivers are in the same ecological region, and the experimental localities were within a radius of 20 km. The climate of the region is warm-temperate with mean annual precipitation ranging from 350 to 600 mm, falling mostly in late summer (March to May) and late winter (August). The stream bed within both rivers predominantly consisted of pebbles

(2–10 cm) and boulder (10–30 cm) substrates interspersed with fine silt. The geology of the area comprises of a variety of sedimentary strata including marine shales, sandstones, mudstones and a complex of dolerite dykes and sills (O'Keeffe and de Moor 1988). The vegetation of the region is characterised by *Acacia* thornbush and xeric thicket and was generally undisturbed around the sampling localities. The major land use is grazing pasture for sheep along the Koonap River and game along the Brak River. River flow is intermittent and occurs when there are floods, usually in summer. As flow ceases, the aquatic habitats become a series of isolated pools that are usually maintained by base flow. The Koonap River was sampled near its confluence with the Great Fish River, whereas the Brak River was sampled within its headwaters beyond the migration limits of the catfish from the Glen Melville Reservoir. The experimental section in the Brak River was a headwater stretch that periodically receives highly mineralised water from the Great Fish River's tertiary IBWT. Mean water temperature within the Koonap and Brak Rivers over the study period was 14.5 ± 1.4 °C and 16.5 ± 0.8 °C, respectively. Conductivity was high in the Brak River, with an average of 1290 ± 46 $\mu S\ cm^{-1}$ compared to the Koonap River that had an average of 552 ± 30 $\mu S\ cm^{-1}$. The pH was less variable and ranged from 7.8 to 8.5 and 8.2 to 8.4 within the Koonap River and Brak River, respectively. Temperature (°C), pH, and conductivity ($\mu S\ cm^{-1}$) were measured during each sampling occasion with a HANNA HI 98129 Combo meter. Both rivers had no flow during the study.

Sampling design and data collection

A pilot study was initially conducted over a period of 6 weeks between July and August 2009 to determine the rate of macroinvertebrate colonisation on different type of artificial substrates. The substrate types used were gravel, pebbles, shredded (2 mm) polythene plastic strips, and a mix of pebbles and polythene plastic strips. Cumulative asymptotes for macroinvertebrate diversity and richness were observed between 3 and 4 weeks. The pebble and polythene strips mixed substrate, which provided a better measure of diversity and richness, was then used in the impact experiment. Each artificial substrate unit consisted of a 4 mm polythene netting container measuring 10 cm × 10 cm × 3 cm in length, width and height, respectively. The artificial substrates were placed within exclusion cages that each measured 1 m × 1 m × 0.5 m in length, width and height, respectively, and were constructed of 4 mm diameter polythene netting. Each cage had 18 artificial substrates. Access by larger macroinvertebrates was facilitated by punching 30 additional holes, each measuring between 1 and 2 cm, into each side and bottom of the cage.

In each of the rivers, fish exclosure cages with artificial benthic invertebrate substrates were used to test the treatment effects of the introduction of catfish. The cages, which were placed in different locations within each of the two rivers, were designed to simulate minimum predation disturbances for the macroinvertebrates before the impact was assessed. The treatments for the cages were Control (catfish exclusion) and Impact (introduction of the catfish) tested Before and After the impact on multiple locations within each river (MBACI design).

Sampling for the impact experiment was conducted between July and October 2010. A multifactorial experimental design was used in this study. Eight exclusion cages (four were randomly assigned as Controls and four as Impacts) were placed into each of the two rivers for a period of 4 weeks prior to the start of the catfish impact experiment to allow for macroinvertebrate colonisation. The cages were placed at a depth between 0.5 and 0.75 m with homogenous cobble and fine silt substrates. Individual cages were placed in different isolated pools within each river. In one large isolated pool within the Koonap River, cages were placed 100 m apart at two sites on either ends of the pool. Treatments (Control and Impact) were randomly assigned to the different sites (cages). After the end of the colonisation period, each river was sampled weekly for 3 weeks by collecting three artificial substrates from each cage to give a total of 24 samples (8 cages × 3 artificial substrates) during each sampling occasion. This was the Before period. After the 3rd week, two catfish (each measuring between 20 and 40 cm) were introduced into each of the four Impact exclusion cages in each river. Sampling after the introduction of the catfish as an Impact was done weekly for another 3 weeks and was the After period. The two catfish per cage corresponded to the average catch per unit effort (CPUE), using gill nets and fyke nets, in the experimental localities during routine sampling within the Koonap River. There was no catfish mortality nor involuntary introduction by other fish species into the exclusion cages during the After period.

At the end of each of the six sampling events, the macroinvertebrates on each of the artificial substrates were visually sorted, identified to family level under a dissection microscope (magnification ×10), counted and weighed for dry mass (overnight at 60°C) in the laboratory. Each artificial substrate was analysed alive to reduce bias associated with moribund macroinvertebrates and took approximately 30 min to complete. The data from the three artificial substrates samples per treatment cage per sampling period were averaged prior to the analysis.

Statistical analysis

Macroinvertebrate diversity, taxa richness, dry mass and abundance were determined for each treatment sample. Diversity was calculated using the Shannon–Wiener's index given as $H' = -\sum_{i=1}^{s} p_i \ln p_i$, where p_i is the proportional abundance of taxa i in the sample given s taxa. Taxa richness was presented as number of invertebrate taxa per 10 cm^2, while dry mass and abundance were expressed as mg per 10 cm^2 and number per 10 cm^2, respectively.

Dry mass and abundance (counts) data were $\ln(x + 1)$ transformed to satisfy the requirements of normally-distributed residuals and homoscedasticity. The MBACI analyses contrasted temporal patterns of taxa mean diversity, mean richness, mean ln(dry mass), mean ln(abundance) for both total and selected individual (most abundant) macroinvertebrate taxa at both the Control and Impact sites. The main interaction of interest in an MBACI experimental design for detecting an environmental impact is the interaction between the Control–Impact treatments and Before–After times (Downes et al. 2002; Quinn and Keough 2002). For each river, a linear mixed-effects model was used and expressed as:

$$y_{ijkl} = CI \times BA_{ij} + L(CI)_k + T(BA)_l + \varepsilon_{ijkl}$$

where the fixed effects were the Control–Impact treatments (*CI*—2 levels) and periods Before–After the introduction of the impact (*BA*—2 levels). Random effects were Locations that were nested within *CI* ($L(CI)$—8 levels), and Times nested within *BA* ($T(BA)$—6 levels).

The null hypothesised contrast, for each river, between Control–Impact sites and Before–After times ($CI \times BA$), $H_0 : (\mu_{CA} - \mu_{CB}) - (\mu_{IA} - \mu_{IB}) = 0$, was assumed to be approximately standard-normally (z) distributed such that $z = \frac{(1,-1,-1,1)\beta}{\sqrt{(1,-1,-1,1)\Sigma(1,-1,-1,1)'}}$, where Σ is the variance–covariance matrix of the parameter vector $\beta = (\mu_{CA}, \mu_{CB}, \mu_{IA}, \mu_{IB})'$.

The analyses were conducted using the library *lme4* in *R* (R Core Development Team 2011).

Multivariate analysis

The macroinvertebrate counts for each family from the data produced a species matrix with 23 taxa × 48 averaged samples for each river and were $\ln(x + 1)$ transformed prior to the analysis. Patterns of invertebrate abundance were analysed using redundancy analysis (RDA). RDA is a direct gradient analysis extension of principal components analysis (PCA). Similar to PCA, RDA identifies orthogonal axes that maximally ''explain'' variation in species composition (Legendre and Legendre 1998) but unlike PCA the axes are constrained to be linear combinations of explanatory variables. The eigenvalue associated with each axis is a measure of this variation. Thus, RDA can be considered to be a form of multivariate regression (Jongman et al. 1995).

As the data were in the form of repeated measurements, a series of ordinations were conducted to test terms analogous to univariate repeated-measures ANOVA. A split-plot design, with a permutation scheme adjusted to suit the repeated-measures design of the data, was used for the analysis. Whole plots were records of each location repeated in time. Explanatory variables were the same as the fixed- and random-effects in the MBACI analysis. The interaction of treatment (Control and Impact) and time over sampling period were of interest in assessing possible impacts.

To test hypotheses related to the impact effects, various combinations of variables, covariates and their interactions were used with an appropriate Monte Carlo permutation in the ordination analyses. In the first ordination, variables coding for sampling time and its interaction with treatments were used as explanatory variables, and sampling locations as covariates. This ordination explained variation in macroinvertebrate community attributed to sampling time and treatments occurring through the experiment. In the second ordination, variables coding for interactions between treatments and sampling time were used to explain variation attributed to changes due to the experimental treatment effect. In this analysis, variables coding for locations and time were used as covariates thereby removing the main treatment effects of the experiment. The third ordination was used to explain variation attributed to change in the control treatment after removing the impact treatment effects. The fourth ordination was used to explain variation attributed change in the impact treatment after removing the control treatment effects. The relationship between individual macroinvertebrate taxa and the treatment effects was further explored using a Generalised Linear Modelling procedure. Ordination analyses were conducted in *CANOCO v4.5.*

Results

Comparison of macroinvertebrate taxa

Twenty-three macroinvertebrate taxa belonging to 11 taxonomic groups were sampled during the experiment (Table 1). Odonata was the most represented group with six families. Fourteen taxa were collected in the Koonap River that had high ambient densities of catfish compared to 22 taxa that were collected in the Brak River that had no catfish. Within the Koonap River, leeches (Hirudinea) were the most abundant taxa with a total count of 4205. In comparison, within the Brak River, aquatic Oligochaeta earthworms were the most abundant with a total count of 2772.

Table 1 The macroinvertebrate taxa collected from the Koonap and Brak River, Eastern Cape, South Africa, and the abbreviations used in the multivariate ordination analyses

Group	Taxa/Family	Abbreviation	Koonap River	Brak River
Ephemeroptera	Baetidae	Baetid	+	+
	Caenidae	Caenid	–	+
	Leptophlebiidae	Leptoph	–	+
Trichoptera	Hydropsychidae	Hysdropy	–	+
Coleoptera	Hydrophilidae	Hydroph	+	+
Hemiptera	Belostomatidae	Belostom	+	+
	Pleidae	Pleid	+	+
Odonata	Aeshnidae	Aeshnid	+	–
	Gomphidae	Gomphid	–	+
	Libellulidae	Libellul	–	+
	Chlorocyphidae	Chlorocy	–	+
	Coenagrionidae	Coenagr	+	+
	Lestidae	Lestid	–	+
Diptera	Ceratopogonidae	Ceratop	+	+
	Chironomidae	Chironom	+	+
	Culicidae	Culicid	–	+
Turbellaria	Planaria	Planar	+	+
Oligochaeta		Oligoch	+	+
Hirudinae		Hirudin	+	+
Mollusca	Ancylidae	Ancylid	–	+
	Lymnaeidae	Lymnaid	+	+
	Physidae	Physid	+	+
Anthomedusae	Hydridae	Hydra	+	+

The signs "+" indicate present and "–" indicate absent

Patterns in macroinvertebrate composition

Within the Koonap River, macroinvertebrate mean diversity and richness were high in the Control treatment relative to the Impact treatment (Fig. 1). This implied that the exclusion of the impact disturbance increased community structure within catfish-invaded localities. The linear mixed-effects model showed that the interactions between treatment and sampling period were significant for both diversity ($P < 0.05$) and taxa richness ($P = 0.02$) in this river (Table 2). In contrast, mean dry mass and abundance did not vary between treatments, and there were no significant interactions between treatment and sampling period ($P > 0.05$). This indicates that there was no detectable impact on biomass and abundance within the invaded river. By comparison, within the uninvaded Brak River, the Impact treatment showed a decrease in macroinvertebrate diversity, richness and dry mass following the introduction of the catfish (Fig. 1). The linear mixed-effects model showed significant interactions for the contrasts of these parameters ($P < 0.05$) (Table 2), indicating that catfish had an impact on community structure and biomass of the macroinvertebrate assemblage within the uninvaded river. Nonetheless, macroinvertebrate abundance did not vary between treatments in the Brak River.

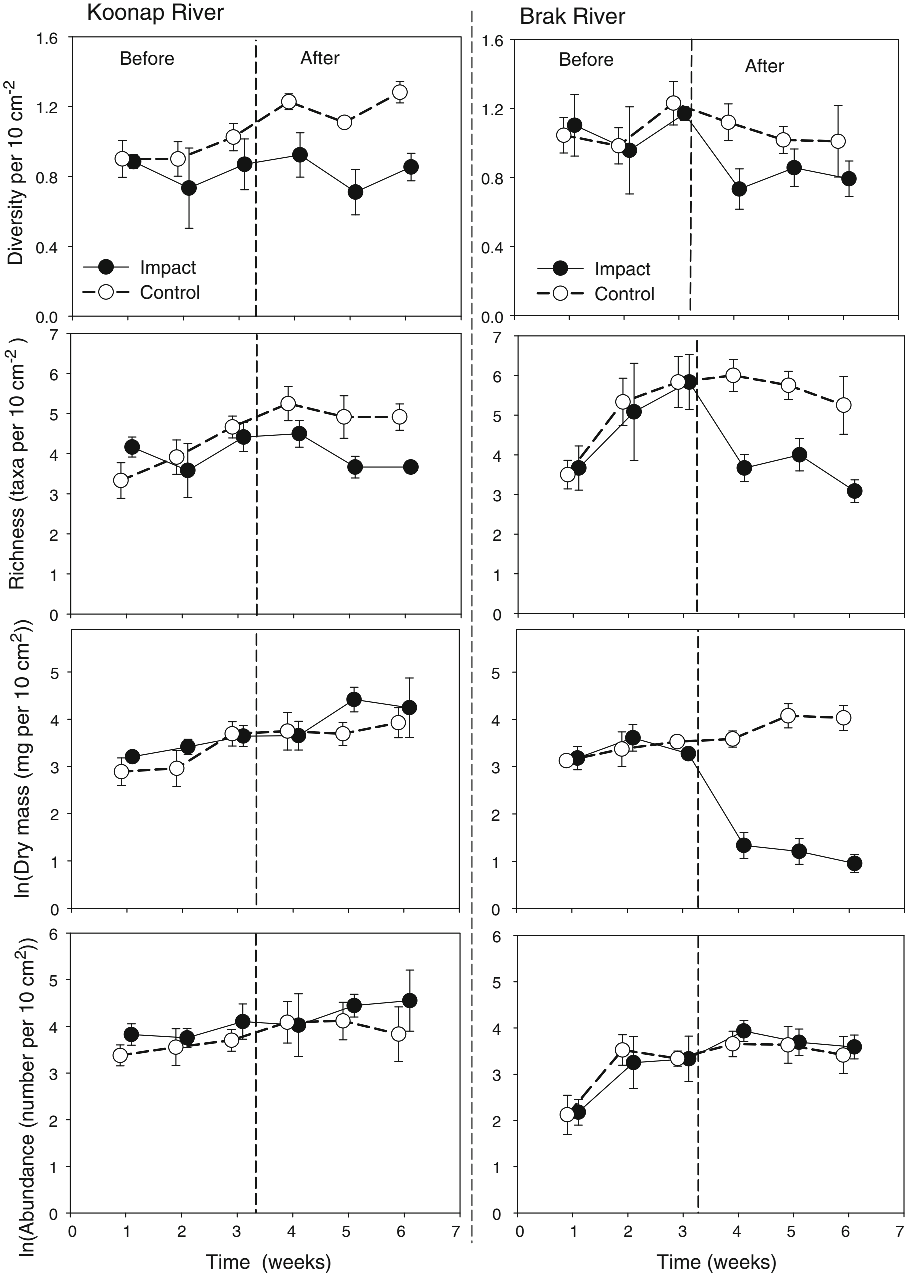

Fig. 1 Temporal patterns in mean (±standard deviation) Shannon–Wiener diversity, richness and dry mass Before and After the introduction of invasive *C. gariepinus* as an Impact within the catfish invaded Koonap River and uninvaded Brak River, Eastern Cape, South Africa

Within the invaded Koonap River, the linear mixed-effects model showed significant interaction between sampling period and treatments ($CI \times BA$) for Baetidae ($P < 0.01$), Belastomatidae ($P = 0.02$) and Ceratopogonidae ($P = 0.03$), which indicates catfish

Table 2 Estimates of the Control–Impact and Before–After interaction contrasts from the mixed-linear MBACI model applied to Shannon–Wiener diversity, taxa richness, ln(Dry mass), ln(Abundance) and individual taxa and in both the invaded Koonap River and the uninvaded Brak River

	Koonap River				Brak River			
		Estimate	z	$P(z)$		Estimate	z	$P(z)$
Diversity	Contrast	0.26	2.64	<0.01	Contrast	0.24	2.13	0.03
	R^2	0.83			R^2	0.77		
Richness	Contrast	1.17	3.00	0.02	Contrast	2.06	4.14	<0.01
	R^2	0.88			R^2	0.81		
ln(Dry mass)	Contrast	−0.07	−0.23	0.81	Contrast	2.75	11.95	<0.01
	R^2	0.88			R^2	0.94		
ln(Abundance)	Contrast	−0.01	−0.01	0.99	Contrast	−0.25	−1.22	0.23
	R^2	0.91			R^2	0.90		
Baetidae	Contrast	8.28	6.87	<0.01	Contrast	–	–	–
	R^2	0.85			R^2	–		
Belostomatidae	Contrast	0.44	2.35	0.02	Contrast	–	–	–
	R^2	0.62			R^2	–		
Caenidae	Contrast	–		–	Contrast	0.44	0.97	0.33
	R^2	–			R^2	0.65		
Ceratopogonidae	Contrast	0.28	2.12	0.03	Contrast	0.22	1.27	0.2
	R^2	0.79			R^2	0.63		
Chironomidae	Contrast	−2.19	−1.55	0.12	Contrast	−14.25	−4.75	<0.01
	R^2	0.94			R^2	0.73		
Coenagrionidae	Contrast	–		–	Contrast	0.89	3	<0.01
	R^2	–			R^2	0.71		
Hirudinea	Contrast	−16.97	−1.49	0.14	Contrast	–	–	–
	R^2	0.69			R^2	–		
Hydridae	Contrast	0.19	0.69	0.49	Contrast	−0.14	−0.46	0.65
	R^2	0.77			R^2	0.73		
Libellulidae	Contrast	–		–	Contrast	3.17	6.66	<0.01
	R^2	–			R^2	0.86		
Oligochaeta	Contrast	−0.69	−0.24	0.81	Contrast	1	0.16	0.87
	R^2	0.78			R^2	0.83		
Planaria	Contrast	–		–	Contrast	0.69	1.99	0.05
	R^2	–			R^2	0.8		

The coefficient of determination (R^2) is provided for each model fit. *Dashes* denote taxa that were not analysed

impact on these taxa (Table 2). These taxa were more abundant in the Control than in the Impact treatments (Fig. 2). By comparison, the Hirudinea, Chironomidae and Oligochaeta were more abundant in the Impact than Control treatments, but did not exhibit significant interaction contrasts indicating that these taxa were not negatively influenced by the catfish impact within the invaded Koonap River. Within the uninvaded Brak River, the odonate taxa Coenagrionidae and Libellulidae, which were more abundant within the Control than the Impact treatments (Fig. 2), exhibited significant interaction contrasts that inferred catfish impacts (Table 2). By comparison, only the Chironomidae midges were more

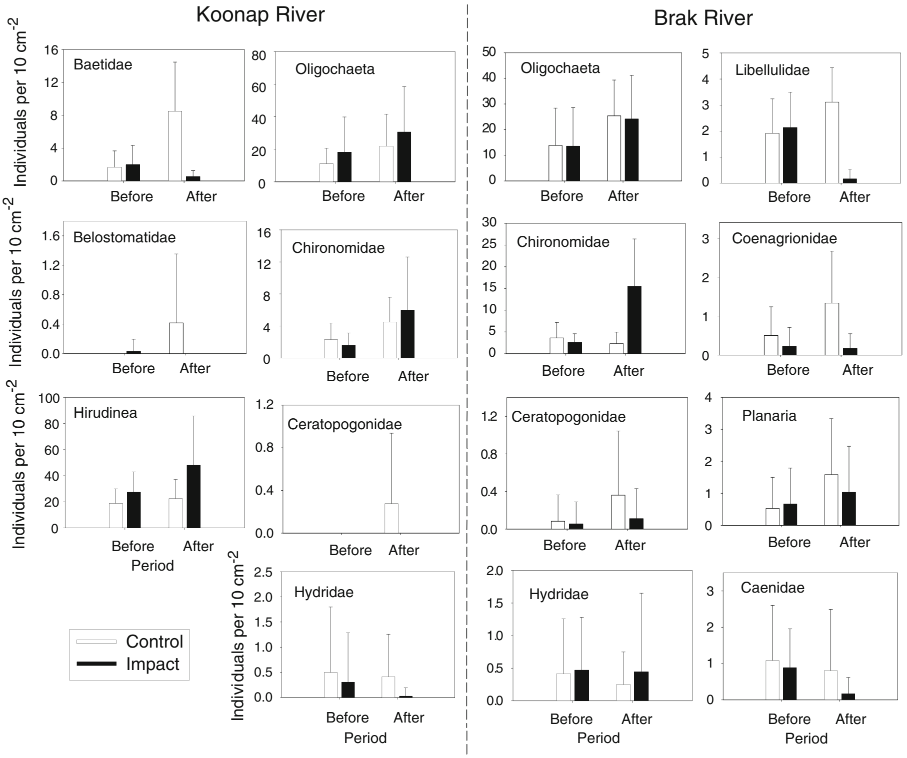

Fig. 2 Changes in mean (±standard deviation) abundance of aquatic macroinvertebrates in the Control and Impact treatments before and after the introduction of *C. gariepinus* in the invaded Koonap River and uninvaded Brak River

abundant in the Impact than the Control treatments, with a significant interaction contrast ($P < 0.01$) indicating a positive catfish impact within the uninvaded river. While oligochaete earthworms increased in abundance between the sampling periods they did not exhibit any significant differences ($P = 0.87$) between treatments.

Multivariate analysis

From a multivariate perspective, the macroinvertebrate communities underwent significant ($P < 0.01$) directional changes associated with the sampling time and its interaction with treatment effects in the Brak River, whereas non-significant changes were noted in the Koonap River (Table 3). These effects explained 21% and 32% of the macroinvertebrate community variation in the Koonap and Brak Rivers, respectively. In the Koonap River, when sampling time was partialled out, the interactive terms of the treatment effects, which explained the variance due to treatment effects that occurred during the experiment, accounted for 9% of the variation. When considered separately, Control treatment effects explained 12% whereas Impact treatments explained 10%, indicating that there was slightly more variation in macroinvertebrate composition within the Control than the Impact treatments. The taxa biplot for the Koonap River showed that the changes in Belastomatidae and Baetidae were most closely associated with the Control treatment (Fig. 3). In contrast, the

Table 3 Partial redundancy analysis examining the patterns of invertebrate communities in the catfish invaded Koonap River and the uninvaded Brak River

Hypothesis	Explanatory variables	Covariates	Variation explained (%)	1st axis		All axes	
				F	*P*(*F*)	*F*	*P*(*F*)
Koonap River							
1	T, C × T, I × T	L	21	6.8	0.71	6.6	0.09
2	C × T, I × T	L, T	9			5.9	0.06
3a	C × T	L, I × T	12			7.7	0.05
3b	I × T	L, C × T	10			6.0	0.15
Brak River							
1	T, C × T, I × T	L	32	14.6	<0.001	11.8	<0.001
2	C × T, I × T	L, T	13			9.9	<0.001
3a	C × T	L, I × T	11			8.2	<0.001
3b	I × T	L, C × T	23			16.8	<0.001

Impact treatment indicated strong association with the leeches, Hirudinea, whereas the Chironomidae and Oligochaeta increased over time but appeared to be uninfluenced by either treatment. By comparison, within the Brak River, the interaction terms of the treatment effects were highly significant ($P < 0.001$) and explained 13% of the variation, indicating a directional change in time and treatment effects for macroinvertebrate composition. When considered separately, both treatment interactions were highly significant ($P < 0.001$), with Control treatment effects explaining 11%, whereas Impact treatments effects explained 23% (Table 3). This indicated that the macroinvertebrate communities were more variable in the Impact than the Control treatments in this river. The biplot for the Brak River indicated that changes in most taxa, which include the odonate taxa, Coenagrionidae, Lestidae and Libellulidae, were closely associated with the Control treatment (Fig. 3). The Impact treatment, by contrast, was strongly associated with the Chironomidae, whereas the Oligochaeta appeared uninfluenced by either treatment.

Generalised Linear Modelling illustrated that, within the Koonap River, Baetidae, Belostomatidae, Chironomidae, Hirudinea and Hydridae underwent significant ($P < 0.05$) directional changes associated with the treatment effects (Fig. 4). Baetidae, Belostomatidae and Hydridae increased in abundance in the Control compared to the Impact treatment whereas Chironomidae and Hirudinae appeared unaffected as they increased in both treatments. By comparison, within the Brak River, eight taxa (Ancylidae, Belostomatidae, Caenidae, Chironomidae, Coenagrionidae, Libellulidae, Oligochaeta and Planaria) underwent significant ($P < 0.05$) directional change associated with the treatment effects (Fig. 4). All taxa, except the Chironomidae and Oligochaeta, increased in abundance within the Control compared to the Impact treatment. The Chironomidae increased in the Impact treatment while the Oligochaeta were unaffected and increased in both treatments.

Discussion

Comparisons of macroinvertebrate communities between catfish invaded and uninvaded streams revealed contrasting temporal patterns. Within the invaded Koonap River, high

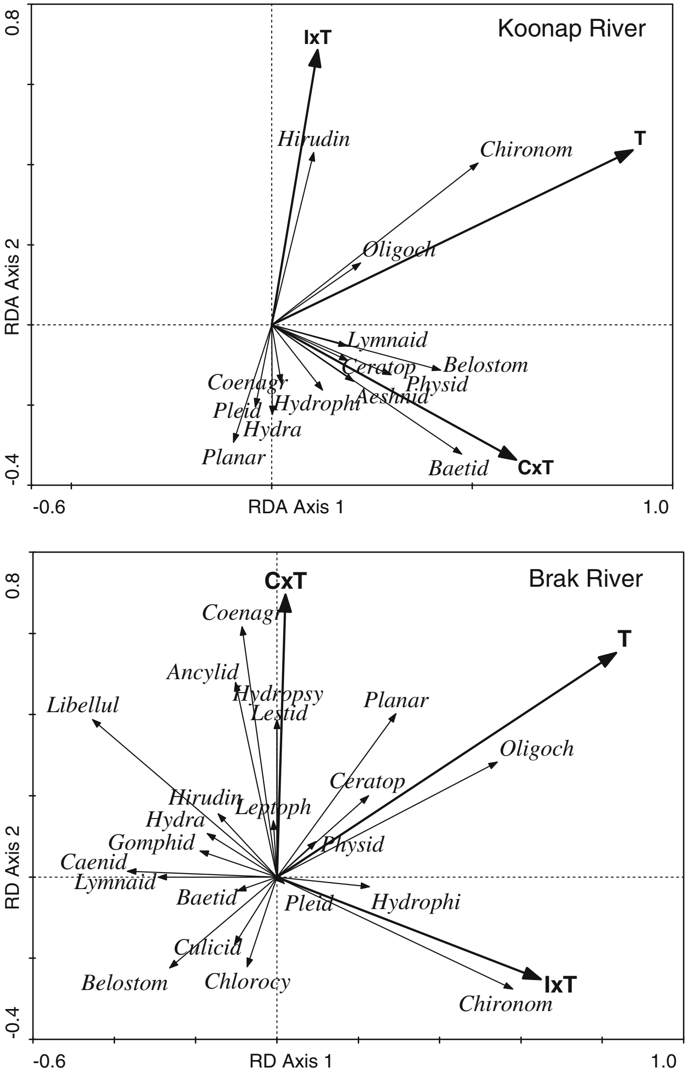

Fig. 3 Partial RDA ordination plots for total macroinvertebrate counts indicating the invertebrate communities in the catfish invaded Koonap River (*top*) and uninvaded Brak River (*bottom*). C = Control, I = Impact (the introduction of *C. gariepinus*), T = Time, and × indicates interactions between variables

macroinvertebrate diversity and richness were observed in the Control treatment that excluded catfish relative to the Impact treatment that had catfish where macroinvertebrate community structure varied less between sampling periods. This demonstrated that, within invaded habitats, excluding the non-native catfish increased community structure, whereas catfish presence was associated with less temporal variation in macroinvertebrate composition. In contrast, biomass and abundance were uninfluenced by either treatment, indicating that the macroinvertebrate community within the invaded river was dominated by taxa that were less responsive or adapted to the impact. By comparison, within the

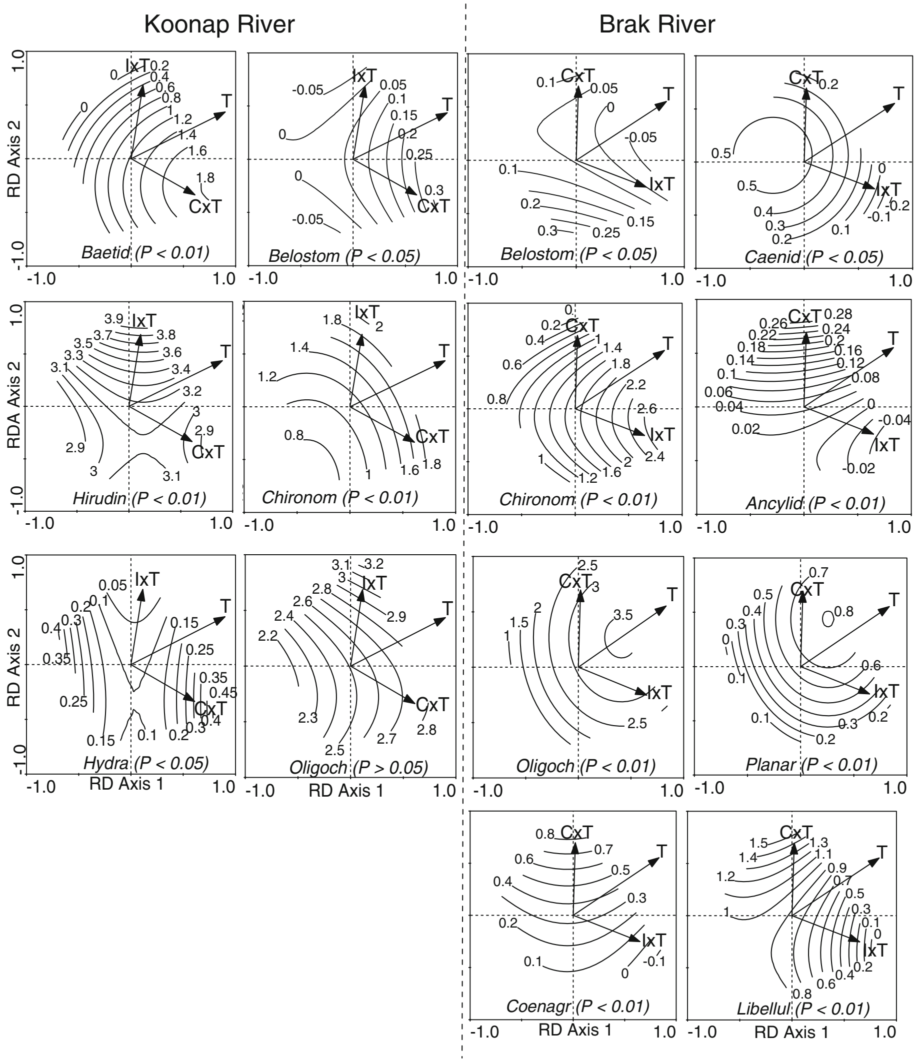

Fig. 4 Generalised Linear Models indicating the relationship between macroinvertebrate taxa and treatment effects within the invaded Koonap River and the uninvaded Brak River. Contours on each plot indicate the predicted abundance patterns for each taxa in relation to the treatments, and the values on each contour indicate the associated predicted ln(abundance). C = Control, I = Impact (the introduction of *C. gariepinus*), T = Time, and × indicates interactions between variables

uninvaded Brak River, catfish introduction demonstrated an impact on macroinvertebrate composition, a pattern that was consistent with observations from other studies on effects of introduced fish on macroinvertebrates in previously uninvaded habitats (Carlisle and Hawkins 1998; Knapp et al. 2001; Simon and Townsend 2003). This study, therefore, revealed different macroinvertebrate responses to the presence of non-native catfish within invaded and uninvaded streams, and suggests that the invasive catfish plays a role as a disturbance in influencing macroinvertebrate communities.

Although some studies indicate that macroinvertebrate communities can resist change to disturbances through rapid colonisation and use of alternative refugia (Collier and Quinn 2003), this study suggests that adaptive responses to invasive predators may differ in habitats with and without fish. Macroinvertebrates in fish-containing habitats tend to develop anti-predator responses to fish (Schilling et al. 2009). In addition, within habitats where invasive predators have establishment, macroinvertebrates may evolve to become less vulnerable through behavioural and morphological adaptations in response to predation (Simon and Townsend 2003; Abjornsson et al. 2004; Meissner and Moutka 2006; Kitano et al. 2009). In contrast, within fishless or recently invaded habitats, macroinvertebrates often lack such adaptations and may not recognise or respond appropriately to the invader (Nyström et al. 2001). These contrasts may therefore explain the macroinvertebrate composition and their different responses within the catfish-invaded Koonap River that had other fish species, which include longfin eel (*Anguilla mossambica*), moggel (*Labeo umbratus*) and smallmouth yellowfish (*Labeobarbus aeneus*), compared to the Brak River that was fishless.

Several studies have shown that introduced predatory fish exert a pronounced negative effect on macroinvertebrates in recently invaded habitats. This is because of the inability of native macroinvertebrate prey to respond to predators that they do not naturally co-exist with (Knapp et al. 2001; Stoks et al. 2003; Schilling et al. 2009), due to lack of co-evolved adaptive mechanisms (Simon and Townsend 2003). Within the uninvaded Brak River, catfish impact was reflected by a decrease in taxa diversity, richness and biomass. Catfish impact was further supported by multivariate analysis that showed high variation in macroinvertebrate composition in the Impact treatment plots, which suggests disruption of the community by the invader. Macroinvertebrate abundance was, nonetheless, uninfluenced by catfish presence. Although some studies have demonstrated impacts on macroinvertebrate abundance (Englund and Polhemus 2001; Maezono et al. 2005), others indicate that loss of certain taxa is mediated by an increase in abundance of those taxa that are not negatively affected by the predators, suggesting that impacts may be related to the response of individual macroinvertebrate taxa (Meissner and Moutka 2006). Assessment of macroinvertebrate composition within the uninvaded Brak River reflected different responses by individual taxa to catfish impact. In particular, the results indicated low abundance of Coenagrionidae and Libellulidae odonates in the Impact treatment plots, whereas the Chironomidae midges and Oligochaeta appeared uninfluenced by the presence of the predator. The most common response of macroinvertebrates to predation by non-native fish is a decline in the densities of vulnerable taxa (Kadye and Magadza 2008; Johnson et al. 2009; Duxbury et al. 2010). Large-bodied prey, such as odonates, are usually the most vulnerable group in recently invaded habitats (Englund and Polhemus 2001; Maezono and Miyashita 2003; Maezono et al. 2005) because invasive predators are opportunistic feeders that tend to target the most conspicuous and accessible prey (Miller and Crowl 2006; Johnson et al. 2009; Weyl et al. 2010). Odonates are usually dominant macroinvertebrate predators that play a crucial role as keystone predators, especially in fishless and uninvaded habitats (Donald and Anderson 2003), and their elimination by invasive predators has been observed to correspond to an increase in the abundance of their potential prey, which reflects trophic cascades (Maezono and Miyashita 2003; Phillips et al. 2009). Within the Brak River, the high abundance of Chironomidae midges in the Impact treatment relative to the Control treatment may suggest a positive response to low abundance of odonate predators. Other studies have also reported invasion paradoxes whereby the elimination of keystone predators by invasive predators facilitates invasions by other species (Shurin 2001). Such facilitative invasions can have detrimental effect as the multiple invaders can interact at the expense of the native biota causing invasion “meltdown” (Simberloff and Von Holle 1999).

In contrast to the uninvaded stream, within the invaded Koonap River, macroinvertebrates showed little response to catfish impact. Some studies indicate that when non-native predators become established, macroinvertebrates assemblages become less responsive as they become dominated by taxa that are either uninfluenced by the presence of predators (Meissner and Moutka 2006) or those that show local adaptation to predator presence (Simon and Townsend 2003; Abjornsson et al. 2004). Local adaptations include predator avoidance behaviour, such as altered drift patterns, use of interstitial spaces for refuge and rapid dispersal by mobile taxa into habitat patches without predators (Douglas et al. 1994; Englund et al. 2001; Schilling et al. 2009), and morphological adaptations, such as change in size-structure of prey (Huryn 1998). Within the invaded Koonap River, the lack of a macroinvertebrate response was particularly reflected by patterns in both abundance and biomass that did not differ between treatments, and little variation in diversity and richness within the Impact treatment, which suggest dominance of resilient taxa. Predator avoidance behaviour was likely explained by high taxa diversity and richness observed within the Control treatment plots relative to the Impact treatment plots in the invaded Koonap River. This avoidance behaviour was also inferred from multivariate analyses that indicated strong association of some taxa, such as Baetidae, Belostomatidae and Hydridae with the Control treatment. In particular, the small-bodied baetid mayflies, *Baetis* spp., have been observed to quickly recover under experimentally-induced predation disturbances, and they actively searched for patches that provided more refuge (Meissner and Moutka 2006). Mayflies are also known to disperse over a large area and to quickly adapt within disturbed environments (Gibbs et al. 1998; Knapp et al. 2001; Effenberger et al. 2008). This suggests that persistent disturbances induce changes to macroinvertebrate communities (Muehlbauer et al. 2011), which result in assemblages dominated, in addition to the resistant taxa, by those that can either quickly recolonise or find alternative refuge if the disturbance does not impair the habitat (Niemi et al. 1990).

Resilient taxa were reflected by the Impact treatment within both the invaded and uninvaded rivers. This was particularly reflected by the abundance of taxa such as leeches (Hirudinea), earthworms (Oligochaeta) and midges (Chironomidae). Assessment of community attributes based on multivariate analysis further indicated the association of the leeches, midges and earthworms with Impact treatment in both rivers. These taxa usually show little negative response to disturbances (Miller and Crowl 2006), including predation (Knapp et al. 2001). Some studies have attributed the resilience of these macroinvertebrate taxa to both their lifestyle because they are less active benthic-dwelling deposit-feeders that are usually not preyed upon by the invasive predators (Carlisle and Hawkins 1998), and indirect positive effects through elimination of their competitors (Knapp et al. 2001; Johnson et al. 2009). Maezono et al. (2005) found no evidence of predation pressure on these predation-resilient taxa in experimental treatments with non-native largemouth bass (*Micropterus salmoides*) and bluegill sunfish (*Lepomis macrochirus*) that eliminated large-bodied taxa in Saitama Prefecture, eastern Japan. In the present study, leeches and midges appeared to benefit from predation impact as they were more abundant in the presence of catfish relative to its absence, whereas earthworms appeared to be unaffected by either treatment. Leeches were unlikely to be negatively affected by the impact because they are generally less mobile and tend to cling firmly to substrates by means of posterior sucker. Some leeches are generally known to feed on a wide range of prey, whereas other leeches are strictly parasitic (Graf et al. 2006; Sket and Trontelj 2008), although there was no evidence of the latter in this study. Their high abundance during this study suggests that they were probably detritovorous. Similarly earthworms and midges are detritivores that are known to be abundant within impacted habitats because they tend to burrow into or live within soft substrata, and benefit from both the elimination of their competitors and increased exposure to resources when a detritus-based food web dominates within disturbed environments (Knapp et al. 2001; Ruetz et al. 2002; Miller and Crowl 2006; Weyl et al. 2010).

From a disturbance perspective, this study reflected different levels of responses to catfish impact within invaded and uninvaded streams. The overall impact patterns within the two rivers supports Parkyn and Collier's (2004) observations on press disturbances whose initial impact result in immediate changes in communities, as observed in the Brak River, before they reach a new level comprising of a less responsive community, or a community that is dominated by taxa that adapt quickly to the disturbance, and possible maintained following a shift in species composition, as suggested by the patterns observed in the Koonap River. Within the Eastern Cape region, the catfish has established in many rivers and dams, and the main concern is on both its predation impact and potential to influence trophic interrelationships (Kadye and Booth 2012). Macroinvertebrate recolonisation and within stream-refugia may be compromised because the catfish can utilise a wide range of habitats. This study revealed that the invasive catfish can influence macroinvertebrate communities, which may have an effect on trophic dynamics. Efforts should be made to protect uninvaded tributaries and, where possible, eradicate the invasive catfish.

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