

Body shape variation in relation to resource partitioning within cichlid trophic guilds coexisting along the rocky shore of Lake Malawi

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Abstract—To appreciate better how cichlids segregate along the trophic, spatial and temporal dimensions, it is necessary to understand the cichlids' body design, and its role in resource partitioning. We investigated body shape variation, quantified using landmark-based geometric morphometrics, among cichlid species belonging to algal and zooplankton feeders coexisting along the rocky shores of Lake Malawi, in order to elucidate the adaptive significance of body shape. Significant differences were found within zooplankton feeders in which *Copadichromis borleyi* had a shorter gape, smaller eyes and shorter caudal peduncle relative to *Ctenopharynx pictus* and, within algal feeders, *Labeotropheus fuelleborni* had a shorter and inferior subterminal gape, and shorter head relative to *Petrotilapia genalutea*. Variation among species is discussed with reference to trophic and feeding microhabitat differentiation which enables us to appreciate the role of body shape in enhancing ecological separation, and thus leads to coexistence among cichlid species.

Keywords: Cichlidae; geometric morphometrics; Lake Malawi; resource partitioning; trophic guild.

INTRODUCTION

Two classic hypotheses have been posited to explain why there are many cichlid species in the African Great Lakes, viz.; Lakes Victoria, Malawi and Tanganyika (but see Kornfield and Smith, 2000). The first states that the cichlid morphological design, particularly of the feeding apparatus, is a key innovation for rapid speciation

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(Liem, 1973; Greenwood, 1991; Galis and Metz, 1998; but see Seehausen, 2000). The second promotes that sexual selection is the major force driving speciation (Turner and Burrows, 1995; Seehausen et al., 1997). Though the two theories seem to be in conflict, a scientific approach embracing both ideas may be the best way to understand why Cichlidae is the most speciose family in the Great Lakes of Africa (Galis and Metz, 1998). Sexual selection may be a mechanism that produces reproductively isolated forms/species, but it falls short of accounting for the adaptive radiation that enables cichlids to exploit almost all available resources within the great lakes (Bouton et al., 1999). In addition to understanding how cichlid radiation evolved, another important question is: ecologically, how do so many cichlid species coexist? Ribbink et al. (1983) reported that the haplochromine cichlids of Lake Malawi are found at high densities especially on the rocky shore areas (e.g., 15 species at West Thumbi Island with ca. 20 adults/m²) and Hori et al. (1983) found many adult fishes (13 species with ca. 18/m²) inhabiting the rocky shores of Lake Tanganyika. Such high densities suggest intense competition for space as well as for food resources. Therefore, the way in which these cichlids partition available resources is likely to be one of the main factors that enhance their coexistence.

Cichlids, like other fishes, are known to partition resources in three major dimensions namely; trophic, spatial and temporal (Witte, 1984; Ross, 1986; Bouton et al., 1997). Trophically, cichlids segregate through food size partitioning, quantitative differences in food composition, differences in food collecting strategies and feeding microhabitat niche partitioning (Yamaoka, 1982, 1997; Hori, 1983, 1991; Witte, 1984; Goldschmidt, 1990; Reinthal, 1990; Yuma, 1994; Kohda and Tanida, 1996; Genner et al., 1999a, b). In most cases, such trophic groups are identified by structural differentiation of their trophic morphology, even though such differentiation is related more to the way the food is captured and processed than to the type of food consumed (Barel, 1983; Yamaoka, 1997). However, instead of studying the trophic apparatus, which has received much attention from previous researchers (e.g., Reinthal, 1989; Albertson and Kocher, 2001), we investigated overall cichlid body shape. Differentiation in overall body shape tends to be ignored, despite the fact that diversity in body shape has been reported in this group by Fryer and Iles (1972), and has been shown to be important in the evolution of some lineages of Tanganyikan cichlids (e.g., Rüber and Adams, 2001).

In this study, we used four species that coexist along the rocky shores of Lake Malawi representing zooplankton feeders (*Ctenopharynx pictus* and *Copadichromis borleyi*), and epilithic algal feeders (*Petrotilapia genalutea* and *Labeotropheus fuelleborni*). Zooplankton and algal feeders were chosen since they are the most dominant trophic guilds among Lake Malawi's cichlid fishes. *Ctenopharynx pictus* is benthophagous, but also feeds from the water column when zooplankton is in abundance (T. Sato, pers. comm.), while its counterpart *Copadichromis borleyi* is reported to feed from the open water (Ribbink et al., 1983; Konings, 1990). The two algal feeders favour shallow rocky areas, although there is some segregation between them such that *L. fuelleborni* is commonly found on the sediment-free,

wave-beaten sides of the rocks (Ribbink et al., 1983; Konings, 1990). It is in the light of this partitioning of food (zooplankton versus algae) and feeding microhabitat, that prompted us to conduct this study in order to investigate if there are any morphological differences among species that may reflect adaptive significance of body shape to such resource partitioning. Hence our main purpose is to answer the following question; is there body shape variation among these species that can be related to resource partitioning (i.e. trophic and spatial dimensions) and thus enhance ecological separation that may facilitate their coexistence?

MATERIALS AND METHODS

SCUBA divers, using hand nets and gill nets, captured the following species from West Thumbi Island in the Cape Maclear region of Lake Malawi (14°00'S 34°50'E): *P. genalutea* ($n = 30$, standard length, SL, 75.9-116.4 mm, in April 2001) and *Copadichromis borleyi*, *Ctenopharynx pictus*, *L. fuelleborni* ($n = 30$ per species, SL, 64.2-127.5, 65.6-101.3, 69.7-104.2, respectively, in November 2001). Fishes were placed in 10% formalin solution soon after capture and each specimen was injected with formalin. They were then transferred to 70% ethanol and stored until examination.

Geometric morphometric and statistical analyses. Landmark-based geometric morphometric (GM) techniques (Rohlf and Marcus, 1993) were used to quantify cichlid body shape. GM methods are preferable to quantifying body shape over linear distances because the geometric relationships among the variables are preserved throughout the analysis. Thus, in addition to a statistical assessment of shape differences, graphical representations of shape change can also be presented. An OLYMPUS digital camera, with a resolution of 3.3 megapixels, was used to take images of all specimens. The x , y coordinates of 12 homologous landmarks (fig. 1) were digitised from the left side of each individual using the software TPSDIG32 (Rohlf, version 1.19, 2001). These landmarks were chosen for their capacity to capture overall body shape. Unfortunately, direct analysis of the landmark coordinates is not possible, as they contain components of both shape and non-shape variation. To obtain shape variables, non-shape variation (due to size, location and orientation) in the landmark coordinates was removed through the Generalised Procrustes Analysis (GPA) (Rohlf and Slice, 1990). GPA removes non-shape variation by scaling all specimens to unit size, translating them to a common location, and rotating them so that their corresponding landmarks line up as closely as possible. From the aligned GPA coordinates, an overall average (consensus) configuration is estimated and used in later analyses. Shape variables are then obtained from the aligned specimens using the thin-plate spline (Bookstein, 1989, 1991) and the standard formula for the uniform shape components (Bookstein, 1996). Together, the uniform and non-uniform components are treated as a set of shape variables for statistical comparisons of shape variation within and among groups (e.g., Caldecutt and Adams,

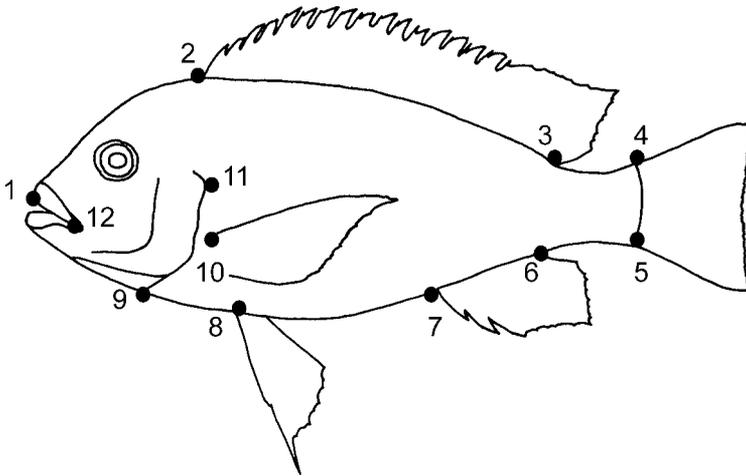


Figure 1. Positions of landmarks used to define body shape collected from the left side of each fish; 1. anterior tip of snout; 2 and 3. anterior and posterior insertion of the dorsal fin; 4 and 5. upper and lower insertion of caudal fin; 6 and 7. posterior and anterior insertion of the anal fin; 8. insertion of the pelvic fin; 9. insertion of the operculum on the profile; 10. upper insertion of pectoral fin; 11. posterior extremity of the operculum; 12. posterior extremity of the gape.

1998; Adams and Rohlf, 2000; Rüber and Adams, 2001; Kassam et al., in press). In addition to the overall consensus configuration, we calculated the consensus configurations for each individual group. These were used to generate representations of shape of each group relative to the overall mean shape. The above-mentioned procedures were implemented with the software TPSRELW (Rohlf, version 1.24, 2002a).

Several statistical procedures were used to investigate variation among species. First, to determine if body shape varied significantly among species, a multivariate analysis of variance (MANOVA) was performed (e.g., Rohlf et al., 1996; Adams and Funk, 1997; Caldecutt and Adams, 1998; Kassam et al., in press). Secondly, pairwise multiple comparisons were performed to determine which species (if any) significantly differed from one another. These were based on generalised Mahalanobis distance (D^2) from a canonical variates analysis (CVA) with the critical α (0.05) for these tests being adjusted using the Bonferroni procedure. TPSSPLIN software (Rohlf, version 1.16, 2002b) was used to generate thin-plate spline deformation representations of group means.

Supplemental measurements. Because of their significance in the feeding ecology of fishes (Fryer and Iles, 1972; Rüber and Adams, 2001), the following traditional morphometric characters were also measured; interorbital width, measured as the distance on the dorsal part of the head giving the least width between bony margin of the left and right orbit; gape width, the distance between the ends of the mouth slit on the left and right side. All measurements were taken by using digital

calipers to the nearest 0.1 mm. Analysis of variance (ANOVA) was performed to determine if these characters differed significantly among species.

Finally, a two-block partial least squares analysis was performed to investigate if there was any association between body shape and the two trophic characters measured. Two-block partial least squares analysis is a multivariate correlation technique that describes the covariance between two sets of variables (e.g., Rohlf and Corti, 2000; Rüber and Adams, 2001). This analysis was performed in TPSPLS software (Rohlf, version 1.09, 2002c).

JMP software (Sall et al., version 3.2, 1998), and NTSYS-PC software (Rohlf, version 1.80, 2000) were used for the ANOVA and CVA analyses, respectively.

RESULTS

Body shape variation. Significant differences in body shape among species were revealed through MANOVA (Wilks' $\Lambda = 0.0040283$, $F = 27.536$, $P < 0.0001$). Planned pairwise comparisons among species using Generalised Mahalanobis distances indicated significant differences in body shape among all species (table 1). To visualise shape differences, thin-plate spline deformation plots were generated for the average specimen for each species for both zooplankton feeders (fig. 2a, b) and algal feeders (fig. 2c, d).

For the zooplankton feeders, *Copadichromis borleyi* had a shorter gape, a shorter but deeper head, and a shorter caudal peduncle relative to *Ctenopharynx pictus*. Additionally, the vent of *Ctenopharynx pictus* was more anteriorly positioned relative to that of *Copadichromis borleyi* (fig. 2a, b). For the algal feeders, *L. fuelleborni* had a shorter and inferior subterminal gape, a shorter head, and a more anteriorly placed pectoral fin relative to *P. genalutea* (fig. 2c, d).

Supplemental measurements. ANOVA revealed significant differences in the trophic characters among the species ($F = 55.539$, $df = 4$, $P < 0.0001$). The post-hoc multiple pairwise comparisons indicated that there was significant difference in interorbital width between zooplankton feeders (Tukey-Kramer test, $P < 0.05$, table 2), where *Copadichromis borleyi* had a larger interorbital width (mean \pm

Table 1.

Pairwise comparisons based on Generalised Mahalanobis distances among the four species belonging to algal and zooplankton trophic guilds. All pairs are significantly different (at $\alpha = 0.05$, after Bonferroni correction) since the calculated critical D^2 was 4.8452.

Species	<i>C. borleyi</i>	<i>C. pictus</i>	<i>L. fuelleborni</i>	<i>P. genalutea</i>
<i>C. borleyi</i>	0.0000			
<i>C. pictus</i>	7.0607	0.0000		
<i>L. fuelleborni</i>	5.9251	9.9158	0.0000	
<i>P. genalutea</i>	5.1429	7.8905	6.7377	0.0000

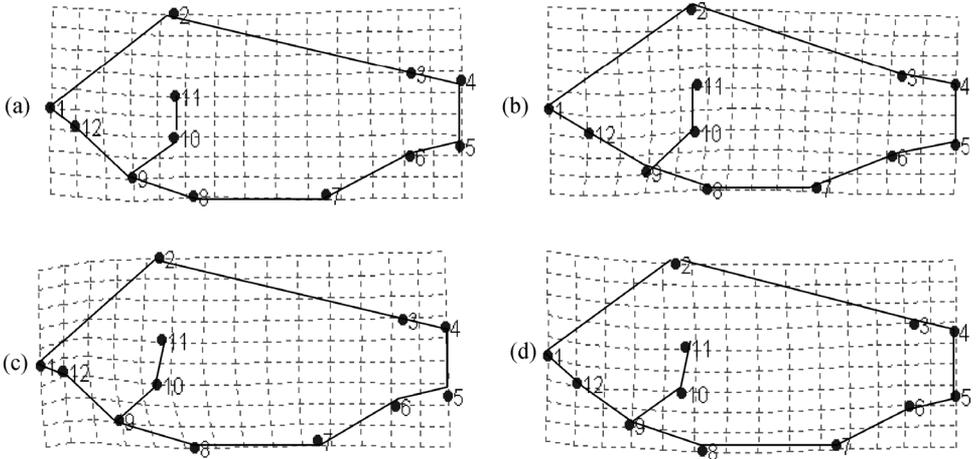


Figure 2. Thin-plate spline deformation grids representing each species; (a) *Copadichromis borleyi*; (b) *Ctenopharynx pictus*; (c) *Labeotropheous fuelleborni*; (d) *Petrotilapia genalutea*.

Table 2.

Multiple comparisons based on Tukey-Kramer test for two trophic characters. Right half represents comparisons for gape width, left half for interorbital width. Positive values denote significantly different pairs whereas negative values denote pairs that are not significantly different.

Species	<i>C. borleyi</i>	<i>C. pictus</i>	<i>L. fuelleborni</i>	<i>P. genalutea</i>
<i>C. borleyi</i>		-0.914	3.659	4.586
<i>C. pictus</i>	1.521		3.933	4.859
<i>L. fuelleborni</i>	0.903	3.674		-0.260
<i>P. genalutea</i>	1.468	4.238	-0.685	

SD; 8.3 ± 2.7) than *Ctenopharynx pictus* (5.5 ± 0.7). There was no difference in gape width between the two species (*Copadichromis borleyi*; 7.2 ± 0.3 and *Ctenopharynx pictus*; 6.9 ± 0.3). There was also no significant difference in either interorbital width or gape width between the two algal feeders, but the means for the two trophic characters were higher than those in zooplankton feeders (interorbital width, 10.5 ± 1.4 and gape width, 12.1 ± 0.3 for *L. fuelleborni*, while in *P. genalutea*, 11.1 ± 1.5 and 12.9 ± 0.3 , respectively).

The shorter interorbital width in the two zooplankton feeders might mean that the orbit is larger, resulting in possession of larger eyes than is the case for algal feeders. As an a posteriori test, eye diameter was measured and a significant difference was revealed among species (ANOVA, $F = 101.9$, $P < 0.0001$). Subsequent pairwise comparisons indicated significant differences between all pairs (Tukey-Kramer test, $P < 0.05$) except that of *L. fuelleborni* (6.7 ± 0.5) and *P. genalutea* (7.2 ± 0.6), whereas zooplankton feeders have larger eye diameter (*Copadichromis borleyi*, 9.4 ± 0.9 and *Ctenopharynx pictus*, 10.5 ± 1.1).

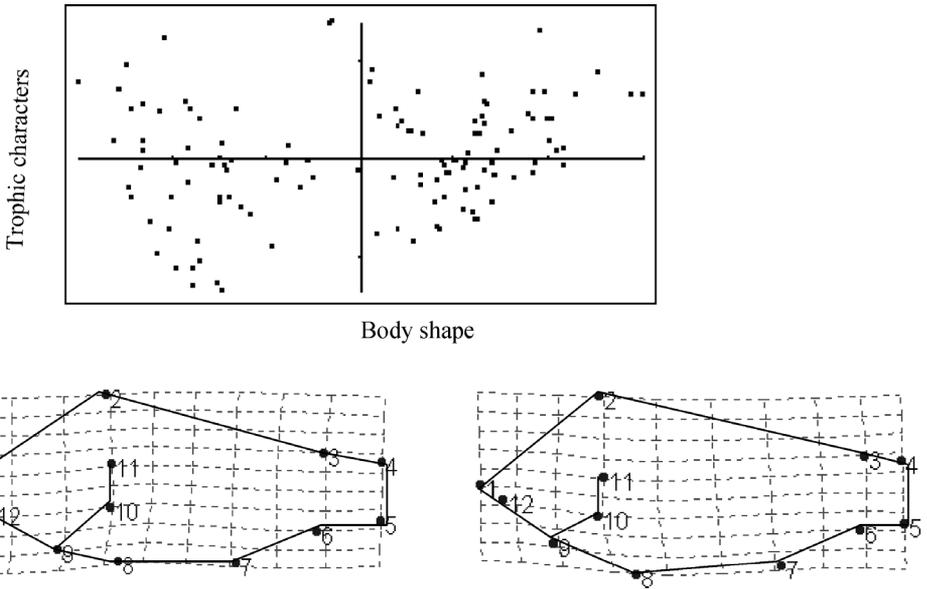


Figure 3. Relationship between body shape and trophic morphological characters using partial least squares analysis. Deformation grids are shown representing an individual towards the positive and negative ends of the body shape axis. Individuals found on the positive side of the body shape axis correspond to algal feeders, while individuals found on the negative side of the body shape axis correspond to plankton feeders.

The two-block partial least squares analysis revealed a significant positive correlation between body shape and the trophic characters ($r = 0.779$; $P = 0.001$), which is shown in figure 3. Individuals towards the positive end of the body shape axis had a shorter but wider gape, a larger interorbital width, a short and narrow head, a short but deep caudal peduncle, and a deep midbody. Specimens with this shape correspond to the two algal feeders. Individuals towards the negative end of the body shape axis show the opposite pattern and represent the two zooplankton feeders. They have a longer but narrower gape and a shorter interorbital width.

DISCUSSION

A longstanding question in studies of ecomorphology is: does morphology relate to trophic ecology? Surprisingly, this is not always a straightforward question to answer. In some cases, the relationship cannot be made because differentiation in trophic ecology does not always correspond to substantial variation in the trophic morphology. In such cases, modulation of behavioural patterns may drive the observed differences in trophic ecology (e.g., Hori, 1983; Yuma, 1994). Our results, however, provide some evidence linking morphology and trophic ecology in the species investigated. Using landmark-based morphometric methods, we found significant differences in overall body shape. Furthermore, body shape

variation was significantly correlated with gape width and interorbital width, two characters commonly associated with trophic ability (Fryer and Iles, 1972). The most pronounced variation was found in the head region, particularly with respect to gape size and gape position. This result implies that trophic morphology has been adapted to different feeding strategies among these coexisting species. Such differential trophic morphology helps to shed light on how resources are partitioned, be it along food or spatial axes.

The relationship between feeding habit and trophic morphology of species within trophic guild appears consistent with ecological specialisation. In zooplankton feeders, for example, differences in gape size may be related to feeding microhabitat partitioning. *Copadichromis borleyi*, which feeds mainly from the water column, has a smaller gape, while *Ctenopharynx pictus* (a benthophagous feeder) has a larger gape. This morphology-habitat association in the small-gaped, limnetic *Copadichromis borleyi* matches the classic description of a suction feeder (Liem, 1991). By contrast, the larger gape of *Ctenopharynx pictus* may enable the fish to take large volumes of loose sediment into the mouth, from which the prey (mainly copepods) are sieved with long and numerous gill rakers (Ribbink et al., 1983). Thus, it appears that in Lake Malawi's zooplankton feeders, the classic benthic-limnetic niche partitioning is seen within this trophic guild. Besides the gape size, eye size variation between these two species seems to play a vital role. Hart and Gill (1994) reported that limnetic threespine stickleback have larger orbits to accommodate a larger eye, which increases their resolving power for detecting small zooplanktonic prey. We found that these two zooplankton feeders, who have to detect tiny prey visually (Fryer and Iles, 1972), also have larger eyes, a result consistent with findings in threespine stickleback. However, *Ctenopharynx pictus* being benthophagous, we hypothesise that searching for prey in such a habitat requires a higher resolving power, which is consistent with its larger eyes than those in its counterpart, *Copadichromis borleyi*.

In the algal-feeding trophic guild, segregation along a behavioural axis seems to play a significant role in morphological divergence. Ribbink et al. (1983) reported that *L. fuelleborni* prefers foraging in shallow water, where the surge is a prominent part of the environment and where interspecific competition is reduced. Its inferior subterminal mouth, a characteristic feature of this species, is used to scrape algae from rock surfaces while the body is oriented almost parallel to the substrate (Fryer and Iles, 1972; Ribbink et al., 1983; Albertson and Kocher, 2001). This foraging behaviour is contrasted with that of *P. genalutea* which scrapes the rocks with its terminal mouth while its body is almost perpendicular to the substrate. Such subtle variation in foraging techniques have been demonstrated to play a significant role in resource partitioning in other guilds, such as epilithic algal-feeding and benthophagous-feeding cichlid species in Lake Tanganyika (see Yamaoka, 1982, 1983, 1991, 1997; Yuma, 1994). The larger gape width revealed in the two algal feeders concords with Fryer and Iles (1972) who stated that a wider gape is

important for algal feeding, as it enables the fish to scrape a wide band of rock surface at a single application of the mouth.

Barel's (1983) observation that in most cases trophic groups are morphologically identified by particular 'facies' (appearances) seems to concur with our findings in the species examined. There appear to be morphological features unique to each particular group which are directly related to the prey consumed, and how and where the prey is collected. We suggest that this variation in collection strategies, coupled with trophic morphological divergence, may enhance ecological separation, which is probably a key factor leading to coexistence through reduced interspecific competition for resources. It can also be argued that ecological separation followed by morphological divergence may not only help in reducing competition among species, but may also lead to ecological speciation in sympatry, which is one of the proposed modes of rapid speciation in African cichlids (see Dieckmann and Doebeli, 1999; Schluter, 1999; Kornfield and Smith, 2000).

The ability to correlate trophic morphology and trophic ecology using landmarks collected from body shape shows the vital role which body shape plays in these cichlids. In other fishes, body shape is functionally related to feeding mode, where limnetic feeders are shallow bodied with long snouts, and benthic feeders are deeper bodied with shorter snouts (Lavin and Mcphail, 1985; Caldecutt and Adams, 1998). This does not diminish the importance of direct studies of trophic structures, but rather complements them by providing additional information on the morphological variation within and between species. Further, by assessing the association between body shape and trophically important traits (e.g., gape width), one may better understand the morphological diversity present in these amazing animals. Our study demonstrates that correlating body shape and trophic morphological characters allows us to gain knowledge of how cichlids capture their prey. Thus, an integrative approach addressing both levels of morphological variation is the best way of understanding the diversity of cichlid fauna.

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