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Biological Invasions

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# Ecomorphology of largemouth bass relative to a native trophic analogue explains its high invasive impact

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**Abstract** Predicting and understanding the impact of biological invaders is a global ecological imperative. Progress has been made through the application of phenomenological analysis via comparative functional response analysis. However, little is known about the mechanisms which drive high-magnitude functional responses of invasive species, especially when compared to trophically analogous natives. Largemouth bass *Micropterus salmoides* is a freshwater invasive species evaluated as a more efficient

predator, with a higher-magnitude functional response, compared to a native analogue, the Cape kurper *Sandelia capensis*. In order to determine what traits drive this difference we quantified handling time behaviours (detection time, catch time, processing time) of both predator species and prey/predator size ratio, and employ an ecomorphological approach to determine whether largemouth bass is a more specialised predator than Cape kurper. There was no difference in detection time between the species, but largemouth bass were significantly and on average five times faster at catching prey than Cape kurper. Both species' processing time was positively related to prey size, but Cape kurper was on average 4.5 times faster

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than largemouth bass. Ecomorphological data indicate that largemouth bass was the more specialised pursuit hunter for fish, whereas Cape kurper was better at ambush hunting. This suggests that the ecological impact of largemouth bass may be exacerbated in areas where there is habitat simplification which can lead to the extirpation of local small-bodied fish. In addition, there may be non-consumptive detrimental effects on trophically analogous natives through competitive exclusion.

**Keywords** Competition · Functional traits · Freshwater · Handling time · Conservation

## Introduction

The continued spread of invasive species across the globe is contributing to biodiversity loss in many ecosystems (Meyerson et al. 2019). As a consequence, invasive species confer substantial economic cost due to the necessity of constant management and mitigation protocols in order to reduce their vast potential ecological effects (Pimental et al. 2005; Oreska and Aldridge 2011; Meyerson et al. 2019). The burden of this makes management somewhat prohibitive, especially within developing countries. Consequently, research has focused on developing predictive methodologies to identify species that will confer the most ecological damage in order to triage potential and emerging invasive species for management purposes (Courtois et al. 2018).

A predictive method that has gained traction is the use of comparative functional response (CFR) analysis (Dick et al. 2014, 2017a,b; Alexander et al. 2014; Dickey et al. 2018). This describes the density-dependent resource utilisation of a consumer (Solomon 1949; Holling 1959) and operates under the assertion that invasive species exert a higher impact, i.e. *per capita* effect, on resources than native species do (Ricciardi et al. 2013; Dick et al. 2014). In numerous systems, this hypothesis has been experimentally corroborated by showing that successful invasive species do indeed show superior performance with regards to resource utilisation (Dick et al. 2017a,b; Laverty et al. 2017). As the functional response of a species describes resource use in a phenomenological manner [with the functional

response relationship being defined by the parameters attack (or search) efficiency  $a$ , handling (or processing) time  $h$ , and maximum feeding rate  $1/h$ ]; the causal mechanism of higher ecological impact can only be inferred from the results of functional response experiments. While being a useful tool to describe phenomenological patterns seen in the field and a rapid assessment of relative differences in predation rate, the CFR approach does not give an ultimate cause to explain impacts of invasive species seen in the field.

Predation shapes community structure in ecological systems by controlling the dynamics of predator and prey populations (Sih et al. 1985). In the case that an invasive predator has a higher functional response than the native analogue, it is possible that 1) the invasive species will exert a higher predatory pressure on native prey species and 2) that the population dynamics of shared resources will be disrupted and the native predator will suffer due to being outcompeted by the invader (Alexander et al. 2014; Laverty et al. 2017). Predatory performance (i.e. *per capita* effect) is affected by a species' physiology, behaviour, hunting strategies, and morphology (Eklöv and Diehl 1994; Takamura 2007; Deurs et al. 2017). These variables drive niche differentiation in species to allow similar species to persist in sympatry. Understanding the way in which invasive species are specialised in comparison to their native analogues can help to inform prediction metrics in order to determine mechanisms that facilitate invasive species impact. Morphological traits ultimately determine the capacity of a species to locate, attack and consume different prey items (Wainwright and Reilly 1994; Sibbing and Nagelkerke 2000), therefore it is an obvious link that these traits contribute to the ecological impact exerted on native species. Dietary overlap and similar trophic profiles, as imbued from morphological trait similarities, of invasive and native species can result in exploitative competition (Nagelkerke et al. 2018). Hence, incorporating an assessment of morphological differences can clarify the causal organismal drivers of high resource consumption and possible out-competition.

The largemouth bass *Micropterus salmoides* was introduced into South Africa to enhance recreational fisheries (Ellender and Weyl 2014) and has since established in a wide range of habitats throughout the country (Khosa et al. 2019). As a result of its persistence in freshwater systems and high degree of ecological impact it confers on the recipient systems

(e.g., Weyl et al. 2010; Kimberg et al. 2014; Ellender et al. 2018) it is considered as one of the “World’s Worst Invaders” (Lowe et al. 2000). Largemouth bass is a highly efficient piscivore, and while predominantly piscivorous it shows some flexibility in diet preferences (Taylor et al. 2019). In the South African context one of the trophically analogous native species that has been impacted is the Cape kurper *Sandelia capensis* (Cuvier 1829) (Ellender et al. 2017). Cape kurper is a data-deficient species but has trophic similarities with largemouth bass, being a generalist piscivore with flexible omnivory (Shelton et al. 2018). In most cases, Cape kurper have disappeared from stream reaches invaded by largemouth bass (Ellender et al. 2011).

In assessing the possible mechanism for these exclusions Alexander et al. (2014) used a CFR approach to demonstrate that largemouth bass have a higher-magnitude CFR when feeding on tadpoles compared to Cape kurper, driven by a shorter handling parameter (sensu FR-terminology) resulting in a higher maximum feeding rate (Alexander et al. 2014). In the case of CFR analysis the modelled handling parameter represents and amalgamates a number of linked processes involved in the subduing, consumption, processing and digestion of prey (Jeschke et al. 2002; Sentis et al. 2013). This suggests that largemouth bass have a morphological or physiological advantage over Cape kurper, which facilitates a shorter handling time and allows them to consume more prey items in the same period of time.

This study looks to determine whether there are behavioural and morphological variables driving the high functional response of largemouth bass compared to Cape kurper. Alexander et al. (2014) demonstrated that the handling time parameter drives largemouth bass impact, therefore we empirically quantify the handling time behaviours of largemouth bass compared to Cape kurper. Handling time can be broken down into different behaviours such as time taken to detect, pursue and catch, and actually consume the prey item (Jeschke et al. 2002). This is further affected by the size of the prey item in comparison to the predator (Hoyle and Keast 1986; Kreuzinger-Janik et al. 2019). We employ an ecomorphological approach, i.e. we study the relationships between the ecological role of an individual and its morphological adaptations, to determine whether differences in feeding-related functional traits indicate whether one

species is more specialised to particular feeding strategies (Wainwright and Reilly 1994; Sibbing and Nagelkerke 2000; Nagelkerke et al. 2018). This describes the potential niche and preferred prey type of a predator, without considering resource availability or environmental contexts. We hypothesise that due to being more morphologically specialised for piscivory, largemouth bass are more efficient at handling fish prey items than Cape kurper.

## Methods

### Animal collection and maintenance

All experiments were completed at the South African Institute for Aquatic Biodiversity in 2013. Largemouth bass ( $n = 9$ ;  $70.2 \pm 4.8$  mm) were collected from Jameson Dam ( $33^{\circ}43'04''S$ ;  $26^{\circ}26'23''E$ ) and Douglas Dam ( $33^{\circ}19'16''S$ ;  $26^{\circ}31'15''E$ ) by seine netting and electrofishing. Cape kurper ( $n = 20$ ;  $59.7 \pm 9.8$  mm) were collected by seine netting in the Blindekloof stream ( $33^{\circ}43'1.42''S$ ;  $25^{\circ}17'27.41''E$ ). All sampling was undertaken in March–April 2013. The two species could not be collected from the same location as areas invaded by largemouth bass have experienced extirpations of Cape kurper. The largemouth bass were collected from dams with some rocky littoral structure, but dominated by submerged and emergent vegetation, while the Blindekloof is a small episodic headwater stream dominated shallow rocky substrate with some marginal vegetation and woody debris in-stream.

Cape kurper and largemouth bass were maintained in species-specific, filtered 300 L holding tanks held at  $21 \pm 1.0$  °C under a 16:8 L:D regime prior to handling-time experiments. Fish were acclimated to the focal prey item, female guppies (*Poecilia reticulata* Peters, 1859) for one week before experimentation and were fed ad libitum once a day. This prey species was chosen because of their general shape, which is very similar to native small-bodied minnows which are natural prey of both predatory species. Further, the native minnows that the guppies represent in this case are highly threatened endemic species which makes using them as prey inconceivable. Guppies were obtained through Hoof and Hound pet store (Makhanda) and maintained in a separate 150 L holding tank and fed commercial fish flakes (JBL,

Germany). All experiments were performed under SAIAB Animal Ethics Clearance (2013/02).

### Handling time

Handling time experiments were completed in 65 L arenas (25 L × 55 W × 47.5 H cm) with no substrate, filled with aged tap water and held at  $21 \pm 1.0$  °C. Largemouth bass ( $n = 9$ ; standard length median and range: 71; 63–81 mm) and Cape kurper ( $n = 9$ ; SL: 56; 45–76 mm) were starved for two days prior to experimentation to standardise hunger levels for the purposes of this experiment. Fish were allowed to acclimate to the experimental arena for 15 min before introduction of prey. All prey items were individually measured for total length (TL) before use in experiments (TL median and range: 22.5; 15.6–37.0 mm for largemouth bass; 22.5; 15.1–32.4 mm for Cape kurper). There was no significant length difference in prey between the predator groups (Student's  $t$  test statistic  $t(47) = 0.39$ ,  $p > 0.05$ ), although Cape kurper were on average 19% smaller than largemouth bass (56.8 vs. 70.2 mm, Student's  $t$ -test statistic  $t(16) = 3.82$ ,  $p < 0.05$ ). To correct for size differences between and among predators and prey, we used the prey-predator size ratio (defined as the ratio of the TL of the prey and the SL of the predator). Predators were allowed 30 min to feed, after which the experiment was terminated even if predation had not occurred. Each individual fish was tested three times with a repeated measures design to reduce number of animals needed, which was especially important considering the declining abundance of Cape kurper in the wild (Ellender et al. 2011; Shelton et al. 2017; Ellender et al. 2018). All trials were filmed using GoPro Hero 1 HD video cameras. Video recordings were then reviewed to determine exact times for: (1) prey detection; (2) catching the prey; and (3) processing the prey.

Detection time ( $t_{\text{det}}$ ) was defined as the time between prey release into the tank and detection of the prey by the predator. The moment of detection could be clearly observed, through increased alert behaviour of the predator, after which it either engaged in pursuit or not. Catch time ( $t_{\text{cat}}$ ) was the time between the moment the predator started its pursuit, until the moment of capture of the prey. Finally, processing time ( $t_{\text{pr}}$ ) was the time between the moment of catch and swallowing of the prey.

Processing of the prey was externally visible, through head movements indicating repositioning and chewing of the prey in the mouth. The moment these head movements stopped, processing of the prey was complete, and the prey was swallowed.

Time data were log-transformed and linear mixed-effects models were fitted, based on maximum likelihood. “Predator species” and “prey-predator size ratio” were used as fixed factors, while “individual fish” was used as a random factor. To account for repeated measures (several experiments were performed with each individual fish), “individual fish” was nested within “predator species”. For each handling component separately, a full model was fitted, containing “predator species”, “prey-predator size ratio”, and their interaction. Non-significant terms were removed stepwise from the model, starting with the interaction term. The final model only contained significant terms. Model residuals were checked for normality through visual inspection of Q–Q plots and Shapiro–Wilk tests, and for homogeneity between groups with Levene's tests. All analyses were performed in an R environment (R Core Team, 2018), using the package nlme (Pinheiro et al. 2018).

### Ecomorphology

Feeding-associated functional morphological traits were measured to compare the trophic capacities of largemouth bass and Cape kurper according to (Sibbing and Nagelkerke 2000) (Table 1). The same fish were used for ecomorphological analysis and for the handling time experiment to reduce the number of animals (SL median and range largemouth bass ( $n = 9$ ): 71; 63–81 mm, Cape kurper ( $n = 20$ ): 58; 45–78 mm). Fish were euthanized with an overdose of clove oil (400 mg/L) and frozen before morphological traits were measured. Traits were selected because they are related to the fish's capacity to prey on particular aquatic prey types, and because they were suitable for the two focal species of this study. Measurements were performed using a standard dissection kit, a set of callipers (Sylvac) for length measurements, and a dissection microscope.

### Analysis

Fifteen feeding-associated functional traits were measured according to (Sibbing and Nagelkerke 2000)

**Table 1** Feeding-associated, morphological traits and their units. Definitions follow (Sibbing and Nagelkerke 2000) and Nagelkerke et al. (2018)

Morphological trait	Unit
Anal fin area	mm <sup>2</sup>
Body depth	mm
Body depth/width	ratio
Caudal peduncle depth	mm
Eye diameter	mm
Gape size	mm <sup>2</sup>
Head length	mm
Hyoid length	mm
Lower jaw closing force efficiency	ratio
Lower jaw length	mm
Opercular volume capacity	ratio
Operculum area	mm <sup>2</sup>
Palatal organ area	mm <sup>2</sup>
Relative gape area	ratio
Velocity suction capacity	ratio

(Table 1). Linear and surface area measures were scaled by taking the residuals of the linear regressions of the log-transformed measures on the log-transformed standard length (SL), while for ratios there was no need for scaling (Nagelkerke et al. 2018). The food-fish model (FFM), as described in (Sibbing and Nagelkerke 2000), was used to systematically and quantitatively relate functional traits of each individual fish to its capacity to utilize aquatic prey types. This was done in two steps. First the effects of morphological traits on the capacity to eat a suite of aquatic food resources were established and quantitatively expressed as positive, negative, or zero values (ranging between  $-2$  and  $+2$ , with zero values indicating that there is no known evidence for an effect). The combined values of all such effects for an aquatic resource form a hypothetical “food specialist profile” (FSP), expressing the ideal relative sizes of morphological traits to exploit that resource (S1). The FSP values for each aquatic food resource were correlated with the morphological measurements of each individual fish (Kendall’s tau correlation), resulting in a correlation coefficient which is considered a measure of the predicted capacity of the fish to feed on this particular food resource. Differences between species in their predicted feeding capacities

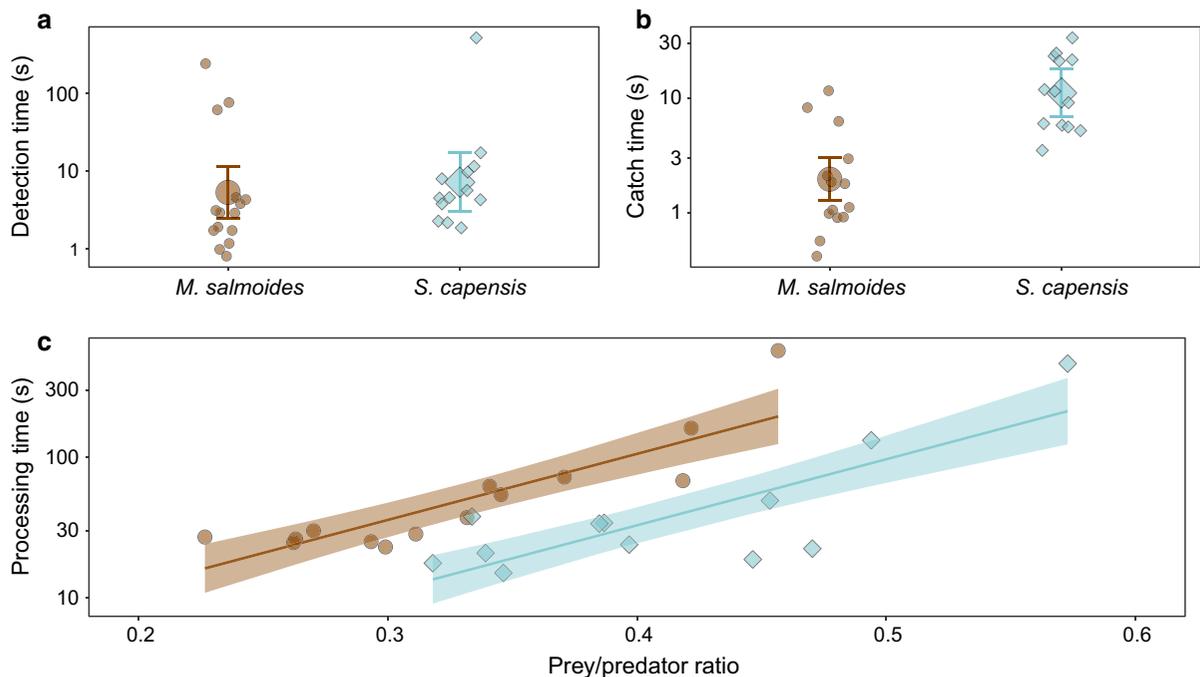
on particular aquatic food resources were tested with a Wilcoxon rank sum test, to avoid problems with non-normal residuals. The combined series of these correlation coefficients for all aquatic food resources was called a trophic profile (TP). The values of measured morphological traits and values of FSPs, were separately standardized before correlation (subtracting the mean value of each variable and dividing by the standard deviation), resulting in a mean value of zero and a standard deviation of one for each variable, thus giving equal weight to all variables (Nagelkerke et al. 2018).

Principal components analysis (PCA) was performed on the functional feeding traits to compare overall trophic morphology, as well as on the TPs for an overall interpretation of trophic capacities. All statistics were performed in an R environment (R Core Team 2018).

## Results

### Handling Times

Detection time ( $t_{\text{det}}$ ) did not vary with predator species ( $b = 0.87$  (SE = 0.69),  $t(10) = 1.26$ ,  $P = 0.24$ ) nor with prey- predator ratio ( $b = -5.20$  (SE = 4.01),  $t(15) = -1.30$ ,  $P = 0.21$ ) and was estimated to have a geometric mean value of 6.1 s (95% CI: 3.3–11.2 s; Fig. 1a). Largemouth bass had a significantly faster  $t_{\text{cat}}$  than Cape kurper ( $b = 1.73$  (SE = 0.33),  $t(10) = 5.22$ ,  $P < 0.0001$ ; Fig. 1b) but prey-predator size ratio did not have a significant effect on  $t_{\text{cat}}$  ( $b = 0.22$  (SE = 2.39),  $t(14) = 0.09$ ,  $P = 0.93$ ; Fig. 1b). Geometric mean of  $t_{\text{cat}}$  for largemouth bass was 2.0 s (95% CI: 1.3–3.0 s) and 11.1 s (95% CI: 6.9–17.9 s) for Cape kurper. Processing time ( $t_{\text{pr}}$ ) was significantly, and on average 4.5 times, shorter for Cape kurper ( $b = -1.17$  (SE = 0.25),  $t(10) = -4.76$ ,  $P < 0.001$ ), and significantly increased with prey-predator size ratio for both species ( $b = 10.82$  (SE = 1.52),  $t(13) = 7.12$ ,  $P < 0.0001$ ; Fig. 1c). Shapiro–Wilk normality tests indicated that the residuals of the final models were not deviating from a normal distribution in case of  $t_{\text{cat}}$  and  $t_{\text{pr}}$ . For  $t_{\text{det}}$  the Shapiro–Wilk test indicated a deviation from a normal distribution, but visual inspection of the Q–Q plots did not. Levene’s tests indicated that for all models residuals were homogeneously distributed.



**Fig. 1** a Overall geometric mean and 95% confidence interval of detection time, b Geometric mean and 95%-confidence interval of catch time c Processing time in relation to prey/

predator size ratio with 95%-confidence intervals. Individual values for *Micropterus salmoides* indicated by brown circles, and for *Sandelia capensis* by blue diamonds

## Ecomorphology

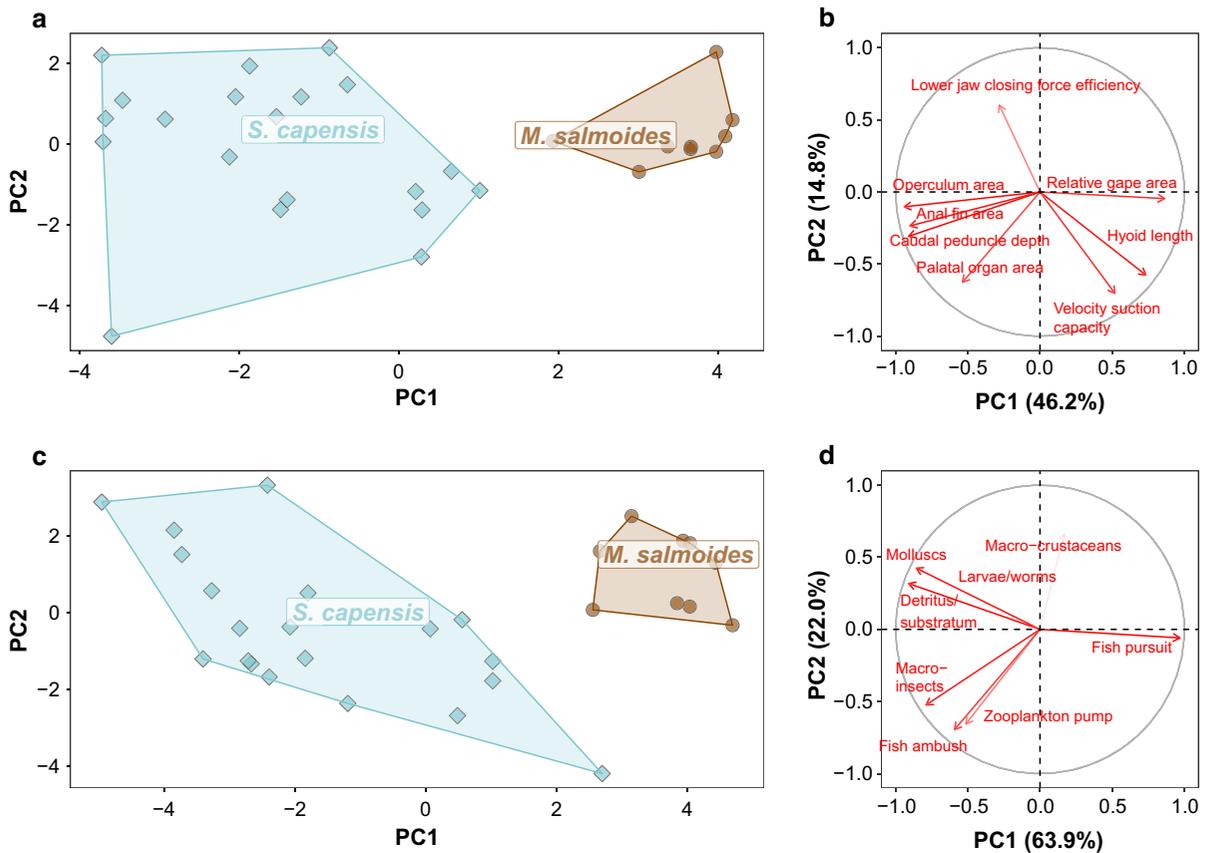
The PCA of the morphological variables explained 61.0% of variance along the first and second axes (Fig. 2a,b). Overall the morphologies of largemouth bass and Cape kurper were clearly separate along the first axis, while still showing considerable intra-specific variation along the first and second axis (Fig. 2a,b). Relative gape area, hyoid length and velocity suction capacity were larger in largemouth bass, while in Cape kurper anal fin area, caudal peduncle depth, and operculum area were clearly larger.

Differences in trophic morphology translated in clear differences in TPs. The PCA of TPs (85.9% of the total variation explained along the first two axes: Fig. 2c,d) revealed that largemouth bass is predicted to be a more specialised pursuit hunter, while Cape kurper is better equipped for ambush hunting and for the exploitation of a wide variety of (smaller-bodied) prey, although there is considerable intra-specific variation. Except for macro-crustaceans, TPs were significantly different between species for all prey types (Wilcoxon rank sum test,  $P < 0.05$ ; Fig. 3).

## Discussion

Predicting and understanding the factors that drive higher ecological impact of invasive species is one of the major challenges and priorities in invasion ecology. While phenomenological methods have proven insightful in predicting which species are likely to cause damage to native biodiversity, the actual mechanisms responsible for ecological impacts remain a black box. We demonstrate here, that by combining an ecomorphological mechanistic approach on the back of a phenomenological approach (such as the handling time experiment here, or the conventional CFR approach: Alexander et al. 2014; Dick et al. 2017), it is possible to specify what traits are instrumental in the interactions between species and potentially contribute to the invasion success and detrimental effects of a global invader.

Time taken to handle prey determines how much a predator can eat within a given period of time. Quantifying differences in handling time behaviours is consequently a powerful way to distinguish between the efficiency of trophically analogous predators. In this case, there was no difference in the time taken to



**Fig. 2** Biplot of a principal component analysis (PCA) of trophic morphological traits (a,b) and of derived trophic profiles (TP: c,d). Markers in the left graphs indicate individual fish belonging to *Sandelia capensis* (blue diamonds) or *Micropterus*

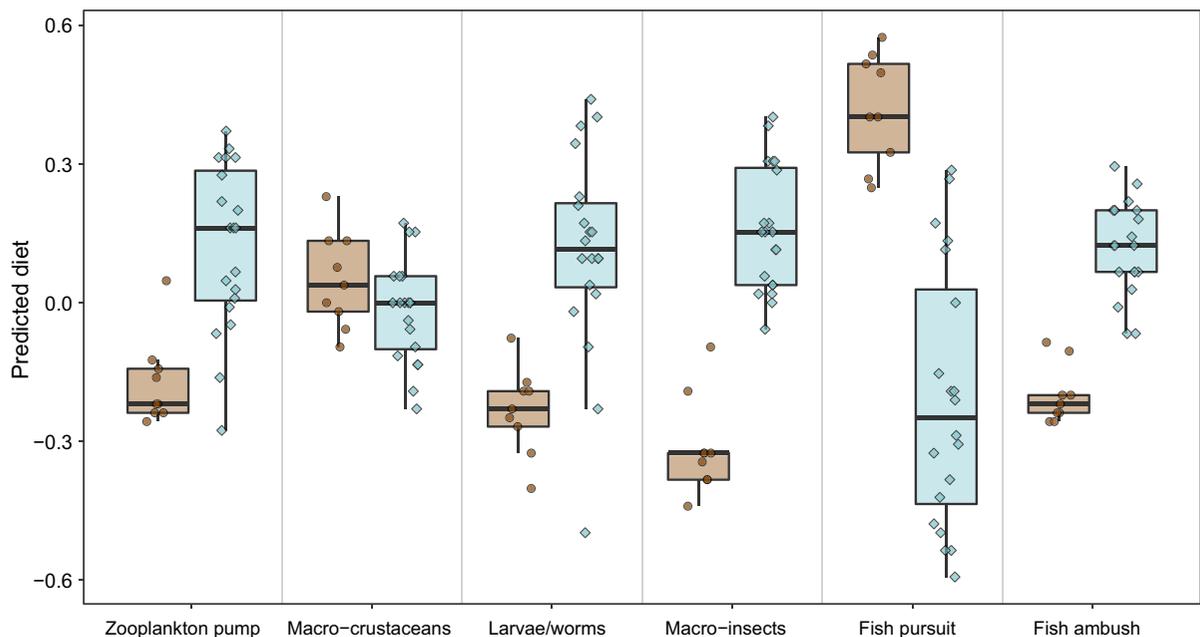
*salmoides* (brown circles). Arrows in the right graphs indicate the loadings of the most influential variables on the PC-axes. Convex hulls show that there is no overlap between the two species

detect prey items between the two predators, therefore predatory efficiency was driven by differences in capability of physically handling and processing the prey items (Jeschke et al. 2002). Nonetheless, this may have been driven by the size of the arena and limited complexity within the arena used in order to film the interactions without obstacle. Prey size was a limiting factor for both species where the larger the prey were, the longer it took for the fish to handle, with regards to catching and processing time. This result is intuitive, given gape size restrictions and ability of the prey to escape (Howick and O’Brien 1983; Gaeta et al. 2018). However, Cape kurper had a faster processing time than largemouth bass, which may make up for its comparatively poor catch rate when preying upon highly abundant prey.

The use of handling time experiments can lead to a better understanding of the feeding process and its

constituent components (detection, catch, and processing), which could potentially serve as an addition to, or an alternative, for the functional-response approach. Moreover, by detailed study of the handling time, probably fewer prey animals are necessary than in the comparative functional response approach. In addition, the ecomorphological approach could be used to predict potential interactions between alien and native species before they actually occur, because the approach gives insights in the potential diet breadth and potential trophic overlap (Nagelkerke et al. 2018) and thus could be used as a “horizon-scanning” tool (Gallardo et al. 2016).

Largemouth bass are a major driver of fish community structure (Jackson 2002) and cause considerable damage to native biota in their invaded ranges (Takamura 2007; Kimberg et al. 2014; Ellender et al. 2018). This is evidently due to their higher



**Fig. 3** Correlations of predicted diet specialisations from the food-fish model (Sibbing and Nagelkerke 2000) for *Micropterus salmoides* (brown) and *Sandelia capensis* (blue). Horizontal lines indicate the median value, boxes show the 25–75%

quantile. Differences between species are all statistically significant ( $P < 0.05$ ), except for macro-crustaceans. Only the six most important prey types (of 14) are shown for clarity

degree of resource exploitation in comparison to native species (Alexander et al. 2014; Alexander et al. 2015). Our results corroborate that largemouth bass are indeed superior piscivores, in comparison to Cape kurper, due to their ecomorphological traits facilitating active pursuit hunting styles (Sullivan and Atchison 1978). Despite Cape kurper having feeding behaviour similar to juvenile centrarchids, i.e. on invertebrates and small fish (Gosse Gosse 1986; Skelton 2001; Shelton et al. 2018), their morphology indicates that they are less specialised in terms of active piscivory than largemouth bass. This implies that Cape kurper performs better in environments with a higher habitat complexity, which is in contrast to largemouth bass which performs better in simplified habitats, especially when feeding on fish prey (Alexander et al. 2015; Shoup and Broderius 2018; Tsunod and Mitsuo 2018). Nonetheless, as the present study and the study by Alexander et al. (2014) both used juvenile largemouth bass, it is important to stress that there can be ontogenetic switches in feeding behaviour that are driven both by individual size, but

also by habitat and environmental factors (García-Berthou 2002; Post 2003; Tsunoda and Mitsuo 2018).

These results give, for the first time, a mechanistic explanation of the process in which juvenile largemouth bass are able to outcompete native species, while, when they are fully grown, they simply directly prey upon Cape kurper. They exert non-consumptive effects upon adult Cape kurper by being superior fish predators (Alexander et al. 2014), but also have a direct consumptive effect on fish prey (Alexander et al. 2014; Shoup and Broderius 2018). Cape kurper are generalist piscivorous fish, but have the potential to show omnivory depending on the need for resource portioning within a system (Shelton et al. 2018). It is possible that a combination of pressure exerted by a more efficient piscivore (i.e. largemouth bass) could drive dietary shift in Cape kurper to less optimal resources, such as invertebrate prey, but also changes in habitat associations (Bøhn and Amundsen 2001).

South African streams have a high degree of endemism which makes them priority conservation areas (Weyl et al. 2014; Ellender et al. 2017). Largemouth bass consistently cause extirpations of

small-bodied, cyprinid minnows, many of which co-occur with Cape kurper (Ellender et al. 2017; Ellender et al. 2018). Field behavioural observations by Ellender et al. (2018) of Eastern Cape redbfin *Pseudobarbus afer* which co-occurs with Cape kurper in its native range, demonstrated that they foraged among benthic cover during the day, but suspended motionless in open water at night. While this was interpreted as a strategy to avoid predation by native anguillid predators, our data suggest that this strategy may also mediate predation by Cape kurper. While the morphology of Cape kurper certainly does not prevent it from preying on small endangered minnow species, it is more effective as an ambush than as a pursuit hunter (Shelton et al. 2018). This exposes the mechanism within which centrarchids exert direct and indirect pressure upon South African native fishes and furthers the need to restore and manage degraded ecosystems to increase habitat complexity. These findings support the necessity to develop impact prediction methods further by combining phenomenological metrics, such as CFR and handling time experiments, with empirical morphological methods such as the fish-food model to fully understand the interplay of traits that drive population dynamics in the field.

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**Author contributions** AML, LAJN, BRE, MEA, OLFW conceived and designed the study. AML collected data. JS and LAJN analysed the data. JS and LAJN led the writing of the manuscript. AML, JS, LAJN, BRE, MEA, OLFW contributed to editing and content of the manuscript.

#### Compliance with ethical standard

**Conflicts of interest** The authors have no conflict of interest to declare.

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