Little evidence for morphological change in a resilient endemic species following the introduction of a novel predator

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Abstract

Human activities, such as species introductions, are dramatically and rapidly altering natural ecological processes and often result in novel selection regimes. To date, we still have a limited understanding of the extent to which such anthropogenic selection may be driving contemporary phenotypic change in natural populations. Here, we test whether the introduction of the piscivorous Nile perch, *Lates niloticus*, into East Africa's Lake Victoria and nearby lakes coincided with morphological change in one resilient native prey species, the cyprinid fish *Rastrineobola argentea*. Drawing on prior ecomorphological research, we predicted that this novel predator would select for increased allocation to the caudal region in *R. argentea* to enhance burst-swimming performance and hence escape ability. To test this prediction, we compared body morphology of *R. argentea* across space (nine Ugandan lakes differing in Nile perch invasion history) and through time (before and after establishment of Nile perch in Lake Victoria). Spatial comparisons of contemporary populations only partially supported our predictions, with *R. argentea* from some invaded lakes having larger caudal regions and smaller heads compared to *R. argentea* from uninvaded lakes. There was no clear evidence of predator-associated change in body shape over time in Lake Victoria. We conclude that *R. argentea* have not responded to the presence of Nile perch with consistent morphological changes and that other factors are driving observed patterns of body shape variation in *R. argentea*.

Introduction

Human activities such as species introductions, habitat modification, ecosystem fragmentation, overharvesting and climate change can lead to marked shifts in selection regimes that may in turn lead to rapid phenotypic changes in resilient organisms (Palumbi, 2001; Stockwell *et al.*, 2003; Hendry *et al.*, 2008). Understanding the magnitude, nature and predictability of phenotypic change in response to anthropogenic perturbations can provide insights into basic evolutionary processes and is also critically important for informing long-term conservation policies.

Human-mediated predator introductions are pervasive, particularly in freshwaters (Strayer, 2010), where the widespread stocking of predatory fish has had negative ecological consequences for native fishes in many regions (Chapman *et al.*, 1996; Whittier *et al.*, 1997; Findlay *et al.*, 2000; Correa & Hendry, 2012). Predator introductions also provide a series of natural experiments that are well-suited to exploring in what ways (and how quickly) novel predators can drive phenotypic change in evolutionarily naïve prey. In natural contexts, predation represents an important agent of divergent selection that can drive intraspecific divergence in morphology (e.g. Nosil & Crespi, 2006), life history (e.g. Reznick & Endler, 1982) and behaviour (e.g. Magurran *et al.*, 1992). Novel predation from

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introduced species may also drive phenotypic changes in prey taxa, but few empirical examples exist to date (Mooney & Cleland, 2001; Strauss *et al.*, 2006; Carroll *et al.*, 2007). For instance, *Daphnia melanica* in alpine lakes in California showed both plastic and genetic declines in age and size at maturity after the introduction of non-native salmonids (Fisk *et al.*, 2007; Latta *et al.*, 2007). Introduced fish predators might select for a suite of adaptations in their prey, including traits that decrease the probability of detection (e.g. crypsis), capture (e.g. improved escape ability) and/or successful handling (e.g. defensive armour) (Langerhans, 2006).

Escape ability is of particular interest because the biomechanics of fast-start swimming in fishes has been studied extensively, and the links between phenotype (morphology), performance (acceleration during fast-starts) and fitness (survival probability) are well established (Webb, 1977, 1982; Weihs, 1989; Domenici & Blake, 1997; Walker, 1997; Blake, 2004; Walker *et al.*, 2005; Langerhans, 2009b; Langerhans & Reznick, 2010). Based on the large body of work linking morphology to locomotor performance in fishes, Langerhans and colleagues (Langerhans *et al.*, 2004; Langerhans, 2010) presented a general ecomorphological paradigm for the evolution of body form in aquatic vertebrates in response to predation. Specifically, they proposed that most fish face a trade-off between selection favouring steady-swimming abilities (e.g. cruising) in the absence of predation and selection favouring unsteady-swimming abilities (e.g. fast-starts, turning) in the presence of predation – two swimming modes optimized by different morphologies. Steady-swimming performance is generally enhanced by a streamlined body shape, that is a fusiform shape with the greatest depth near the anterior and the body tapering off near the caudal region. Conversely, burst-swimming performance is maximized by having a deeper midbody/caudal region and a smaller head/anterior region. These general predictions have now been tested and supported in several species, including threespine stickleback (Taylor & McPhail, 1986; Walker, 1997; Walker & Bell, 2000) and the live-bearing poeciliids *Brachyrhaphis rhabdophora*, *Gambusia affinis*, *G. hubbsi* and *Poecilia reticulata* (Langerhans & Dewitt, 2004; Langerhans *et al.*, 2004, 2007b; Langerhans & Reznick, 2010).

Here, we test these ecomorphological predictions in an East African cyprinid fish, *Rastrineobola argentea*, which is endemic to the Lake Victoria basin of East Africa. In the 1950s and 1960s, a large piscivore, the Nile perch (*Lates niloticus*), was introduced into Lake Victoria and neighbouring lakes to compensate for declining native fisheries, and also, in the case of Lake Victoria, to boost sport fishing (Balirwa *et al.*, 2003; Pringle, 2005). The Nile perch population exploded in the mid-1980s, forming the basis for a highly productive and lucrative export-oriented fishery. The Nile perch boom coincided with the extinction or extirpa-

tion of roughly 40% of Lake Victoria's 400+ endemic haplochromine cichlids, likely due to a combination of overfishing, eutrophication and intense predation from the Nile perch (Kaufman & Module, 1992; Balirwa *et al.*, 2003; Chapman *et al.*, 2008). Once its preferred prey base (the haplochromines) had been depleted, the Nile perch began feeding on alternative prey including *R. argentea*. Although *R. argentea* has always had native predators in the Lake Victoria basin (see below), the high densities of Nile perch observed in most invaded lakes, combined with the occurrence of *R. argentea* in Nile perch stomach contents, suggest that the Nile perch introduction resulted in increased mortality rates for *R. argentea* (Hughes, 1986; Ogutu-Ohwayo, 1990, 1993, 2004; Schofield & Chapman, 1999; Katunzi *et al.*, 2006). Despite this novel predator, *R. argentea* increased dramatically in abundance during the 1980s and 1990s (Wanink, 1999; Tumwebaze *et al.*, 2007) and now supports the most important commercial fishery (by mass) in Lake Victoria (Mkumbo *et al.*, 2007; NaFIRRI, 2008). It also plays a major role in the food web of Lake Victoria (accounting for approximately 60% of the fish biomass of the lake, NaFIRRI, 2008) and is critical for human food security in the region.

This system can provide several novel and important insights into (i) the role of predation in shaping the body form of prey fishes and (ii) the extent to which rapid phenotypic changes occur following anthropogenic perturbations and their potential to contribute to the resilience of species of socio-economic importance. With respect to the former, most examples of predator-induced body shape evolution to date are from live-bearing fishes (Family Poeciliidae) from the Neotropics. Thus, observed convergent responses to predation could partially reflect shared evolutionary histories or constraints in this group of fishes, with some distantly related fishes perhaps responding in alternative ways (Langerhans *et al.*, 2004). To more broadly test this ecomorphological paradigm, we need to examine phylogenetically and geographically distinct taxa. With respect to the latter question, *R. argentea* is one of the few native fishes from Lake Victoria that has managed to thrive alongside the introduced Nile perch, and its apparent resilience may partially reflect adaptive phenotypic change. *Rastrineobola argentea* has undergone rapid life-history changes since the 1960s (Wanink, 1998; Sharpe *et al.*, 2012) that are consistent with an adaptive response to increased mortality (from both Nile perch predation and fishing pressure). Testing whether any changes in morphology have also occurred will shed further light on *R. argentea*'s persistence within this highly anthropogenically disturbed ecosystem, and help to inform management of this important fishery, and the ecosystem as a whole.

We tested for morphological divergence in *R. argentea* in response to predation from the introduced Nile perch

using two approaches. First, we compared body shape of contemporary populations from nine Ugandan lakes that differ in their history of Nile perch invasion. Second, using museum specimens, we compared body shape of *R. argentea* from before versus after the establishment of Nile perch in Lake Victoria. We predicted that in Nile perch-free contexts (uninvaded lakes, and Lake Victoria pre-Nile perch establishment), *R. argentea* would have more streamlined bodies, reflecting selection for steady-swimming abilities. In the absence of predation, steady-swimming should be particularly important for *R. argentea*, as it is a pelagic species that forages over long distances in the open waters of lakes (Kaufman & Ochumba, 1993). Conversely, in contexts with Nile perch (invaded lakes and Lake Victoria post-Nile perch establishment), *R. argentea* should have deeper caudal regions and smaller heads, reflecting selection for increased fast-start escape ability.

Materials and methods

Study sites

Our study focused on nine lakes located in the Lake Victoria basin in Uganda, East Africa (Fig. 1, Table 1), which together with the Upper Nile River, account for *R. argentea*'s known distribution in Uganda, and are described in detail in our previous work (Sharpe *et al.*, 2012). The lakes differed in their Nile perch invasion history, with three being uninvaded, four having established Nile perch populations and two (Bisina and Nawampasa) having experienced a transient Nile perch presence. Lake Bisina was stocked with Nile perch in

the early 1970s and sustained a Nile perch fishery for a time (Mbabazi, 2004). However, the Nile perch population has since collapsed, and repeated surveys in 2001–2003 (Mbabazi, 2004) and 2009–2010 (D. M. T. Sharpe & L. J. Chapman, unpublished) did not uncover any Nile perch in the lake. Lake Nawampasa was free of Nile perch until 1998, when extensive flooding due to El Niño appeared to facilitate dispersal of Nile perch individuals into the lake (S.B. Wandera, unpublished). It is not known whether these individuals have managed to persist, although our sampling in 2009 and 2010 did not uncover any Nile perch (D. M. T. Sharpe & L. J. Chapman, unpublished). Dispersal of *R. argentea* between these lakes is likely low or absent because the dense hypoxic swamps surrounding these lakes should act as a significant dispersal barrier for the hypoxia-sensitive *R. argentea* (Wanink *et al.*, 2001). Thus, we consider these lakes to provide independent replicates of *R. argentea*'s response to Nile perch introduction.

Although Nile perch likely represents the most important predator on *R. argentea* in the Lake Victoria basin, several native catfishes (*Clarias gariepinus*, *Schilbe intermedius* and *Synodontis victoriae*) are known to feed on *R. argentea* to some degree (Mbabazi, 2004). Known avian predators include the pied kingfisher *Ceryle rudis*, the great cormorant *Phalacrocorax carbo lucidus* and the long-tailed cormorant *Phalacrocorax africanus* (Wanink & Goudswaard, 1994; Wanink, 1996).

Data on the distribution and diet of these potential native predators are very scarce; however, the available evidence does not suggest that mortality from these other sources differs systematically between lakes with or without Nile perch (Table S1).
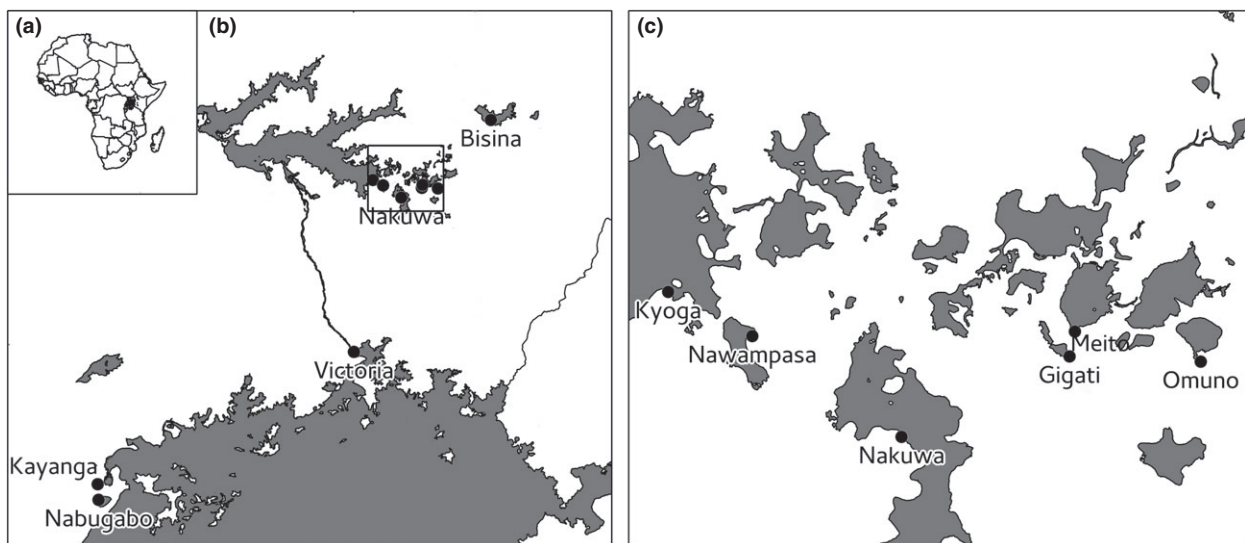
Fig. 1 Map of study sites. Panel a shows the location of the Lake Victoria basin within the African continent. Panel b shows the Ugandan portion of Lake Victoria, and Panel c shows an enlargement of the Kyoga drainage. The lakes that we sampled included three lakes with no history of Nile perch invasion (Kayanja, Gigati and Omuno), two lakes which experienced a transient Nile perch presence (Bisina and Nawampasa) and four lakes with established Nile perch populations (Kyoga, Meito, Nabugabo and Victoria).

Table 1 Summary of populations included in the spatial analysis of body shape. Lakes Bisina and Nawampasa are special cases, because Nile perch were introduced, but seem to have failed to establish (see text for details). Sample sizes (*n*) and the mean (±SE) standard length of each population of *Rastrineobola argentea* included in the geometric morphometric analysis are indicated.

Lake	Nile perch	*n*	Standard length (mm)
Kayanja	Absent	30	37.23 ± 0.59
Omuno	Absent	30	50.77 ± 0.45
Gigati	Absent	30	47.40 ± 0.48
Bisina	Transient (1970s–1990s)	30	37.90 ± 0.49
Nawampasa	Transient (1998–Present)	28	39.93 ± 0.41
Meito	Established	30	40.40 ± 0.27
Nabugabo	Established (1960–present)	30	44.03 ± 0.37
Kyoga	Established (1955–present)	31	45.13 ± 0.74
Victoria	Established (1950s/1960s–present)	29	41.17 ± 0.35

We collected the following environmental data at each lake: water depth (m), water transparency (Secchi depth, m), water temperature (°C) and dissolved oxygen concentration (mg L^{-1}) measured with a Polaris dissolved oxygen meter. These data were collected at three replicate sites in the pelagic zone of each lake, both in the morning and in the afternoon. Although all fish were collected in 2010, environmental measurements were repeated over multiple years (2008, 2009 and 2010) for some lakes and were averaged over time in these cases. We estimated lake surface area (km^2) from satellite images downloaded from Google Earth. Although all of these parameters varied across individual lakes (Table S1), there were no consistent or significant differences between invasion categories for any of the environmental variables quantified (lake area: $F_{2,7} = 2.11$, $P = 0.192$, lake depth: $F_{2,7} = 1.34$, $P = 0.323$, Secchi depth: $F_{2,7} = 1.35$, $P = 0.319$, temperature: $F_{2,7} = 0.12$, $P = 0.893$, dissolved oxygen: $F_{2,7} = 0.22$, $P = 0.812$).

Fish collections

Rastrineobola argentea were collected from the nine lakes described above during the dry season (May–June) in 2010 (Table 1). Fish were captured with a 5-mm-mesh lampara net (the local commercial fishing gear), which was operated as a surface seine in the pelagic zone of each lake. In two lakes, this method of fishing was unsuccessful, so *R. argentea* were collected using other gears (a 5-mm-mesh beach seine in Lake Kayanja and a 5-mm-mesh pelagic trawl in Lake Victoria). We retained approximately 30 individuals per lake (randomly selected from the largest quartile), which were euthanized with clove oil and immediately preserved in 10% formalin for morphological analyses.

Table 2 Summary of populations included in the historical analysis of body shape. Nile perch were introduced into Lake Victoria sometime in the early 1960s, but did not begin appearing regularly in catches until the early 1980s. Sample sizes (n) refer to the number of individuals included in the final analysis. Standard lengths are given as means ± SE. NaFIRRI refers to the National Fisheries Resources Research Institute of Uganda. The precise location for the 1974 sample was not recorded; however, consultation with NaFIRRI scientists indicated that this sample almost certainly came from offshore waters and not the Napoleon Gulf (S.B. Wandera, pers. comm.).

Year	Nile perch	*n*	Standard length	Collectors	Location
1966	Rare	30	55.29 ± 0.77	NaFIRRI	Napoleon Gulf (inshore)
1974	Rare	33	65.86 ± 0.50	NaFIRRI	Lake Victoria (offshore)
1997	Established	22	48.73 ± 0.75	NaFIRRI	Buvuma Channel (offshore)
2003 in	Established	31	44.27 ± 0.62	NaFIRRI	Napoleon Gulf (inshore)
2003 off	Established	34	50.68 ± 0.51	NaFIRRI	Nkata (offshore)
2010	Established	29	41.17 ± 0.35	Sharpe *et al.*	Buvuma Channel (offshore)

For the temporal analysis, we used a combination of preserved museum specimens and collections made by our team over the past decade (Table 2). Museum specimens were photographed, with permission, from collections at the Biodiversity Museum of the National Fisheries Resources Research Institute (NaFIRRI) in Jinja, Uganda, and included *R. argentea* from 1966, 1974, 1997 and 2003. Nile perch were introduced into Lake Victoria sometime in the early 1960s, but did not begin appearing regularly in catches until the early 1980s; hence, we consider 1966 and 1974 to largely reflect pre-invasion conditions. Our team collected *R. argentea* from Lake Victoria in 2010, as described above. All specimens were preserved in 10% formalin. For the most part, historical specimens originated from the Northern waters of Lake Victoria – exact locations are given in Table 2.
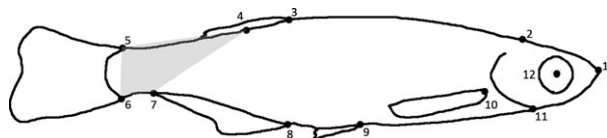
Morphological analyses

Variation in the overall body shape of *R. argentea* was examined using geometric morphometrics, a powerful approach that uses information from spatial coordinates (landmarks) to describe, visualize and analyse shape variation (Rohlf & Marcus, 1993; Adams *et al.*, 2004; Zelditch *et al.*, 2004). Preserved *R. argentea* were photographed in the laboratory using a Canon Powershot

digital camera. We digitized 12 homologous landmarks on the lateral body profile of images (Fig. 2) using TPSDig software (Rohlf, 2006). Landmarks comprised: (1) most anterior point of the premaxilla, (2) indentation at the posterodorsal end of the head, (3) anterior insertion point of the dorsal fin, (4) posterior insertion point of the dorsal fin, (5) dorsal insertion point of the caudal fin, (6) ventral insertion point of the caudal fin, (7) posterior-most point where the anal fin meets the body, (8) anterior insertion point of the anal fin, (9) insertion point of the pelvic fin, (10) dorsal insertion point of the pectoral fin, (11) intersection of the operculum and body profile and (12) centre of the eye orbit.

Photographs were landmarked by two individuals (E. Low-Decarie and D. Sharpe), but all landmarks were individually doubled-checked by D. Sharpe before analyses were conducted. To quantify any potential inter-observer bias, we randomly selected 20 photographs for digitization by both observers. Repeatability was estimated as the intraclass correlation coefficient, that is the proportion of the total variation due to among (rather than within) individual variation (Lessels & Boag, 1987). Repeatability was generally high: 0.99 for centroid size, 0.85 for landmarks (mean for all 24 superimposed landmark coordinates), 0.94 for caudal area and 0.97 for total area, all $P < 0.01$.

Landmark configurations were scaled to a common size, rotated and aligned using generalized Procustes analysis (Rohlf & Slice, 1990) in TPSRelw (Rohlf, 2010). We used TPSRelw to save relative warp scores for each fish, which represent principal components of geometric shape variation and were used as dependent variables in subsequent analyses. TPSRelw was also used to calculate centroid size – a metric of body size commonly employed in geometric morphometrics, which is the square root of the sum of the squared distances from each landmark to the centroid of the landmark configuration. In addition to these geometric morphometrics analyses that explored changes in overall body shape, we also calculated lateral caudal peduncle area from the scaled landmark coordinates, using a minimum convex polygon drawn between landmarks 4, 5, 6 and 7 (shaded area on Fig. 2), and total body area, in R (R Development Core Team 2012).

For all contemporary specimens, we measured standard length (mm) and total wet body mass (mg). Both variables were highly correlated with centroid size (standard length: $r = 0.99$, $P < 0.001$, weight: $r = 0.96$, $P < 0.001$), and so centroid size was used as the body size covariate in all geometric morphometric analyses. Relative body condition (K) was quantified to assess how much variation in overall body shape might be due to variation in condition. For example, heavier, more well-fed individuals would be expected to be deeper bodied than starved individuals, irrespective of predator regime. Following Le Cren (1951), K was calculated as: $K = w_i / a * sl_i b$, where w_i is the weight of individual i (in mg), sl_i is the standard length of individual i (in mm), and a and b are parameters derived from a linear regression of log-transformed weight versus log-transformed length for all individuals in the data-set (a is the back-transformed intercept (0.009), and b is the slope from the linear regression (3.09)).

After the photographs had been taken, we dissected each fish to check for intestinal macroparasites, which can distend the abdomens of infected individuals and so potentially distort overall body shape. We also determined the sex and maturity status of each fish, using a seven-point scale previously developed for *R. argentea* (S.B. Wandera, unpublished, Sharpe *et al.*, 2012)

We were not able to dissect the museum specimens, but we did measure standard length (in mm) for each fish, which we then used to estimate maturity, based on previously published values for length at 50% maturity (L_{50}) for *R. argentea* from Lake Victoria over this same time period (Sharpe *et al.*, 2012). Using this approach, 9 individuals (of 179) fell below the L_{50} threshold for the year in question and were therefore assumed to be immature. We ran the analysis both including and excluding these putatively immature individuals, and the results were unaffected, so we present results only from the first analysis including all individuals. Sex was also unknown for the museum specimens, so we could not explicitly consider this factor in our analysis. If there was a strong and consistent temporal trend in the sex ratio of our samples, this could introduce a systematic bias – however, we consider this to be unlikely.

Statistical analysis

To test for variation in body morphology of *R. argentea* associated with the Nile perch introduction, we performed separate multivariate analyses for the spatial and temporal data sets. First, to test for differences in body shape across lakes with varying Nile perch introduction histories, we performed a mixed-model multivariate analysis of covariance (MANCOVA) with the 20 relative warps as dependent variables, Nile perch regime and sex as main effects, lake nested within Nile perch regime as a random effect and body condition and centroid size as covariates. Statistical significance was determined using an F-test based on Wilks's λ for all terms except Nile perch regime, which used an

Fig. 2 Landmarks used to quantify the body shape variation (see text for details). The caudal peduncle is shaded.

F-test employing restricted maximum likelihood and the Kenward–Roger degrees of freedom adjustment (Kenward & Roger, 1997, 2009), which allowed us to use lake as the unit of replication, effectively treating lake as a random effect (Wesner *et al.*, 2011; Hassell *et al.*, 2012; Riesch *et al.*, 2013). To test for differences in body shape through time, we used a MANCOVA with year as a main effect and centroid size as a covariate (sex and body condition were not included in this model because these data were not available for museum specimens). All *P* values in this model were determined using an F-test based on Wilks's λ. An initial analysis of the historical data (not shown) suggested that there were consistent differences in body shape between *R. argentea* collected from inshore versus offshore habitats, so we subsequently performed separate MANCOVAs for each habitat. In all models, we tested for heterogeneity of slopes across Nile perch categories (or years) and removed any nonsignificant terms and interactions from our final model. Multivariate effect size in these analyses was quantified using Wilks's partial η^2 (Langerhans & Dewitt, 2004).

We took a three-pronged approached to evaluate the magnitude, consistency and nature of possible morphological differences between Nile perch regimes. First, we examined the nature of body shape variation associated with our factors of interest (Nile perch or year) by performing a PCA on the sums of squares and cross-products matrix of those terms from the MANCOVA, following Langerhans (2009b). This allowed us to derive an eigenvector of divergence (d) for each term of interest, that is a vector describing the linear combination of dependent variables that best discriminate between Nile perch regimes/years in Euclidean space. This approach is preferable to traditional canonical variate analysis (CVA) which, when applied in the context of geometric morphometrics, has been shown to distort multivariate space (Klingenberg & Monteiro, 2005; Mitteroecker & Bookstein, 2011). To visualize shape variation along divergence vectors (d), we generated thin-plate spline deformation grids using TPSRegr (Rohlf, 2009). Second, we performed a discriminant function analysis (DFA) using leave-one-out cross-validation to determine how well individuals could be assigned to Nile perch regimes or years based on their morphology (relative warps and centroid size). Third, we calculated pairwise Procrustes distances between sample means to evaluate the overall magnitude of shape differences. Procrustes distances are the square root of the sum of squared differences between homologous landmarks when configurations in Procrustes superimposition (Zelditch *et al.*, 2004) and were calculated in tpsSmall (Rohlf, 2003).

Finally, we tested for variation in caudal peduncle area across lakes/years. For the spatial analysis, we ran a nested ANCOVA, with lake nested as a random effect within Nile perch regime and total body area as a covariate. For the temporal analysis, inshore and offshore populations were analysed using separate ANCOVAS with year as a main effect and total body area as a covariate. All continuous variables were log-transformed to meet the assumption of normality. In each model, we first tested for heterogeneity of slopes and removed the interaction term between total body area and year/lake if not significant. All statistical analyses were performed in R, except for the MANCOVAs, which were performed using JMP (v. 5.1.2, © 2004, SAS). The data underlying our analyses have been archived and are publicly available from the Dryad Digital Repository (http://datadryad.org/, doi:10.5061/dryad.g61d1).

Results

Spatial: body shape variation across lakes

MANCOVA revealed that the body shape of contemporary *R. argentea* was influenced by multiple factors, including Nile perch regime, centroid size, condition, sex and the interaction between centroid size and condition (Table 3). The interactions Nile perch × centroid size, sex × condition and Nile perch × condition were not significant and were therefore removed from the final model.

The greatest amount of partial variance was explained by Nile perch regime (Table 3). This indicated that when controlling for the effects of allometry, condition and sex, body shape varied among lakes with different histories of Nile perch introduction. Visualization of the Nile perch divergence vector (d_{NP}) indicated that *R. argentea* from invaded lakes tended to have smaller heads, larger caudal peduncles, shorter anal fins, ventrally displaced pectoral fins and more upturned mouths relative to *R. argentea* from uninvaded lakes (Figs 3a, 4a and 5). The most heavily invaded lakes (Victoria and Kyoga) displayed the most extreme phenotypes, whereas lakes Nabugabo and Meito (invaded), Bisina and Nawampasa (uninvaded), and Omuno (uninvaded) all had overlapping, intermediate phenotypes (Fig. 5).

Table 3 Mixed-model nested multivariate analysis of covariance (MANCOVA) examining variation in body shape of *Rastrineobola argentea* (relative warps) across Nile perch regimes. Partial variance was estimated based on Wilks's partial η^2. Note that the interactions Nile perch × centroid size, sex × condition and Nile perch × condition were nonsignificant and so were all removed from the final model.

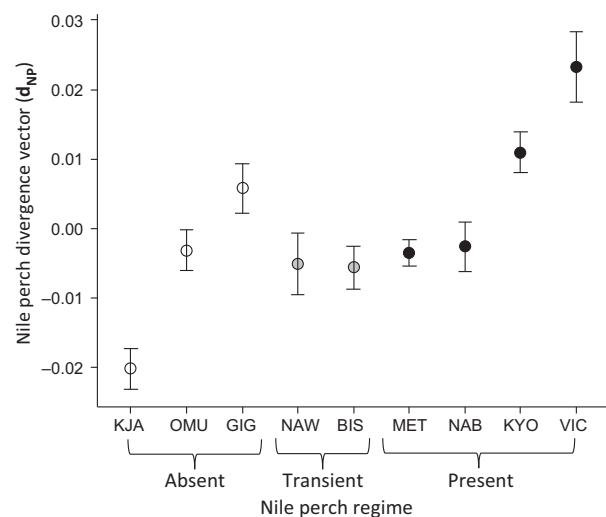| Factor	d.f.	*F*	*P*	Partial variance
Nile perch	38, 2769	5.18	< 0.0001	48.46
Centroid size (CS)	20, 236	4.22	< 0.0001	26.34
Condition	20, 236	6.46	< 0.0001	35.38
Sex	20, 236	5.78	< 0.0001	32.89
Condition X CS	20, 236	2.33	0.0014	16.50
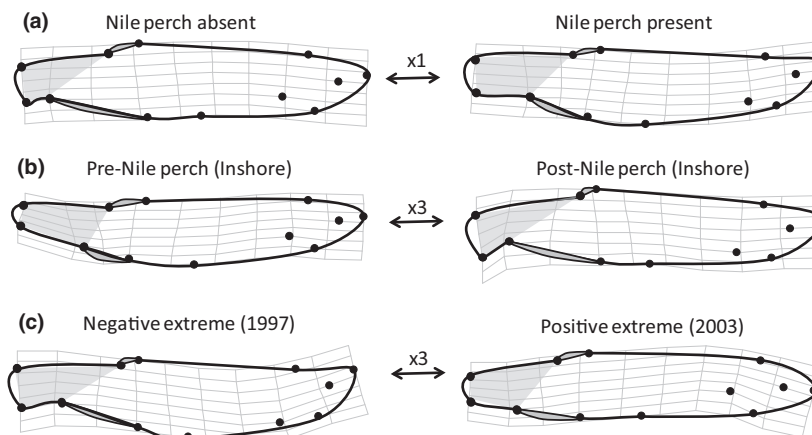
Fig. 3 Variation in overall body morphology of *Rastrineobola argentea*: across lakes (d_{NP}, panel a), through time for inshore populations ($d_{YR.IN}$, panel b) and through time for offshore populations ($d_{YR.OFF}$, panel c). Body shape variation has been illustrated using thin-plate spline transformation grids, which have been magnified by 3 in panels b and c to better illustrate the variation along these divergence vectors. The caudal peduncle has been highlighted. A body outline and the median fins have been sketched in as a visual aid.
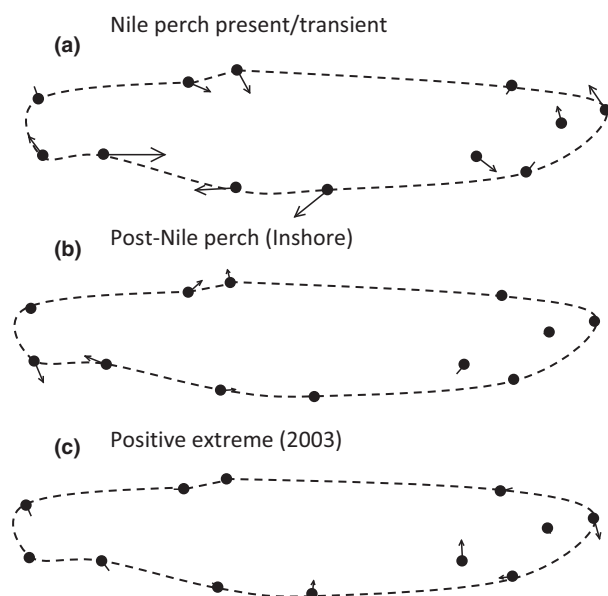
Fig. 4 Landmark vectors illustrating variation in overall body morphology of *Rastrineobola argentea*: across lakes (d_{NP}, panel a), through time for inshore populations ($d_{YR.IN}$, panel b) and through time for offshore populations ($d_{YR.OFF}$, panel c). The vectors convey the direction and relative magnitude of change at each landmark, and the arrows indicate changes in the direction of the population indicated in the title. Vector lengths been magnified by 3 to better illustrate the variation along the divergence vectors, and a body outline has been sketched in as a visual aid.

Fig. 5 Mean scores (±2 SE) along the Nile perch divergence vector (d_{NP}) for lakes where Nile perch were absent (white), transient (grey) or present (black). Lakes are abbreviated as follows: KJA (Kayanja), OMU (Omuno), GIG (Gigati), NAW (Nawampasa), BIS (Bisina), MET (Meito), NAB (Nabugabo), KYO (Kyoga) and VIC (Victoria).

We also uncovered effects of multivariate allometry, condition and sex, with the latter two variables exhibiting the greatest importance (Table 3). Fish with higher centroid sizes (i.e. larger individuals) tended to have smaller heads with more upturned mouths (Fig. S1a). Body condition varied significantly across lakes ($F_{8,261}$ = 19.64, $P < 0.001$), being greatest in the uninvaded lakes Kayanja and Omuno and lowest in the transiently invaded lakes Bisina and Nawampasa (Fig. S2). Fish with higher condition factors (i.e. 'fatter' individuals) tended to have shorter caudal peduncles, larger abdomens and deeper, more robust bodies (Fig. S1b). Females tended to have shorter anal fins and deeper bodies relative to males (Fig. S1c). There was a weak

interaction between centroid size and condition, involving changes in the shape of the head and the depth of the abdomen (not shown).

The DFA showed that *R. argentea* were correctly classified into the appropriate Nile perch category most of the time (77% correctly assigned for invaded lakes, 69% for uninvaded lakes and 87% for transiently invaded lakes, $n = 268$, Wilks' $\lambda = 0.258$, $P < 0.0001$). Median Procrustes distances between pairs of lakes *within* Nile perch regimes were 0.033 (uninvaded lakes), 0.015 (transiently invaded lakes) and 0.031 (invaded lakes). The median distance *between* Nile perch regimes was 0.027 (Table S2).

Caudal peduncle area was positively associated with total body area ($F_{1,260} = 457.04$, $P < 0.0001$), and slopes were homogeneous across Nile perch categories. Although there was a trend for fish from some invaded lakes to have larger caudal peduncles than fish from some uninvaded lakes (Fig. 6), caudal peduncle area did not vary significantly with Nile perch regime overall ($F_{2,6} = 0.508$, $P = 0.63$).

Our dissections indicated that the majority of photographed specimens (83%) were sexually mature and free of intestinal macroparasites (94%). Excluding immature or parasitized individuals from the geometric morphometric analysis did not alter our results (not shown). Across all lakes, linear regressions showed that mean body shape (d_{NP}) was not significantly related to lake area ($R^2 = 0.19$, $P = 0.133$, d.f. = 7), lake depth ($R^2 = 0.16$, $P = 0.156$, d.f. = 7), Secchi depth ($R^2 = 0.00$, $P = 0.748$, d.f. = 7), temperature ($R^2 = 0.01$, $P = 0.326$, d.f. = 7) or dissolved oxygen concentration ($R^2 = 0.00$, $P = 0.361$, d.f. = 7).
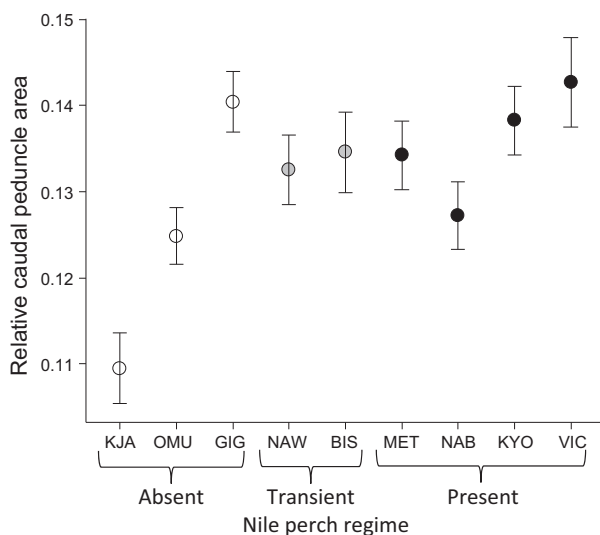
Temporal: body shape variation through time

The body shape of inshore *R. argentea* differed across years (MANCOVA: 1966 vs. 2003, $F_{20,40} = 5.78$, $P < 0.0001$). Centroid size and the interaction between centroid size and year were not significant ($P > 0.05$) and were therefore removed from the final model. Contemporary (post-Nile perch) *R. argentea* from inshore habitats tended to have longer anal fins, deeper caudal peduncles (at the insertion points of the caudal fin), shorter dorsal fins, deeper midbodies and ventrally displaced pectoral fins relative to historical (pre-Nile perch) *R. argentea* (Figs 3b and 4b). There was also a considerable degree of lateral tail bending in these specimens, likely due to the preservation effects. The DFA correctly assigned inshore *R. argentea* to the year of collection at a high rate (1966: 80%, 2003: 87%, F = 283.9, $P < 0.0001$). The median Procrustes distance between 1966 and 2003 inshore samples was 0.019. Caudal area was positively related to total body area for inshore *R. argentea*, and slopes were homogeneous across years (Table S4). Controlling for body size, caudal area was significantly smaller in 2003 than in 1966 ($F_{1,56} = 466.0$, $P < 0.001$; Fig. 8).

In offshore habitats, the body shape of *R. argentea* was influenced by year, centroid size and the interaction between the two (Table 4). Centroid size declined consistently throughout the time series ($F_{1,114} = 474.8$, $P < 0.001$) and explained the greatest amount of partial variance in our MANCOVA (Table 4). Variation in centroid size was associated with changes in midbody depth and head size and shape (Fig. S3a). There was substantial allometry in shape. Five of the first 10 RWs (which cumulatively explained 94% of the total variation in body shape) were significantly correlated with centroid size. However, of these same 10 RWs, in only one case (RW4) did allometry differ significantly across years. The relationship between RW4 and centroid size was positive for two years (1997 and 2010) and negative for two years (1974, 2003, Fig. S4), resulting in divergent effects of size across years (Fig. S3b).

After accounting for this allometry, body shape still varied significantly across years (MANCOVA: $F_{60,272.33} = 2.14$, $P < 0.001$, Figs 3c and 4c). However, there was no clear morphological trajectory through time, with populations from the beginning (1974) and

Fig. 6 Relative caudal peduncle area (ratio of caudal peduncle area to total body area) of *Rastrineobola argentea* across lakes where Nile perch were absent (white), transient (grey) or present (black). Data shown are means ± 2 SE. Lakes are abbreviated as in Fig. 5.

Table 4 Multivariate analysis of covariance (MANCOVA) examining variation in body shape of *Rastrineobola argentea* between years in offshore populations from Lake Victoria. Partial variance was estimated based on Wilks's partial η^2.

Factor	d.f.	F	P	Partial variance
Year	60, 272.33	2.14	< 0.0001	31.88
Centroid Size	20, 91	2.2	0.01	32.67
Year X CS	60, 272.33	1.37	0.05	23.06
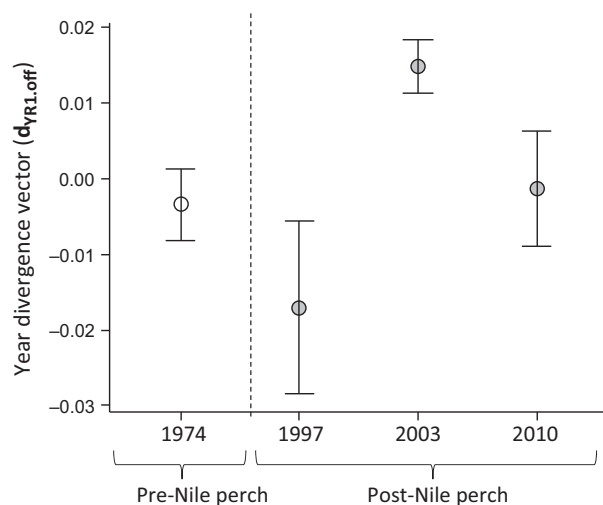
the end of the time series (2010) overlapping along d$_{YR1.off}$ (Fig. 7). Much of the variation was driven by the 1997 population, which had a very upturned mouth and robust body. The DFA correctly assigned offshore *R. argentea* to the year of collection at a high rate (1974: 100%, 1997: 82%, 2003 (offshore): 94%, 2010: 83%, overall correct classification rate: 90%, Wilks' $\lambda = 0.010$, $P < 0.0001$). The median Procrustes distance between years pre- vs. post-Nile perch introduction for offshore samples was 0.024 (Table S3).

Our univariate analysis showed that, for offshore populations, caudal peduncle area varied significantly across years and with total body area (Table S4). Relative caudal area increased significantly in 1997 and then declined again in subsequent years (Fig. 8).

Discussion

We tested the hypothesis that predators can drive rapid and predictable morphological change in natural prey populations, using replicate introductions of the predatory Nile perch in the Lake Victoria basin as a natural experiment. To test this hypothesis, we used two complimentary approaches: examining body shape variation across space (invaded vs. uninvaded lakes) and through time (before vs. after the establishment of Nile perch in Lake Victoria). We predicted that populations of *R. argentea* that co-occurred with Nile perch would exhibit morphologies associated with burst-swimming performance—specifically an increase in the relative area of the caudal region and a decrease in head size.
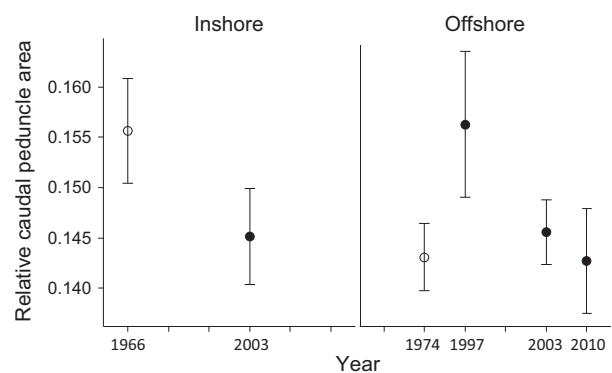
Variation in body shape across lakes

Nile perch regime explained the greatest amount of variation in body shape among *R. argentea* populations, independent of variation attributable to body size, condition and sex. Most notably, our multivariate analysis of body shape suggested an increase in the size of the caudal peduncle and a decrease in head size in *R. argentea* in lakes with Nile perch. This shift in allocation towards the caudal region is consistent with our *a priori* ecomorphological predictions and closely parallels predator-associated morphological changes documented in poeciliid fishes (Langerhans & Dewitt, 2004; Langerhans *et al.*, 2004, 2007b). However, the magnitude of body shape variation observed in *R. argentea* in our study was much less pronounced than that documented previously (median Procrustes distance of 0.027 between Nile perch regimes, vs. 0.030–0.046 between predator regimes in *Gambusia* spp. (Langerhans *et al.*, 2007b; Langerhans, 2009a; Langerhans & Makowicz, 2009)). Furthermore, when caudal peduncle area was analysed separately, there was no significant effect of Nile perch regime. Overall, our data do not provide consistent or unambiguous support for the prediction that Nile perch predation has driven functionally significant morphological divergence in *R. argentea* across invaded versus invaded lakes.

Variation in body shape in Lake Victoria through time

Morphological variation in Lake Victoria through time was much more subtle overall than the variation across lakes. In inshore populations, the only detectable morphological changes were an apparent increase in the depth of the caudal peduncle at the insertion points of the caudal fin and an increase in the length of the anal fin. These trait changes may be functionally important,

given that the area of both the caudal and anal fins is known to strongly influence thrust and fast-start performance (Webb, 1977). However, relative caudal peduncle area declined significantly over time – in contrast to our predictions.

Offshore populations were highly variable through time, but there was no evidence of net morphological change over the time series. Year-to-year variability in body shape could reflect plastic variation in response to ecological factors that have fluctuated over time, such as population density, food availability, water quality and predator pressure. The latter (temporal variation in Nile perch predation pressure) may be particularly important and may not have been adequately captured by our categorization of pre- vs. post-Nile perch periods. This is because the diet of Nile perch has been dynamic, varying with the phase of the invasion and the relative abundance of its apparently preferred prey base, the haplochromine cichlids. In general, the proportion of *R. argentea* in Nile perch stomach contents peaked between the late 1980s and mid-1990s (Ogutu-Ohwayo, 1990, 1993; Schofield & Chapman, 1999) and then declined after 2000, coincident with heavy fishing on Nile perch and haplochromine resurgence (Chapman *et al.*, 2003; Paterson & Chapman, 2009; Hanna, 2014; Nkalubo *et al.*, 2014). Thus, *R. argentea* collected from Victoria in 1997 (which were most divergent morphologically and had larger caudal peduncles) corresponded with a time of peak Nile perch predation; whereas specimens collected in 2003 and 2010 (which grouped more closely with pre-Nile perch specimens) corresponded with a period of reduced predator pressure from Nile perch. Interestingly, a similar pattern of fluctuating morphological change was observed in a recent study of six species of haplochromine cichlids from Lake Victoria (Van Rijssel & Witte, 2012).

Other potential factors

In addition to the potential influence of Nile perch predation, morphological variation in *R. argentea* across space and time may also reflect the influence of other factors not explicitly included in our models. Fish body shape is known to vary with a number of physical and ecological variables, including water flow (Langerhans, 2008), dissolved oxygen (Langerhans *et al.*, 2007a), temperature (e.g. Marcil *et al.*, 2006), relative littoral area (Walker, 1997) and diet/habitat use (e.g. Sharpe *et al.*, 2008).

Dissolved oxygen, temperature, surface area and water depth did not vary significantly across invasion categories. Moreover, these variables exhibited no evidence of association with body morphology, so these are unlikely explanations for the observed patterns of spatial variation in body shape. However, there have been substantial changes in water quality over time. Rapid human population growth in the catchment over

the past century has led to the eutrophication of Lake Victoria and an increase in the severity and frequency of hypolimnetic hypoxia (Hecky *et al.*, 2010). Low-oxygen stress can lead to pleiotropic changes in morphology, such as an increase in head size to accommodate larger gills (e.g. Crispo & Chapman, 2010). However, the observed morphological variation in *R. argentea* over time did not fit this pattern, as head size did not increase over time.

Diet and habitat use have been shown to influence body morphology in a number of fishes. A commonly observed polymorphism in lacustrine fishes is that benthic or littoral-dwelling fish that feed on benthic macro-invertebrates in structurally complex habitats tend to be deeper bodied than pelagic-dwelling fish that feed on zooplankton in open habitats (Malmquist *et al.*, 1992; Schluter & McPhail, 1992; Robinson *et al.*, 1993; Robinson & Wilson, 1994; Svanbäck & Eklöv, 2002). Feeding mode may also influence the orientation of the mouth in fishes: an upturned/dorsally oriented mouth is often correlated with feeding on emerging aquatic insects (Watson & Balon, 1984; Wikramanayake, 1990; Hugueny & Pouilly, 1999).

The diet of *R. argentea* varies considerably across lakes; however, there are no consistent differences in diet between invaded and uninvaded lakes (Sharpe & Chapman, 2014), and no evidence of an association between diet and multivariate body shape (correlation between proportion of zooplankton in the diet and d_{NP}: $r = 0.51$, $P = 0.20$, d.f. = 6, Sharpe, 2012). Through time, the diet of *R. argentea* in Lake Victoria has shifted from a specialized zooplankton diet in the 1960s to a broader contemporary diet that includes insect larvae as well as emerging aquatic insects (Sharpe & Chapman, 2014). However, *R. argentea* from later years that included insects in their diet did not have more upturned mouths than *R. argentea* from earlier years, which were zooplankton specialists. Overall, it seems unlikely that diet is a major driver of the body shape variation observed across lakes or through time; although our study was not specifically designed to test this question.

Why no evidence of predator-induced morphological change?

Despite several decades of moderate to high levels of predation from the introduced Nile perch, *R. argentea* did not unequivocally show the morphological changes often observed in prey fish that co-occur with piscivores. There are several potential explanations for this apparent lack of adaptation to a novel stressor. First, there may be a lack of heritable variation in body shape in *R. argentea* for selection to act upon. Body shape has been shown to have a genetic basis in some fishes (e.g. Langerhans *et al.*, 2004; Sharpe *et al.*, 2008); however, its heritability in *R. argentea* is unknown. Second,

although *R. argentea* have a short generation time (0.3–0.9 years, Wanink, 1998), too little time may have elapsed since the Nile perch introduction for detectable morphological changes to have accumulated. This seems unlikely; however, given evidence for rapid phenotypic change in this same population over the same time period for life-history traits (Sharpe *et al.*, 2012). Third, some fishes are capable of very rapid, phenotypically plastic changes in body shape in response to the presence of predators, including for example Crucian carp (Brönmark & Pettersson, 1994) and juvenile perch and roach (Eklöv & Jonsson, 2007). However, *R. argentea* may lack the capacity to produce such inducible defences, which are presumably costly to maintain. Fourth, *R. argentea* may be responding to Nile perch predation primarily through other means. For instance, shifts in life-history strategies (Sharpe *et al.*, 2012) and/or the adoption of antipredator behaviours could also improve survival in the face of Nile perch predation and thus weaken selection on morphology. Many prey fish reduce activity levels, use shelters more frequently and/or shift to more complex habitats in the presence of piscivores (Werner *et al.*, 1983; Rahel & Stein, 1988). Schooling is another common antipredator behaviour in fish (Magurran, 1990a) that has been shown to be adaptive and heritable in several taxa (e.g. in Trinidadian guppies, *Poecilia reticulata* (Seghers, 1974; Huizinga et al., 2009) and European minnow, *Phoxinus phoxinus* (Magurran, 1990b). *R. argentea* is a pelagic schooling species (Kaufman & Ochumba, 1993; Tumwebaze *et al.*, 2007) and so may have responded behaviourally to the Nile perch introduction by forming larger and more cohesive schools and/or schooling more frequently. This might potentially select for increased steady-swimming performance and thus more streamlined bodies – the opposite of our ecomorphological predictions for increased burst-swimming performance. More generally, ecomorphological predictions that hold for prey fish in small streams or ponds may not apply to pelagic species in large lakes, and a focus on solely morphological traits may be too narrow to capture important behavioural components of an antipredator response. Testing for divergence in schooling tendency and other types of antipredator behaviour (e.g. changes in diel activity patterns or habitat use) between contemporary populations of *R. argentea* that do or do not co-occur with Nile perch would be an interesting avenue for future work.

Conclusions

As human impacts on the natural world intensify, evolutionary biologists have become increasingly interested in understanding the extent to which adaptation may be able to buffer natural populations against anthropogenic stressors. *Rastrineobola argentea* provides a particularly interesting case study for understanding human-induced phenotypic change and for exploring what classes of traits might respond most readily to novel selective regimes. We have previously shown that *R. argentea* has undergone rapid changes in trophic ecology (Sharpe & Chapman, 2014) and life-history traits (Sharpe *et al.*, 2012) in response to the Nile perch introduction and fishing pressure. In contrast, in our current study, we found little clear evidence for predator-induced morphological change in *R. argentea*.

Aside from a handful of examples (the thickening of shells of marine molluscs in response to the introduced green crab (Vermeij, 1982); body shape changes in yellow perch in response to the recolonization of previously extirpated piscivores (Lippert *et al.*, 2007)) – to date, there are few documented cases of adaptive morphological responses in native prey to introduced predators (Strauss *et al.*, 2006). With freshwater introductions increasing at an accelerating rate (Hall & Mills, 2000), understanding the likelihood and nature of adaptation in native prey is critical for their conservation.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Physical attributes of the nine lakes sampled for this study (modified from Sharpe *et al.*, 2012).

Table S2 Pairwise Procrustes distances between lakes.

Table S3 Pairwise Procrustes distances between years in Lake Victoria.

Table S4 Results from ANCOVAS examining variation in caudal peduncle area of *Rastrineobola argentea* between years in inshore and offshore populations from Lake Victoria.

Figure S1 Variation in body shape of contemporary *Rastrineobola argentea* asociated with centroid size (d_{CS}, Panel a), body condition (d_{COND}, Panel b), and sex (d_{SEX}, Panel c).

Figure S2 Variation in relative condition factor (K) across lakes where Nile perch were absent (white), transient (grey), or present (black).

Figure S3 Variation in body shape of *Rastrineobola argentea* in the offshore waters of Lake Victoria associated with centroid size ($d_{CS.off}$, Panel a) and the interaction between year and centroid size ($d_{YR.CS.off}$, Panel b).

Figure S4 Scatterplot illustrating the interaction between centroid size and year for RW4 for *Rastrineobola argentea* from offshore water of Lake Victoria.