

# Morphological distinctness despite large-scale phenotypic plasticity—analysis of wild and pond-bred juveniles of allopatric populations of *Tropheus moorii*

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**Abstract** Cichlids are an excellent model to study explosive speciation and adaptive radiation. Their evolutionary success has been attributed to their ability to undergo rapid morphological changes related to diet, and their particular breeding biology. Relatively minor changes in morphology allow for exploitation of novel food resources. The importance of phenotypic plasticity and genetically based differences for diversification was long recognized, but their relationship and relative magnitude remained unclear. We compared morphology of individuals of four wild populations of the Lake Tanganyika cichlid *Tropheus moorii* with their pond-raised F<sub>1</sub> offspring. The magnitude of morphological change via phenotypic plasticity between wild and pond-bred F<sub>1</sub> fish exceeds pairwise population differences by a factor of 2.4 (mean Mahalanobis distances). The genetic and environmental effects responsible for among population differentiation in the wild could still be recognized in the pond-bred F<sub>1</sub> fish. All four pond populations showed the same trends in morphological change, mainly in mouth orientation, size and orientation of fins, and thickness of the caudal peduncle. As between population differentiation was lower in the wild than differentiation between pond-raised versus wild fish, we suggest the narrow ecological niche and intense interspecific competition in rock habitats is responsible for consistent shape similarity, even among long-term isolated populations.

**Keywords** Cichlids · Geometric morphometrics · Interlandmark distances · Microsatellites · Lake Tanganyika

## Introduction

A central goal in evolutionary biology is answering the question about the origin of phenotypic divergence and the influence of environment on shaping phenotypes (e.g., Via and Lande 1985; Barel 1993; West-Eberhard 2003; 2005). Divergent natural selection has long been put forward as a major mechanism in the evolution of trophic specialization (Barel 1983; Bouton et al. 1997). Thereby natural selection acts on polymorphic traits by sorting variation towards novel niches in conjunction with the origin of novel species. More specifically, the evolution of reproductive isolation between populations by divergent natural selection arising from differences between ecological niches was named ecological speciation. This type of speciation was thought to be a general phenomenon that might occur in allopatry or sympatry, involve many agents of natural selection, and results from a combination of adaptive processes (Schluter 2000, 2001; McKinnon et al. 2004; Rundle and Nosil 2005). Particular circumstances induce periods of intensive innovation, a phenomenon termed adaptive radiation (Sturmbauer 1998; Robinson and Schluter 2000; Schluter 2000). Such periods occurred repeatedly during the history of our planet and are best studied in suitable model systems in which the process is currently ongoing or in an advanced stage. The enormously diverse species flocks of cichlid fishes in the East African Great Lakes are such model systems in which the occurrence and relative importance of parameters promoting speciation can be addressed (Meyer 1993).

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Phenotypic variation among individuals and populations may be due to genetic and/or environmental factors. West-Eberhard (1989) defined phenotypic plasticity as follows: the ability of a single genotype to produce an array of alternative phenotypes in response to environmental conditions. This may be manifested in morphology, physiological state, and/or behavior. The study of phenotypic plasticity has progressed significantly over the past few decades (Pigliucci 2005). Plasticity has been hypothesized to act as an important strategy for organisms to cope with environmental variation (Stearns 1989; Scheiner 1993), and a plastic response to a changing environment might be adaptive in that individuals displaying such a response have higher fitness than those that do not (Price et al. 2003). The role of phenotypic plasticity for evolution has been a hotly debated topic since West-Eberhard's book (2003), in which she postulated that the sequence of developmental plasticity, phenotypic accommodation and subsequently genetic accommodation, is the mechanism responsible for almost all evolutionary novelty, speciation, adaptive radiation, and macroevolution. In other words, evolution would proceed through adaptive developmental phenotypic plasticity. A number of different studies, reviews, and opinions followed, but the exact role of phenotypic plasticity in evolution remains controversial (e.g., De Jong and Crozier 2003; Pigliucci and Murren 2003; Behera and Nanjundiah 2004; de Jong 2005; Chapman et al. 2008).

Phenotypic plasticity in body shape and trophic morphology in response to different food types and feeding orientation was demonstrated for a variety of organisms (reviewed in Via et al. 1995; Agrawal 2001; West-Eberhard 2003). Fishes and especially cichlid fishes have been shown to be particularly plastic in their trophic morphology and behavior (Meyer 1987; Meyer et al. 1990; Wimberger 1991; Day et al. 1994; Huysseune 1995; Robinson and Wilson 1995; Hofmann 2003; Wintzer and Motta 2005; Solem et al. 2006; Aubin-Horth et al. 2007; Burmeister 2007), and this plasticity was put forward as one of the key factors promoting their evolutionary success (Greenwood 1965, 1984; Hoogerhoud 1986; Meyer 1987; Witte et al. 1990; Stauffer and Gray 2004). This group of fishes has successfully colonized several rivers and lakes, and these colonizers split into numerous species by colonizing all thinkable ecological niches. The East African Great lakes are particularly species rich, and each lake comprises hundreds of endemic species. The cichlids of Lake Tanganyika are morphologically, ecologically, and behaviorally the most diverse within the family Cichlidae (Fryer and Iles 1972; Greenwood 1984; Chakrabarty 2005; Koblmüller et al. 2008). To date only few studies on phenotypic plasticity on Lake Tanganyika cichlids exist. These focused on the plasticity of a variety of life history traits (growth, size and time of reproduction, social skills,

and cognitive abilities) using the split-brood approach (Taborsky 2006a, b; Arnold and Taborsky 2010; Kotrschal and Taborsky 2010).

The genus *Tropheus*, of which about 120 color morphs in six nominal species (Poll 1986) are currently described, is an ideal model to study evolutionary processes (Sturmbauer and Meyer 1992; Egger et al. 2007). *Tropheus* is one of the most abundant algae grazers in the upper littoral zone living in all types of rocky habitats (Sturmbauer et al. 2008). Consequently, sandy or muddy shores and river estuaries are strictly avoided and constitute barriers to gene flow (Sefc et al. 2007). Almost every continuous stretch of rocky shoreline is inhabited by its own color morph. In contrast to coloration, morphology turned out to be highly similar among allopatric populations and sister species (Sturmbauer and Meyer 1992), most probably due to the fact that *Tropheus* occupies the same niche in all allopatric habitats and due to stabilizing selection. However, recent studies showed that there are small but clear differences between populations in body shape (Maderbacher et al. 2008) as well as in a single viscerocranial element (Postl et al. 2008). Thus, the existence of patterns in the degree of phenotypic plasticity can be addressed by comparing allopatric populations or sister species which are morphologically constrained in similar ways.

This study compared the overall morphology of wild fish and pond-raised  $F_1$  offspring of the Lake Tanganyika cichlid *Tropheus moorii*. To this end, we raised offspring of four populations as independent replicates to test for common effects. This study design tested the hypothesis that environment-induced morphological differences do not affect shape differences among populations (Maderbacher et al. 2008; Postl et al. 2008). We asked if morphological differences among populations remain intact in a standardized pond environment or if morphological plasticity can annihilate population differentiation, in order to explore the relative proportion of genetically fixed and environment-induced effects on body shape. We quantified genetic variation among investigated populations and examined the pattern and extent of plasticity of body shape caused by the pond environment. We considered only a narrow size class of juveniles due to the known sexual dimorphism in adults of the study species *T. moorii* (Herler et al. 2010).

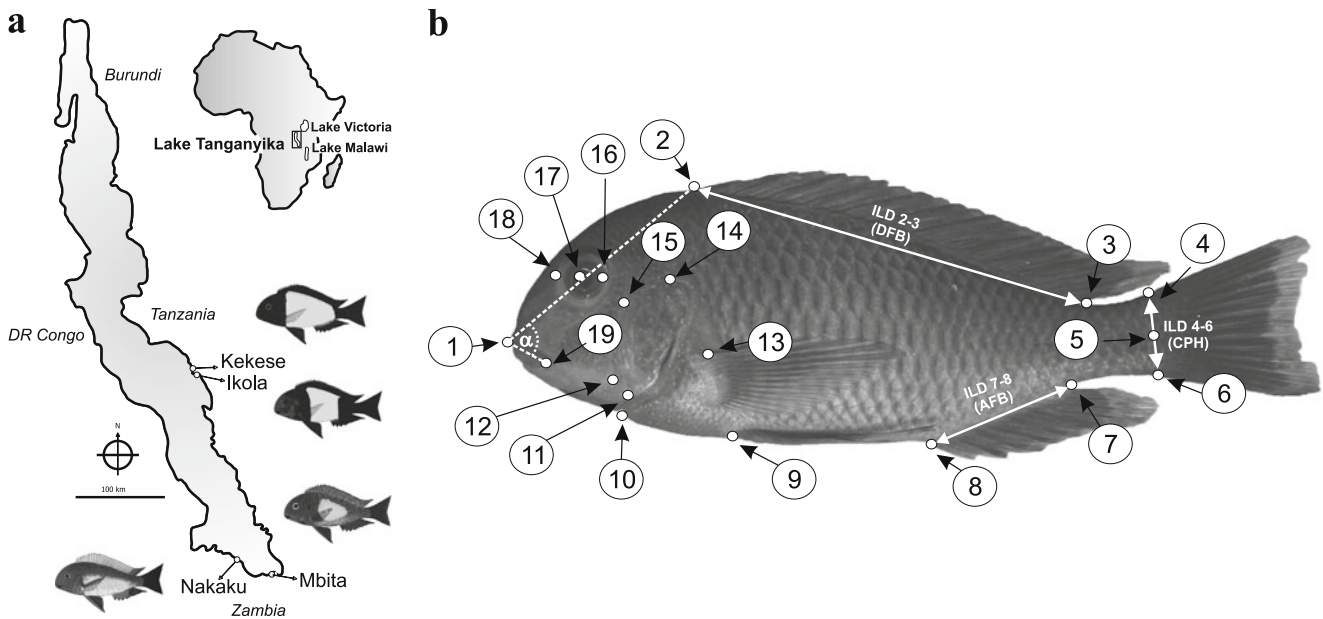
## Materials and methods

This study is based on specimens of four different populations of *T. moorii*. In March 2004, population samples were taken at Mbita Island (8°44'S, 31°06'E) and at Nakaku (8°38'S, 30°52'E). Both localities were located in the southern section of the lake. The other two populations were from the central eastern section of the lake. These fish were collected near

Ikola (6°41'S, 30°21'E) and Kekese (6°36'S, 30°17'E) in February 2007 (Fig. 1a). The population at Kekese is one of the few in which two *Tropheus* coexist and the study species *T. moorii* lives deeper than its ally *Tropheus polli*. Just after capture, a portion of the catch was sent to the University of Graz alive. Simultaneously, four identical breeding ponds of a size of 2×5 m and 70 cm water depth were stocked with wild adults from the four populations next to Lake Tanganyika to produce F<sub>1</sub> offspring. For Mbita and Nakaku, each pond was stocked with 25 males and 75 females; for Kekese and Ikola, ponds were stocked with ten males and 30 females. The number of stocked individuals was reduced for the Ikola–Kekese experiment as it turned out that few fish actually bred and thus territorial stress among adults could be reduced. Parental fish were removed after 1 year. Each pond was equipped with a standardized cobble landscape. Fish were fed daily with flake food in addition to naturally available algae growing on rocks within the pond. Ponds were cleaned daily including a water change of 25% of the pond water with freshly pumped lake water (temperature 27°C, pH 9.1). Thus, there was no difference in water chemistry between the wild and the pond environment. F<sub>1</sub> offspring were investigated as they reached about the size of our wild-juvenile sample. A small fin clip of each individual was taken for genetic analysis.

For determination of genetic differentiation among investigated populations, we analyzed nine microsatellite loci UNH154, UNH130, Pzep3, UNH908, Pzep2, UME003, UME002, TmoM11, and TmoM27 (Lee et al. 1995; Parker and Kornfield 1996; Zardoya et al. 1996; van Oppen et al. 1997; Carlton et al. 2002; Albertson et al. 2009). Methods of DNA extraction and PCR conditions are described in Koch et al. (2008). The inferred genotypic information (241 Mbita, 177 Nakaku, 201 Kekese, and 207 Ikola) from nine microsatellite loci was evaluated for deviations from Hardy–Weinberg equilibrium and linkage disequilibrium using the software package Arlequin 3.11 (Excoffier et al. 2006). All nine microsatellite loci confirmed Hardy–Weinberg expectations and testing for linkage equilibrium revealed that markers were inherited independently. Genetic characterization was based on estimates of allele and genotype frequencies, gene diversity, and allelic richness. Pairwise F<sub>ST</sub> values were calculated in Arlequin.

For morphological analysis, we restricted our comparisons to a narrow size class between 30 and 65 mm standard length. The data considered in morphometric analysis included 114 juveniles from wild populations (23 Mbita, 22 Nakaku, 32 Kekese, and 19 Ikola) and 335 pond-bred F<sub>1</sub> offspring (114 Mbita, 158 Nakaku, 31 Kekese, and



**Fig. 1** Sampling locations and landmark set. **a** Map of Lake Tanganyika with details on sampling locations and drawings of the four color morphs from Schupke (2004). **b** Landmark positions for geometric morphometric analysis and the angle ( $\alpha$ ) describing mouth orientation. 1 Anterior tip of the snout; 2, 3 anterior and posterior insertion of the dorsal fin; 4, 6 upper and lower insertion of caudal fin; 5 midpoint of the origin of the caudal fin; 7, 8 posterior and anterior insertion of the anal fin; 9 insertion of the ventral fin; 10 ventral tip of

cleithrum; 11 most ventral point of the border between inter-operculum and sub-operculum; 12 the point where pre-operculum, inter-operculum, and sub-operculum get in contact; 13 upper insertion of the pelvic fin; 14 dorsal origin of the operculum; 15 dorsal end of the pre-opercular groove; 16 and 18 lie at the extreme of the orbit along the antero-posterior body axis; capture the width of the bony orbit. 17 Center of the eye, 19 most posterior point of the lips

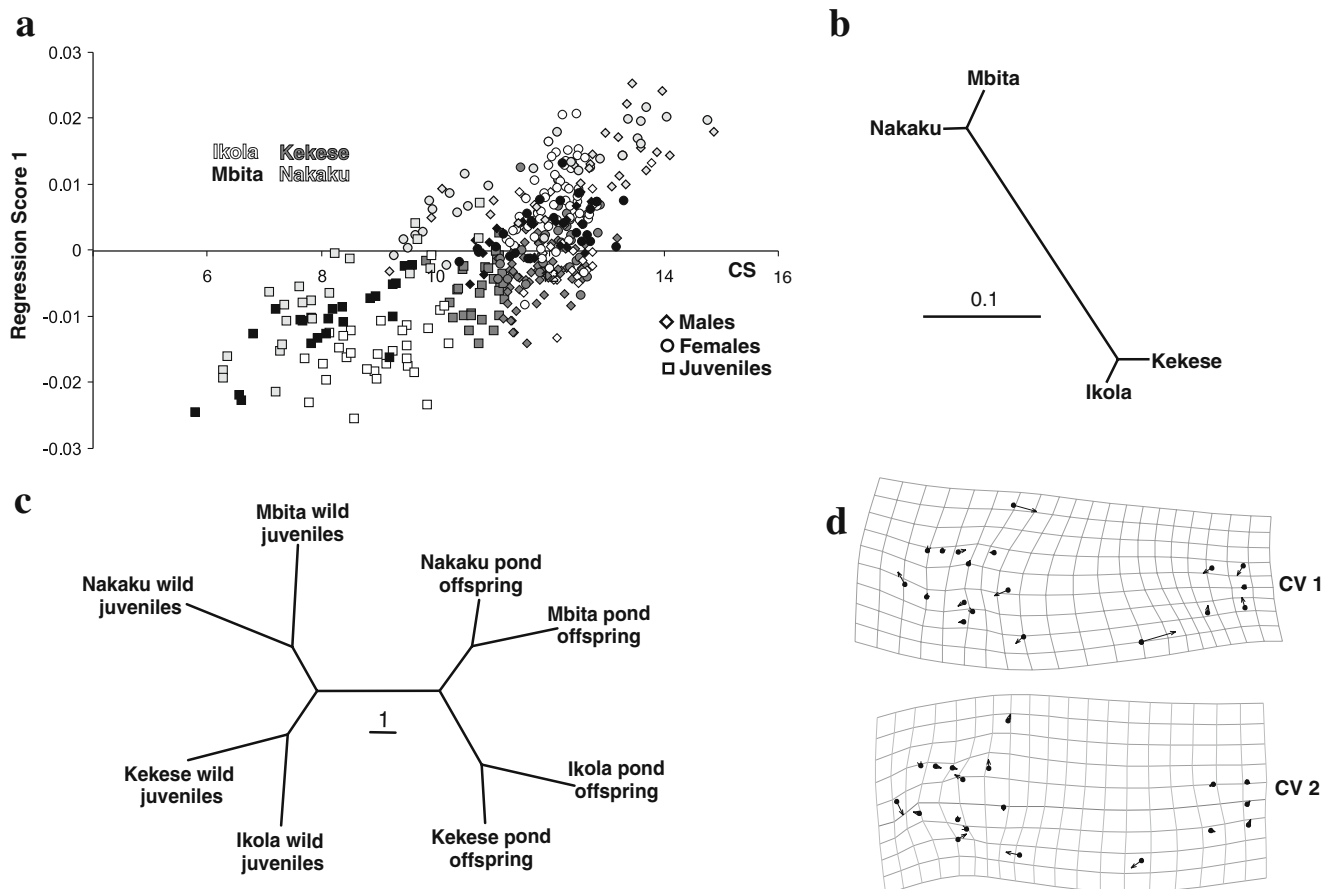
32 Ikola). Digital images of anesthetized specimens were obtained using a flatbed scanner (Herler et al. 2007). Coordinates of 19 landmarks (Fig. 1b) were digitized using TpsDig 2.10 (Rohlf 2006).

We used a geometric morphometric approach based on Procrustes methods (Bookstein 1996; Dryden and Mardia 1998). By using residual components of regression of shape on size, the allometric component of within-group variation as well as size-related differences between groups were considered. To examine the variation among populations and environment, we performed a canonical variate analysis (CVA; Mardia et al. 1979). An unrooted neighbor-joining tree based on Mahalanobis distances was created using the program PAST (Hammer et al. 2001). A principal component analysis (PCA) based on the covariance matrix of landmark data, including all individuals, was carried out to investigate overall effects of environment on morphology. A discriminant function analysis was done to find features of shape that have a maximal difference between environments relative to the variation within populations. Analyses

were carried out in MorphoJ (Klingenberg 2011). In addition to the comparisons of overall shape, we applied discrete measurements in form of interlandmark distances (ILD). All possible distances between 19 landmarks (Modicos; Carvajal-Rodríguez and Rodríguez 2005) were generated. Selected distances (distance between landmarks 2 and 3; 4 and 6; 7 and 8) were related to standard length and compared by Kruskal–Wallis tests among wild juveniles and pond-bred  $F_1$  generation. To test if there are any differences in mouth orientation, we additionally measured the angle  $\alpha$  between landmarks 1, 2, and 19 for a random sub-sample of 40 wild juveniles and 40 pond  $F_1$  offspring on digital images in TpsDig 2.10. Statistical analyses were performed in PAST (Hammer et al. 2001).

## Results

Moderate genetic differentiation was observed between Mbita and Nakaku ( $F_{ST}=0.055$ ;  $p<0.0001$ ), and Ikola and



**Fig. 2** Genetic and morphological discrimination between populations and environments. **a** Regression of shape (Procrustes coordinates) on centroid size (estimating the specimen size) including wild male, female, and juvenile individuals of the four study populations. **b** Unrooted tree by the neighbor-joining method on the  $F_{ST}$  distance

matrix based upon nine microsatellite loci of the populations at Nakaku, Mbita, Kekese, and Ikola. **c** Unrooted neighbor-joining tree based on Mahalanobis distances obtained from a CVA on landmark data of the four populations in two different environments. **d** Deformation grids according to the two CV axes

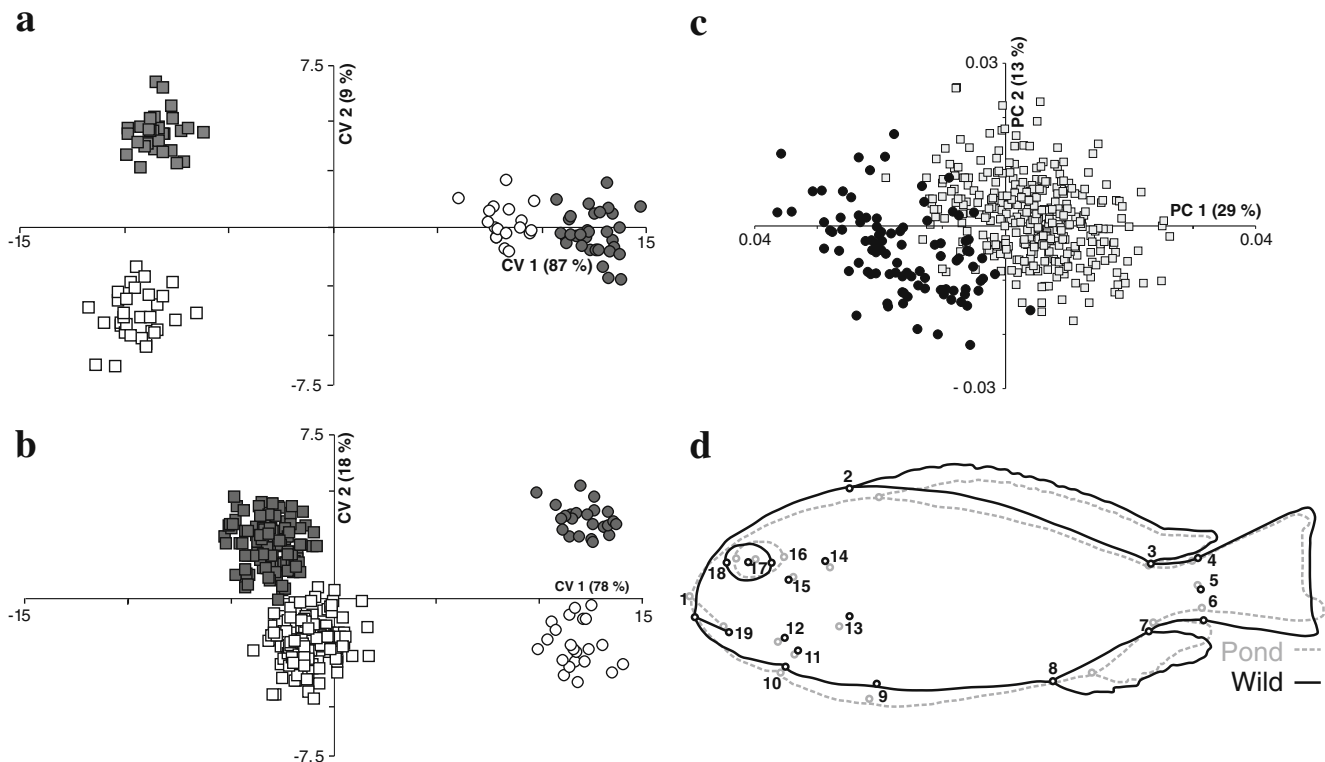
Kekese ( $F_{ST}=0.049$ ,  $p<0.0001$ ), while high genetic differentiation was detected among eastern versus southern populations ( $F_{ST}>0.25$ ,  $p<0.0001$ ; Fig. 2b, Table S1). Morphometric data showed a linear size–shape relationship (Fig. 2a), albeit we restricted our comparisons to a narrow size class between 30 and 65 mm standard length.

Overall, the pattern of morphological differentiation among populations paralleled that seen with genetic differentiation (Fig. 2c). There is also high morphological differentiation between southern and eastern populations. However, analysis of pond-bred juveniles of the four study populations yielded a surprisingly large change in morphology reflected by 2.4-fold larger Mahalanobis distances among wild versus pond-bred specimens, irrespective of population (Fig. 2c; Table S2). The deformation grids shown in Fig. 2d highlight these marked differences, whereby canonical variate axis 1 predominantly reflects the differences between the two environments and CV axis 2 those between populations. When the two population pairs from the eastern and southern region were analyzed separately, the CVA scatter plots visualized the notable excess of environmentally induced plasticity in relation to

the morphological divergence among the wild populations (Fig. 3a, b). In both CVA scatter plots, wild juveniles and pond-bred F<sub>1</sub> offspring could be clearly separated along CV axis 1, which means the pond effect goes in consistent direction in all four populations. Populations are clearly separated from each other along CV axis 2, except the wild Ikola and Kekese individuals.

To test for the generality of the phenomenon of a pond effect, a PCA of the complete landmark data set was carried out without pre-defining group assignment.

Wild juveniles and pond-bred F<sub>1</sub> offspring overlapped somewhat along both of the first two PC factors, but a relatively strong differentiation was nevertheless observed in multivariate space with most wild individuals positioned to the lower left (more negative) of the graph, and most pond-bred F<sub>1</sub> individuals to the upper right (more positive) (Fig. 3c). We found that the most pronounced shape changes concerned the orientation of the mouth, a backward movement of the origin of the dorsal fin and the anal fin resulting in a surface reduction and a narrower caudal peduncle (Fig. 3d). In all four populations, the discriminant function could separate wild and pond juveniles without



**Fig. 3** Shape change as a cause of different environment. **a** Canonical variate analysis on shape data including wild juveniles and pond-bred F<sub>1</sub> offspring of Kekese and Ikola (Kekese wild juveniles shaded circles; Ikola wild juveniles open circles; Kekese pond offspring shaded squares; Ikola pond offspring open squares) and **b** Mbita and Nakaku (Mbita wild juveniles shaded circles; Nakaku wild juveniles

open circles; Mbita pond offspring shaded squares; Nakaku pond offspring open squares). **c** Principal component analysis on shape data including all wild juveniles (filled circles) and pond-bred F<sub>1</sub> offspring (shaded squares) of four populations of *T. moorii*. **d** Demonstration of shape changes in different environments using a warped outline drawing (scaling factor=0.08) according to PC 1



any overlap, so that every specimen can be correctly allocated. Individually, each population showed the same direction and nearly the same magnitude of shape change from wild to pond individuals (Fig. 4).

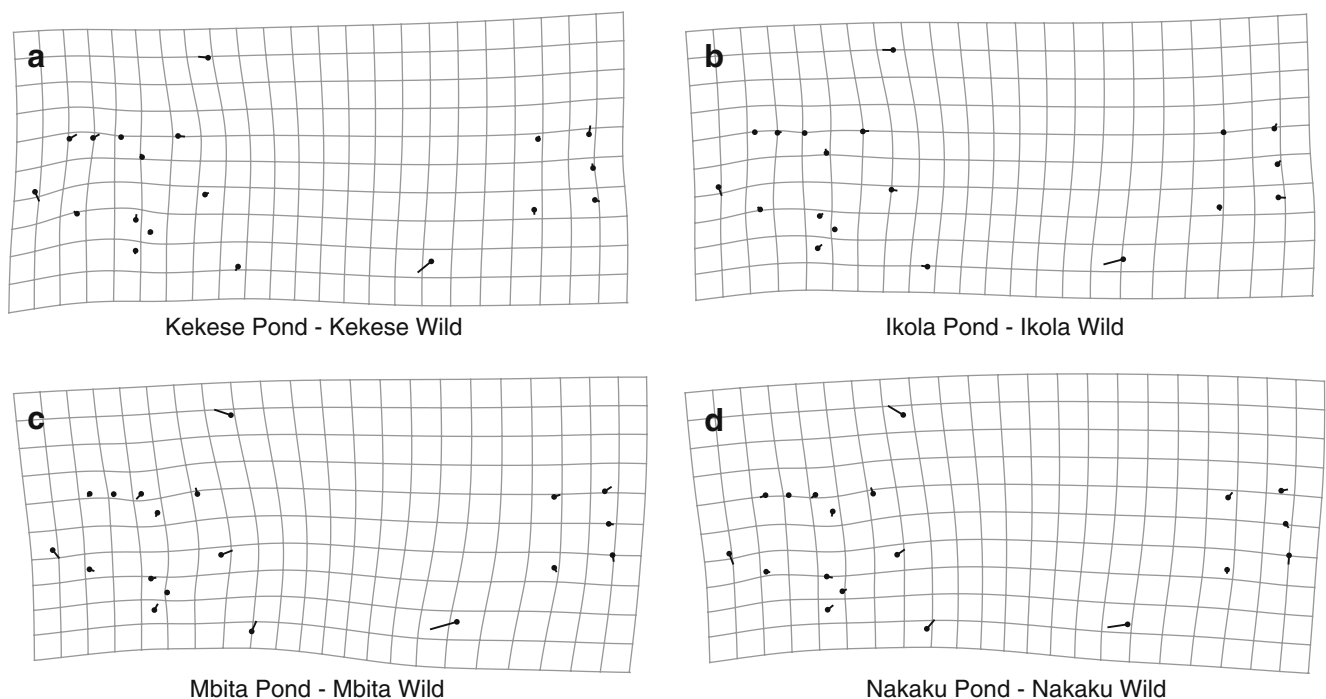
Selected body measurements were significantly different ( $p < 0.0001$ ) between wild juveniles and pond-bred  $F_1$  offspring and could be equalized with traditional measurements (ILD 2–3=dorsal fin base length, 4–6=caudal peduncle height, and 7–8=anal fin base length; Fig. 5a–c). The angle between insertion of the dorsal fin, tip of the snout, and most posterior tip of the lips was about  $4^\circ$  larger in pond-bred  $F_1$  juveniles than in wild juveniles, meaning that wild fish had a more inferior mouth position (Fig. 5d).

## Discussion

The innovative aspect of our study was to consider the degree and pattern of phenotypic plasticity in relation to morphological differences found in natural populations which are subject to similar selective forces. Therefore, we contrasted the wave-exposed and competitor- and predator-driven natural rock environment of *Tropheus* with the fully calm and predator-free environment of a concrete pond with standardized rock architecture and feeding regime. In this environment, we produced  $F_1$  offspring of four different populations and color morphs, which were tested for Hardy–Weinberg equilibrium. This design was

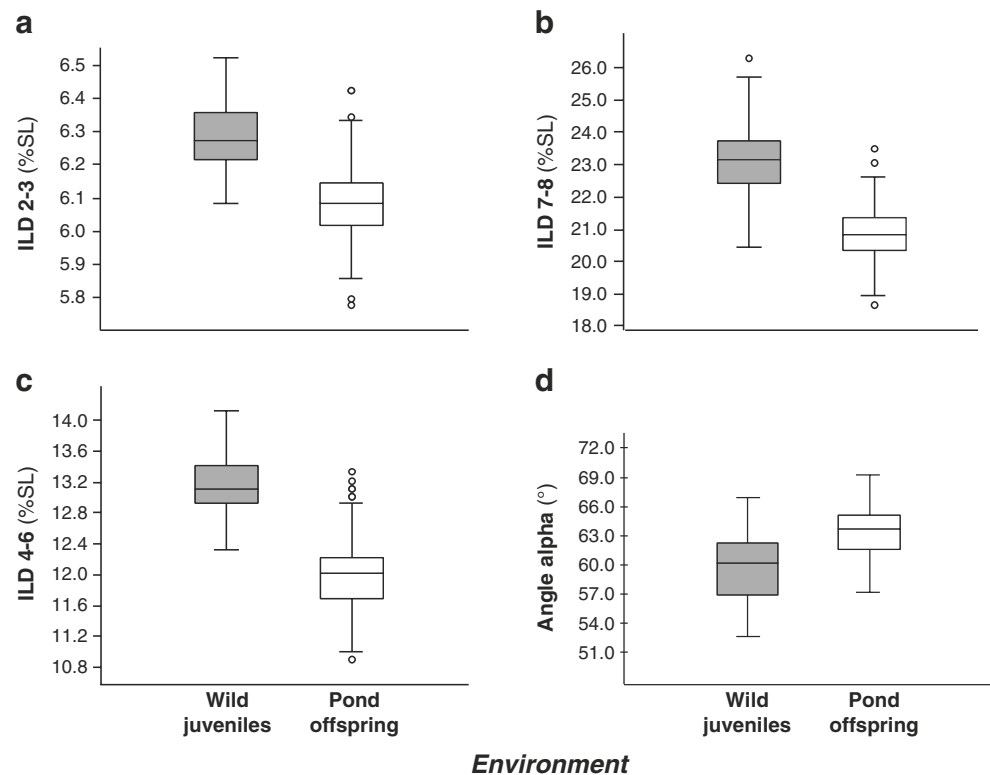
chosen to demonstrate the relative magnitude of phenotypic and genetic contribution to population differences in evolving populations. As argued by Price et al. (2003), phenotypic plasticity may be a fitness-relevant trait subject to natural selection. In fact, the degree of morphological plasticity can have profound influences on evolutionary and ecological outcomes. It could, for example, influence the ability to track environmental changes and thus regulate the potential for character divergence. Furthermore, competitive interactions between species might be altered if one of the competitors has a highly plastic morphology that enables it to efficiently utilize a wider range of resources than would otherwise be possible (Olsson and Eklöv 2005). It was also shown that phenotypic plasticity involves life history traits with adaptive significance such as growth, size and time of reproduction, social skills, and cognitive abilities (Taborsky 2006a, b; Arnold and Taborsky 2010; Kotrschal and Taborsky 2010).

Our study species is a highly specialized algae feeder that lives in a variety of rock habitats, ranging from moderately sloping cobble shores to steeply descending solid rock, so that phenotypic plasticity might be relevant for its fitness and evolution. In previous studies, we have shown that populations of *Tropheus* could be discriminated based on subtle morphological differences. Even if such low levels of variation are expected between populations at early stages of evolutionary divergence, they may even be superimposed by phenotypic plasticity. Thus, the genetic



**Fig. 4** Magnitude and positions of shape differences among pond-bred  $F_1$  offspring and wild juveniles shown for each population separately (a Kekese; b Ikola; c Mbita; d Nakaku). Grids derived from discriminant analysis in MorphoJ

**Fig. 5** Comparison of discrete measurements between the two environments (pond offspring *open squares*; wild juveniles *shaded squares*). Box–whisker plots of three significantly different interlandmark distances ( $p < 10^{-41}$ ): **a** dorsal fin base length, **b** caudal peduncle height, and **c** anal fin base length (wild juveniles  $n=96$ , pond offspring  $n=335$ ) and of measurements of **d** the angle  $\alpha$  between landmarks 2, 1, and 19 (wild juveniles  $n=40$ , pond offspring  $n=40$ ) on specimens from the two environments ( $p=3.5 \times 10^{-6}$ )



component of population variation is particularly difficult to demonstrate in evolutionarily young populations. Therefore, it is crucial to assess the degree of phenotypic plasticity in a standardized design. Our experiment indeed showed that the magnitude of morphological change via phenotypic plasticity can exceed population differences by a factor of 2.4 even though populations of *Tropheus* were separated for about 100,000 years (Sturmbauer et al. 2005). At the same time, we demonstrated that there are also population-specific differences that remain intact in individuals raised in a standardized environment.

The observed changes in the common pond environment were consistent in all four study populations. The most impressive change concerns orientation of the mouth. In cichlids, but also in other fish families, structural differences in trophic morphology have been related more to the way food is captured and processed than to the type of food consumed (Barel 1983; Yamaoka 1997; Wintzer and Motta 2005). Hence, the change in the angle of the mouth could be interpreted as a response to less scraping from the rocks, in addition to more sucking in the water column, as a consequence of the availability of flake food in the ponds. In the wild, an inferior subterminal mouth is characteristic for *Tropheus* and is used to scrape algae from rocks. Various studies demonstrate linkage between functional morphology in cichlid jaws and differences in feeding

performance for Lake Victoria cichlids (Bouton et al. 1997, 1998, 2002). Albertson and Kocher (2001) compared jaw morphologies between two closely related cichlid species of Lake Malawi and found that many aspects of shape differences clearly reflect different modes of feeding. Fin size and shape is expected to affect swimming performance. High aspect ratios, defined as the square of the span divided by the fin area, characterize fast-swimming fishes, while low ratios are measured in fishes with low swimming performance but better maneuvering abilities (Weihs 1989; Videler 1993). Changes in fin structure of pond individuals could be a response to more quiet water and lack of predation within the ponds. Another interesting aspect concerns the population of Kekese, as it lives in deeper water than the remaining study populations due to the sympatry of a second *Tropheus*. While the pond effect goes in consistent direction (Fig. 3a, left side; Fig. 4), there are population-specific components in body morphology. We observed a somewhat distinct segregation among the populations from Ikola and Kekese (Fig. 3a, right side). This may be due to the fact that the Kekese population shifted towards greater water depths due to the presence of a second *Tropheus* species in its habitat, but this remains to be tested in a future study.

From the non-random pattern of the observed morphological changes, we conclude that they were not caused by a simple release of selection pressure but rather as a plastic

response to a novel environment. A second issue concerns the magnitude of change between the wild populations and the pond fish. We observed that the magnitude of morphological change via phenotypic plasticity outreaches that found among natural populations by a factor of 2.4. This indicates that *Tropheus* has a higher potential for phenotypic plasticity than the degree of population variation observed. Our interpretation concerning the evolutionary significance of phenotypic plasticity is that there is intense selection within each of those spatially and genetically isolated species communities, keeping *Tropheus* in its relatively narrow trophic niche. This type of stabilizing selection is enforced by both biological interactions with other species in the habitat and similar selective forces from abiotic characteristics of the rock habitats of the four study populations. Because observed morphological variation among the four study populations remained intact after being exposed to a common environment, we also conclude that part of the morphological differences among *Tropheus* populations are indeed genetically determined.

To conclude, our study connects to West-Eberhard's hypothesis that the sequence of developmental plasticity, phenotypic accommodation, and subsequently genetic accommodation might be the most important mechanism for the origin of evolutionary novelty, speciation, adaptive radiation, and macroevolution. In allopatric populations of *Tropheus*, the scope of phenotypic plasticity is not fully exploited, so that there is still potential for adaptive developmental phenotypic plasticity should the environment change more radically. An organism's phenotype is affected by both internal (genetic and developmental processes) and environmental factors (Albertson and Kocher 2006) and thus both can contribute to the fitness of an individual. Ontogenetic plasticity can be subject to natural selection, as each genotype has the potential to produce a range of phenotypes, as a second-order response to more short-term fluctuations of the environment. However, current research in adaptation is predominantly focused on uncovering the genetic basis of specific traits of evolutionary importance through quantitative genetic analysis. A more explicit consideration of phenotypic plasticity will necessarily complicate such approaches, and we suggest that it is equally important to assess the scope of phenotypic plasticity when addressing the genetic basis of differentiation.

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**Conflict of interest** The authors declare that they have no conflict of interest.

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