

Comparisons of isotopic niche widths of some invasive and indigenous fauna in a South African river

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SUMMARY

1. Biological invasions threaten ecosystem integrity and biodiversity, with numerous adverse implications for native flora and fauna. Established populations of two notorious freshwater invaders, the snail *Tarebia granifera* and the fish *Pterygoplichthys disjunctivus*, have been reported on three continents and are frequently predicted to be in direct competition with native species for dietary resources.

2. Using comparisons of species' isotopic niche widths and stable isotope community metrics, we investigated whether the diets of the invasive *T. granifera* and *P. disjunctivus* overlapped with those of native species in a highly invaded river. We also attempted to resolve diet composition for both species, providing some insight into the original pathway of invasion in the Nseleni River, South Africa.

3. Stable isotope metrics of the invasive species were similar to or consistently mid-range in comparison with their native counterparts, with the exception of markedly more uneven spread in isotopic space relative to indigenous species. Dietary overlap between the invasive *P. disjunctivus* and native fish was low, with the majority of shared food resources having overlaps of <0.26. The invasive *T. granifera* showed effectively no overlap with the native planorbid snail. However, there was a high degree of overlap between the two invasive species (~0.86).

4. Bayesian mixing models indicated that detrital mangrove *Barringtonia racemosa* leaves contributed the largest proportion to *P. disjunctivus* diet (0.12–0.58), while the diet of *T. granifera* was more variable with high proportions of detrital *Eichhornia crassipes* (0.24–0.60) and *Azolla filiculoides* (0.09–0.33) as well as detrital *Barringtonia racemosa* leaves (0.00–0.30).

5. Overall, although the invasive *T. granifera* and *P. disjunctivus* were not in direct competition for dietary resources with native species in the Nseleni River system, their spread in isotopic space suggests they are likely to restrict energy available to higher consumers in the food web. Establishment of these invasive populations in the Nseleni River is thus probably driven by access to resources unexploited or unavailable to native residents.

Keywords: diet, ecological impacts, Nseleni River, *Pterygoplichthys disjunctivus*, *Tarebia granifera*

Introduction

Invasive species are a threat to both ecosystem biodiversity and integrity. Freshwater ecosystems, which can be effectively considered biogeographic islands, are particularly susceptible to the establishment of invasive species because their ecological space is often 'unsaturated' with native species (Oberdorff *et al.*, 1997; Strayer, 2010; Kadye

& Booth, 2012). Ecological effects of invaders may include behavioural shifts in native species, alteration of native habitat, alteration of food webs and trophic dependencies and, in some cases, extirpation of native biota (Simon & Townsend, 2003). Two notorious freshwater invaders have established populations on three continents, the planorbid snail *Tarebia granifera* (Lamarck, 1822; Pointer *et al.*, 2003; Ben-Ami, 2006; Appelson, Forbes & Demetriades,

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2009) and the vermiculated sailfin catfish *Pterygoplichthys disjunctivus* (Loricariidae; Weber, 1991; Page & Robins, 2006; Hossain *et al.*, 2008; Levin, Phuong & Pavlov, 2008; Jones *et al.*, 2013), with potentially serious implications for native flora and fauna.

Tarebia granifera (or 'Quilted Melania' in the aquarium trade) is a member of the freshwater prosobranch family Thiaridae from South-East Asia and has been suggested to alter community structure and diversity in invaded habitats (Appelton *et al.*, 2009). Data from several habitats where *T. granifera* occurs sympatrically with indigenous species show that the invasive snail always becomes numerically dominant (Appelton *et al.*, 2009) and, given the well-known top-down effects of grazers in marine and freshwater ecosystems (Pillay, Branch & Steyn, 2009), current research predicts negative feedback in food webs as a result of direct and/or indirect resource competition between the invader and native biota. Miranda, Perissinotto & Appelton (2011) reported high gut pigment content in *T. granifera*, indicating that despite being categorised as a detritivore by Larned, Chong & Punewai (2001), it may also significantly affect microphytobenthos biomass and thus potentially compete with indigenous species for food resources. Indeed, *T. granifera* may deleteriously affect indigenous fauna due to its ability to utilise large amounts of microphytobenthos (March & Pringle, 2003) as well as detritus and, coupled with very high feeding rates (Miranda *et al.*, 2011; Miranda & Perissinotto, 2012), could potentially cause significant top-down and cascading effects.

The second invader, *Pterygoplichthys disjunctivus*, is a member of the Loricariid family, native to the Paraná River basin in South America (Nico *et al.*, 2012). It has been blamed in numerous cases for decreases in marketable fish catch both in subsistence and commercial fisheries as well as destroying fishing nets and cages (Chavez *et al.*, 2006; Levin *et al.*, 2008; Wu, Liu & Lin, 2011). Despite the potentially significant economic implications of loricariid invasions, comparatively little work has been done on their ecosystem impacts. Numerous studies suggest that the potential negative ecological effects of loricariid invasions include increased water turbidity (Chavez *et al.*, 2006; Nico, 2010), bank destabilisation due to tunnelling (Devick, 1989; Page & Robins, 2006; Nico, Loftus & Reid, 2009), predation of native fish eggs (S.L. Cook-Hildreth, unpubl. data), alteration of habitat quality (Amarasinghe, Shirantha & Wijeyaratne, 2006; Krishnakumar *et al.*, 2009), alteration/disruption of food-web dynamics (Nico & Martin, 2001; Levin *et al.*, 2008), declines/displacement of native species (M.J. Cohen, unpubl. data; Neilson & Cannister, 2013) and competi-

tion with native fish for food resources (Page & Robins, 2006; Nico *et al.*, 2009; Neilson & Cannister, 2013). However, although many of these potential consequences imply direct food competition between *Pterygoplichthys* spp. and indigenous fauna, to date this has been difficult to test.

Quantifying the impacts of invasive species can be challenging due to the complexity of ecological interactions (Miranda & Perissinotto, 2012), particularly in aquatic ecosystems. Recently, stable isotope analysis (SIA) has been shown to be a useful tool for tracking changes in trophic structure and energy flows in a system, contributing to the further understanding of how an ecosystem may be affected by indigenous and non-indigenous species (Caut *et al.*, 2006). Isotopic ratios are conserved up through the food web, with predictable isotopic shifts (or fractionation) at every trophic step (DeNiro & Epstein, 1978, 1981; Fry & Sherr, 1984). As such, stable carbon ($\delta^{13}\text{C}$; information on food resources) and nitrogen ($\delta^{15}\text{N}$; information on trophic position) isotopic ratios can provide time-integrated information about feeding relationships and energy flow (e.g. Peterson & Fry, 1987; Cabana & Rasmussen, 1996; Vander Zanden & Rasmussen, 1999). Thus, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can be used to conceptualise trophic niches within communities and habitats because they vary both temporally and spatially (Bearhop *et al.*, 2004; Layman *et al.*, 2007; Newsome *et al.*, 2007; Kadye & Booth, 2012) and provide a powerful approach to predicting the invasion impacts of non-indigenous species and the degree of dietary competition pressure felt by endemic species (Schmidt *et al.*, 2007; Olsson *et al.*, 2009).

Innovative developments in isotope ecology have recently provided statistical Bayesian frameworks for investigating variation in isotopically defined groups (see Layman *et al.*, 2007; Hammerschlag-Peyer *et al.*, 2011). Layman *et al.* (2007) proposed a series of quantitative stable isotope metrics to define the trophic ecology and structure of a system using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ population values. Jackson *et al.* (2011) refined these techniques and bolstered their ability to cope with sample size disparities (see also Jackson *et al.*, 2012), allowing the degree of resource sharing (i.e. competition) between sympatric species to be quantified more easily (Cucherousset *et al.*, 2012; Jackson & Britton, 2013).

The Nseleni River in KwaZulu-Natal, South Africa, is a highly invaded ecosystem, documented to contain numerous established populations of invasive species, including both *T. granifera* and *P. disjunctivus* (Appelton *et al.*, 2009; Jones *et al.*, 2013). Using SIA and subsequent comparisons of species isotopic niche widths and their degree of overlap, our study aimed to (i) investigate

whether the invasive snail *T. granifera* and the invasive fish *P. disjunctivus* are likely to be directly competing with native fauna for dietary resources in the Nseleni River and (ii) resolve diet composition of both invaders.

Methods

Study site

The study was conducted in the freshwater Nseleni River system located in the subtropical KwaZulu-Natal Province of South Africa (Fig. 1). The study area included the Mposa tributary and the lower 16 km of the Nseleni River above its inflow into the 286-ha Lake Nsezi. The study area is described in detail in Jones *et al.* (2013), but a brief overview follows. In the study area, the river is approximately 100 m wide and 3 m deep with a predominantly muddy substratum (Jones *et al.*, 2013). The Nseleni River system does not flow in only one direction (natural flow) because when the level

of the lake is raised at Lake Nsezi, through an interbasin transfer scheme, the water is pushed back up the system. Consequently, all branches of the river system have relatively similar physico-chemistry (Jones R.W., Hill J.M., Hill M.P. and Weyl O.L.F. unpub. data).

Riparian vegetation is dominated by large stands of powder puff *Barringtonia racemosa*, *Ficus* spp. trees and grasses. Emergent aquatic vegetation is dominated by the papyrus *Cyperus papyrus*, water lilies *Nymphaea* sp. and the floating aliens water hyacinth *Eichhornia crassipes* and *Azolla filiculoides*. Aquatic vegetation includes the submerged macrophytes *Ceratophyllum demersum* and *Stuckenia pectinata*. In addition to *P. disjunctivus* and the six most common native fishes sampled during this study (Table 1), additional nine native freshwater fishes have been recorded (in low numbers) from the river (*Anguilla mossambica*, *Anguilla bicolor*, *Aplocheilichthys myaposa*, *Barbus paludinosus*, *Barbus trimaculatus*, *Barbus viviparus*, *Labeo molybdinus*, *Labeobarbus natalensis* and *Coptodon rendalli*; South African Institute for Aquatic Biodiversity Database).

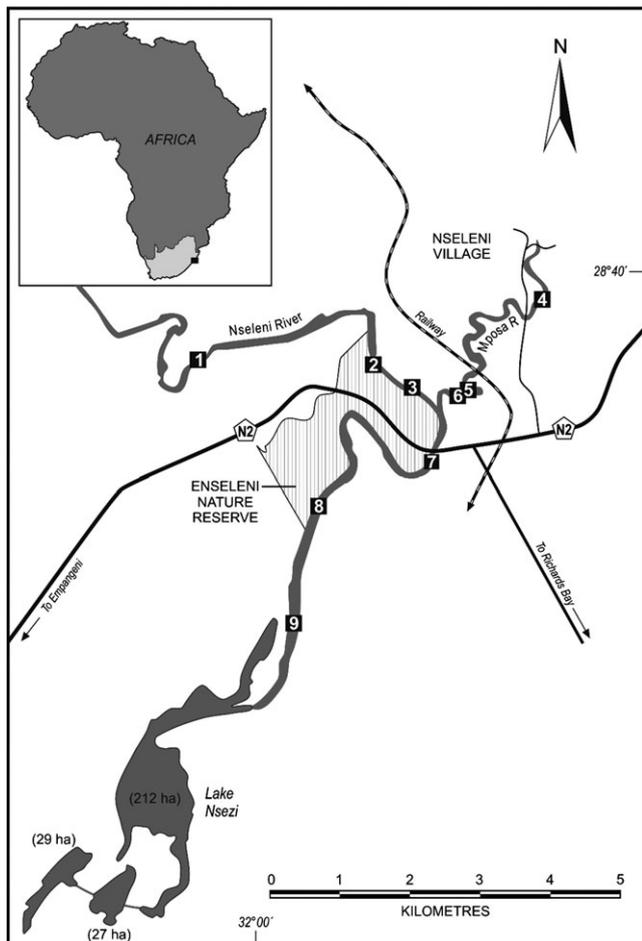


Fig. 1 Map of the Nseleni River system, in KwaZulu-Natal, South Africa.

Sample collection

The most common fish and plant taxa (Table 1) were collected together with the two species of snail that occur at nine different sites on the Nseleni River (Fig. 1) over a 2-week period in February 2012, with the exception of *Pterygoplichthys disjunctivus* samples, which were collected at the same sites over 5 months from November 2011 to February 2012 (permit number: OP 4868/2011). Fish tissue samples were taken from white muscle just in front of the caudal fin, above the lateral line, with all skin and scales removed. All samples (fish, invertebrates and plants) were rinsed in distilled water, oven-dried (48 h at 50 °C) and ground into homogenous powder. Prior to isotope analysis, a small number of samples of each type were acidified using methods described by Cloern, Canuel & Harris (2002) and Jacob *et al.* (2005); as no effervescence was apparent (1N HCl under a 15× dissection microscope), no acid washing was performed on any further samples.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of all samples were determined using a Europa Scientific 20-20 IRMS interfaced to an ANCA SL Elemental Analyser at the IsoEnvironmental Laboratory, South African Institute for Aquatic Biodiversity, Grahamstown, South Africa. All $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were reported as ‰ versus Vienna PeeDeeBelemnite (VPDB) and air, respectively, and normalised to internal standards calibrated to the International Atomic Energy reference materials (IAEA-CH6 for $\delta^{13}\text{C}$

Table 1 Species collected, tissue type, sample size and their mean stable isotope metrics (where applicable): $dNR_b = \delta^{15}N$ range; $dCR_b = \delta^{13}C$ range; CD_b = mean distance to centroid; $SDNND_b$ = SD mean nearest neighbour distance; SEA_c = standard ellipse area; % overlap = the percentage of *Pterygoplichthys disjunctivus* niche area (SEA_c) which overlaps with indigenous fish and mollusc species* or % overlap = the percentage of *Tarebia granifera* niche area (SEA_c) which overlaps with the indigenous planorbid snail[†]

Species	Tissue type	<i>n</i>	dNR_b	dCR_b	CD_b	$SDNND_b$	SEA_c	SEAc overlap
Fish								
<i>Pterygoplichthys disjunctivus</i> (I)	Muscle tissue	42	7.14 (4.70–8.36)	9.07 (6.75–9.72)	2.34 (1.83–2.88)	0.51 (0.31–0.80)	10.8	–
<i>Barbus paludinosus</i>	Muscle tissue	7	4.52 (2.93–5.10)	2.56 (1.36–2.90)	1.87 (1.21–2.35)	0.93 (0.32–1.46)	6.3	0.17*
<i>Clarias gariepinus</i>	Muscle tissue	9	10.24 (5.81–11.91)	11.06 (4.94–12.95)	3.21 (1.66–5.06)	1.07 (0.31–2.30)	9.14	0.91E ^{-18*}
<i>Glossogobius callidus</i>	Muscle tissue	7	1.57 (0.64–2.13)	3.03 (1.07–3.98)	1.13 (0.55–1.72)	0.66 (0.00–1.25)	2.43	0.19*
<i>Marcusenius pongolensis</i>	Muscle tissue	24	4.54 (2.52–5.68)	12.57 (6.42–15.92)	2.76 (1.70–4.10)	0.97 (0.24–2.03)	8.83	0.48*
<i>Oreochromis mossambicus</i>	Muscle tissue	18	10.21 (5.81–11.91)	11.00 (4.94–12.95)	3.19 (1.63–5.03)	1.07 (0.31–2.30)	9.11	0.25*
<i>Pseudocrenilabrus philander</i>	Muscle tissue	21	4.16 (2.84–4.72)	6.27 (3.23–7.72)	1.77 (1.19–2.36)	0.6 (0.26–0.98)	5.86	0.89E ^{-17*}
Snails								
<i>Tarebia granifera</i> (I)	Soft tissue, pooled (<i>n</i> = 3)	17	4.54 (3.80–4.73)	2.13 (1.55–2.29)	1.40 (0.91–1.79)	0.25 (0.14–0.35)	2.97	0.86*
Planorbella sp.	Soft tissue, pooled (<i>n</i> = 3)	10	3.9 (0.64–5.45)	2.19 (0.44–2.78)	1.58 (0.44–2.63)	1.08 (0.59–2.04)	1.73	0.18E ^{-12*} 0.10E ^{-14†}
Plants/diet items								
<i>Ceratophyllum demersum</i>	Leaves	6	–	–	–	–	–	–
<i>Azolla filiculoides</i> (I)	Leaves	6	–	–	–	–	–	–
Biofilm		6	–	–	–	–	–	–
<i>Eichhornia crassipes</i> (I)	Leaves	6	–	–	–	–	–	–
Sediment		6	–	–	–	–	–	–
Epiphytic algae		6	–	–	–	–	–	–
<i>Echinochloa pyramidalis</i>	Leaves	6	–	–	–	–	–	–
<i>Barringtonia racemosa</i>	Leaves	6	–	–	–	–	–	–
<i>Nymphaea</i> sp.	Leaves	6	–	–	–	–	–	–
<i>Cyperus papyrus</i>	Leaves	6	–	–	–	–	–	–

Numbers in parentheses represent the 2.5–97.5% quantile range (see Jackson & Britton, 2013), and (I) indicates an invasive species. Values in bold are the two invasive species of interest in this study.

and IAEA-N2 for $\delta^{15}N$). Results are expressed in standard delta notation, δX ($[R_{\text{sample}}/R_{\text{standard}}] - 1$)1000, where X is the element in question and R is the ratio of the heavy over the light isotope. Precision of replicate determinations for both $\delta^{13}C$ and $\delta^{15}N$ was ± 0.06 and $\pm 0.09\text{‰}$, respectively.

Data analysis

As all fish and snail species are potentially mobile between sites, the $\delta^{13}C$ and $\delta^{15}N$ values were pooled and used to derive quantitative population metrics (Layman *et al.*, 2007) for each species to investigate trophic structure and dietary resource competition between the indigenous and invasive fauna in the Nseni River ecosystem. Metrics and analysis were completed using the Stable Isotope Bayesian Ellipses in R (SIBER; Jackson *et al.*, 2011) model. Metrics included nitrogen (dNR_b) and carbon (dCR_b) ranges, providing a univariate measure of the total nitrogen and carbon ranges exploited by a species; mean distance to the

centroid (CD_b), which provides a description of trophic diversity; standard deviation of nearest neighbour distance ($SDNND_b$), which provides a measure of trophic evenness; and standard ellipse area (SEA_c), which provides a bivariate measure of mean core isotopic niche (Jackson *et al.*, 2011). See Jackson *et al.* (2011) for a fully detailed methodology and Layman *et al.* (2007) for original descriptions of stable isotope metrics. The calculation of SEA_c subsequently allows for a measure of the degree of niche overlap (%; absolute limit of 100% indicating complete overlap), which can then be used as a quantitative measure of dietary similarity between populations and was quantified according to Jackson *et al.* (2012) and Jackson & Britton (2013). To allow comparisons between species populations with varying sample sizes, all metrics were bootstrapped ($n = 10\,000$, indicated with subscript 'b') based on the minimum consumer sample size in the data set (see Table 1). A small sample size correction for improving accuracy to SEA values is indicated by the subscript 'c' (Jackson *et al.*, 2011).

Probability estimates of the relative contribution of dietary resources assimilated by the invasive *P. disjunctivus* and *T. granifera* were obtained using bivariate, separate single-group mixing models in the Stable Isotope Analysis in R package (SIAR; Parnell *et al.*, 2010), incorporating elemental source concentrations as per Inger *et al.* (2010). All food resources used in the model had sufficiently distinct isotope values. Discrimination factors between resources and consumers for *P. disjunctivus* were assumed to be -0.1 ± 0.05 ‰ ($\Delta^{13}\text{C}$) and 5.13 ± 0.05 ‰ ($\Delta^{15}\text{N}$) (German & Miles, 2010), and 0.4 ± 0.17 ‰ ($\Delta^{13}\text{C}$) and 2.3 ± 0.28 ‰ ($\Delta^{15}\text{N}$) for *T. granifera* (McCutchan *et al.*, 2003).

Both SIBER and SIAR models were run in the R environment (R Development Core Team, 2007; available at <http://cran.r-project.org/web/packages/siar/index.html>).

Results

Stable isotope metrics showed the invasive fish *Pterygoplichthys disjunctivus* to be occupying a medium-sized niche with a more diverse diet than four native fish (*Barbus paludinosus*, *Glossogobius callidus*, *Marcusenius pongolensis* and *Pseudocrenilabrus philander*), but less than two native fish species (*Clarias gariepinus* and *Oreochromis*

mossambicus) (Table 1; Fig. 2). The medium ranges of dNR_b (7.14) and dCR_b (9.07) for the invasive fish indicate that it utilises a wider range of food resources and trophic levels than the majority of indigenous fish, with the exception of *Clarias gariepinus* and *Oreochromis mossambicus* (see Table 1). This is consistent with the SEA_c value for *P. disjunctivus* describing a large isotopic niche space (10.8; Table 1). Concurrently, a medium CD_b value (2.34) for the invasive fish describes medium trophic diversity, with three native species possessing higher diversity and three possessing lower diversity (Table 1). SDNND_b values for the invasive fish were much lower than any of the indigenous fish (Table 1), representing a lower degree of trophic evenness. Niche overlaps (i.e. overlap of standard ellipse areas (SEA_c) between the invasive fish and its native counterparts) were very low, with the majority of shared food resources having overlaps of less than 0.26, with the exception of *M. pongolensis*, which had a moderate niche overlap with *P. disjunctivus* (0.48). Interestingly, the niche overlap between the invasive fish and the invasive snail (*T. granifera*) was high at 0.86 (Table 1; Fig. 2).

Comparison of stable isotope metrics between the invasive and native snail showed similar dNR_b and dCR_b ranges. The isotopic niche area occupied by *T. granifera* ($\text{SEA}_c = 2.97$) was larger than that of the

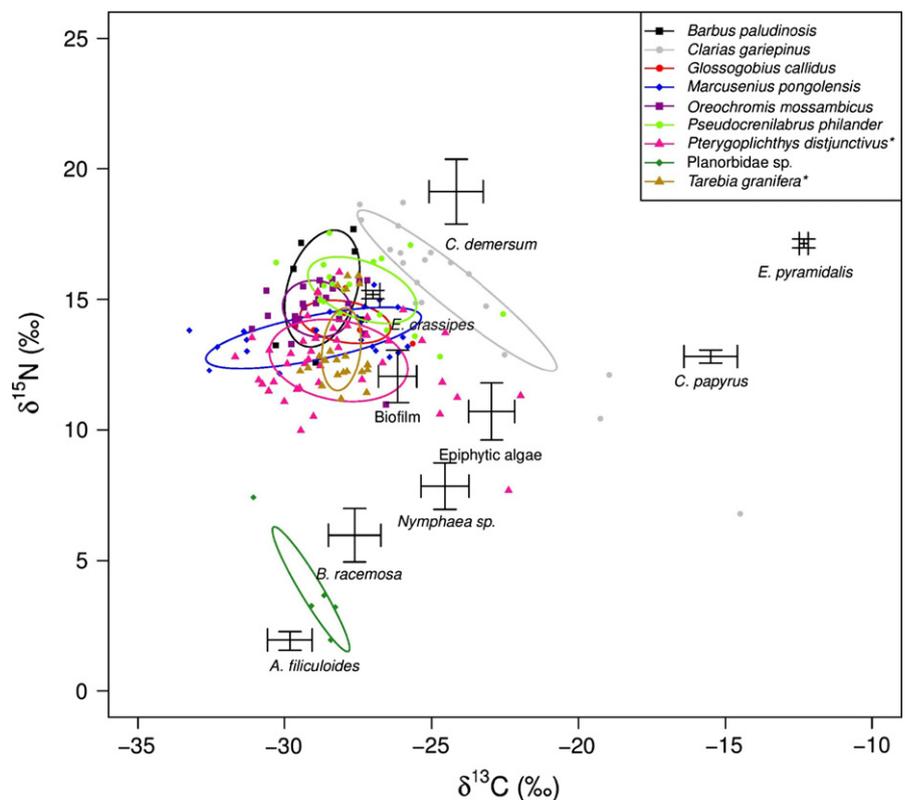


Fig. 2 Corrected standard ellipse areas (SEA_c), representing core isotopic niche space of invasive and indigenous fish and snails as determined through SIBER models (Jackson *et al.*, 2011). The invasive *Pterygoplichthys disjunctivus* and *Tarebia granifera* are marked with an asterisk.

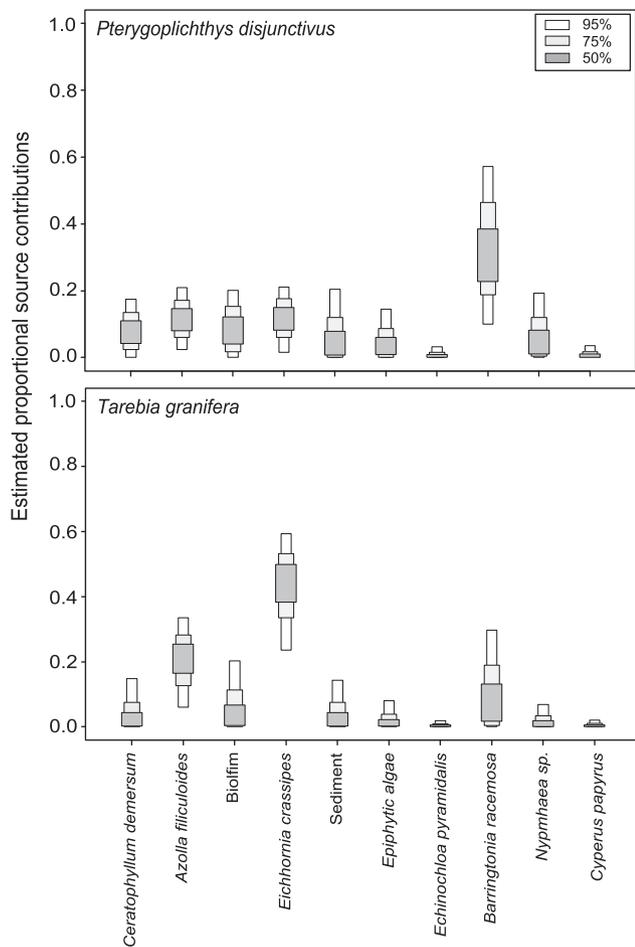


Fig. 3 Estimated proportional source contributions (with 50, 75 and 95% credibility intervals) as determined by SIAR (Parnell *et al.*, 2010) for *Pterygoplichthys disjunctivus* and *Tarebia granifera* diet.

indigenous *Planorbella* species (1.73), and *T. granifera* possessed a lower degree of trophic diversity ($CD_b = 1.40$) and evenness ($SDNND_b = 0.25$) (Table 1). The niche overlap between the invasive and native snail was effectively zero ($0.102E^{-14}$), indicating no shared food resources (Table 1; Fig. 2).

SIAR mixing models indicated that detritus from the mangrove *B. racemosa* probably contributes the largest proportion (on a scale of 0.00–1.00) to *P. disjunctivus* diet (0.12–0.58), with proportional contributions of remaining sources ranging between 0.00 and 0.21 (Fig. 3a). Conversely, SIAR models showed that diet composition of *T. granifera* was more mixed, with detritus from the invasive plant *E. crassipes* contributing the largest proportion (0.24–0.60), followed by detrital *A. filiculoides* (0.09–0.33) and detrital *B. racemosa* (0.00–0.30). Remaining sources contributed proportionally less, with all inputs below 0.20 (Fig. 3b).

Discussion

As the time integration of isotope signals in fish muscle, for example, is usually on the order of the previous few months (Buchheister & Latour 2010), results from this study describe ecosystem dynamics for the period of austral summer. Isotope metrics for both invasive species were either similar (*T. granifera*) or consistently mid-range (*P. disjunctivus*) when compared to those of their native counterparts, with one exception ($SDNND_b$). For *P. disjunctivus*, these metrics show utilisation of a medium range of resources and trophic levels and an intermediate level of trophic diversity when compared to the native fish species. The $SDNND_b$ metric, however, was comparatively lower for both invasive species than those of the native ones, suggesting that both *P. disjunctivus* and *T. granifera* are much less evenly spread in isotopic space than any of the indigenous sympatric species. It is possible that this high level of packing (or clumping) in isotopic space may conform in part to the fluctuating resources theory of invasibility (Davis, Grime & Thompson, 2000; Davis & Pelsor, 2001), which suggests that any species will have a higher degree of invasion success if it does not encounter intense competition from residents for required resources. This unevenness of isotopic spacing may indicate that *P. disjunctivus* and *T. granifera* are exploiting resources otherwise unavailable to native fauna. Interestingly, despite low trophic evenness and intermediate levels of resource use and trophic diversity, the two invasive species had the largest isotopic niche widths (SEA_c) of all the species sampled.

Although information on proportional abundance of dietary items was not collected in this study, consumer isotopic ratios are directly linked to an organisms' diet and thus may be validated using Schoener's index of diet similarity (Schoener, 1968; where 0 = no overlap and 1 = complete overlap between two species). Typically, values greater than 0.6 infer ecologically significant dietary overlap (Schoener, 1968; Layman & Allgeier, 2012) and thus potentially direct resource competition. Overlap of standard ellipse areas between *P. disjunctivus* and native fish from the Nseleni River system was less than 0.60 in all comparisons; however, a moderate degree of overlap (as described by Knickle & Rose, 2013) was seen with *M. pongolensis*. Thus, despite some resource sharing with *M. pongolensis*, the overall degree of potential direct dietary resource competition between *P. disjunctivus* and resident fish species was low, with the invasive fish occupying a distinct part of isotopic niche space. These results are in contrast to the direct

resource competition interactions reported for numerous other highly successful freshwater fish invaders, such as the topmouth gudgeon *Pseudorasbora parva* (Britton, Davies & Harrod, 2010; Jackson & Britton, 2013), small-mouth bass (Vander Zanden *et al.*, 2004) and numerous salmonids (e.g. Vander Zanden *et al.*, 2003; McHugh *et al.*, 2006; Cucherousset *et al.*, 2007). Similarly, a complete lack of dietary overlap was seen between *T. granifera* and the native *Planorbella* sp., with the two snails occupying entirely different positions in isotopic niche space and, more importantly, feeding at different trophic levels. This is perhaps not surprising as planorbid snails are pulmonate gastropods and thus, by necessity, occupy different microhabitats (shallow aquatic vegetation) than the invasive *T. granifera* (primarily a substratum grazer; Seuffert & Martin, 2010). However, there is some evidence to suggest that thiarids and sympatric pulmonates can have similar diets; thus, *T. granifera* may limit shared food resources (Miranda & Perissinotto, 2012) and in some cases may outcompete native pulmonates, despite their different microhabitats (Perez, Vargas & Malek, 1991).

The lack of significant direct competition for food resources between invasive and native fauna in this study was surprising based on the potential for ecological damage speculated or reported by numerous studies on both *P. disjunctivus* (Page & Robins, 2006; Nico *et al.*, 2009; Neilson & Cannister, 2013) and *T. granifera* (March & Pringle, 2003; Appelton *et al.*, 2009; Miranda & Perissinotto, 2012). It is likely, however, that strong indirect dietary resource competition is at work, as both invasive species and the majority of native fauna occupy a similar range in $\delta^{13}\text{C}$ (a descriptor of food source), with separation based primarily on $\delta^{15}\text{N}$ values. This suggests that the majority of the fauna sampled in the Nseleni River system during austral summer may be ultimately dependent on the same food resources, but utilise the derived energy at different trophic levels. Although *P. disjunctivus* and *T. granifera* are clearly not in direct competition for food with native sympatric species, high abundances of these invaders are likely to be reducing the energy available, probably through nutrient limitation, to individuals further up the food chain, thus significantly altering the food web. This is a particular concern given the increasing numbers of *P. disjunctivus* documented in the Nseleni River system over the past 5 years (Jones *et al.*, 2013). This scenario of energy reduction was first suggested by Page & Robins (2006), and was predicted to have long-term indirect effects on community composition, where high numbers of invaders would reduce energy available to other herbivores/detritivores such as

aquatic insects and other arthropods. This reduction in invertebrates would subsequently lead to reduced populations of other animals that feed on arthropods, and so on up the food chain (Page & Robins, 2006), including many native fishes. Furthermore, there is the potential for these invasive species to increase interspecific resource competition (Britton *et al.*, 2010) further up the food web if basal resources become limited. Results from this study are inconclusive in these regards, but warrant further investigation.

Interestingly, SEA_c comparisons between the two invasive species show an ecologically significant dietary overlap of more than 0.85, indicating that *P. disjunctivus* and *T. granifera* may be directly competing with each other for food (but not with their respective native counterparts). The application of mixing models to identify important dietary source contributions for both invaders showed that the largest single contribution to *P. disjunctivus* diet was mangrove leaf detritus (*B. racemosa*). *Tarebia granifera* showed highest contributions of detritus from two invasive species, *E. crassipes*, followed by *A. filiculoides*, but also included a significant mangrove leaf detritus component. Detritus originating from all three of these principal diet components possess significant physical (*E. crassipes*; Casca *et al.*, 2003) and/or chemical (*A. filiculoides*; Cohen *et al.*, 2002) deterrents to consumers, or are highly refractory and thus difficult for many consumers to digest (mangrove leaf litter; Kristensen *et al.*, 2008), potentially rendering this food source inaccessible to native species. Both *P. disjunctivus* and *T. granifera* are documented detritivores, with the catfish reportedly being very efficient at separating out and digesting the soluble components of detritus (German & Bittong, 2009; German & Miles, 2010) while the snail's generalist feeding approach means it can utilise large amounts of microphytobenthos in addition to detritus (Miranda *et al.*, 2011; Miranda & Perissinotto, 2012). These feeding traits, combined with the identified food resources and the large dietary overlap in niche space between the invasive species, conform with the fluctuating resources theory of invasibility (Davis *et al.*, 2000; Davis & Pelsor, 2001), which suggests that both *P. disjunctivus* and *T. granifera* are exploiting food resources underutilised and/or unavailable to resident sympatric species. Furthermore, there is a suggestion of invasion facilitation, as the primary components of *T. granifera* diet are themselves invasive species (Simberloff & Von Holle, 1999; Schultz & Dibble, 2012).

The long-term ecosystem effects of invasion by both *P. disjunctivus* and *T. granifera* are not yet well understood, and numerous other factors must be considered

when investigating alien species impacts, particularly in terms of biodiversity. These include life history, physiological and environmental tolerance, reproduction, behaviour and abundance. For example, increased alien abundance may also result in fewer young, reduced hatching and/or survivorship and slower growth rates in indigenous species (Appleton, 2003; Wu *et al.*, 2011). In the case of *T. granifera*, there is also some evidence to suggest that large aggregates of snails secrete chemical cues that induce avoidance behaviour and negative taxis in heterospecifics (Perez *et al.*, 1991; Raw, Miranda & Perissinotto, 2013), resulting in increases in thiarid competitiveness and the displacement of native species. Increased competitiveness in the cases of the invasive loricariid catfish and planorbid snail, however, does not appear to be achieved through direct dietary resource competition in the Nseleni river system, although increasing abundance probably restricts the energy available to higher consumers in the food web, with the potential for bottom-up alterations to food webs and ecosystem functioning. The establishment of populations of *P. disjunctivus* and *T. granifera* is probably driven by access to resources underutilised or unavailable to native species, and further studies of these species are required to determine whether population sizes can be brought down to acceptable levels that will sustain environmental and ecological integrity.

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