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ORIGINAL PAPER

Adaptive responses in resurgent Lake Victoria cichlids over the past 30 years

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Abstract Textbook examples of adaptive radiation like the Galapagos finches and the East-African cichlids form a subject of major interest in evolutionary biology. Many of these species often show rapid morphological changes in response to a perturbed environment. The dramatic ecological changes in Lake Victoria during the past three decades, e.g. Nile perch predation and eutrophication, provide a unique opportunity to study environmental effects on cichlid morphology. Preliminary research has revealed that the lake's haplochromines tend to be extremely plastic and sensitive to these environmental changes. So far, long-term ecomorphological studies at short-term intervals are extremely rare. In this study, we examined morphological changes over a 30 year period in six haplochromine species. Geometric morphometric analyses at intervals of approximately 3 years revealed adaptive responses. Three out of four resurgent haplochromines had a smaller head surface/caudal peduncle area (HS/CPA) ratio during the upsurge of the predatory Nile perch. During the same period, all four resurgent species had a larger cheek depth and a smaller eye size. The smaller HS/CPA ratio and larger cheek depth are likely to be adaptive responses to a high predation pressure and a diet shift to larger prey. The smaller eye size seems to be the result of a trade off between the eyes and other morphological structures in the smaller head of these species. Interestingly, the direction of the morphological changes was different between the four resurgent cichlid species and two species that became extremely rare or even may have gone extinct. The HS/CPA ratio increased in the extinct species where it decreased in the resurgent species. This study suggests that predation is a major driver of these morphological changes, which may be due to either phenotypic plasticity or adaptive changes.

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Introduction

Adaptive radiation of species has attracted the interest of many evolutionary biologists resulting in multiple studies on this speciation process in vertebrates (Streelman and Danley 2003). Well known examples of adaptive radiation are the Galapagos finches, Anolis lizards and the African cichlids. These and other model organisms (like the peppered moth and the three-spined stickleback), often show rapid morphological changes through selection by (human-induced) alteration of their environment (Clarke et al. 1985; Grant and Grant 1995; Losos et al. 1997; Reznick et al. 1997; Bell et al. 2004; Aguirre and Bell 2012). However, with the exception of studies on the Galapagos finches (Grant et al. 2004; Grant and Grant 2006) and three-spined sticklebacks (Aguirre and Bell 2012), there are no long-term ecomorphological studies where samples have been taken at short time-intervals. By focusing on the ecomorphology of species at short time intervals, we can pinpoint the changes in morphology (including reversals and stasis) possibly induced by environmental changes (Gingerich 1983, 2001; Hendry and Kinnison 1999; Reznick and Ghalambor 2001; Hairston et al. 2005).

Lake Victoria cichlids have experienced major environmental changes for almost 30 years, and this makes them ideal model species to study environmentally-induced morphological changes. In the 1950s the predatory Nile perch was introduced, and its population boomed in the 1980s (Ogutu-Ohwayo 1990; Pringle 2005; Goudswaard et al. 2008). Concurrently, eutrophication through increasing human population densities and inappropriate agricultural practices resulted in increased phytoplankton blooms, especially of cyanobacteria (Hecky 1993; Mugidde 1993; Verschuren et al. 2002). This caused the lake water to become murky and low in dissolved oxygen (DO; Hecky et al. 1994; Seehausen et al. 1997; Witte et al. 2005). Along with these dramatic changes, a greater abundance of shrimps, molluscs, insects and small cyprinid fish (*Rastrineobola argentea* Pellegrin) were observed (Kaufman 1992; Witte et al. 1992a; Hecky 1993; Hecky et al. 1994; Wanink and Witte 2000; Goudswaard et al. 2006). These environmental changes had a major impact on cichlid diversity and resulted in a 40 % decline in the number of species (Witte et al. 1992b, 2000; Seehausen et al. 1997).

During the 1990s, when overfishing caused the Nile perch to decline, some haplochromines were able to recover (Witte et al. 2007, 2012). These resurgent species shifted their diet during the environmental changes from zooplankton and detritus to larger and more robust prey items (Van Oijen and Witte 1996; Katunzi et al. 2003; Kishe-Machumu et al. 2008). One of them was *Haplochromis (Yssichromis) pyrrhocephalus* Witte & Witte-Maas, now the most common zooplanktivore in the Mwanza Gulf (Witte et al. 2000; J. C. van Rijssel & F. Witte pers. obs.). This species adjusted its head morphology in response to the low DO levels and the changed diet by enlarging its gills and increasing the crushing muscles of the pharyngeal jaw apparatus (Witte et al. 2008).

Major environmental changes which can initiate rapid morphological responses in fish include, amongst others, increase of predation, eutrophication (turbidity and low dissolved oxygen levels), and a diet shift (e.g. Wootton 1998; Bittner et al. 2010; Langerhans 2010). A common morphological response to predation in fishes is a decreased head surface and an increased caudal peduncle area. A literature review revealed 16 different species that have a smaller anterior region and a larger caudal region at high-predation localities or treatments (Langerhans 2010). However, the decrease of the size of a fish head may limit the size of structures in the head, like the eyes (Barel et al. 1989).

For most fish species, vision is the main source of sensory information (Guthrie and Muntz 1993). Increasing turbidity of freshwater lakes due to eutrophication is becoming a common phenomenon and results in a loss of fish biodiversity (Seehausen et al. 1997; Taylor et al. 2006; Witte et al. 2012). For a fish, one way to cope with increasing turbidity, is to increase the cones in the eye in order to capture the decreased incoming light (Van der Meer and Anker 1984). The enlargement of the cones will involve an increase in eye size, given that the density of the cones remain unchanged.

Changes in vision can be the cause or result of a diet shift in fish (Hairston and Li 1982; Li et al. 1985; Hobson 1991; Wainwright and Bellwood 2002). Next to vision, gape width and buccal cavity size are limiting factors for a fish's diet (Werner 1974; Wainwright and Richard 1995; Carroll et al. 2004). Therefore, a shift to larger prey is likely to increase the buccal cavity and with it, cheek depth (Witte et al. 2008). Cheek depth, eye size and head profile are interrelated as is shown by Barel et al. (1989).

Cichlid morphology shows phenotypically plastic responses to changes in diet, light conditions and DO levels in the lab (Meyer 1987; Witte et al. 1990; Van der Meer 1993; Smits et al. 1997; Chapman et al. 2000; Bouton et al. 2002a; Stauffer and Van Snik Gray 2004; Terai et al. 2006; Rutjes et al. 2009; Crispo and Chapman 2010a, b) as well as in the field (Smits et al. 1996; Chapman et al. 2000; Terai et al. 2006; Crispo and Chapman 2010a, b). As Witte et al. (2008) noticed, it is not yet clear whether the morphological changes found in *H. pyrrhocephalus* are the result of phenotypic plasticity or genetic changes. Moreover, it still has to be proven that the observed morphological changes have indeed led to enhanced chances of survival in the changed environment, i.e. that they constitute adaptive responses. When morphological responses would occur in the same direction in several Lake Victoria haplochromine species, it becomes more likely that these responses are adaptive.

By studying morphological changes that have occurred in concert with environmental changes, this is the first study comparing morphological changes over a time span of 30 years at about 3 year time intervals in six different cichlid species; five zooplanktivores, *Haplochromis (Yssichromis) laparogramma* Greenwood & Gee (lap), *H. (Y.) pyrrhocephalus* (pyr), *H. (Y.) heusinkveldi* Witte & Witte-Maas (heus), *H. tanaos* Van Oijen & Witte (tan), *H. piceatus* Greenwood & Gee (pic) and a mollusci-/detritivore *Platytaeniodus degeni* Boulenger (deg). Four of these species have successfully recovered (pyr, lap, tan and deg) and two are extremely rare or extinct (pic and heus; Witte et al. 2000, 2007). We expected adjustments in body shape and morphology of the resurgent species in relation to the environmental changes. Predictable adaptive responses to the environmental changes in external body shape, are i) a smaller head surface (HS)/caudal peduncle area (CPA) ratio to facilitate burst swimming in order to escape predation by Nile perch; ii) a larger buccal cavity (represented by cheek depth) to facilitate swallowing larger prey; iii) an increase in eye size to harbour larger, and consequently more light sensitive cones, to cope with the decreased light conditions. Moreover, in case of adaptive responses, we expected the resurgent species to change into a similar direction, whereas we predicted the extinct species not to change, or to change in a different morphological direction.

Materials and methods

Fish collection

Fish were collected during the years 1978–2006, in the northern part of the Mwanza Gulf, Lake Victoria, Tanzania. Fish samples were divided into three different periods; (1) the pristine period (1978–1981), which is considered as the period before the severe environmental changes (2) the perturbed period (1984–1999), which is during the severe environmental changes (3) the recovery period (2001–2006), in which the environmental changes are less severe compared to the previous period (Table 1). Most fish were caught with bottom trawls along a 5 km transect at a depth range of 6–14 m (for catch locations see Witte et al. 1992b; Bouton et al. 2002b) and were taxonomically classified in the field. Fish were preserved in 4 % formaldehyde solution (buffered with borax) and, after shipment to Leiden, transferred to 70 % ethanol. The fish were stored in the Netherlands Centre for Biodiversity (NCB), Naturalis, in Leiden. For the present study, we selected fish from multiple year groups that differed by approximately 3 years. The sex of each specimen was determined by examination of the gonads in the lab. In total, 1,019 adult fish [standard length (SL) 44.1–86.3 mm] of six species were selected (Appendix Table 1 in Electronic Supplementary Material).

Geometric morphometry

To ensure reliable measurements we selected the most straight fish that had not been deformed during preservation and transport; slightly bent fish were pinned down and straightened. Based on homologous structures that are also used for taxonomic measurements (e.g. Barel et al. 1977), 21 landmarks (LM) were placed by a single researcher (JCVR) with a waterproof marker pen (Appendix Fig. 1 in Electronic Supplementary Material). The left side of each fish was, together with a reference scale, photographed with a Canon EOS 450D digital photo camera and a Sigma 70 mm macro lens. The landmarks

Table 1 Periods of environmental changes

Years*	1978–1981	1984–1999	2001–2006
Period	Pristine period	Perturbed period	Recovery period
Environment	No Nile perch[a], high number of cichlids[b], no hypoxic conditions[c], diet of studied cichlids consists of small prey[d]	Nile perch boom[a], low number of cichlids[b], increased hypoxia[c], diet shift towards larger prey[d]	Lower Nile perch numbers than in perturbed period[e], high number of cichlids[b], less severe hypoxia than in perturbed period[f], diet shift towards smaller prey[g]

* Years represent the years of sample collection

[a] Goudswaard et al. (2008)

[b] Witte et al. (2012)

[c] Wanink et al. (2001)

[d] Van Oijen and Witte (1996), Katunzi et al. (2003), Kishe-Machumu et al. (2008)

[e] Matsuishi et al. (2006), Mkumbo et al. (2007), Kayanda et al. (2009)

[f] Sitoki et al. (2010)

[g] Kishe-Machumu (2012)

on the photographs were digitized in TpsDig 2.15 (Rohlf 2001). Past 2.05 (Hammer et al. 2001) was used to check for landmark displacement errors and aberrant specimens.

Geometric morphometrics were performed using MorphoJ 1.02 g (Klingenberg 2011) following Klingenberg et al. (2003). To avoid the effect of sexual dimorphism, males and females were analyzed separately. A procrustes superimposition was applied to extract shape co-ordinates. This method translates the shape to a common origin, scales to unit centroid size and rotates to minimize the procrustes distance between landmarks (Rohlf 1999; Zelditch et al. 2004; Mitteroecker and Gunz 2009). An allometry correction was applied to all data, which were divided in subgroups (e.g. species or year) by performing a multivariate regression of the procrustes coordinates on the centroid size (Monteiro 1999; Klingenberg et al. 2003). For multiple group comparison between years, a Canonical Variate Analysis (CVA) was used to calculate body shape differences (variation). The Discriminant Function Analysis (DFA) was used for pairwise group comparison between years. Each analysis was accompanied with a permutation test (10,000×) to test for significance. To visualize body shape differences between groups, the thin plate spline technique was applied. This technique interpolates between landmarks and landmark displacements (e.g. Zelditch et al. 2004). The average body shape (consensus) of each group of the DFA was visualized by applying an outline to the shape differences which were exaggerated three-fold for better visualization.

To check if body shape differences were predominantly caused by year, we tested these shape differences for the effects of centroid size (allometry) and catch location (Appendix in Electronic Supplementary Material).

Morphological character measurements

Morphological characters that might be influenced by environmental parameters were measured by calculating the distance between the coordinates of the different landmarks in Excel 2007. For each fish, SL, body depth, head length (HL), an estimation of head surface (HS) by considering the head as a triangular shape (LM 8,14,21), eye length, eye depth, cheek depth, caudal peduncle depth and an estimation of the caudal peduncle area (CPA) by considering the tail as rectangular shape (LM 15, 16, 18, 19) were measured and a simplified HS/CPA ratio was calculated (Appendix Fig. 1 in Electronic Supplementary Material).

Statistical analysis

A general linear model (GLM) with SL or HL as covariate and year as independent factor was applied to test for the effect of time on the morphological characters. In this selective model, dependent variables, independent factors and their interactions were inserted. With the use of Multivariate Analyses of Covariance (MANCOVA), non-significant interactions were removed stepwise from each model; thereafter non-significant independent factors were removed stepwise. Significant interactions (int.act.) between SL and year were plotted to determine the effect of each factor. Estimated marginal means of all dependent variables were used to plot morphological character changes in time. We assumed that our dataset was representative for the natural population of haplochromines and expected a normal distribution of morphological characters. Almost all residuals of each of the 360 GLMs were normally distributed ($P > 0.05$, Shapiro–Wilk test, Shapiro and Wilk 1965). Six non-normally distributed residuals were found. Nonetheless, we included in these residuals in the GLMs as the observed values did not show large deviation from the expected normal distribution in the Q–Q plots. The *P* values of the GLM were corrected with a sequential Bonferroni test (Posch and Futschik 2008). To test the effect of year on SL, an analysis of variance (ANOVA) was used. A linear regression with the morphological characters as dependent and the SL as independent factor was performed. The residuals of this regression were used to test for randomness in the dataset with a Runs test (with mean as cut point). All statistical tests on the morphological characters were performed with SPSS 16.

Results

Shape changes in resurgent species, pristine versus perturbed period

Both sexes of all six species showed significant body shape changes between the pristine and the perturbed period (pairwise comparison between years, $P < 0.05$, Figs. 1, 2, 3) and a reduction of SL ($P < 0.01$; Fig. 3). The most pronounced changes occurred during the perturbed period (Figs. 2, 3; Appendix Tables 2 and 3 in Electronic Supplementary Material). Besides the effect of year, there was a significant effect of the covariates SL and HL for each GLM ($P < 0.001$). Males and females showed changes in the same direction. As males showed more pronounced changes than females (Appendix Table 4 in Electronic Supplementary Material), primarily the results of males are discussed.

As hypothesized, for the two resurgent species pyr and deg, the head surface/caudal peduncle area (HS/CPA) ratio decreased significantly in the perturbed period ($P < 0.05$). The resurgent species, lap, showed a similar trend although the decrease of the HS/CPA ratio was not significant. In contrast with our expectations, the other resurgent species, tan, increased its HS/CPA ratio in the perturbed period ($P = 0.049$; Fig. 3), mainly by increasing its body depth and head length (Appendix Fig. 2 in Electronic Supplementary Material).

All four resurgent species showed similar other morphological changes in time. The cheek depth (with SL and HL as covariates) increased significantly in the perturbed period for pyr, lap and deg ($P < 0.05$, Fig. 3; Appendix Table 5 in Electronic Supplementary Material). Against our expectations, the eye depth and length showed a similar inverse trend, ($P < 0.05$; Fig. 3; Appendix Fig. 2 in Electronic Supplementary Material). In the resurgent species tan, eye depth ($P = 0.001$), eye length and cheek depth showed the same trend as in the other resurgent species, though changes in eye length were not significant

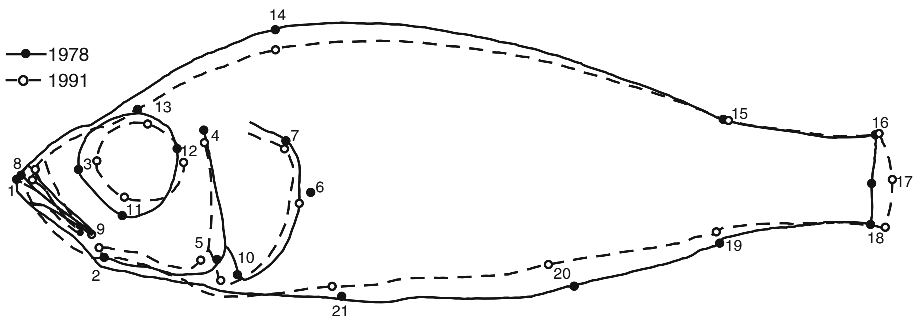


Fig. 1 Body shape outline of pyr males obtained from the DFA. The *continuous lines* and the *filled landmarks* represent the consensus of the year 1978. The *dashed line* and *blank landmarks* represent the consensus of the year 1991. Differences were enlarged three times for better visualization

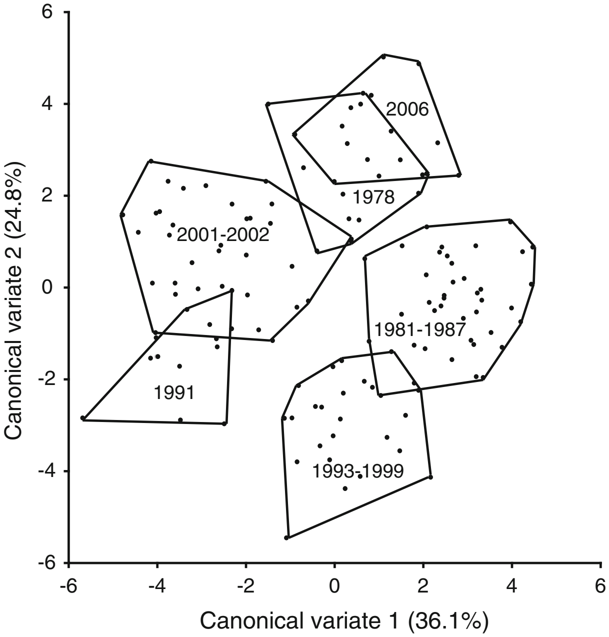


Fig. 2 Plot of pyr males from 1978 to 2006 obtained from the CVA. Each dot represents the body shape of one specimen. CV 1 and CV 2 explain together 60.9 % of the total body shape variation in years

and a significant interaction with SL was found for cheek depth (int.act. $P = 0.016$; Fig. 3; Appendix Fig. 2, Table 5 in Electronic Supplementary Material).

The changes in HS/CPA ratio for pyr were non-random ($P < 0.05$), but not for the other resurgent species. The changes in body depth, cheek depth, eye depth and eye length were non-random for all four resurgent species ($P < 0.05$).

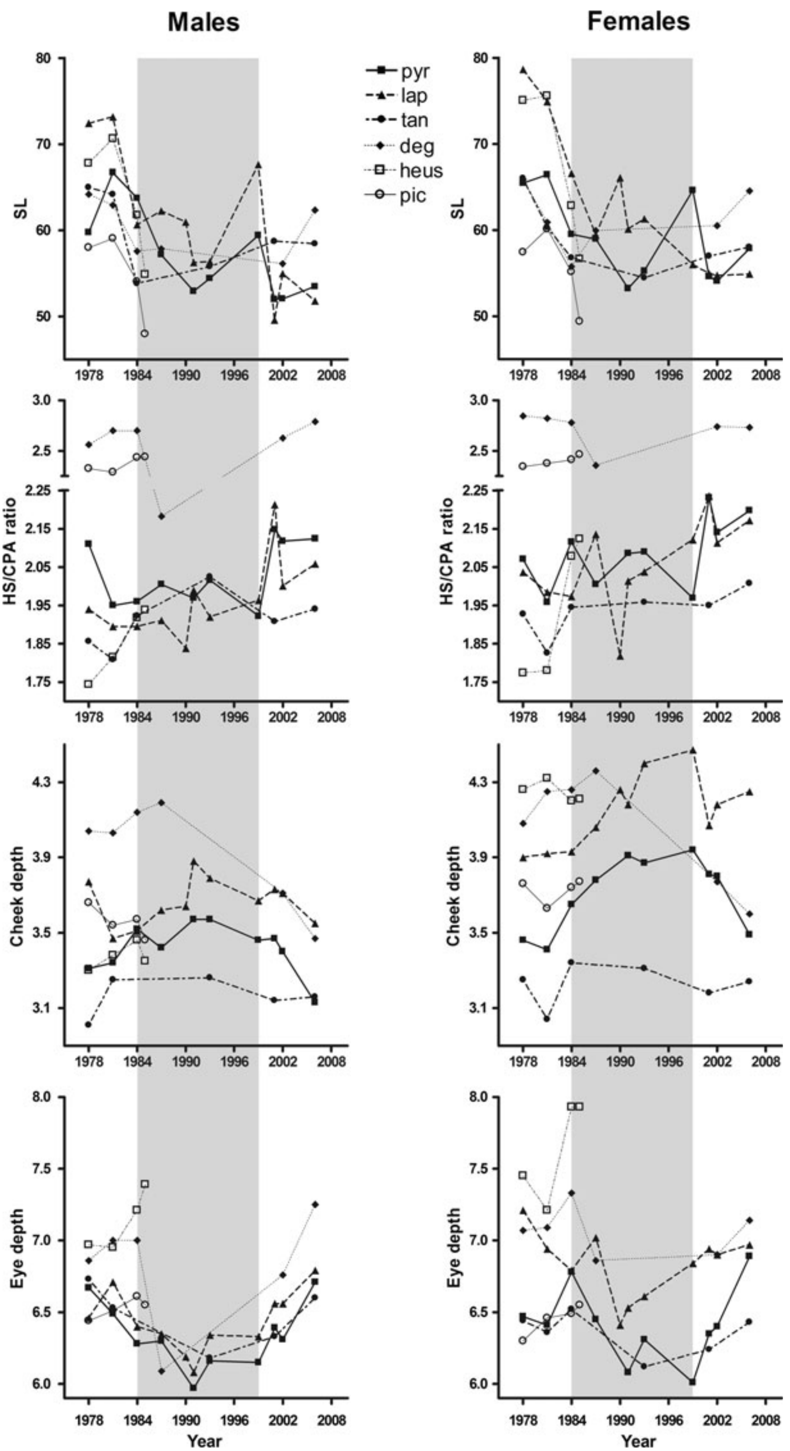
Shape changes in the extinct species, pristine versus perturbed period

There were some morphological changes that went into a different direction in the resurgent species compared to the extinct species. The extinct species heus showed an increase in the HS/CPA ratio during the perturbed period ($P = 0.002$; Fig. 3), while it decreased for the resurgent species pyr, deg and lap. In the resurgent species, the caudal peduncle area remained the same, or even increased in the deep bodied deg females ($P = 0.003$), whereas this character decreased in the extinct species pic and heus ($P = 0.012$ and int.act. $P = 0.063$ respectively), mainly due to the decrease of the caudal peduncle depth ($P < 0.001$ and $P = 0.001$ respectively; Appendix Fig. 2 in Electronic Supplementary Material).

In addition, the extinct species showed an increase in eye length during the perturbed period ($P < 0.05$, Appendix Fig. 2 in Electronic Supplementary Material), whereas three out of four of the resurgent species showed a significant decrease of this morphological character in the perturbed period.

Reversal in morphology in resurgent species, perturbed versus recovery period

During the recovery period, in three out of the four resurgent species (pyr, tan and lap), overall body shape changed back into the form of the pristine period ($P < 0.05$; Figs. 2, 4).


Males
Females
pyr
lap
tan
deg
heus
pic
SL
80
70
60
50
HS/CPA ratio
3.0
2.5
2.25
2.15
2.05
1.95
1.85
1.75
Cheek depth
4.3
3.9
3.5
3.1
Eye depth
8.0
7.5
7.0
6.5
6.0
1978
1984
1990
1996
2002
2008
Year

◀**Fig. 3** Plots of the estimated marginal means of the GLM of all species (plots of SL show means based on raw data). Each *line* represents the morphological character changes in time per species with SL as covariate. *Filled symbols* represent resurgent species, *blank symbols* represent extinct species. The *grey shade* represents the period when major ecological and morphological changes occurred. Plots of estimated marginal means with HL as covariate are not shown as they did not differ much from those with SL as covariate

Although lap showed a similar body shape alteration as tan and pyr, the 2006-form differed slightly from the 1978-form by having a somewhat smaller body depth, smaller caudal peduncle area and a slightly larger eye length and depth (Procrustes distance 0.0163, $P = 0.028$).

Morphological characters that showed a reversal of changes during the recovery period in all four species were the HS/CPA ratio, cheek depth, eye depth and eye length ($P < 0.05$; Fig. 3; Appendix Fig. 2 in Electronic Supplementary Material).

Discussion

Just like peppered moths, Galapagos finches, Bahamian lizards, Trinidadian guppies and threespine sticklebacks (Clarke et al. 1985; Grant and Grant, 1995; Losos et al. 1997; Reznick et al. 1997; Bell et al. 2004; Aguirre and Bell 2012), Lake Victoria haplochromines showed morphological changes within a decade. As in Galapagos finches, the most pronounced changes occurred during, and just after, major fluctuations in the environment.

Adaptations to Nile perch predation

Nile perch predation was associated with the major morphological changes found in this study. The decrease of SL in all six species has been reported before for some of these species, as well as a decrease in size at first maturity (Witte et al. 1995). Next to intensive trawling in the 1970s and early 1980s with mesh sizes that selectively caught the larger individuals (Witte et al. 1995), these size changes could be the result of Nile perch predation, which also may have been size selective (Witte et al. 1992a).

Conforming with our expectations, Nile perch predation resulted in a smaller HS/CPA ratio during the perturbed period in three out of four resurgent species (pyr, deg and lap,

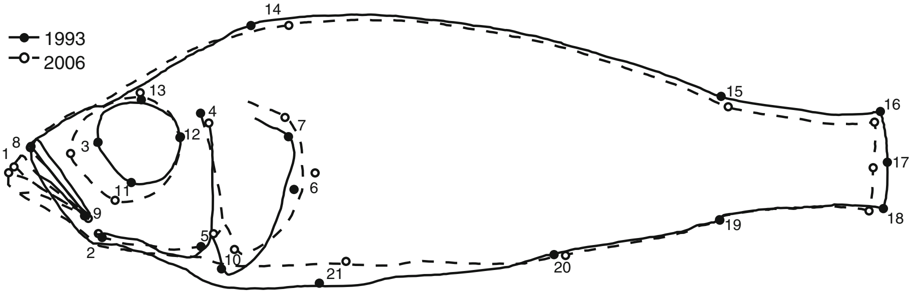


Fig. 4 Body shape outline of pyr males obtained from the DFA. The *continuous lines* and the *black landmarks* represent the consensus of the year 1993. The *dashed line* and *white landmarks* represent the consensus of the year 2006. Differences were enlarged three times for better visualization

although not significant for lap). Additional data from another successful resurgent species, the detritivore *H.* “paropius-like” showed a decreased HS/CPA ratio in specimens of 2006 compared to specimens from 1977 to 1984 (respectively 3.41 and 4.90, measured from average body outline; C. van Geest, J. C. van Rijssel, F. Witte, unpublished data). A smaller HS/CPA ratio has proven to be beneficial for mosquitofish (Langerhans et al. 2004; Langerhans 2009), threespine sticklebacks (Hendry et al. 2011) and guppies (Hendry et al. 2006) at high-predation sites, to enhance burst swimming speed, which is essential for predator escape performance (Blake 2004). Like in these species, the smaller HS/CPA ratio observed in the present study is in line with a response to increased predation by predatory fish.

Surprisingly, the resurgent species tan showed an increase in the HS/CPA-ratio in the perturbed period. As tan is the most slender haplochromine in the lake and the average width and volume of its head is much smaller than that of the other species (J.C. van Rijssel, unpublished data), we speculate that it might have been forced to increase its head surface (and thus HS/CPA-ratio) because of possible trade-offs (see below) with for instance a larger gill size. Despite the increase of the HS/CPA-ratio of the resurgent tan, the ratio remained in the same range as that of the other resurgent zooplanktivores (Fig. 3).

Nile perch predation did not have the same effect on the morphological changes and constraints of the two extinct or poorly recovering species. These species showed caudal peduncle area- and eye size- changes in the opposite direction of those of the resurgent species. This resulted in, amongst other things, a larger HS/CPA ratio for pic and heus (Table 2). Supplementary data for another poorly recovering zooplanktivore, *H.* “argens” showed an increase of the HS/CPA ratio as well, from 2.75 in 1979 to 3.75 in the 2000s (measured from average body outline). Although we lack an explanation for these changes in the opposite direction, negative impacts of an increased HS/CPA ratio may include impaired burst swimming speed. During the last decade, morphology-performance mapping has received increased attention in fish literature and it has been suggested that morphology-performance related changes can determine an individual’s fitness (Hendry et al. 2011). Our data support the suggestion that the ability to change the morphology in a performance enhancing direction may be beneficial to species survival.

Adaptations to larger prey with an inevitable trade-off

As a possible adaptation to larger prey consumed during the perturbed period (Van Oijen and Witte 1996; Katunzi et al. 2003; Kishe-Machumu 2012; J. H. Wanink, unpublished data; E. van Reenen and F. Witte, unpublished data), the present study found an increase in cheek depth in all four resurgent species. The increase in cheek depth could also have affected the eye size, as cheek depth and eye size are negatively correlated (Barel et al.

Table 2 Direction of morphological changes in all species

Character	Resurgent zooplanktivores (3)		Resurgent *P. degeni* (1)		Extinct/rare zooplanktivores (2)
	1970s–1990s	1990s–2000s	1970s–1980s	1980s–2000s	1970s–1980s
HS/CPA ratio	2↓, 1=	↑	↓	↑	↑
Cheek depth	↑	↓	↑	↓	=
Eye size	↓	↑	↓	↑	↑

Numbers represent the number of species changed, no numbers indicate changes in all species, ↑, increase; ↓, decrease; =, no change

1989). The latter is likely to be the case as the eye size of all four resurgent species showed a decrease in the perturbed period (both with respect to SL and HL). This decrease has been reported for pyr by Witte et al. (2008) as a possible trade-off for the accommodation of the larger gills. Most likely, both the larger cheek depth and larger gills in a smaller head have resulted in smaller eyes of these haplochromines. A study of the retinas of pyr and tan suggests that the reduction of eye size only had an influence on the blue light-sensitivity (single cones) and the visual resolution (for pyr), but not on the photopic sensitivity of the double cones. So, although the eyes did not increase in size, these species may have found a way to cope with the turbid environment by changing their retinal features (Van der Meer et al. 2012).

Reversal of morphology in resurgent species

During the recovery period, the environmental conditions in the lake were less harsh than in the perturbation period. Firstly, the Nile perch biomass was, during the recovery period, well below the level of the perturbed period (Matsuishi et al. 2006; Mkumbo et al. 2007; Kayanda et al. 2009). Secondly, some zooplanktivores (including *H. pyrrhocephalus* and *H. laparogramma*) have partly shifted their diet back to that of the pristine period, including again more zooplankton (Kishe-Machumu 2012; R. C. van der Stelt, J. C. van Rijssel, F. Witte, unpublished data). Thirdly, water transparency in the Mwanza Gulf in 2006 has increased again compared to the late 1980s (M. A. Kishe-Machumu, unpublished data). Fourthly, the lake-wide low oxygen levels seemed to be less harsh in the recovery period (Sitoki et al. 2010). It is likely that all these changes have resulted in the reversal of the body shape, the HS/CPA ratio, cheek depth and eye size in the studied species during the recovery period.

Haplochromines are not the only organisms showing this reversal in morphology. Peppered moths, Galapagos finches, Bahamian lizards and threespine sticklebacks all showed reversed morphological changes after restoration of the perturbed environment through fluctuating directional selection (Clarke et al. 1985; Grant and Grant 2006; Losos et al. 2006; Kitano et al. 2008), hybridization (Taylor et al. 2006), or by a form of reverse or relaxed selection (Teotonio and Rose 2001). So far, we lack sufficient (genetic) data to confirm if this is the case for the resurgent haplochromines as well.

Possible mechanisms behind the morphological changes

Phenotypic plasticity has been found to play a major role in body shape changes of African cichlids (Crispo and Chapman 2010a) and many other morphological traits (Chapman et al. 2000; Bouton et al. 2002a; Rutjes et al. 2009). Crispo and Chapman (2010a) found larger gills driven by hypoxia, which had an influence on body shape (deeper heads and shorter bodies), and similar results were found in the cyprinid *Barbus neumayeri* (Langerhans et al. 2007). A review of phenotypic changes in wild animal populations indicated that human induced environmental changes are an important source of phenotypically plastic responses (Hendry et al. 2008). However, haplochromine numbers were extremely low during the end of the 1980s and early 1990s (Witte et al. 1992b, 2012) and a strong selection pressure might have acted on these fishes. The morphological characters measured in this study show enough variation on which natural selection could have acted. Fast evolution of morphological traits by natural selection is not uncommon in vertebrates, which show adaptive radiation (Grant and Grant 2006; Losos et al. 2006; Kitano et al. 2008).

Unfortunately, so far, we lack the genetic data to confirm whether the rapid morphological changes are the result of phenotypic plasticity or natural selection.

Conclusions

From this study we conclude that rapid changes of morphological traits and their reversal occurred in Lake Victoria cichlids within a couple of decades. Predation appears to be a major driver of these changes. Natural selection and phenotypic plasticity or a combination of these two mechanisms are likely to be responsible for the contemporary morphological changes. Ongoing morphological and genetic studies, in combination with plasticity experiments in the laboratory, will provide us with a more detailed insight in the adaptive radiation of these fast evolving species.

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