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The introduced *Micropterus salmoides* in an equatorial lake: a paradoxical loser in an invasion meltdown scenario?

J. Robert Britton · David M. Harper · Dalmas O. Oyugi · Jonathan Grey

Abstract *Micropterus salmoides* is a North American piscivorous fish on the IUCN list of 100 of the world's worst invasive alien species. Introduced into Lake Naivasha (Kenya) in 1929, their current population abundance is significantly depressed in a lake that has recently become dominated by fishes of the *Cyprinidae* family; the introduced cyprinid *Cyprinus carpio* now dominates catches in the commercial fishery and *Barbus paludinous* is now numerically dominant in the fish community. Long-term diet studies of *M. salmoides* based on gut contents analysis (GCA) have defined their diet spectrum, feeding preferences and ontogenetic dietary shifts. Between 1987 and 1991, diet was size-structured; fish <260 mm were mainly insectivorous and fish >260 mm fed mainly on invasive crayfish *Procambarus clarkia* with *B. paludinosus* rarely taken. More recent GCA data revealed that up to 2003, these size-structured trophic relationships were still evident, but there has been a subsequent shift to their feeding almost exclusively on small (<100 mm) *B. paludinosus*, coincident with a size-related functional switch whereby *M. salmoides* >120 mm were now piscivorous. However, a Bayesian stable isotope mixing model (SIAR) suggested *M. salmoides* diet actually remained relatively varied in 2006 and 2007; it indicated *P. clarkii* were still contributing more to their diet than *B. paludinosus* in fish <260 mm and provided only partial support for the functional shift. The consequence of the *M. salmoides* depressed population abundance is their predation pressure on prey fishes is limited and preventing top-down effects. This is in contrast to their invasive populations elsewhere in the world and the likely result of invasion meltdown processes in Naivasha involving the introduced *C. carpio* and *P. clarkii* that have produced sub-optimal foraging conditions for *M. salmoides*.

Keywords Largemouth bass · *Procambarus clarkii* · *Barbus paludinosus* · *Cyprinus carpio* · Diet composition · Invasive species

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Introduction

Introductions of alien fish predators into freshwater ecosystems are of significant ecological concern due to their potential for causing deleterious, top-down effects on native fish assemblages, such as the effect of Nile perch *Lates niloticus* (L.) on the endemic haplochromines of Lake Victoria (Ogutu-Ohwayo and Hecky 1991; Goldschmidt et al. 1993). The piscivorous largemouth bass, *Micropterus salmoides* Lacépède, has been introduced from North America into numerous countries around the world for sport fishing, including in Asia (Takamura 2007), Europe (Godinho et al. 1997; Elvira and Almodovar 2001) South America (Welcomme 1992) and Africa (Weyl and Hecht 1999; Gratwicke and Marshall 2001). The predation pressure exerted by established populations is usually sufficient to incur significant ecological impacts in invaded ecosystems, including major shifts in the species composition and size structure of communities (Cambray and Stuart 1985; Gratwicke and Marshall 2001), and major shifts in the habitat utilisation, foraging behaviour and somatic growth of their prey populations (Werner et al. 1983; Werner and Hall 1988). Consequently, *M. salmoides* is listed on the IUCN list of 100 of the world's worst invasive alien species (Lowe et al. 2000).

Interactions between invasive fishes and native fish communities are frequently revealed through dietary studies (Matern and Brown 2005; Kalogirous et al. 2007; Britton et al. 2009a). Gut contents analyses (GCA) provide evidence of whether the invading population has increased predation pressure on prey species (Carol et al. 2009) or has increased competition for resources (Britton et al. 2007). Contemporary methods such as stable isotope analyses (SIA) complement GCA by providing a longer-term perspective on assimilated diet (Grey 2006). Studies tend to focus on species that have been recently introduced or are newly invasive (e.g. Nobriga and Feyrer 2008; Grabowska et al. 2009). This is the period when interest from the scientific community is usually highest as ecological data are required to support the emerging strategies needed to manage the invasion (Britton et al. 2009b). However, established populations of alien fish with functional roles as generalized macro-predators often have the capacity for substantial trophic adaptability in response to shifts in

prey availability (Nobriga and Feyrer 2008). Thus, the long-term diet composition of an invasive piscivore is a function of prey preferences, availability, and their ease of capture and handling.

Although the introduction and establishment of *M. salmoides* into Lake Naivasha, Kenya, occurred in the 1920 and 1930s, there were limited data available on their population until their specific inclusion in commercial gill-net fishery statistics from 1987. Subsequent studies in the 1990s using GCA revealed significant size-structuring in their diet; insect prey were the main food source of fish of up to 260 mm; larger fish were then primarily feeding selectively on another invasive species, the crayfish *Procambarus clarkii* Girard (Hickley et al. 1994). There was a key predator-prey relationship between the abundances of *M. salmoides* and *P. clarkii*, which had a regulatory role in determining macrophyte areal cover (Hickley and Harper 2002). Since then, however, there have been sustained periods of macrophyte absence, depressed *P. clarkii* abundance, and substantial changes in the fish community following the introduction and establishment of the invasive common carp *Cyprinus carpio* L. (Britton et al. 2007). Consequently, in this paper we test the hypothesis that the diet composition of *M. salmoides* in Lake Naivasha has recently shifted in accordance with the availability of their prey communities and in doing so, has elicited a top-down effect in structuring prey fish populations, similar to other *M. salmoides* populations across their invasive range. We use Lake Naivasha as the model system because of the wealth of background data and well documented history of species invasions (e.g. Harper and Mavuti 2004). These invasions also conform with the concept of 'invasion meltdown' (Simberloff and Von Holle 1999), whereby recent invasions by species such as *C. carpio* were facilitated by the earlier invasions of *P. clarkii* due to the modified environmental conditions provided by their ecological engineering (Smart et al. 2002; Britton et al. 2007). The objectives were to determine their population abundance in relation to their prey communities between 1987 and 2008, assess the temporal relationships between their diet composition and prey communities between 2001 and 2008, and identify whether their predatory activity has been sufficient to induce measurable effects on the fish community.

Materials and methods

Lake Naivasha is a shallow, freshwater lake in Kenya's Rift Valley located 190 km south of the equator at an elevation of 1,890 m a.s.l. It is approximately 100 km^2 in area and 3 to 6 m deep. Water temperatures are generally >20°C (Hickley et al. 2004). Although it was designated a Ramsar site in 1995 (Wetlands International 2003), considerable pressures remain on the lake and the riparian zone, for example eutrophication, habitat degradation, introduced species and lake level fluctuations (Kitaka et al. 2002; Harper and Mavuti 2004; Britton et al. 2007). In the 1970s, the lake was described as having clear waters and an extensive papyrus fringe, with dense growth of submerged macrophytes within lagoons (Siddiqui 1977). In more recent years, water clarity has declined substantially, with secchi disk depths often recorded <40 cm (Harper and Mavuti 2004). The fish assemblage now includes *M. salmoides*, *C. carpio*, *Tilapia zillii* (Gervais) and *Oreochromis leucostictus* (Trewavas) (all introduced), with *Barbus paludinosus* Peters the only fish in the lake that was naturally present in the catchment (Britton et al. 2007).

Temporal patterns in the population abundance of *M. salmoides* were provided by two measures of relative abundance. The first used catch statistics data from the commercial fishery that provided species-specific monthly catch totals between January 1987 and May 2009. This fishery comprised up to 43 boats licensed to use up to 10 gill nets each of 100 m length, with a minimum mesh size (knot to knot) of 2.5 inches (64 mm); the minimum fish landing size is 180 mm. All captured fish have to be taken to landing beaches where all fish are measured and weighed, enabling the catch statistics to be collated. As the minimum mesh sizes meant the majority of captured bass were >260 mm, to provide data on the population below this size threshold, the second methodology utilised multi-mesh gill net gangs of up to 60 m length and 1.5 m depth. Each 60 m net comprised 12 panels of 5 m length of mesh size (knot to knot) 8, 10, 13, 16.5, 19, 22, 25, 30, 33, 38, 45 and 50 mm, with up to four nets joined together. Samples were collected once each year (July to October) between 1987 and 2008 (with the exception of 2001), with each sampling period lasting for up to 10 days. The nets were set at locations covering various spatial areas across the major habitat types of the lake. They were set from the surface on a daily basis, usually at first light, and lifted after between 3 to 6 h fishing. After lifting, the fish were removed from the net, identified to species level, measured (fork length, L_F, nearest mm) and weighed (nearest g). The relative abundance of each species captured was calculated using a standardised catch per unit effort index (CPUE), using the method of Hickley and Harper (2002) that provided an output measured in the number of fish per gill net gang per hour (n gang h^{-1}) and enabled comparison of fish relative abundance between annual sampling periods. Values of CPUE for the fishes for the period between 1987 and 1999 were available from Hickley and Harper (2002). From 2002, the relative population abundance of crayfish was also assessed during the same sampling periods as the fish populations. A combination of traps (adults) and sweep netting (juveniles) were used. A full description of the methodology is available in Britton et al. (2007).

The size-structured interactions and trophic relationships of *M. salmoides* and their principal prey items were assessed using GCA on fish samples collected between 2002 and 2008. Following dissection, stomach contents were examined using a binocular microscope, with taxa identified and counted. Frequency of occurrence for each dietary item was expressed as the number of guts in which the item was recorded divided by the total number of guts examined. The number of empty stomachs was negligible in the samples due to the sample collection during daylight hours when the foraging activities of *M. salmoides* peak in the lake (Hickley et al. 1994). Due to the relatively low representation of *M. salmoides* in all of the gill net catches since 2003 then the sample size used for GCA was relatively low (cf. Sect. "Results") and so to provide greater insight into their diet composition, SIA was completed on samples of fish muscle and their major prey species collected between 2001 and 2008. Fish and crayfish were collected as described previously and samples of *Micronecta scutellaris* were collected using dip nets from the same areas. Samples were oven-dried at 60°C, pulverised in an agate pestle and mortar, and stored in sealed Eppendorf vials. Stable isotope ratios were determined by continuous flow isotope ratio mass spectrometry and reported using the δ notation expressed in units of per mille as follows:

δ (‰) = [(R sample/ R standard)-1] × 1,000, and R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The reference materials used were secondary standards of known relation to the international standards of Vienna Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen. Typical precision for a single analysis was ±0.1‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$. Fish $\delta^{13}C$ data were arithmetically lipid-normalised according to Kiljunen et al. (2006). These data were analysed by estimating the percentage contributions to bass biomass from the putative prey species by substituting individual bass $\delta^{13}C$ and $\delta^{15}N$ values in a Stable Isotope Analysis in R (SIAR) model (Jackson et al. 2009). Prey annual mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values derived from $n > 3$ pooled samples of 20 individual *M. scutellaris*, $n > 15$ individual *Procambarus*, and $n > 10$ individual *B. paludinosus* (cf. Results) were used as potential sources, and trophic fractionation factors of 0.5–1‰ and 2.5–3.5‰ were used for carbon and nitrogen, respectively.

With the exception of SIAR, all statistical analyses were completed in SPSS v. 16.0 (©SPSS Inc., Chicago, Illinois). Where the error is provided with mean values, they express 95% confidence limits unless stated otherwise.

Results

The indices of relative abundance suggest the population abundance of *M. salmoides* is currently depressed compared with the levels recorded between 1987 and 1991, the period of their initial dietary study (Figs. 1, 2). In the commercial fishery statistics (i.e. mainly fish >260 mm), mean monthly catches were significantly higher between 1987 and 1991 (3,035 ± 496 kg) than between 2001 and 2009 (914 ± 187 kg) (ANOVA $F_{1,121} = 66.93$, $P < 0.001$). This decrease in their relative abundance was also measured in the multi-mesh gill net samples (i.e. fish <260 mm) that revealed a similar difference between the two periods, with CPUE between 1987 and 1991 (36.8 ± 14.8 fish per gang h^{-1}) significantly higher than between 2002 and 2008 (2.4 ± 2.7 fish per gang h^{-1}) (ANOVA $F_{1,10} = 28.3$, $P < 0.001$).

This temporal shift in catches of *M. salmoides* was also coincident with other changes in the lake, as revealed by catches in the fishery that have shifted in recent years from overall dominance by
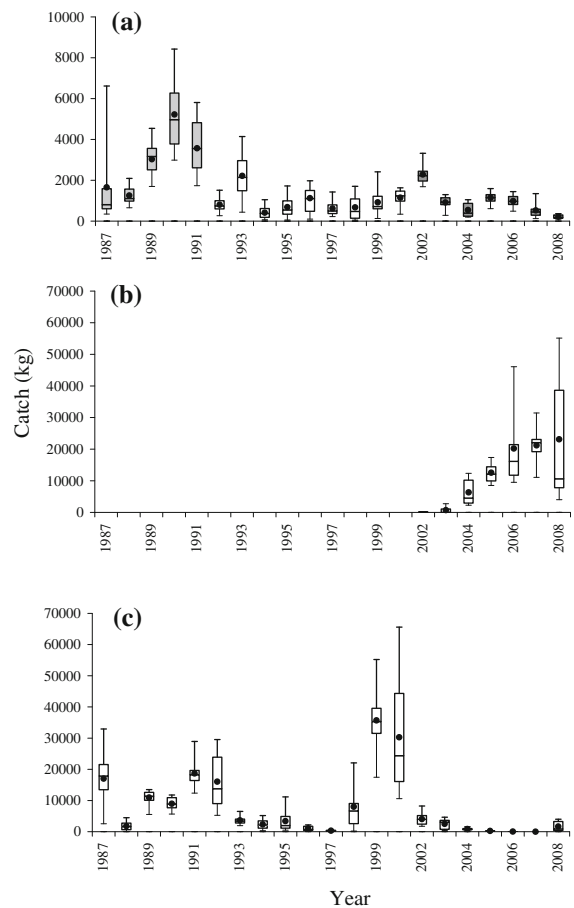
Fig. 1 a *Box plot* of mean monthly catch of *Micropterus salmoides* by year from the Lake Naivasha commercial fishery. *Boxes shaded* in light grey represent the period of the initial dietary study (Hickley et al. 1994) and dark grey represent the present period of study; **b** *Box plot* of mean monthly catch of *Cyprinus carpio* by year; and **c** *Box plot* of mean monthly catch of *Oreochromis leucostictus* by year. In each *box plot*, the *top*, *mid-line* and *bottom* of each *box plot* represent the 75, 50 and 25th percentiles, the *horizontal lines* represent the 10 and 90th percentiles and *filled circle* = the mean. Note the difference in the scale of the Y-axis between **a** and **b**, **c**

O. leucostictus to *C. carpio*, with the latter species comprising >90% of catches since 2005 (Fig. 1). This switch to the exploitation of an introduced cyprinid fish also corresponded with a significant increase in the multi-mesh gillnet catches of *B. paludinosus* (Fig. 2); the CPUE of this small cyprinid fish between 1987 and 1991 was 1.4 ± 1.3 fish per gang h^{-1} compared with 71.2 ± 38.4 fish per gang h^{-1} between 2002 and 2008 (ANOVA $F_{1,11} = 10.8$, $P < 0.001$). Their length range was dominated by fish of 50 to 90 mm fork length, with
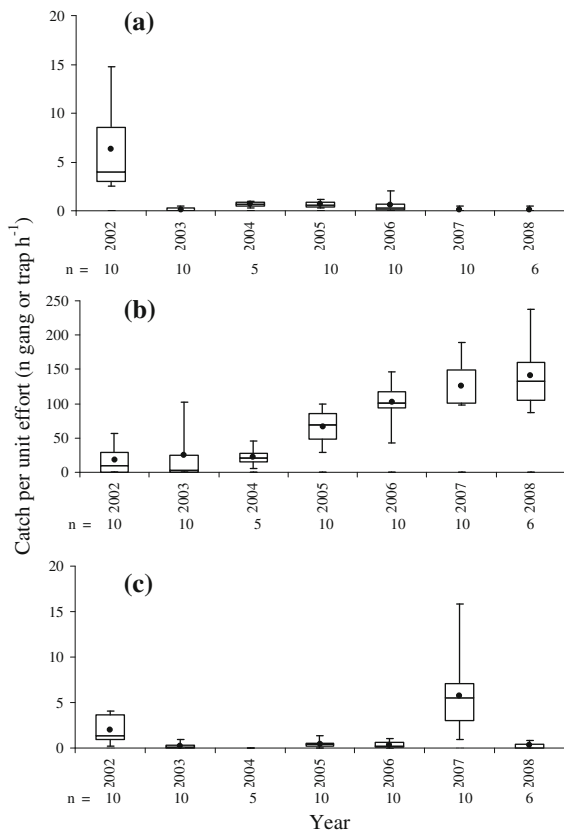
Fig. 2 a *Box plot* of catch per unit of multi-mesh gill net samples of *Micropterus salmoides*, 2002 to 2008 (n gang h^{-1}); **b** *Box plot* of catch per unit of multi-mesh gill net samples of *Barbus paludinosus*, 2002 to 2008 (n gang h^{-1}); **c** *Box plot* of catch per unit of *Procambarus clarkii* from crayfish trap samples, 2002 to 2008 (n trap h^{-1}). In each *box plot*, the *top*, *mid-line* and *bottom* of each *box plot* represent the 75, 50 and 25th percentiles, the *horizontal lines* represent the 10 and 90th percentiles and *filled circle* = the mean

no fish caught >128 mm. In contrast to *B. paludinosus*, the CPUE of *C. carpio* sampled using the same methodology between 2003 and 2008 never exceeded 15.4 fish per gang h^{-1}. Regarding *P. clarkii*, abundance data were not available for the period 1987 and 1991, although the high relative abundances of *M. salmoides* and their known relationship with crayfish abundance (Hickley and Harper 2002) would suggest their population abundance was relatively high. Between 2002 and 2008, *P. clarkii* CPUE appeared relatively low, with the exception of 2007 when their CPUE increased following a brief period of macrophyte regeneration (Fig. 2).

The use of GCA on 163 *M. salmoides* sampled in 2002 and 2003 that had food items in their stomachs

revealed the diet contribution by their principal prey species was similar to that observed between 1987 and 1991. The majority of stomachs of bass <260 mm contained up to 55 individual *M. scutellaris* and fish >260 mm usually contained at least one *P. clarkii* (Fig. 3). The frequency of occurrence of *P. clarkii* in fish <260 mm was less than 5% in both of these years and a similar pattern was observed for *M. scutellaris* in the stomachs of fish >260 mm. Piscivory of *B. paludinosus* was not apparent in *M. salmoides* of any size (Fig. 3). Although samples collected in subsequent years comprised of fewer fish (total number of sampled *M. salmoides* with food items in their stomachs between 2004 and 2008 = 87; Fig. 3), GCA did strongly suggest a marked shift in the contribution of these prey items to *M. salmoides* diet from 2004/05, indicating a functional shift from a size-structured diet dependent on either *M. scutellaris* (<260 mm) or *P. clarkii* (>260 mm) to one dominated by *B. paludinosus*. This involved a significant decrease in the body size at which *M. salmoides* switched to piscivory and predation of *P. clarkii*, with the mean length of fish with *B. paludinosus* or crayfish in their stomach reducing significantly between 2002 to 2003 (313 ± 25.3 mm) and 2005 to 2008 (189 ± 32.1 mm) (ANOVA F$_{1,92}$ = 59.8, P < 0.001) (Fig. 3). Between 2006 and 2008, up to 6 individual *B. paludinosus* were found in the stomachs of *M. salmoides* as small as 120 mm. Regarding piscivory, *B. paludinosus* was the principal fish species recorded by GCA in diet between 2005 and 2008, with only one recording of *C. carpio* despite their increase in population abundance; *P. clarkii* has not been recorded in diet by GCA since 2005. Despite this shift in piscivory by *M. salmoides*, there was no evidence of deleterious effects on the *B. paludinosus* population (Figs. 2, 3). Rather, as *B. paludinosus* CPUE increased, so did their contribution to *M. salmoides* diet, with these relationships significant between 2002 and 2008 (*B. paludinosus* CPUE × contribution to diet of *M. salmoides* <260 mm: R^2 = 0.63, F$_{1,5}$ = 8.24, P < 0.04; *B. paludinosus* CPUE × contribution to diet of *M. salmoides* >260 mm: R^2 = 0.58, F$_{1,5}$ = 6.6, P < 0.05).

Although GCA suggested a functional shift to piscivory of *B. paludinosus* by *M. salmoides* in recent years, modelled contributions from isotope-derived data inferred that their feeding interactions and

Fig. 3 a Frequency of occurrence of *Micronecta scutellaris* in the diet of Micropterus salmoides <260 mm, 2002 to 2008; **b** Frequency of occurrence of *Barbus paludinosus* in the diet of *Micropterus salmoides* <260 mm, 2002 to 2008; **c** Frequency of occurrence of *Procambarus clarkii* in the diet of *Micropterus salmoides* >260 mm, 2002 to 2008; **d** Frequency of occurrence of *Barbus paludinosus* in the diet of *Micropterus salmoides* >260 mm, 2002 to 2008. In each *box plot*, the *top*, *mid-line* and *bottom* of each *box plot* represent the 75, 50 and 25th percentiles, the *horizontal lines* represent the 10 and 90th percentiles and *filled circle* = the mean, and *n* = the number of fish used for the stomach contents analysis
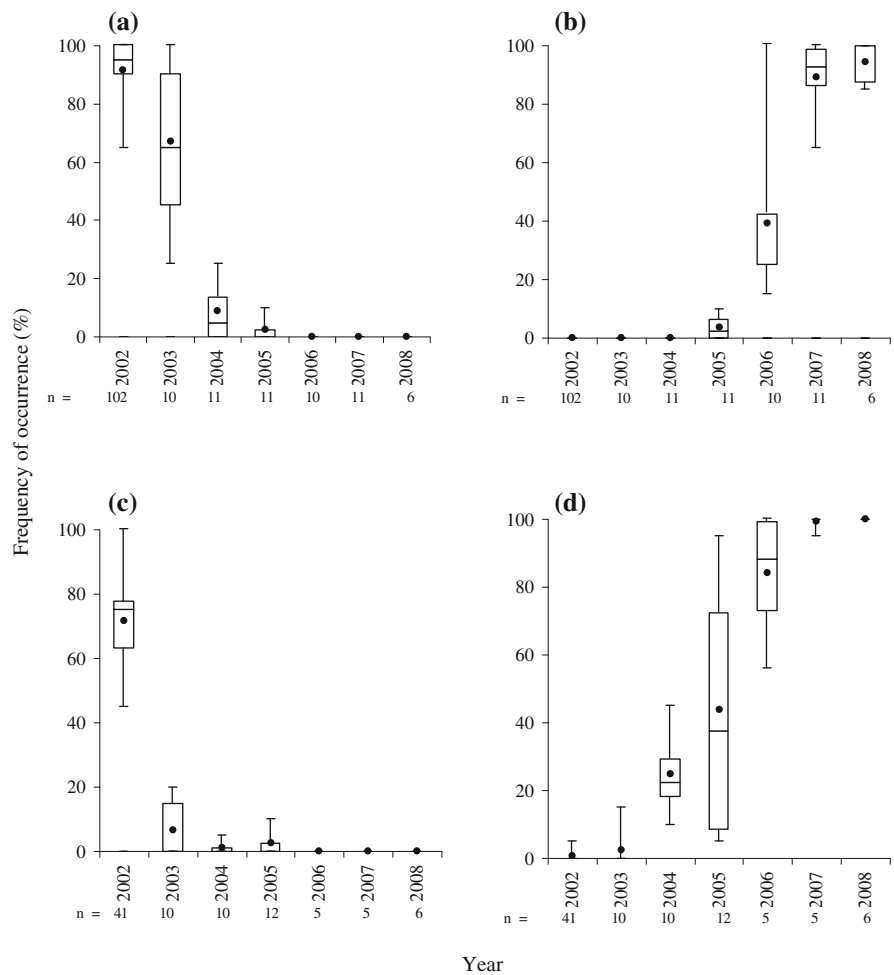
trophic relationships remained more diverse (Fig. 4). In fish <260 mm, the decrease in the proportion of diet comprising *M. scutellaris* and increase of that comprising *B. paludinosus* (from GCA) was also apparent from the stable isotope data (Fig. 4). However, whereas *P. clarkii* has never been recorded as a major prey item in this length class by GCA, the outputs from SIAR imply their contribution to diet was actually relatively high throughout the period, and especially in 2006. In fish >260 mm, SIAR outputs partially corroborated the findings of GCA in that *M. scutellaris* was only a minor prey item making little contribution to *M. salmoides* diet, and the contribution of *P. clarkii* also reduced in the period. However, whereas this change was identified from GCA in 2005, it was only apparent from stable isotope data in 2007, when there was a functional shift to *B. paludinosus* predation.

Discussion

There was strong evidence of a shift in the diet composition of *M. salmoides* in Lake Naivasha that was related to changes in the availability of their prey. This was principally the result of a prolonged depression in the population abundance of *P. clarkii* and more recent increases in the *B. paludinosus* population. The dietary shift was accompanied by an ontogenetic shift in piscivory; whereas in previous years *M. salmoides* of <260 mm were primarily insectivorous, fish as small as 120 mm were feeding upon the abundant *B. paludinosus* in the latter part of our study. Despite this apparent increased predation pressure by *M. salmoides* on the prey fish community, there was no evidence to suggest that it had elicited a top-down effect in size-structuring the *B. paludinosus* population. Rather, increased predation pressure
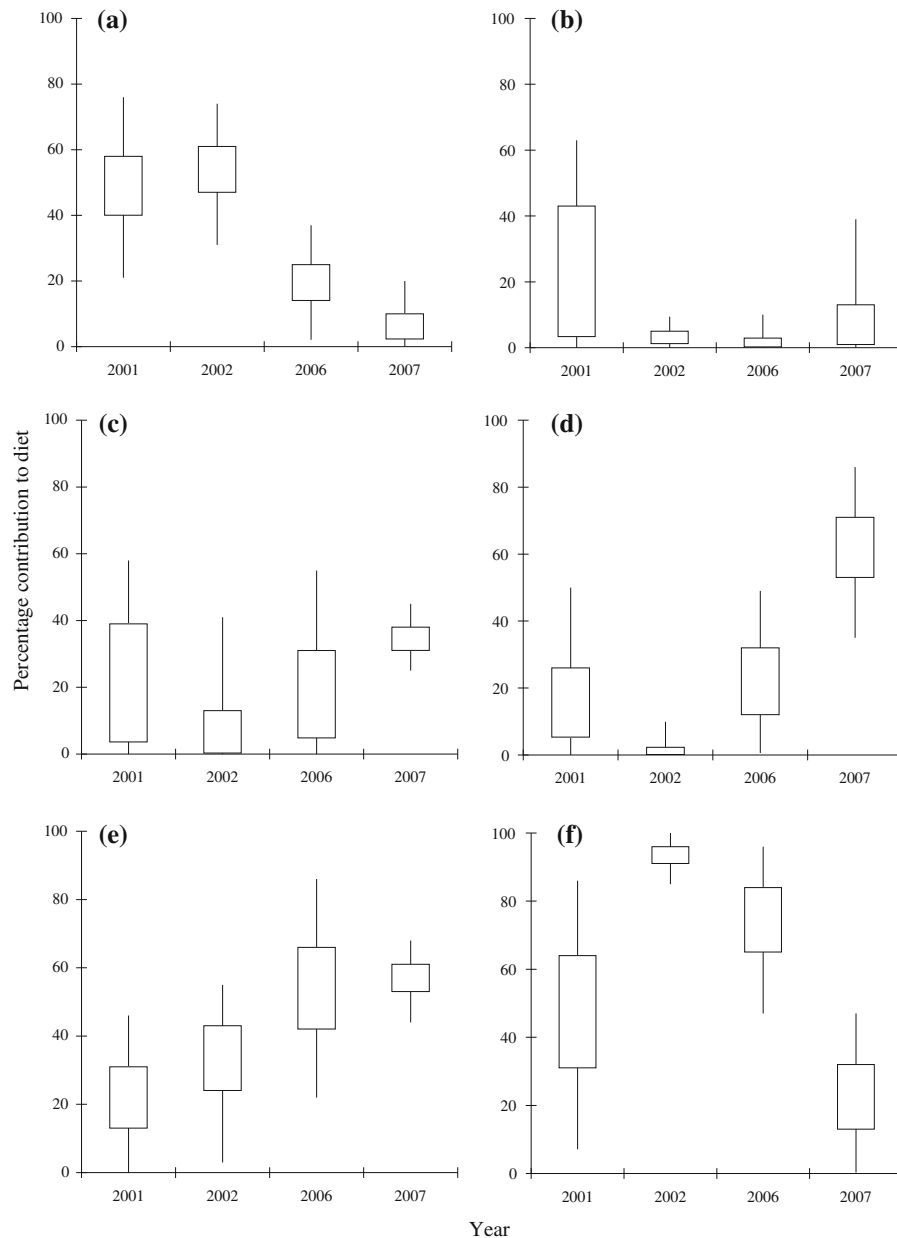
Fig. 4 Percentage contributions (reported as a probable range in confidence intervals) of three prey species to *Micropterus salmodies* diet derived from stable isotope data input into SIAR; **a** Contribution of *Micronecta scutellaris* to the diet of *M. salmoides* <260 mm; **b** contribution of *Micronecta scutellaris* to the diet of *M. salmoides* >260 mm; **c** contribution of *Barbus paludinosus* to the diet of *M. salmoides* <260 mm; **d**

contribution of *Barbus paludinosus* to the diet of *M. salmoides* >260 mm; **e** contribution of *Procambarus clarkii* to the diet of *M. salmoides* <260 mm; and **f** contribution of *Procambarus clarkii* to the diet of *M. salmoides* >260 mm. The *clear boxes* represent the Gaussian likelihood bound by 50% confidence intervals and the *vertical lines* bound by 95% confidence intervals

appears to have been inconsequential to the population growth of *B. paludinosus*, with this likely to have been facilitated by the increasing eutrophic conditions of the lake providing enhanced planktonic food

resources (Cambray and Stuart 1985; Harper and Mavuti 2004). Thus, *M. salmoides* appears to have been taking advantage of an abundant prey item with little adverse effect on the prey population. This is

contrary to all other case studies on invasive *M. salmoides* populations around the world which have shown significant top-down effects on their prey fish populations, especially when the prey fishes comprise cyprinid species (e.g. Cambray and Stuart 1985; Azuma and Motomura 1998; Yonekura et al. 2004; Katano et al. 2005; Jang et al. 2006; Sammons and Maceina 2006; Takamura 2007). For example, in other African countries, *B. paludinosus* populations have been heavily impacted by *M. salmoides* predation, with Gratwicke and Marshall (2001) revealing that the population densities of small *Barbus* species, including *B. paludinosus*, were reduced by up to 99% in their presence across 42 lakes in Harare, Zimbabwe. In Japanese farm ponds, fish species richness was three times higher in *M. salmoides* absence and native fish abundance was suppressed in their presence (Maezono and Miyashita 2003; Yonekura et al. 2004; Maezono et al. 2005).

This apparent paradox in the predation effects of *M. salmoides* on the cyprinid fishes of Lake Naivasha is likely to be due to their depressed population abundance resulting in relatively low predation pressure. The reasons for their depressed abundance remain unclear, especially in light of the recent significant increases in the population abundances of cyprinid prey fishes. Moreover, the macrophyte denudation of the lake should have enhanced their foraging success, as studies have revealed macrophyte growth inhibits *M. salmoides* foraging efficiency by providing increased prey refugia (Schramm and Zale 1985; Savino and Stein 1989; Dionne and Folt 1991; Sammons and Maceina 2006). However, the shift from clear water to high turbidity that has occurred in the lake since the 1970s (Harper and Mavuti 2004), a combined result of macrophyte loss through crayfish introduction (Smart et al. 2002; Britton et al. 2007), and frequent algal blooms that result from increased eutrophication (Kitaka et al. 2002; Harper and Mavuti 2004), may all contribute, and are not mutually exclusive. This is because *M. salmoides* foraging efficiency is adversely impacted by increased turbidity due to its reliance on visual cues (McMahon and Holanov 1995; Takamura 2007). Thus, whilst the earlier introduction of *P. clarkii* may have provided *M. salmoides* with an abundant and profitable food source during the 1990s, the destructive foraging behaviour and denudation of the macrophyte flora by crayfish ultimately appears to

have changed the lake conditions sufficiently to their detriment. The benthic foraging behaviour of introduced *C. carpio* has also exacerbated the turbidity problem, and further reduced the likelihood of return to the former clear water state (Britton et al. 2007). It was also apparent that the establishment of *C. carpio* in Naivasha was facilitated by the prior invasion by *P. clarkii* through their ecological engineering activities that provided an environment denuded of macrophytes, rich in nutrients, and subject to high turbidity and algae blooms (Harper and Mavuti 2004); i.e. good conditions for *C. carpio* but not a piscivore reliant on visual cues (Koehn 2004). Thus, the invasion of crayfish facilitating the invasion of carp in Lake Naivasha was conforming to the concept of invasion meltdown (Simberloff and Von Holle 1999).

Although the low sample size between 2004 and 2008 (a function of the low population abundance of *M. salmoides* in that period) limits the conclusions that can be drawn solely from the GCA data, these were augmented by SIA data from further individuals. However, comparison of the data derived from the two complementary methods did reveal some apparent differences in output. Gut contents analyses suggested that the trophic relationships of *M. salmoides* in Lake Naivasha have shifted considerably in recent years, moving from dominance of feeding on insect prey (fish <260 mm) and *P. clarkii* (fish >260 mm) to feeding primarily on *B. paludinosus* (all fish >120 mm). However, SIAR indicated that *M. salmoides* diet had remained more varied and reliant on other species. For example, it suggested that in *M. salmoides* <260 mm, *B. paludinosus* never contributed more than 55% of the assimilated diet and that *P. clarkii* was actually an increasingly important contributor, despite not being recorded in samples by GCA. There are several possible reasons for the difference in outputs from the two approaches. GCA tends to provide a 'snapshot' of ingested diet and the samples we analysed only represent a 10 days period per annum. SIA of fish muscle represents a temporal integration of carbon and nitrogen assimilated from diet, dependent upon metabolic turnover, growth and the temperature of the surrounding water (Perga and Gerdeaux 2005, Grey 2006) but cannot provide the taxonomic resolution of GCA. As such, it would appear prudent to use the information gleaned from both approaches (Grey et al. 2002), with the

appropriate caveats provided for GCA in relation to low sample sizes.

In summary, changes in the prey communities of *M. salmoides* has resulted in a shift in their trophic relationships, with a recent ontogenetic shift to piscivory at smaller sizes detected from GCA data, but with SIAR emphasizing that other prey species such as *P. clarkii* remain important contributors. Despite a switch to piscivory that has enabled exploitation of an extremely abundant prey resource, this has not resulted in their population abundance returning to former levels and so their predation was not a major determinant of fish community structure. Consequently, in an aquatic ecosystem invaded by multiple species, *M. salmoides* appears to be the paradoxical loser due to the effects of invasion meltdown processes on the lake environment.

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