

# Fast adaptive responses in the oral jaw of Lake Victoria cichlids

Jacco C. van Rijssel,<sup>1,2,3,4,5</sup> Ellen S. Hoogwater,<sup>1</sup> Mary A. Kische-Machumu,<sup>1,6</sup> Elize van Reenen,<sup>1</sup> Kevin V. Spits,<sup>1</sup> Ronald C. van der Stelt,<sup>1</sup> Jan H. Wanink,<sup>1,7</sup> and Frans Witte<sup>1,2</sup>

<sup>1</sup>Department of Integrative Zoology, Institute of Biology Leiden, Leiden University, P.O. Box 9505, 2300 RA Leiden, The Netherlands

<sup>2</sup>Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands

<sup>3</sup>Current Address: Fish Ecology and Evolution, EAWAG Center of Ecology, Evolution and Biogeochemistry, 6047 Kastanienbaum, Switzerland

<sup>4</sup>Current Address: Institute of Ecology and Evolution, University of Bern, CH-3012 Bern, Switzerland

<sup>5</sup>E-mail: [jacco.vanrijssel@eawag.ch](mailto:jacco.vanrijssel@eawag.ch)

<sup>6</sup>Tanzania Fisheries Research Institute (TAFIRI), 9750 Dar Es Salaam, Tanzania

<sup>7</sup>Koeman & Bijkerk B.V., Ecological Research and Consultancy, P.O. Box 111, 9750 AC Haren, The Netherlands

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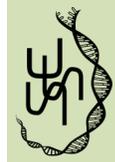
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Rapid morphological changes in response to fluctuating natural environments are a common phenomenon in species that undergo adaptive radiation. The dramatic ecological changes in Lake Victoria provide a unique opportunity to study environmental effects on cichlid morphology. This study shows how four haplochromine cichlids adapted their premaxilla to a changed diet over the past 30 years. Directly after the diet change toward larger and faster prey in the late 1980s, the premaxilla (upper jaw) changed in a way that is in agreement with a more food manipulating feeding style. During the 2000s, two zooplanktivorous species showed a reversal of morphological changes after returning to their original diet, whereas two other species showed no reversal of diet and morphology. These rapid changes indicate a potential for extremely fast adaptive responses to environmental fluctuations, which are likely inflicted by competition release and increase, and might have a bearing on the ability of haplochromines to cope with environmental changes. These responses could be due to rapid genetic change or phenotypic plasticity, for which there is ample evidence in cichlid fish structures associated with food capture and processing. These versatile adaptive responses are likely to have contributed to the fast adaptive radiation of haplochromines.

**KEY WORDS:** Diet change, microevolution, morphological response, phenotypic plasticity, premaxilla, selection.

Adaptive radiation is considered to be caused by divergent natural selection as a result of environmental differences and competition (Schluter 2000). Many model organisms that undergo adaptive radiation often have two features in common: (1) diversification of the feeding apparatus (e.g., Darwin's finches, Hawaiian honeycreepers), which is thought to be one of the major causes of adaptive radiation (Kocher 2004); and (2) rapid morphological changes to a changing environment, as for example is found in Darwin's finches and three-spined sticklebacks (Grant and Grant 1995; Aguirre and Bell 2012).

The East-African cichlids, which are a textbook example of adaptive radiation, also show both features (Kocher 2004; van Rijssel and Witte 2013). For many model organisms, the observed rapid morphological changes could be attributed to directional natural selection (e.g., Grant and Grant 1995; Losos et al. 1997; Aguirre and Bell 2012); for cichlids, selection on both heritable traits and plasticity, as well as plasticity in itself, is thought to have contributed to the evolution of morphological divergence (Chapman et al. 2000; Kerschbaumer et al. 2014) and to morphological adaptive responses through time (van Rijssel and Witte 2013).



Especially the cichlids of Lake Victoria seem to be an excellent model to study adaptive responses to environmental changes as they (1) represent the fastest adaptive vertebrate radiation on earth (Schluter 2000) suggesting the ability to use fast adaptation mechanisms; (2) underwent severe environmental changes in the past decades to which a number of species were able to adapt to (Witte et al. 2008; van Rijssel and Witte 2013).

Lake Victoria is a relatively young lake and the origin of its haplochromine species flock is estimated to be 100,000–400,000 years old or even less (Meyer et al. 1990; Johnson et al. 1996; Seehausen 2002; Verheyen et al. 2003). There is evidence that the lake was completely dry about 14,600 years ago (Johnson et al. 1996), implying that the Lake Victoria species flock evolved even faster, although this has been heavily debated (Fryer 2004; Elmer et al. 2009). The 500+ species of Lake Victoria haplochromines are divided into 15 trophic (sub) groups. In the Mwanza Gulf, south of the lake (which has been studied extensively in the past 40 years), 13 species of detritivores and more than 12 species of zooplanktivores made up 50% and 25% of the haplochromine biomass, respectively (Witte and van Oijen 1990; Goldschmidt et al. 1993; Witte et al. 2007b). Although very species rich in the recent past, the Lake Victoria cichlids met severe environmental and ecological changes during the past 35 years resulting in a 40% biodiversity loss (200 endemic species, Witte et al. 1992).

In the years 1983/1984, the introduced Nile perch boomed in the Mwanza Gulf (Goudswaard et al. 2008) and is thought to be a major contributor to decline of haplochromine cichlids (Witte et al. 2007a). Concurrently, eutrophication resulted in lower dissolved oxygen levels (Hecky et al. 2010; van Rijssel 2014) and a turbidity increase (Seehausen et al. 1997; van Rijssel 2014). All these changes combined contributed to the decline of the haplochromine cichlid species and numbers (Witte et al. 2000, 2007a, 2013). The piscivores, molluscivores, and insectivores were the first to disappear during the early 1980s, whereas the detritivores showed a steep decline during that time and disappeared only after 1985/1986. The zooplanktivores declined during the early- and mid-1980s as well and were the last to disappear from the research transect in the Mwanza Gulf in 1987/1988 (Witte et al. 2007a; Kische-Machumu 2012).

At the same time (mid- and late 1980s), the relative abundance of large-bodied calanoids in the copepod-dominated zooplankton decreased (Wanink et al. 2002), whereas macroinvertebrates such as insects, mollusks, and shrimps, and the small zooplanktivorous cyprinid fish *Rastrineobola argentea* (locally known as dagaa) increased in abundance (Kaufman 1992; Wanink 1999; Goudswaard et al. 2006; Table S1).

During the 1990s, some haplochromine species, predominantly detritivores (four species) and zooplanktivores (three species), recovered along the research transect in the Mwanza Gulf

(Witte et al. 2007b) and haplochromine numbers almost reached levels similar to that before the environmental changes (Kische-Machumu 2012). The zooplanktivores became the most abundant trophic group during the 1990s and 2000s and comprised 71% of the catches along the research transect in the Mwanza Gulf in 2006, whereas detritivores only comprised 21%. Oral mollusc shellers (5+ species) used to comprise about 1% of the catches before the environmental changes but increased in abundance making up 3–6% of the catches in 2006 and 2008 (four species). From 2008 onwards, trophic group composition changed and detritivores became the dominant trophic group again (Kische-Machumu 2012). Both zooplanktivores and detritivores shifted their diet toward larger and more robust prey such as macroinvertebrates and fish during the 1990s (van Oijen and Witte 1996; Katunzi et al. 2003; Kische-Machumu et al. 2008). As a possible adaptive response to that, van Rijssel and Witte (2013) found that cheek depth increased in these haplochromines probably to facilitate swallowing of the larger prey.

Among the Cichlidae, three general modes of feeding are observed: inertial suction, ram feeding, and manipulation (Liem 1980). Manipulation includes a broad range of feeding behaviors with the actual use of oral teeth during, for example, gripping and biting. Earlier studies revealed that suction-feeding cichlids generally have a premaxilla with a longer ascending (asc.) arm and an angle ( $\beta$ ) between asc. and dentigerous (dent.) arm smaller than 90°. The reverse held for fish that “bite” or scrape food from a substrate (Otten 1983; Witte 1984; Bouton et al. 2002). Past plasticity studies showed that the premaxilla of the cichlids that used a more biting-like feeding style had, among others, a less acute angle  $\beta$  and a shorter asc. arm (Witte 1984; Meyer 1987; Wimberger 1991; Bouton et al. 2002).

To investigate whether an important part of the cichlid feeding apparatus, the premaxilla, showed adaptive responses to the changed environment/ecology of the haplochromines, we analyzed the diet of four endemic haplochromine species from Lake Victoria over a period of 33 years and compared a dataset of premaxilla morphology with a dataset on diet item frequency. By grouping the samples into three periods according to environmental changes and diet class abundance, we tested whether changes in the proportion of small-, medium-, and large-sized diet items were correlated to premaxilla morphology. For this study, we used two zooplanktivores *Haplochromis (Yssichromis) laparogramma* (*lap*) and *H. (Y.) pyrrhocephalus* (*pyr*), which mostly occur in the sublittoral part of the Mwanza Gulf; a zooplankti/insectivore *H. tanaos* (*tan*) and a mollusci/detritivore *Platytaeniodus degeni* (*deg*), which tend to occur more in the littoral parts of the Mwanza Gulf.

Assuming that larger and more robust prey will involve a more biting-like feeding style, we expected the premaxilla to have shorter asc. arm and a smaller angle  $\beta$  in all four species when

feeding on larger and tougher prey (Otten 1983; Witte 1984; Bouton et al. 2002).

## Material and Methods

### FISH COLLECTION

Fish were collected during the years 1978–2011, in the northern part of the Mwanza Gulf, Lake Victoria, Tanzania. In total, 450 adult males of four species (an average of 12 specimens per species per year, at intervals of approximately three years) were selected from the specimens used in van Rijssel and Witte (2013) (Table S2).

Fish and diet samples were divided into three different periods that were based on environmental changes in the Mwanza Gulf and dietary changes in the haplochromines of this study: (1) the pristine period (1978–1984), which is considered as the period before the severe environmental and diet changes; (2) the perturbed period (1987–2002), which is the period of severe environmental changes and observed diet changes; (3) the recovery period (2006–2011), in which the environmental changes are considered less severe compared to the previous period (van Rijssel and Witte 2013). The three periods differ somewhat from the periods described in van Rijssel and Witte (2013), as in this study, the periods are also based on the dietary shifts of the fish (which occurred from 1987 onwards), instead of on environmental changes alone.

We obtained volume percentages of stomach and intestine contents for all four species. For *lap*, a selection of the specimens used for the premaxilla morphology was made. For *deg*, we used fish from the pristine and recovery periods (Table S3) as no sufficient material from the perturbed period was available. For *pyr* and *tan*, we used data from the dietary studies of van Oijen and Witte (1996), Katunzi et al. (2003), and Kische-Machumu (2012).

### DIET ANALYSIS

Volume percentages of stomach and intestine contents of all four species were averaged and analyzed following the procedure described in Kische-Machumu et al. (2008). Our method differs in that volume percentages were corrected for empty stomach and intestine contents by considering the volume percentages of present prey as 100%, even though the stomach and intestine were not always completely filled. Fish with stomachs and intestines filled with <25% were discarded. The prey types were classified in three size categories based on their smallest diameter: small (zooplankton, phytoplankton, detritus, and ostracods <0.5 mm), intermediate (midge larvae and pupae and insect remains, up to approximately 2 mm), and large (fish, shrimps, molluscs, and leeches >2 mm; Katunzi et al. 2003; Kische-Machumu et al. 2008).

### PREMAXILLA MORPHOLOGY

We dissected the right premaxilla directly from the fish by making a rostral incision between the ascending arms of left and right premaxillae. The right premaxilla was separated from the fish by making an incision between the right maxilla and the dorsal side of the dentigerous arm. Remaining tissue was removed with tweezers. Eight landmarks were placed on photographs made from the dissected right premaxilla with TPSDig2 (Rohlf 2001). Additionally, seven morphological characteristics were derived from these photographs; the asc. arm length, dent. arm length, angle  $\beta$ , teeth coverage (teeth cov.), the number of teeth (teeth nr), tooth length, and tooth shape (Text S1). The teeth cov. was measured because, in contrast to most other Lake Victoria haplochromines, the zooplanktivores *lap* and *pyr* have the caudal 1/4 to 1/3 of the premaxillary dentigerous arm edentulous, which was one of the autapomorphic features used to define the genus *Yssichromis* (Greenwood 1980). Geometric morphometrics were performed using MorphoJ 1.05a (Klingenberg 2011) following van Rijssel and Witte (2013). All four species showed a significant effect of centroid size on premaxilla shape ( $P < 0.05$ ). Therefore, all analyses were conducted on the residuals of the multivariate regression. For multiple and pairwise group comparison between years, canonical variate analysis (CVA) and discriminant function analysis (DFA) were used, respectively. The average premaxilla shape (consensus) of each group of the DFA was visualized by applying an outline to the shape differences that were exaggerated threefold for better visualization.

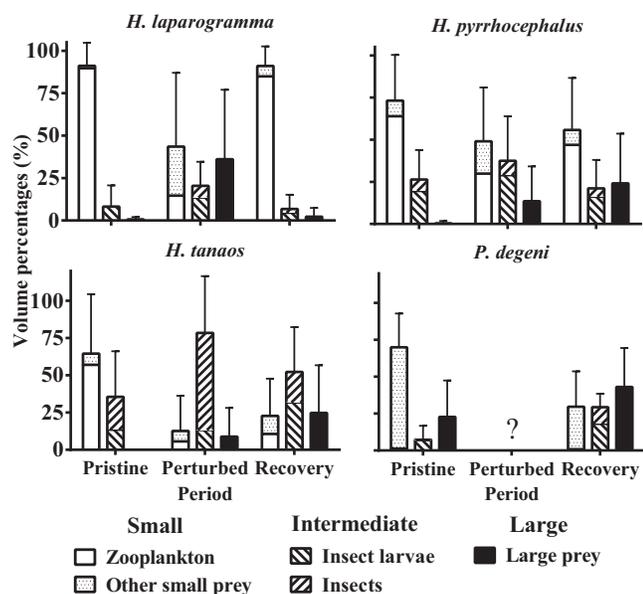
### STATISTICAL ANALYSIS

The volume percentages of prey sizes per period were compared for each species separately with a Mann–Whitney  $U$ -test. For *lap*, a Spearman correlation test between prey size and the morphological characters was conducted. For all four species, a general linear model (GLM) with standard length as covariate and year as independent factor was applied to test for the effect of year on the morphological characters of the premaxilla following van Rijssel and Witte (2013). All residuals of the GLMs were normally distributed ( $P > 0.05$ , Shapiro–Wilk test). The  $P$ -values of all tests were corrected with a sequential Bonferroni test. All statistical tests were performed with SPSS 20.

## Results

### DIETARY CHANGES, PRISTINE VERSUS PERTURBED PERIOD

For all four species, the diet consisted mainly (65–91%) of small prey (zooplankton or detritus) during the pristine period. In the perturbed period, there was a significant decrease of small prey and a significant increase of intermediate and large prey for the



**Figure 1.** Volume percentages of prey sizes of the four studied species in the pristine, perturbed, and recovery periods. Zooplankton and other small prey; and insect larvae and insects are combined in stacked bars.

species *lap*, *pyr*, and *tan* ( $P < 0.05$ ; Figure 1). The diet during the perturbed period consisted mainly of intermediate and large prey such as insects, shrimps, fish, molluscs, and leeches (Table S4).

**PREMAXILLA CHANGES, PRISTINE VERSUS PERTURBED PERIOD**

In the pristine period, interspecific differences in the shape of the premaxilla were mainly (1) teeth coverage (Fig. 2A) and (2) thickness/robustness of the premaxilla (not presented). The two zooplanktivorous species (*pyr* and *lap*) have teeth up to two-thirds of the dentigerous arm, whereas the zooplankti/insectivore *tan* and mollusci/detrivore *deg* have a completely covered dentigerous arm. Especially *deg* had a more robust premaxilla compared to the other three species, which concurs with its molluscivorous diet.

In the perturbed period, three of four studied species (*pyr*, *lap*, and *tan*) showed significant premaxilla shape changes (DFA,  $P < 0.001$ ; Fig. 2A). Premaxilla changes for *deg* were extensive but not significant due to low sample size. In general, the asc. arm length of these three species decreased ( $P < 0.001$ ; Figs. 2A, 3A, B) and the dent. arm length increased for *pyr* and *lap* ( $P < 0.01$ ; Figs. 2A, 3C). The angle  $\beta$  decreased for *lap* and *pyr*, although for the latter species,  $\beta$  also increased again during the perturbed period ( $P < 0.001$ ; Figs. 2A, 3D). The zooplanktivores *lap* and *pyr* both showed a significant increase in teeth cov. and teeth nr ( $P < 0.01$ ; Figs. 2A, 3E, F), whereas *tan* and *deg* showed a slight decrease of these characters ( $P < 0.05$ , teeth nr *deg*  $P = 0.06$ ;

Fig. 3E, F). The tooth length did not change significantly in all four species, whereas the tooth shape for *pyr* and *deg* changed significantly from predominantly bicuspid and some tricuspid to more unicuspid ( $P < 0.05$ ; Fig. 3G, H).

**DIETARY CHANGES, PERTURBED VERSUS RECOVERY PERIOD**

In the recovery period, the two zooplanktivores (*lap* and *pyr*) showed a reversal (for *pyr* only partly) in diet towards that of the pristine period; implying for *lap* an increase of small prey and a decrease of intermediate and large prey compared to the perturbed period ( $P < 0.05$ ). A similar trend was found for *pyr* (although only significant for intermediate prey; Fig. 1; Table S5). The diet of *tan* and *deg* did not show a reversal toward smaller prey; the amount of intermediate prey remained relatively high whereas the amount of large prey increased even further for *tan* (Fig. 1;  $P < 0.05$ ).

**PREMAXILLA CHANGES, PERTURBED VERSUS RECOVERY PERIOD**

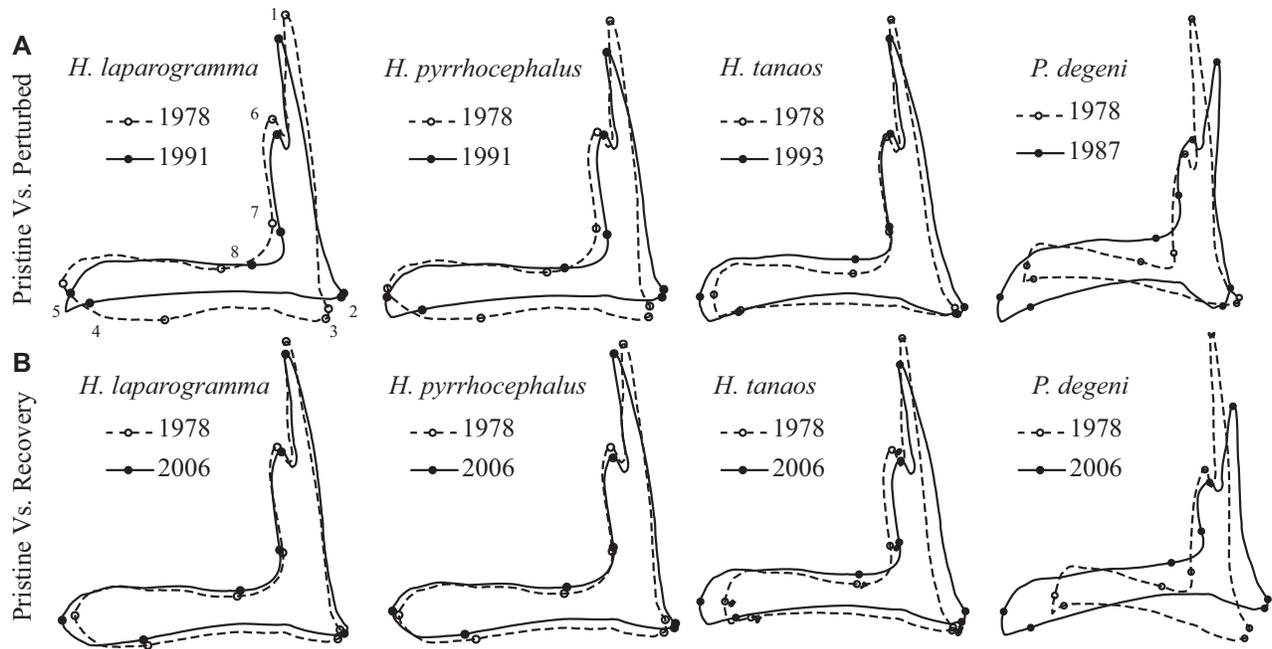
Concomitant with the (partly) diet reversal, the shape of the premaxilla of both zooplanktivores returned to the form of the pristine period (DFA,  $P > 0.05$ ). The changes in asc. arm (not for *pyr*), dent. arm, teeth cov., and teeth nr reversed between 1999 and 2011 (Figs. 2B, 3A, C, E).

The shape of the premaxilla of *tan* and *deg* continued to change significantly during the recovery period ( $P < 0.001$ ; Fig. 2B). In agreement with the increase of larger prey, the asc. arm length decreased ( $P < 0.001$ ; Figs. 2B, 3B), whereas the dent. arm length increased ( $P < 0.01$ ; Figs. 2B, 3C) and the angle  $\beta$  increased for *deg* ( $P < 0.001$ ; Figs. 2B, 3D). The average tooth length and number of unicuspid teeth (Fig. 3G, H) increased in *deg* ( $P < 0.001$ ; Table S6).

**COMPARISON OF ECOMORPHOLOGICAL CHANGES AMONG SPECIES**

In general, the dietary and morphological changes began in 1987, at the beginning of the perturbed period (Figs. 3, 4), although a few morphological changes in some species started as early as 1984 (e.g., decrease asc. arm length in *pyr*; Fig. 3A).

The zooplanktivorous species *lap* and *pyr* showed the largest morphological changes in the perturbed period when they had shifted to larger prey (Figs. 1–3). The species *tan* and *deg* show the most pronounced morphological changes in the recovery period when feeding on larger prey (Figs. 1–3). However, both species did already show extensive morphological changes in the perturbed period (Figs. 2, 3), when (presumably for *deg*) feeding on larger prey (Fig. 1). The zooplanktivorous species (*lap* and *pyr*) showed a reversal of morphological changes concurrent with a (partly) reversal to small prey in their diet, whereas the species



**Figure 2.** Premaxilla shape changes found in the four haplochromine species illustrated by the outlines derived from the DFA. (A) Comparison between pristine and perturbed periods, (B) comparison between pristine and recovery periods. The dashed line with blank circles represents the year 1978 from the pristine period. The continuous line with filled dots represents a year from the perturbed period (A) or the year 2006 from the recovery period (B). Differences are exaggerated threefold for better visualization. The sharp corners of the caudal end of the dentigerous arm in *lap* and *deg* are artifacts due to the exaggeration and should be rounded.

*tan* and *deg* showed increased morphological changes compared to the perturbed period.

#### CORRELATION BETWEEN DIET AND PREMAXILLA MORPHOLOGY

For *lap*, significant correlations between large prey and the premaxilla characters dent. arm, angle  $\beta$ , and teeth cov. were found ( $P < 0.05$ ; Fig. 4). Significant correlations for small prey with these characters were found as well, although these were not significant after sequential Bonferroni correction (Table S7).

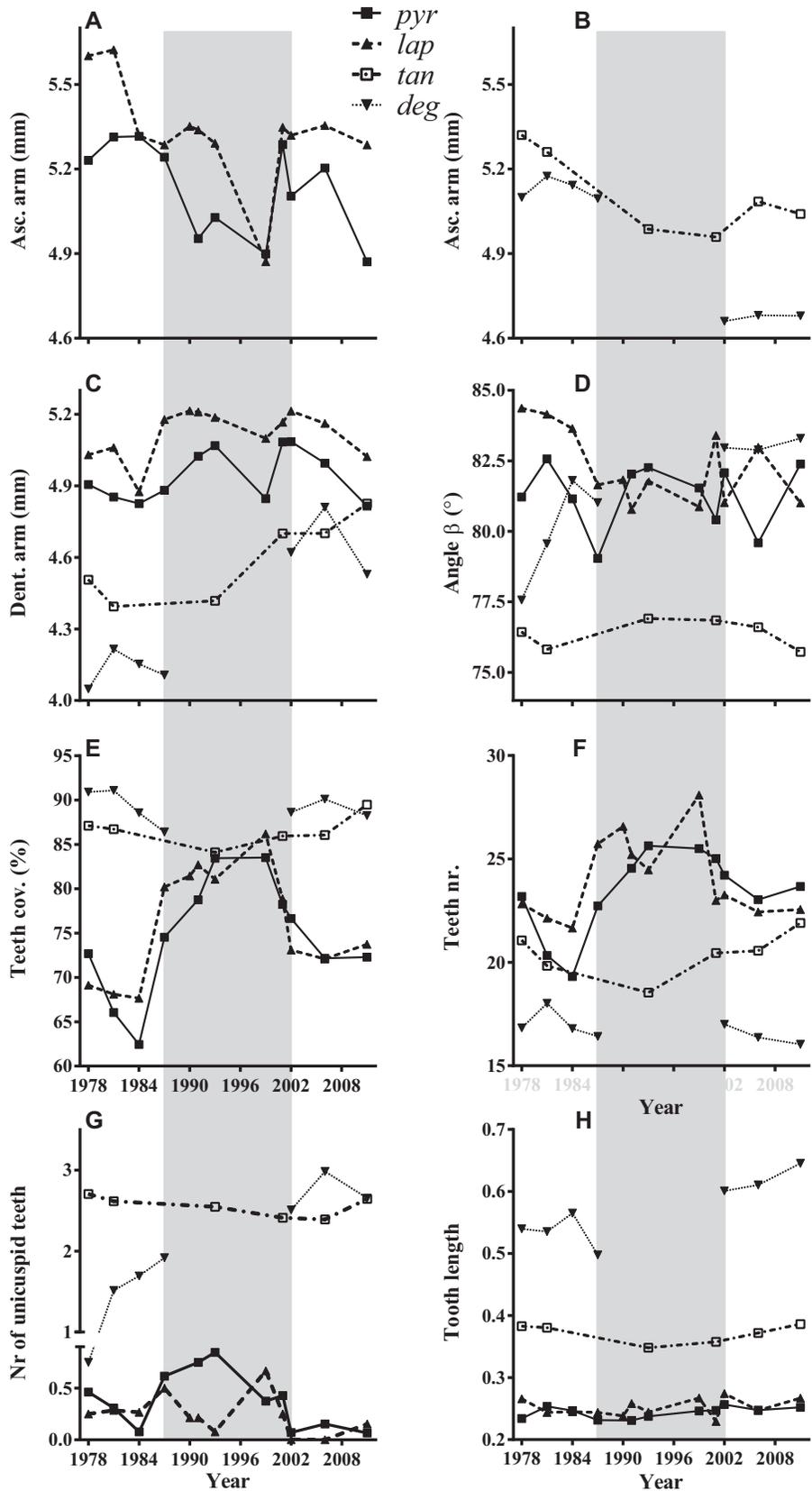
## Discussion

### DIET CHANGE AND REVERSAL

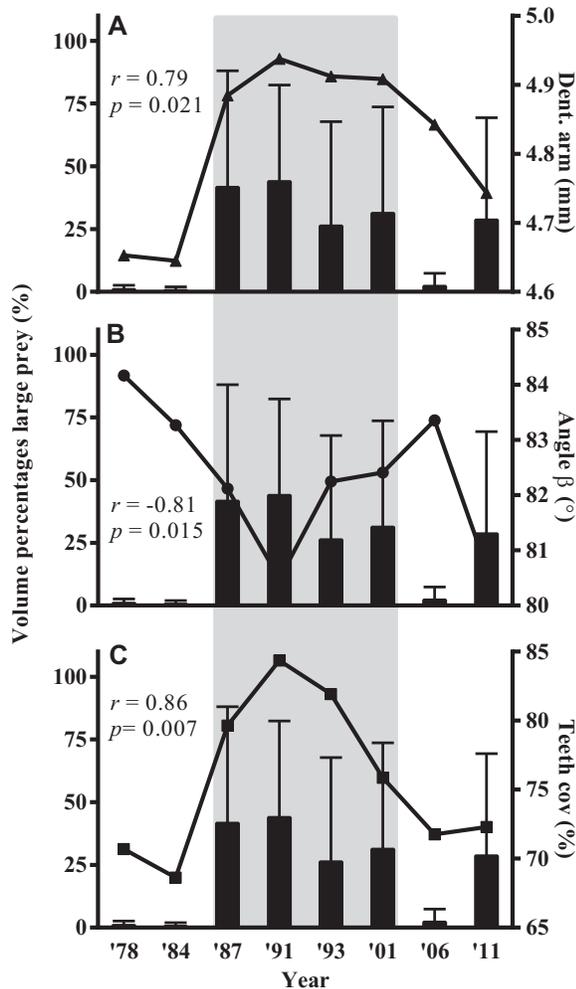
This study shows that, under natural conditions, the premaxilla in several cichlid species rapidly adjusts to, most likely, a change in diet (see below). Although there is some variability in the observed diet change, stable isotope analysis of the same specimens confirmed the diet change (Kishe-Machumu 2012; van Rijssel 2014). Three possible explanations for the shift towards larger prey in the perturbed period have been proposed by Kishe-Machumu et al. (2008). First, the increased abundance of larger prey types (Table S1; Kaufman 1992; Wanink 1999; Goudswaard et al. 2006) in combination with the increased ratio of large prey/haplochromines (Table S1). Second, the dramatic decline

in haplochromine species, resulting in competitive release. Third, the decreased water transparency of the lake and decreased eye size of the resurgent cichlids (van Rijssel and Witte 2013). These smaller eyes (which are probably due to a morphological trade-off), but especially the lower resolution of the eyes of some species (van der Meer et al. 2012), may have made it harder to distinguish small-sized prey types (e.g., zooplankton) in more turbid water.

Remarkably, in one of the two originally zooplanktivorous species, the diet returned toward smaller prey during the recovery period, whereas the other showed a partial reversal of the diet. Although some of the large prey were still abundant in the lake (Budeba and Cowx 2007; Kayanda et al. 2009; J. C. van Rijssel and F. Witte, pers. obs.; Table S1), the strong increase of haplochromines during the recovery period (Witte et al. 2007a; Kishe-Machumu 2012) likely has increased competition. This hypothesis is supported by the decreased large prey/zooplanktivores ratio in 2006 (Table S1), the year in which the zooplanktivores included a lot of zooplankton in their diet again (Fig. 4; Table S4). In addition to intraspecific competition, interspecific competition might have played a role in the diet reversal too. The detritivorous species *Haplochromis* “paropus-like” increased tremendously in abundance during the 2000s. It occurs in the same habitat as the zooplanktivores, and has shifted its diet toward larger prey as well (Kishe-Machumu et al. 2008; Kishe-Machumu 2012). The increased abundance of this and other species is likely to have



**Figure 3.** Estimated marginal means through time for all four species of: (A, B) ascending arm, (C) dentigerous arm, (D) angle  $\beta$ , (E) teeth coverage, (F) teeth number, (G) number of unicuspid teeth, and (H) tooth length through time of all four species. Estimated marginal means of the ascending arm are illustrated in two panels for better visualization. The gray shade represents the perturbed period.



**Figure 4.** Volume percentages of large prey (bars, left axis) and estimated marginal means through time for *H. laparogramma* (solid lines, right axis) of: (A) dentigerous arm, (B) angle  $\beta$ , (C) teeth coverage. The coefficient ( $r$ ) and  $P$ -value of the Spearman correlation are given per morphological character. The gray shade represents the perturbed period.

increased competition for these larger prey and might have forced the zooplanktivores to specialize on zooplankton again. The relative small abundance of *Haplochromis* “paropius-like” in the littoral area of the Mwanza Gulf might also be the reason why the species *H. tanaos* and *P. degeni* might have been subjected to less heavy competition and hence did not reverse their diet back to smaller prey again.

In addition to competition, water transparency in the Mwanza Gulf has improved again in the recovery period compared to the perturbed period (van Rijssel 2014). Finally, the eye size of the studied haplochromines increased again during the recovery period (van Rijssel and Witte 2013). Probably a combination of the three above-mentioned events has resulted in the (partly) reversal of the diet in the two zooplanktivorous species.

## ADAPTIVE RESPONSES OF PREMAXILLA

The diet change from small zooplankton/detritus to larger and more robust prey (such as insects and shrimps) has most likely induced the found premaxillary changes as they (1) show large similarities with the results of the cichlids that used more biting-like feeding style in the phenotypic plasticity experiments (smaller ascending arm, larger angle  $\beta$ , Witte 1984; Meyer 1987; Wimberger 1991; Bouton et al. 2002), (2) agree with the higher number (for the zooplanktivores) and a more unicuspid shape of teeth found in insectivorous and piscivorous cichlids (Witte and van Oijen 1990), (3) have enlarged the gape width to enable the larger prey (larger dentigerous arm), as was found for the cheek depth of the same individuals (van Rijssel and Witte 2013).

Although the exact feeding mode of the studied cichlids on their new prey types is unknown, all these changes suggest a feeding style that mainly involves manipulation (Liem 1980) of the larger and more robust prey with the use of the oral teeth. Apart from a shorter asc. arm, a larger angle  $\beta$  is supposed to increase biting force (Otten 1983). Only *P. degeni* showed a significant increase in the angle  $\beta$ . Although, like in the other three species, the angle  $\beta$  did hardly reach the range found for biters ( $83^\circ$ – $103^\circ$ , Witte 1984). These findings suggest that the feeding style of these fish did not switch to extreme biting as is found in true oral mollusc shellers and epilithic algae scrapers.

The increase in teeth coverage in the zooplanktivores during the perturbed period is remarkable. In his generic revision of the haplochromines, Greenwood (1980) described the edentulous part of the premaxilla as a diagnostic character for the genus *Yssichromis*. However, our findings indicate that the toothless part of the dentigerous arm is not a proper diagnostic feature.

## POSSIBLE MECHANISMS BEHIND MORPHOLOGICAL CHANGES

Essentially, three possible mechanisms (selection, phenotypic plasticity, hybridization) might have contributed to the observed morphological changes that are far from mutually exclusive. The direct responses of the premaxilla to the diet shifts we found for *H. laparogramma* are likely to have occurred at the same rate in the other studied species and suggest a fast adaptation mechanism.

Directional selection might be involved in the rapid morphological changes in the oral jaws (Albertson et al. 2003a). Albertson et al. (2003b) found that the oral jaw apparatus is controlled by relatively few genes and some parts of it by only one gene (e.g., tooth shape), which can result in an extremely quick response to selection. In addition, recent studies on Tanganyika cichlids have shown that traits such as mouth position have a high additive genetic variance and heritability, which suggests a genetic basis for the mode of food uptake (Postl et al. 2008; Koch et al. 2012). However, the variation in morphological traits of the cichlid premaxilla in this study is generally low. For example, features such

as a completely covered dentigerous arm have only been encountered for the zooplanktivores in the perturbed period (1987–2002,  $n = 179$ ) and never in the pristine period (1978–1984,  $n = 75$ ) or the recovery period (2006–2011,  $n = 54$ ). An additional 30 specimens of *H. laparogramma* collected in 1985 all had an edentulous area. In addition, although not included in the analysis, females (also an average of 12 specimens per species per year) revealed similar shape changes as found for the males, and none of the individuals showed a completely covered dentigerous arm during the pristine or recovery period. Nonetheless, despite the rarity of a completely covered dentigerous arm in these periods, the possibility of genetically based changes remains quite likely. Numbers used in this study are only a subsample and do not reflect the complete population, which may harbor rare phenotypes that can increase in frequency by selection. Selection can act within a few generations on relatively little variation as has been shown for several taxa (including fish) in the field (Reznick et al. 1990; Rundle 2003; Zbinden et al. 2008), in the laboratory (Kawecki et al. 2012 and references therein), and in domesticated systems (e.g., Hillman and Davies 1990; Trut et al. 2009). Even when a trait does not occur within a population, the expression of a new phenotype could be the result of genetically based changes by selection on polygenic traits.

Phenotypic plasticity might have played an important role in the observed morphological changes as well. Phenotypic plasticity is described as the environmentally sensitive production of alternative phenotypes by given genotypes (DeWitt and Scheiner 2004). Plasticity is a common phenomenon in cichlids and laboratory experiments have confirmed the ability of many cichlid species to change the jaw apparatus in response to different diets (Witte 1984; Hoogerhoud 1986; Meyer 1987; Wimberger 1991; Huysseune 1995; Smits et al. 1997; Bouton et al. 2002; Stauffer and Van Snik Gray 2004; Kerschbaumer et al. 2011; Muschick et al. 2011; Gunter et al. 2013), although different diets in the wild do not always lead to divergence in morphology in cichlids (see Odhiambo et al. 2011). Some of these studies tested plasticity of the premaxilla and showed a shorter ascending arm and a larger angle  $\beta$  of the premaxilla as a phenotypic response to a feeding style involving manipulation of prey (especially biting, Witte 1984; Wimberger 1991; Bouton et al. 2002). The results of these plasticity studies concur with the results found in our study. In all four species, we found a shorter ascending arm and in *P. degeni*, the species with the most robust premaxilla, which indicates a biting-like feeding style, a larger angle  $\beta$ . Recent plasticity experiments on Lake Tanganyika cichlids, three-spined sticklebacks, and Trinidadian guppies have shown morphological responses resembling adaptive phenotypes evolved under natural conditions (Kerschbaumer et al. 2011; Torres-Dowdall et al. 2012; Wund et al. 2012). These studies all suggest that phenotypic plasticity might play an important role in the colonization of novel

environments, which we think is likely to be the case for Lake Victoria cichlids.

The role of plasticity in speciation and adaptive radiation tended to be little appreciated, but has attracted more attention recently (Pfennig et al. 2010). Some even argue that changes in traits through phenotypic plasticity have a greater evolutionary potential than mutationally induced ones and eventually can be selected on through genetic accommodation (West-Eberhard 2005) as for example by genetic assimilation (Pigliucci and Murren 2003; Schlichting and Wund 2014). For the cichlid genus *Tropheus* from Lake Tanganyika, it has been proposed that phenotypic differences among populations in sympatry as in allopatry have a genetic basis but are also sensitive to plasticity and that selection is likely to act on both plasticity as on the phenotypic traits themselves (Kerschbaumer et al. 2014). In addition, as is supposed for the cichlid mandible, it might be that regions that come in contact with prey (dentition) evolve independently from regions involved in opening and closing of the premaxilla (Albertson et al. 2005; Parsons et al. 2012). As our results tend to be similar to above-mentioned plasticity studies, we hypothesize that plasticity has played a role in the observed morphological changes and speculate that this plasticity (and the selection on it) might have played a role in cichlid speciation.

It is quite probable that hybridization has occurred in the studied haplochromine population. Seehausen et al. (1997) found that the increased water turbidity in the perturbed period had blocked reproductive isolation by constraining color vision, which interfered with mate choice and relaxed sexual selection for rock cichlids in the Mwanza Gulf. Hybridization through reversed speciation is not only found for cichlids but has been reported for European whitefish and sticklebacks as well (Taylor et al. 2006; Vonlanthen et al. 2012). In these cases, hybridization resulted in a loss of biodiversity, however, hybridization might also be beneficial to speciation in early adaptive radiation events (Seehausen 2004). Evidence for introgressive hybridization and much reduced genetic differentiation has been found for *H. laparogramma* and *H. pyrrhocephalus* in the Mwanza Gulf based on mtDNA sequences (Mzighani et al. 2010; Takeda et al. 2013). In addition, body shapes of these two zooplanktivores converged in the perturbed period and specimens could not be separated from each other anymore based on this trait, whereas the body shapes diverged again in the recovery period (J. C. van Rijssel and F. Witte, unpubl. data). If hybridization has occurred in these fish, it would also offer a plausible explanation for the sudden appearance of a completely covered dentigerous arm in both zooplanktivores *H. pyrrhocephalus* and *H. laparogramma*. The zooplanktivores from the genus *Yssichromis* are the only species of Lake Victoria known to have this large edentulous part of the dentigerous arm (Greenwood 1980). This implies that any hybridization event with species from another genus could have

resulted in a higher teeth coverage. These “new” phenotypes were probably not constrained by competition and could have rapidly spread through the population at the end of perturbed period especially because many ecological niches and adaptive peaks were virtually unoccupied.

Although the mechanism behind the observed morphological changes remains unclear, this study showed that haplochromine cichlids are able to rapidly respond to environmental changes and that changes in diet are likely to be caused by a competition release and increase. The fast and sometimes immediate morphological responses indicate a fast adaptation mechanism. Genetically based changes as well as phenotypic plasticity are likely to have contributed to observed morphological responses. Experimental studies on trait plasticity and selection with the use of genetic analysis of traits (epigenetics, quantitative trait analyses) will enhance our understanding of the role of each mechanism in the adaptive radiation of species. Whatever the outcome of these studies, the fact that these haplochromines are able to show these fast adaptive responses is likely to have contributed to their fast adaptive radiation.

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#### DATA ARCHIVING

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#### LITERATURE CITED

- Aguirre, W. E., and M. A. Bell. 2012. Twenty years of body shape evolution in a threespine stickleback population adapting to a lake environment. *Biol. J. Linn. Soc.* 105:817–831.
- Albertson, R. C., J. T. Strelman, and T. D. Kocher. 2003a. Directional selection has shaped the oral jaws of Lake Malawi cichlid fishes. *Proc. Natl. Acad. Sci. USA* 100:5252–5257.
- . 2003b. Genetic basis of adaptive shape differences in the cichlid head. *J. Hered.* 94:291–301.
- Albertson, R. C., J. T. Strelman, T. D. Kocher, and P. C. Yelick. 2005. Integration and evolution of the cichlid mandible: the molecular basis of alternate feeding strategies. *Proc. Natl. Acad. Sci. USA* 102:16287–16292.
- Bouton, N., F. Witte, and J. J. M. van Alphen. 2002. Experimental evidence for adaptive phenotypic plasticity in a rock-dwelling cichlid fish from Lake Victoria. *Biol. J. Linn. Soc.* 77:185–192.
- Budeba, Y. L., and I. G. Cowx. 2007. The role of the freshwater shrimp *Caridina nilotica* (Roux) in the diet of the major commercial fish species in Lake Victoria, Tanzania. *Aquat. Ecosyst. Health Manage.* 10:368–380.
- Chapman, L. J., F. Galis, and J. Shinn. 2000. Phenotypic plasticity and the possible role of genetic assimilation: hypoxia-induced trade-offs in the morphological traits of an African cichlid. *Ecol. Lett.* 3:387–393.
- DeWitt, T. J., and S. M. Scheiner. 2004. Phenotypic plasticity: functional and conceptual approaches. Oxford Univ. Press, Oxford, U.K.
- Elmer, K. R., C. Reggion, T. Wirth, E. Verheyen, W. Salzburger, and A. Meyer. 2009. Pleistocene desiccation in East Africa bottlenecked but did not extirpate the adaptive radiation of Lake Victoria haplochromine cichlid fishes. *Proc. Natl. Acad. Sci. USA* 106:13404–13409.
- Fryer, G. 2004. Speciation rates in lakes and the enigma of Lake Victoria. *Hydrobiologia* 519:167–183.
- Goldschmidt, T., F. Witte, and J. Wanink. 1993. Cascading effects of the introduced Nile perch on the detritivorous phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conserv. Biol.* 7:686–700.
- Goudswaard, K. P. C., F. Witte, and J. H. Wanink. 2006. The shrimp *Caridina nilotica* in Lake Victoria (East Africa), before and after the Nile perch increase. *Hydrobiologia* 563:31–44.
- Goudswaard, K. P. C., F. Witte, and E. F. B. Katunzi. 2008. The invasion of an introduced predator, Nile perch (*Lates niloticus*, L.) in Lake Victoria (East Africa): chronology and causes. *Environ. Biol. Fish.* 81:127–139.
- Grant, P. R., and B. R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* 49:241–251.
- Greenwood, P. H. 1980. Towards a phyletic classification of the genus *Haplochromis* (Pisces, Cichlidae) and related taxa. Part II; the species from Lakes Victoria, Nabugabo, Edward, George and Kivu. *Bull. Br. Mus. Nat. Hist. Zool.* 39:1–101.
- Gunter, H. M., S. H. Fan, F. Xiong, P. Franchini, C. Fruciano, and A. Meyer. 2013. Shaping development through mechanical strain: the transcriptional basis of diet-induced phenotypic plasticity in a cichlid fish. *Mol. Ecol.* 22:4516–4531.
- Hecky, R. E., R. Mugidde, P. S. Ramlal, M. R. Talbot, and G. W. Kling. 2010. Multiple stressors cause rapid ecosystem change in Lake Victoria. *Freshw. Biol.* 55:19–42.
- Hillman, G. C., and M. S. Davies. 1990. Domestication rates in wild-type wheats and barley under primitive cultivation. *Biol. J. Linn. Soc.* 39:39–78.
- Hoogerhoud, R. J. C. 1986. Taxonomic and ecological aspects of morphological plasticity in molluscivorous haplochromines (Pisces, Cichlidae). Pp. 131–134 in 3rd European Workshop on Cichlid Biology. *Annales du Musée royal de l’Afrique Centrale Sciences Zoologiques, Bielefeld, West-Germany.*
- Huysseune, A. 1995. Phenotypic plasticity in the lower pharyngeal jaw dentition of *Astatoreochromis alluaudi* (Teleostei, Cichlidae). *Arch. Oral Biol.* 40:1005–1014.
- Johnson, T. C., C. A. Scholz, M. R. Talbot, K. Kelts, R. D. Ricketts, G. Ngobi, K. Beuning, I. Ssemmanda, and J. W. McGill. 1996. Late pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* 273:1091–1093.
- Katunzi, E. F. B., J. Zoutendijk, T. Goldschmidt, J. H. Wanink, and F. Witte. 2003. Lost zooplanktivorous cichlid from Lake Victoria reappears with a new trade. *Ecol. Freshw. Fish.* 12:237–240.

- Kaufman, L. 1992. Catastrophic change in species rich fresh water ecosystems. *Bioscience* 42:846–858.
- Kawecki, T. J., R. E. Lenski, D. Ebert, B. Hollis, I. Olivieri, and M. C. Whitlock. 2012. Experimental evolution. *Trends Ecol. Evol.* 27:547–560.
- Kayanda, R., M. A. Taabu, R. Tumwebaze, L. Muhoozi, T. Jembe, E. Mlaponi, and P. Nzungi. 2009. Status of the major commercial fish stocks and proposed species-specific management plans for Lake Victoria. *Afr. J. Trop. Hydrobiol. Fish.* 12:15–21.
- Kerschbaumer, M., L. Postl, M. Koch, T. Wiedl, and C. Sturmbauer. 2011. Morphological distinctness despite large-scale phenotypic plasticity—analysis of wild and pond-bred juveniles of allopatric populations of *Tropheus moorii*. *Naturwissenschaften* 98:125–134.
- Kerschbaumer, M., P. Mitteroecker, and C. Sturmbauer. 2014. Evolution of body shape in sympatric versus non-sympatric *Tropheus* populations of Lake Tanganyika. *Heredity* 112:89–98.
- Kishe-Machumu, M. A. 2012. Inter-guild differences and possible causes of the recovery of cichlid species in Lake Victoria, Tanzania. Ph.D. thesis, Leiden University, Leiden, The Netherlands.
- Kishe-Machumu, M. A., F. Witte, and J. H. Wanink. 2008. Dietary shift in benthivorous cichlids after the ecological changes in Lake Victoria. *Anim. Biol.* 58:401–417.
- Klingenberg, C. P. 2011. MorphoJ: an integrated software package for geometric morphometrics. *Mol. Ecol. Res.* 11:353–357.
- Koch, M., A. J. Wilson, M. Kerschbaumer, T. Wiedl, and C. Sturmbauer. 2012. Additive genetic variance of quantitative traits in natural and pond-bred populations of the Lake Tanganyika cichlid *Tropheus moorii*. *Hydrobiologia* 682:131–141.
- Kocher, T. D. 2004. Adaptive evolution and explosive speciation: the cichlid fish model. *Nat. Rev. Genet.* 5:288–298.
- Liem, K. F. 1980. Acquisition of energy by teleosts: adaptive mechanisms and evolutionary patterns. Pp. 299–334 in M. A. Ali, ed. *Environmental physiology of fishes*. Plenum Publishing Corporation, New York.
- Losos, J. B., K. I. Warheit, and T. W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* 387:70–73.
- Meyer, A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. *Evolution* 41:1357–1369.
- Meyer, A., T. D. Kocher, P. Basasibwaki, and A. C. Wilson. 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial-DNA sequences. *Nature* 347:550–553.
- Muschick, M., M. Barluenga, W. Salzburger, and A. Meyer. 2011. Adaptive phenotypic plasticity in the Midas cichlid fish pharyngeal jaw and its relevance in adaptive radiation. *BMC Evol. Biol.* 11:116.
- Mzighani, S. I., M. Nikaido, M. Takeda, O. Seehausen, Y. L. Budeba, B. P. Ngatunga, E. F. B. Katunzi, M. Aibara, S. Mizoiri, T. Sato, et al. 2010. Genetic variation and demographic history of the *Haplochromis laparogramma* group of Lake Victoria—an analysis based on SINEs and mitochondrial DNA. *Gene* 450:39–47.
- Odhiambo, E. A., M. Kerschbaumer, L. Postl, and C. Sturmbauer. 2011. Morphometric differentiation among haplochromine cichlid fish species of a satellite lake of Lake Victoria. *J. Zool. Syst. Evol. Res.* 49:216–223.
- Otten, E. 1983. The jaw mechanism during growth of a generalized *Haplochromis* species—*H. elegans* Trewavas 1933 (Pisces, Cichlidae). *Neth. J. Zool.* 33:55–98.
- Parsons, K. J., E. Marquez, and R. C. Albertson. 2012. Constraint and opportunity: the genetic basis and evolution of modularity in the cichlid mandible. *Am. Nat.* 179:64–78.
- Pfennig, D. W., M. A. Wund, E. C. Snell-Rood, T. Cruickshank, C. D. Schlichting, and A. P. Moczek. 2010. Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol. Evol.* 25:459–467.
- Pigliucci, M., and C. J. Murren. 2003. Perspective: genetic assimilation and a possible evolutionary paradox: can macroevolution sometimes be so fast as to pass us by? *Evolution* 57:1455–1464.
- Postl, L., J. Herler, C. Bauer, M. Maderbacher, L. Makasa, and C. Sturmbauer. 2008. Geometric morphometrics applied to viscerocranial bones in three populations of the Lake Tanganyika cichlid fish *Tropheus moorii*. *J. Zool. Syst. Evol. Res.* 46:240–248.
- Reznick, D. A., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357–359.
- Rohlf, F. J. 2001. TPSDig2: a program for landmark development and analysis. Available at <https://life.bio.sunysb.edu/morph/>.
- Rundle, H. D. 2003. Divergent environments and population bottlenecks fail to generate premating isolation in *Drosophila pseudoobscura*. *Evolution* 57:2557–2565.
- Schlichting, C. D., and M. A. Wund. 2014. Phenotypic plasticity and epigenetic marking: an assessment of evidence for genetic accommodation. *Evolution* 68:656–672.
- Schluter, D. 2000. *The ecology of adaptive radiation*. Oxford Univ. Press, Oxford, U.K.
- Seehausen, O. 2002. Patterns in fish radiation are compatible with Pleistocene desiccation of Lake Victoria and 14 600 year history for its cichlid species flock. *Proc. Roy. Soc. Lond. Ser. B Biol. Sci.* 269:491–497.
- . 2004. Hybridization and adaptive radiation. *Trends Ecol. Evol.* 19:198–207.
- Seehausen, O., J. J. M. van Alphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277:1808–1811.
- Smits, J. D., G. C. Anker, F. Witte, and K. D. N. Barel. 1997. Comparative functional anatomy of the pharyngeal jaw apparatus in two morphs of *Astatoreochromis alluaudi* (Pisces, Cichlidae). *Neth. J. Zool.* 47:313–347.
- Stauffer, J. R., and E. V. Van Snik Gray. 2004. Phenotypic plasticity: its role in trophic radiation and explosive speciation in cichlids (Teleostei: Cichlidae). *Anim. Biol.* 54:137–158.
- Takeda, M., J. Kusumi, S. Mizoiri, M. Aibara, S. I. Mzighani, T. Sato, Y. Terai, N. Okada, and H. Tachida. 2013. Genetic structure of pelagic and littoral cichlid Fishes from Lake Victoria. *PLoS One* 8:9.
- Taylor, E. B., J. W. Boughman, M. Groenenboom, M. Sniatynski, D. Schluter, and J. L. Gow. 2006. Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. *Mol. Ecol.* 15:343–355.
- Torres-Dowdall, J., C. A. Handelsman, D. N. Reznick, and C. K. Ghalebomb. 2012. Local adaptation and the evolution of phenotypic plasticity in Trinidadian guppies (*Poecilia reticulata*). *Evolution* 66:3432–3443.
- Trut, L., I. Oskina, and A. Kharlamova. 2009. Animal evolution during domestication: the domesticated fox as a model. *BioEssays* 31:349–360.
- van der Meer, H. J., J. C. van Rijssel, L. C. Wagenaar, and F. Witte. 2012. Photopic adaptations to a changing environment in two Lake Victoria cichlids. *Biol. J. Linn. Soc.* 106:328–341.
- van Oijen, M. J. P., and F. Witte. 1996. Taxonomical and ecological description of a species complex of zooplanktivorous and insectivorous cichlids from Lake Victoria. *Zool. Verh. Leiden* 302:1–56.
- van Rijssel, J. C. 2014. Adaptive responses to environmental changes in Lake Victoria cichlids. Ph.D. thesis, Leiden University, Leiden, The Netherlands.
- van Rijssel, J. C., and F. Witte. 2013. Adaptive responses in resurgent Lake Victoria cichlids over the past 30 years. *Evol. Ecol.* 27:253–267.

- Verheyen, E., W. Salzburger, J. Snoeks, and A. Meyer. 2003. Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. *Science* 300:325–329.
- Vonlanthen, P., D. Bittner, A. G. Hudson, K. A. Young, R. Muller, B. Lundsgaard-Hansen, D. Roy, S. Di Piazza, C. R. Largiader, and O. Seehausen. 2012. Eutrophication causes speciation reversal in whitefish adaptive radiations. *Nature* 482:357–362.
- Wanink, J. H. 1999. Prospects for the fishery on the small pelagic *Rastrineobola argentea* in Lake Victoria. *Hydrobiologia* 407:183–189.
- Wanink, J. H., E. F. B. Katunzi, K. P. C. Goudswaard, F. Witte, and W. L. T. van Densen. 2002. The shift to smaller zooplankton in Lake Victoria cannot be attributed to the ‘sardine’ *Rastrineobola argentea* (Cyprinidae). *Aquat. Living Res.* 15:37–43.
- West-Eberhard, M. J. 2005. Developmental plasticity and the origin of species differences. *Proc. Natl. Acad. Sci. USA* 102:6543–6549.
- Wimberger, P. H. 1991. Plasticity of jaw and skull morphology in the neotropical cichlids *Geophagus brasiliensis* and *G. steindachneri*. *Evolution* 45:1545–1563.
- Witte, F. 1984. Consistency and functional significance of morphological differences between wild-caught and domestic *Haplochromis squamipinnis* (Pisces, Cichlidae). *Neth. J. Zool.* 34:596–612.
- Witte, F., and M. J. P. van Oijen. 1990. Taxonomy, ecology and fishery of haplochromine trophic groups. *Zool. Verh. Leiden* 262:1–47.
- Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas, and N. Bouton. 1992. The destruction of an endemic species flock—quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environ. Biol. Fish.* 34:1–28.
- Witte, F., B. S. Msuku, J. H. Wanink, O. Seehausen, E. F. B. Katunzi, K. P. C. Goudswaard, and T. Goldschmidt. 2000. Recovery of cichlid species in Lake Victoria: an examination of factors leading to differential extinction. *Rev. Fish Biol. Fish.* 10:233–241.
- Witte, F., J. H. Wanink, and M. Kische-Machumu. 2007a. Species distinction and the biodiversity crisis in Lake Victoria. *Transac. Am. Fish. Soc.* 136:1146–1159.
- Witte, F., J. H. Wanink, M. Kische-Machumu, O. C. Mkumbo, P. C. Goudswaard, and O. Seehausen. 2007b. Differential decline and recovery of haplochromine trophic groups in the Mwanza Gulf of Lake Victoria. *Aquat. Ecosyst. Health Manage.* 10:416–433.
- Witte, F., M. Welten, M. Heemskerk, I. van der Stap, L. Ham, H. Rutjes, and J. H. Wanink. 2008. Major morphological changes in a Lake Victoria cichlid fish within two decades. *Biol. J. Linn. Soc.* 94:41–52.
- Witte, F., O. Seehausen, J. H. Wanink, M. A. Kische-Machumu, M. Rensing, and T. Goldschmidt. 2013. Cichlid species diversity in naturally and anthropogenically turbid habitats of Lake Victoria, East Africa. *Aquat. Sci.* 75:169–183.
- Wund, M. A., S. Valena, S. Wood, and J. A. Baker. 2012. Ancestral plasticity and allometry in threespine stickleback reveal phenotypes associated with derived, freshwater ecotypes. *Biol. J. Linn. Soc.* 105:573–583.
- Zbinden, M., C. R. Haag, and D. Ebert. 2008. Experimental evolution of field populations of *Daphnia magna* in response to parasite treatment. *J. Evol. Biol.* 21:1068–1078.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s website:

**Table S1.** Abundance of haplochromine trophic groups and some of their prey types in the Mwanza Gulf through time.

**Table S2.** Catch locations and number of specimens per species per year.

**Table S3.** Origins and number of fish used per period for the diet analysis, *n* is given in parentheses.

**Table S4.** Volume percentages of different prey types per period per species.

**Table S5.** *P*-values of the Mann–Whitney *U*-test between prey sizes and periods.

**Table S6.** *P*-values of the effect of year from the GLM per species with SL as covariate.

**Table S7.** Correlation coefficients of the Spearman correlation between the estimated marginal means of the morphological characters and prey size.

**Text S1.** Premaxilla and teeth measurements.