

Morphological Divergence Predicts Habitat Partitioning in a Lake Malawi Cichlid Species Complex

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In Lake Malawi cichlids, comparisons of feeding morphology have typically been performed at the genus level, with little emphasis on interspecific comparisons. Variation in jaw shape can be a powerful predictor of feeding performance and habitat preference. Jaw morphology and habitat partitioning were examined among species in the Lake Malawi rock-dwelling species complex, *Tropheops*. Although *Tropheops* species varied in a variety of craniofacial characters, lower jaw shape was the focus of this study because of its close association with feeding performance in bony fishes. Significant differences were observed among five microhabitat variables measured *in situ* for six *Tropheops* species at two field sites in southern Lake Malawi in July and August, 2001. Depth was identified as a major axis of trophic niche partitioning, and species-specific differences in lower jaw shape and foraging strategy were correlated with depth distributions among species. These data are consistent with the hypothesis that competition for trophic resources (epilithic organisms) has led to habitat partitioning and the establishment and maintenance of distinct trophic morphologies within the *Tropheops* species complex. Detailed morphological analyses of inter- (and intra-) specific trophic variation in Lake Malawi cichlids will likely lead to important insights into the proximate mechanisms that underlie cichlid trophic diversity.

THE Lake Malawi rock-dwelling cichlid community (locally referred to as *mbuna*) embodies several characteristics that make it an attractive model for the study of important questions in ecology and evolution. Mbuna species tend to exhibit high levels of philopatry accompanied by low rates of dispersal (van Oppen et al., 1997; Arnegard et al., 1999; Markert et al., 1999; Danley et al., 2000), and are both species rich and densely packed (Fryer, 1959; Ribbink et al., 1983). For decades evolutionary biologists have used the rocky habitat and its associated cichlid fauna to study the factors that have contributed to both the evolution and maintenance of morphological diversity among East African cichlids (reviewed by Kornfield and Smith, 2000; Genner and Turner, 2005).

Many important questions have focused on the apparent stable co-existence of closely related mbuna species with highly similar diets and habitats. In his classic study, Fryer (1959) noted the discrete horizontal and vertical distributions of many rock-dwelling species, but suggested that competition is minimized within this community due to a balance between a superabundance of algae and low levels of predation. To Fryer, it was this attribute of the mbuna that could explain the coexistence of species, and that the possession of different trophic morphologies was simply a case of “different mechanisms hav[ing] evolved in order to achieve the same end” (Fryer, 1959).

It was further postulated that trophic specializations among cichlid species might not be adaptive (Liem, 1980). In a series of laboratory studies, Liem found that different morphological “specialists” often employ the same range of feeding modes (Liem, 1980, and references therein). The crux of Liem’s paradox is morphological specialization without functional divergence. If one design is sufficient to perform multiple tasks, then how could trophic diversity have evolved as the result of natural selection? This discordance between morphological differences and func-

tional similarities among species was supported by several field studies where specialized taxa were observed feeding opportunistically on other food resources (Ribbink and Lewis, 1982; McKaye and Marsh, 1983; Ribbink et al., 1983; Stauffer, 1991). However, a reevaluation of this conundrum in the context of “ecological bottlenecks” has led to a potential solution to Liem’s paradox, and renewed interest in competition as a force behind the origin and maintenance of cichlid trophic diversity (McKaye and Marsh, 1983; Robinson and Wilson, 1998; Liem and Summers, 2002). Much like in Darwin’s finches, the selective advantage of specializations in trophic anatomy will become most relevant during periods of stressful environmental conditions (Grant and Grant, 2002, and references therein).

Indeed, a growing body of evidence suggests that competition is a prominent aspect of life in the rocky habitats of Lake Malawi and that morphological specialization is associated with habitat and dietary partitioning. Reinthal (1990a) identified four general feeding behaviors among Lake Malawi’s rock-dwelling cichlids: nipping, brushing, mowing, and pelagic foraging. Moreover, he found that these four feeding behaviors are broadly associated with differences in trophic morphology, diet, and habitat. Bouton et al. (1997) showed that species with different oral morphologies differed in their efficiency to collect as well as process different prey items in the lab. In a complementary field study, both inter- and intraspecific differences in diet and microhabitat were shown to correspond to local and seasonal resource abundance (Bouton et al., 1998). Competition for food was interpreted to play an important role in structuring mbuna communities since dietary overlap among species decreased with an increase in fish abundance and a decrease in resource availability. Microhabitat partitioning has also been observed among Lake Malawi’s rock-dwelling cichlids (Genner

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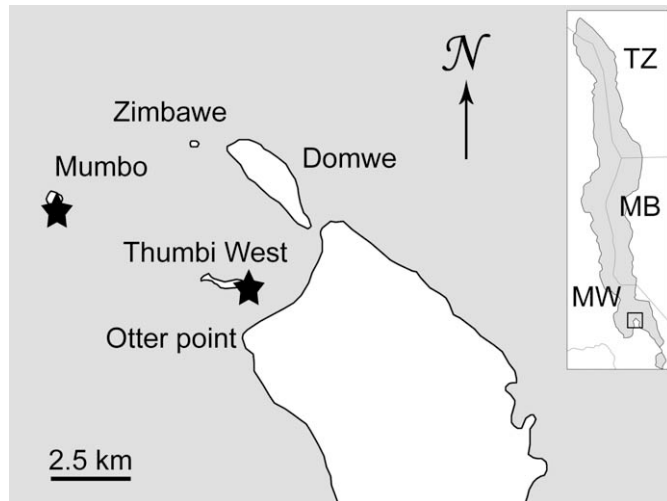


Fig. 1. The Nankumba Peninsula and surrounding islands in southern Lake Malawi. Dive sites from Thumbi West (14°05'S, 34°50'E) and Mumbo (13°59'S, 34°45'E) islands are labeled with a star. Abbreviations: TZ, Tanzania; MB, Mozambique; MW, Malawi.

et al., 1999). A common theme of this work is that fine-scale foraging-niche partitioning does occur among cichlid species.

This report adds to the growing body of evidence that competition is a common feature of cichlid communities, and that it manifests itself as habitat partitioning and morphological divergence. It was predicted that depth is a major factor contributing to habitat partitioning among *Tropheops* species, and given the differences in the epilithic community at different depths (Ribbink et al., 1983), species with distinct vertical distributions will exhibit divergent jaw morphologies. To test these predictions, five microhabitat variables (including depth distribution) were measured for six *Tropheops* species at two sites, and jaw morphology was assessed in 12 *Tropheops* species that exhibit discrete depth distributions. The goal of this paper is to use statistical associations between variation in jaw morphology and microhabitat preference to provide evidence that competition for trophic resources helps shape cichlid communities, and that the lower jaw is an adaptive feature of cichlid anatomy.

MATERIALS AND METHODS

Study sites.—Mumbo and Thumbi West Islands are part of Lake Malawi National Park, located in the southern part of the lake (Fig. 1). Thumbi West Island is 2 km long and 500 m at its widest point. It is located 2.6 km from Domwe Island, 1.5 km from Otter Point, and less than 1 km from Chembe Beach. Its shoreline is a continuous rocky habitat with the exception of two small sand/weedy beaches. Rocks around Thumbi West are variable in size and shape. Observations and collections at Thumbi West were performed at the eastern-most end of the island, Mitande Cove. This area is characterized by slabs, boulders, and large, medium, and small rocks. The rock-sand interface was found at approximately 15 m in 2001, with small pockets of sand and weeds occurring below 10 m. Most rocky surfaces below 5 m were covered with a layer of sediment. Over 30 mbuna species coexist at Mitande Cove (Ribbink et al., 1983; Albertson, pers. obs.).

Mumbo Island is approximately 600 m long and 400 m wide, and is located 5.9 km northwest of Thumbi West. The water that separates Mumbo Island from other islands is at least 100 m deep (Ribbink et al., 1983). Like Thumbi West, its shore is continuously rocky except for two small beaches at the northern and southern ends of the island. The rocky shore of Mumbo Island is lined mainly by large to medium sized rocks. Coarse gravel is also a prominent feature of Mumbo Island, which lies at the base of rocks and along the rock-sand interface at approximately 30 m. Observations and collections were made along the western side of the Island. This area is characterized by a gentle slope of medium sized rocks and gravel to about 15 m, and then a steeply descending slope of large rocks and boulders to the sandy plain at 30 m.

Study species.—All *Tropheops* species are characterized by a steeply descending snout and a slightly sub-terminal mouth, and typically feed from the rocky substratum while oriented 45° to the substrate with a sideways and upward jerking motion, referred to as 'nipping' (Ribbink et al., 1983; Reinthal, 1990a). Six abundant species within the *Tropheops* complex were chosen for behavioral observations. Four *Tropheops* species were sampled at Thumbi Island West: *T. 'red cheek'* (RC), *T. 'lilac'* (LIL), *T. 'orange chest'* (OC), and *T. 'intermediate'* (INT). These were the predominant *Tropheops* species found at Mitande Cove. Both *Tropheops* species endemic to Mumbo Island were also sampled, *T. 'mumbo'* (MUM) and *T. 'lilac mumbo'* (LM).

Depth distribution.—One hundred-meter transects were run parallel to the shoreline at 1.5 m intervals, down to 20 m (below the peak depth distribution of all species). Using SCUBA, the number of males and females of each species was counted along transects. Individuals were counted if they were on or up to 1.5 m below the transect. Each transect was traversed three times and the number of fish was averaged and rounded to the nearest whole number. Since depth distribution was shown to violate the assumptions of homoscedasticity and normality, differences in depth distribution of species at each study site were determined via Kruskal-Wallis nonparametric ANOVA (Sokal and Rohlf, 1981).

Focal behavioral study.—Focal observations of feeding were carried out between 10 July and 14 August 2001. Twenty individuals from each species were observed along the same 100 m stretch of rocky habitat as where the depth distribution analysis was performed. Each focal observation lasted ten minutes and was carried out between 0700 and 1600 h.

A feeding bout was defined as a continuous feeding event that was interrupted by 20 or more seconds of non-feeding, a change of substrate, or a social interaction (i.e., courting, defending territory). Several microhabitat characters (see below) were scored for each bout of feeding. Differences among species for each character were assayed via a Kruskal-Wallis nonparametric ANOVA (Sokal and Rohlf, 1981). A principal component analysis was also performed on averaged microhabitat variables for each individual (including the depth at which each animal was sampled) to identify major axes of variation.

The surface area of the rock on which fish were feeding was recorded by measuring the length and width of the

Table 1. *Tropheops* Species. Samples collected for morphometric analysis, and the populations from which they were collected are listed. Species abbreviations in parentheses are used in the text.

Species	<i>n</i>	Population(s)
<i>T. microstoma</i>	15	Otter Island
<i>T. otter gold</i>	5	Otter Island
<i>T. gracilior</i>	23	Otter Point, Domwe Island
<i>T. orange chest (OC)</i>	48	Domwe Island, Thumbi West Island, Zimbabwe Rock
<i>T. intermediate (INT)</i>	31	Thumbi West Island, Mazinzi Reef, Otter Island
<i>T. lilac (LIL)</i>	16	Thumbi West Island, Otter Island
<i>T. red cheek (RC)</i>	20	Thumbi West Island
<i>T. chinyankwazi</i>	17	Chinyankwazi Island
<i>T. chinyamwezi</i>	20	Chinyamwezi Island
<i>T. broad mouth</i>	5	Otter Island
<i>T. lilac mumbo (LM)</i>	20	Mumbo Island
<i>T. mumbo (MUM)</i>	10	Mumbo Island

rocky surface in centimeters. The surface area, rather than the size of the rock itself, was chosen for several reasons. First, animals often showed a clear preference for one particular side of a rock (i.e., top instead of bottom). Moreover, when the rock on which a fish was feeding was a slab, or when many rocks were stacked upon each other, the size of the entire rock was difficult to measure. The slope of each rocky surface was also measured underwater to the nearest ten degrees with a protractor, from 0 to 90, and the shelter offered by each foraging surface was estimated as follows. A rocky surface was given a score of (1) if there were no other perpendicular surfaces within 30.5 cm of the foraging area, (2) if there was one other perpendicular surface within 30.5 cm, (3) if there were two other surfaces, (4) if there were three, and (5) if an animal was effectively foraging in a cave. For each feeding bout, the foraging surface was described as being either sediment-covered or sediment-free, and the proportion of each was estimated visually. Importantly, this variable does not measure whether the rock itself was sediment-covered, just if the foraging surface was covered with sediments (see below).

Morphology.—In bony fishes, lower jaw shape is predictive of feeding behavior (Westneat, 1990, 2004; Albertson and Kocher, 2001). To assess morphological variation across *Tropheops* species, lower jaw morphology was measured in 12 species collected from the southern end of Lake Malawi in or around Lake Malawi National Park (Table 1). Species used for the focal behavioral study described above were collected for morphological analysis at the sites where the behavioral and transect data were obtained. It is important to note that *Tropheops* species varied in other craniofacial characters aside from the lower jaw, but these differences will be the focus of another study. Specimens were collected using gill nets and SCUBA, dried on site in Malawi, and shipped back to the United States. Dried specimens were fed to dermestid beetles, which cleaned and disarticulated skeletal elements of the head. Cleaned specimens were then placed at -75°C for 10–15 minutes to kill the remaining beetle larvae, and stored in labeled boxes.

The lower jaws from each specimen were mounted in modeling clay and digitized in the lateral view using a Zeiss Axiocam digital imaging system mounted to an M2 Bio stereomicroscope (Zeiss). Geometric morphometric analysis was then performed using Morphometrika (J. Walker, [\[jaw.fmnh.org/Software/Morphometrika.html\]\(http://jaw.fmnh.org/Software/Morphometrika.html\)\). Landmarks used to describe the geometry of the lower jaw are shown in Figure 3 and described in Alberston and Kocher \(2001\). Essentially, landmarks were chosen that are known to capture the functional consequences of variation in jaw shape, and are thus suited to predict differences in feeding performance \(Albertson and Kocher, 2001\). Superimposition of landmark data was achieved using a Generalized Procrustes Analysis \(GPA; Gower, 1975; Rohlf and Slice, 1990\), which aligned landmark configurations such that the sum of squared distances between corresponding landmarks was minimized by scaling, translating, and rotating specimens with respect to a mean consensus configuration. A thin-plate spline \(TPS\) analysis was then performed to obtain partial warps, which are a series of geometric descriptors of shape. TPS models the form of an infinitely thin metal plate that is constrained at some combination of points \(i.e., landmarks\) but is otherwise free to adopt a target form in a way that minimizes bending energy \(Bookstein, 1991\). In morphometrics, this interpolation is applied to a Cartesian coordinate \(\$x, y\$ \) system in which deformation grids are constructed from two landmark configurations \(Bookstein, 1991\). The total deformation of the spline can be decomposed into geometrically orthogonal components based on scale \(Rohlf and Marcus, 1993\). These components \(partial warps\) can be localized to describe precisely what aspects of shape are different. A principal component analysis \(PCA\) was then performed on partial warp scores, formally referred to as relative warp analysis \(RWA; Bookstein, 1996\), to identify and visualize major axes of shape variation.](http://</p>
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RESULTS

Depth distribution.—Results from the Kruskal-Wallis test showed a discrete split between species with respect to depth, producing shallow- and deep-water species groups at each site (Tables 2, 3). At Thumbi West, *Tropheops* species RC and LIL (Table 1) were never found below 7 m and were rarely observed below 3 m of water, whereas OC and INT were rarely observed above 3 m and were most abundant at 7–9 m, respectively. At Mumbo Island, LM was most abundant between 1.5–3.5 m and was rarely seen below 7 m, whereas MUM was most abundant at 12 m and was rarely observed above 7 m.

Table 2. Microhabitat Variables. Means and 95% confidence intervals for the sample means of microhabitat variables are shown for each species. Twenty individuals were measured for each microhabitat variable.

	Thumbi West				Mumbo	
	RC	LIL	OC	INT	LM	MUM
depth (m)	3.11 (± 0.55)	2.44 (± 0.46)	6.28 (± 0.52)	7.41 (± 0.52)	3.75 (± 0.31)	10.61 (± 0.40)
surface area (cm ²)	245 (± 89)	326 (± 104)	1458 (± 478)	195 (± 102)	2946 (± 1204)	315 (± 340)
sediments (%)	0.07 (± 0.06)	0.25 (± 0.09)	0.26 (± 0.10)	0.96 (± 0.05)	0.01 (± 0.00)	0.98 (± 0.03)
shelter (1–5)	2.1 (± 0.2)	2.0 (± 0.18)	1.2 (± 0.1)	3.0 (± 0.3)	1.4 (± 0.2)	2.1 (± 0.3)
slope (degrees)	54.1 (± 7.1)	55.5 (± 6.8)	37.0 (± 8.1)	30.5 (± 8.4)	33.3 (± 11.2)	15.8 (± 7.8)

Principal component analysis confirmed that depth distribution was an important variable involved in habitat partitioning among *Tropheops* species. Along with sedimentation, depth had the highest factor loadings on PC1 for species at both Thumbi West and Mumbo Island (Table 4). For both field sites, deep-water species had positive factor scores along PC1, whereas shallow-water species had negative factor scores (Fig. 2). Depth was correlated with other microhabitat variables including sedimentation (Table 5).

Foraging surface area.—Species also partitioned their habitat according to the surface area of the rocks on which they fed (Tables 2, 3). At Thumbi West, RC, LIL, and INT consistently foraged from smaller surface areas, whereas OC foraged from large, flat rocky surfaces. At Mumbo Island, LM fed from much larger areas than MUM, which mainly reflected MUM's preference for feeding from coarse gravel at the base of larger rocks and boulders. Differences in foraging surface area were not related to differences in depth distribution (Table 5). Rather, partitioning of the size of the foraging surface area appeared to be another important, orthogonal dimension of divergence in foraging niche. For species at Thumbi West, surface area had high loadings on PC2 (Table 4), and nearly every OC individual had a negative factor score on PC2, whereas all other species had mean positive factor scores (Fig. 2). For both field sites, only the first two PC axes had eigenvalues greater than 1.

Sediment.—*Tropheops* species differed in the proportion of feeding bouts from sediment-free versus sediment-covered substrates (Tables 2, 3), and sediments had the highest loadings on PC1 at both sites. This variable was also highly correlated with depth (Table 5), which had comparable loadings on PC1. At Mumbo Island the deep-water species, MUM, foraged almost exclusively from sediment-covered surfaces, whereas the shallow-water species, LM, foraged

exclusively from sediment-free surfaces (Table 2). In general, this trend was observed at Thumbi West as well. The shallow-water species, RC and LIL, more consistently foraged from sediment-free surfaces than did the deep-water species, INT. It is noteworthy, however, that OC tended not to forage from sediment-covered surfaces in spite of it occupying a depth distribution where most rocks were covered with sediments. This was likely due to OC's preference to forage from the tops of large, flat, rocks where wave action served to keep exposed surfaces relatively clear of sediments and detritus, whereas INT fed from the base of rocks where the foraging surface was covered by a thick layer of organic sediment. Another notable observation was that RC fed more often from sediment-free substrate than did

Table 3. Kruskal-Wallis Nonparametric ANOVA for Microhabitat Variables. All X^2 values were significant at the $P < 0.001$ level (**).

	Thumbi West	Mumbo
	$X^2_{(3)}$	$X^2_{(1)}$
depth	87.9**	246.5**
surface area	53.5**	120.1**
sediments	151.2**	87.9**
shelter	94.8**	16.9**
slope	30.2**	11.3**

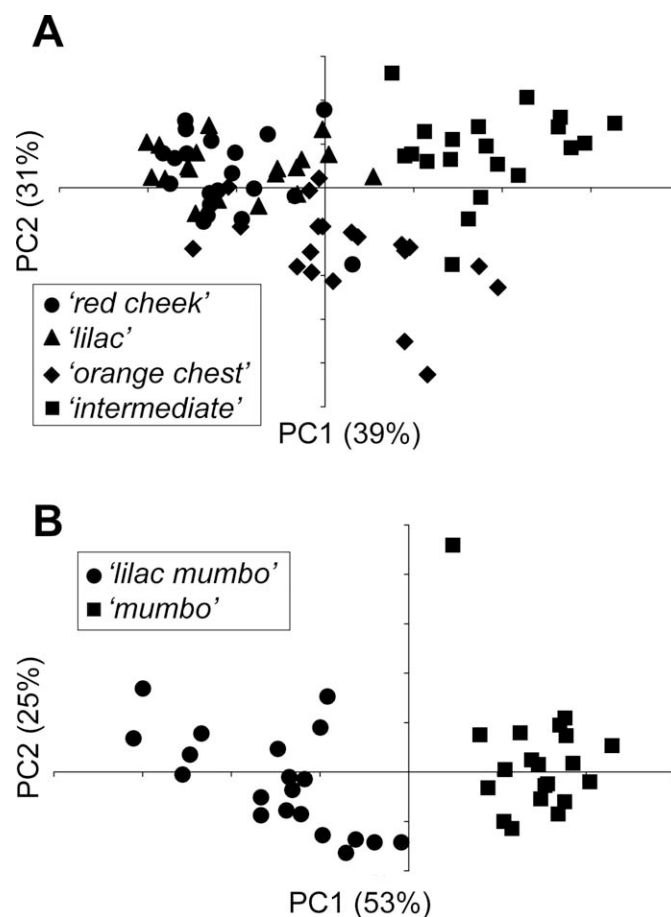
**Fig. 2.** Results of the principal component analysis for habitat variables. The scatterplot of factor loadings for the first two axes are shown for Thumbi West (A), and Mumbo Island (B). In both graphs, the major units for both axes (which are unlabeled) are 1.0.

Table 4. Principal Component Analysis. Factor loadings for different habitat variables, eigenvalues, and variabilities (%) are listed.

Factor loadings:	Thumbi West		Mumbo	
	PC1	PC2	PC1	PC2
depth	0.831	-0.122	0.796	0.311
surface area	0.119	-0.816	-0.719	0.392
sediments	0.836	0.197	0.907	0.214
shelter	0.350	0.829	-0.719	0.619
slope	-0.667	0.384	0.371	0.768
eigenvalue	1.971	1.554	2.628	1.269
Variability (%)	39.419	31.073	52.565	25.380

LIL. In fact, this was the only variable in which RC and LIL differed (Table 2).

Both RC and OC were also unique among *Tropheops* species in that they were regularly seen foraging with species in another genus that employed a brushing mode of feeding. Members of the genus *Petrotilapia* forage from the substrate by brushing loose filamentous algae, diatoms, and other detritus that have settled onto algal beds. Both RC and OC would often wait until a *Petrotilapia* species "cleaned" an area of sediment before feeding on the attached algae beneath. In this way RC and OC could forage from sediment-free substrate even if the rock itself was covered with sediments.

Shelter.—*Tropheops* species also partitioned their habitat according to shelter offered by the foraging area (Tables 2, 3). Both INT and MUM tended to forage from surfaces that were highly sheltered. At Mumbo Island, this trend was largely attributable to MUM's preference of feeding from the coarse gravel that accumulated around the base of rocks and boulders and within cracks and crevices between rocks. At Thumbi West Island, both territorial male and non-territorial female INTs exhibited high affinity for sheltered foraging areas. This trend was consistent with the tendency of male INTs to excavate nests beneath rocks (Ribbink et al., 1983; Albertson, pers. obs.). On the other hand, OC and LM fed almost exclusively from exposed surfaces at Thumbi West and Mumbo Island, respectively. Both RC and LIL foraged from surfaces that offered intermediate levels of shelter.

Slope.—At Thumbi West, habitat partitioning by *Tropheops* species in terms of slope recapitulated partitioning according to depth (Tables 2, 5). Specifically, the shallow-water species, RC and LIL, fed from surfaces that were steeply sloped relative to the deep-water species. This observation was likely due to differences in the physical habitat around Thumbi West. The shallows (>5 m) were comprised of small

and medium sized rocks piled on top of one another, whereas the depths were dominated by large, flat, and interspersed rocks and slabs that gradually sloped toward the rock-sand interface. At Mumbo Island, the shallow-water species, LM, foraged from surfaces with a greater slope than the deep-water species, MUM. This difference was not related to depth (Table 5). Rather, it was likely a consequence of LM's preference to feed from the tops and exposed sides of large rocks and boulders and MUM's tendency to feed at the base of rocks where slope was negligible.

Morphology and feeding mode.—The relative warp analysis identified a major axis of morphological variation that also distinguished deep- and shallow-water *Tropheops* species (Fig. 3). The first principal component axis explained 39% of the morphological variation in lower jaw shape among *Tropheops* species. Most shallow-water species had positive factor scores along PC1 (circles, Fig. 3), whereas species typically found at depth had negative factor scores (squares, Fig. 3). The shallow-water morphotype was characterized by a long ascending arm of the articular and retroarticular process relative to the total length of the lower jaw, whereas the deep-water morphotype possessed short articular and retroarticular processes relative to the length of the lower jaw. These morphological differences are consistent with divergent modes of feeding. Shallow-water *Tropheops* had jaws characterized by high mechanical advantage (i.e., greater predicted force transmission, Westneat [1990], data not shown), which is typical of species that employ a powerful biting mode of feeding. Deep-water species, on the other hand, possessed jaws with low mechanical advantage (i.e., greater predicted velocity transfer, Westneat [1990], data not shown), consistent with modes of feeding that require a less powerful, but more rapid, jaw rotation, including shifting and suction feeding.

Despite the fact that OC was found in deep water at Thumbi West, it grouped morphologically with shallow-water species. This species is extremely common in southern

Table 5. Pearson Correlation Matrix for Microhabitat Variables. Correlation among variables at Mumbo Island are above the diagonal. Those for Thumbi West are below. Asterisks indicate significance at $\alpha = 0.05$.

	depth	surface area	sediments	shelter	slope
depth	—	-0.236	0.813*	-0.382*	0.310
surface area	0.134	—	-0.472*	0.677*	-0.182
sediments	0.532*	0.039	—	-0.486*	0.378*
shelter	0.133	-0.446*	0.404*	—	0.161
slope	-0.450*	-0.190	-0.335*	0.083	—

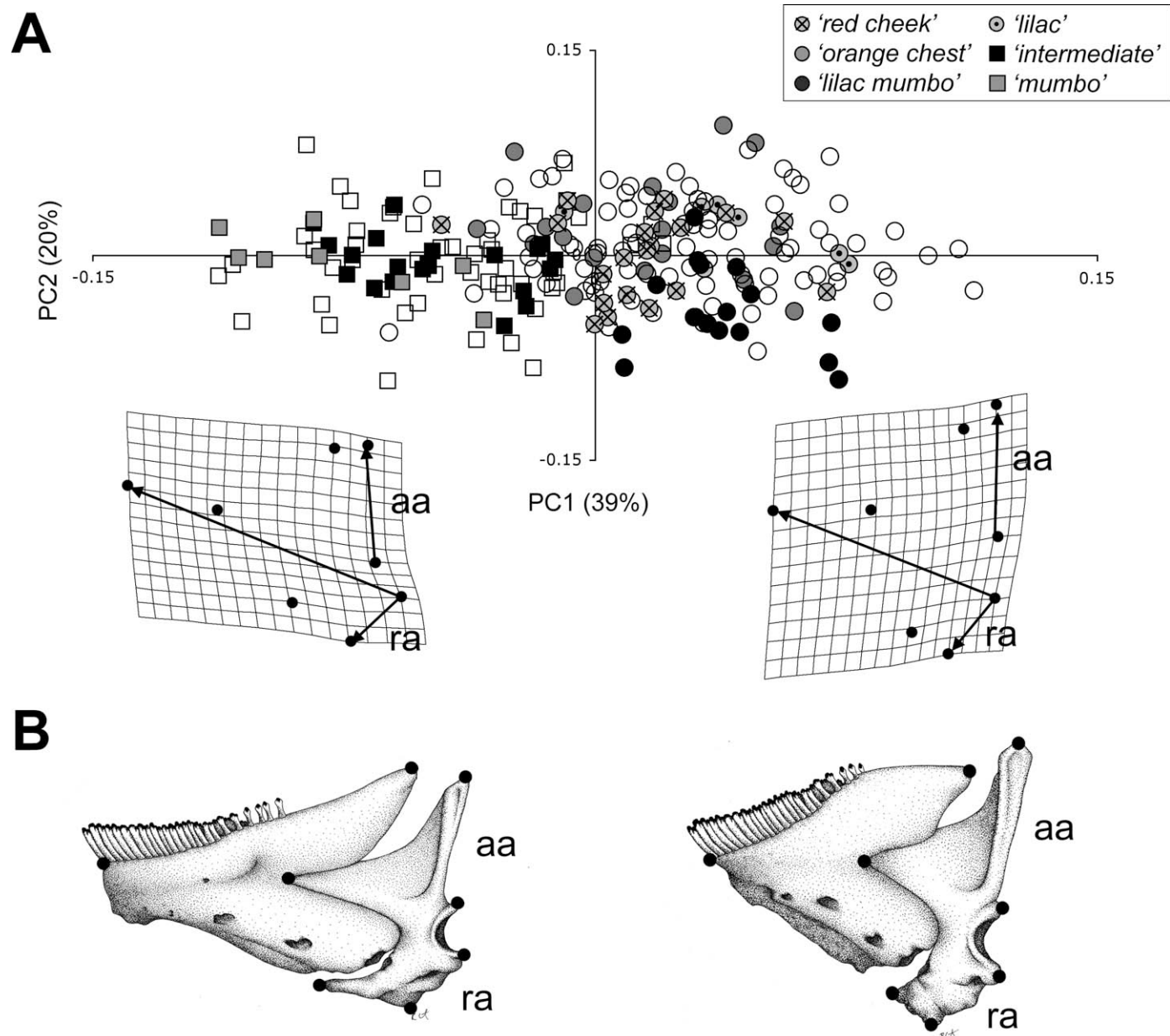


Fig. 3. (A) Results of the relative warp analysis. Species that are generally found in the shallow-water habitat are denoted as circles, whereas species that are found at depth are drawn as squares. Species used for focal study are labeled. (B) Examples of deep- (left) and shallow-water (right) lower jaw morphologies are illustrated, and the articular (aa) and retroarticular (ra) processes are labeled.

Lake Malawi, and had a very broad depth distribution from the extreme shallows to 30+ meters (Ribbink et al., 1983; Albertson, pers. obs.). Notably, the depth at which OC was found among locations appears to be related to what other *Tropheops* species are present. For example, OC was sympatric with two shallow-water species (LIL and RC) at Thumbi West, and was restricted to the deeper habitat. At Domwe Island, OC was sympatric with the deep-water species *T. gracilior*, and it was found in relatively shallow water (Ribbink et al., 1983; Albertson, pers. obs.). At Zimbabwe Rock, OC was the only *Tropheops* species present, and it had a very broad vertical distribution from 1–30 m (Ribbink et al., 1983; Albertson, pers. obs.). Interestingly, OC found at each of these sites were anatomically distinct from one another ($F_2 = 6.54$, $P = 0.003$), which is consistent with the hypothesis of local adaptation to different trophic

environments, or character displacement in trophic morphology.

All species whose behavior was observed spent some time foraging from the substrate with a classic *Tropheops* 'nipping' mode of feeding, where attached filamentous algae was plucked from the substrate with a sideways rotation and upward jerk of the head. In the case of species that lived in the shallows (RC, LIL, and LM) and/or sediment-free (OC) areas, this was the exclusive mode of feeding observed. These species also possessed shallow-water, biting jaw morphologies (Fig. 3). Deep-water species that inhabited sediment-rich areas (INT and MUM), on the other hand, were also observed feeding with a sifting mode, where they took mouthfuls of sand and sediment and sifted them through their gill rakers. In addition, INT was observed foraging on plankton in the water column with a suction

mode of feeding. Both INT and MUM possessed jaws with low mechanical advantage, which is consistent with the prediction that these species demonstrate less powerful, but more rapid, jaw rotation.

DISCUSSION

This study shows that species within the *Tropheops* species complex partition their habitat in many dimensions, but that jaw morphology predicts divergence in terms of depth and sedimentation. While other studies have demonstrated habitat partitioning in Lake Victoria (Bouton et al., 1998), Tanganyika (Yamaoka et al., 1986), and Malawi (Genner et al., 1999), the role of fine-scale foraging niche partitioning in the maintenance of cichlid species diversity remains debated.

Two types of *Tropheops*.—*Tropheops* species are classically defined by a slightly sub-terminal mouth and steep craniofacial profile (Ribbink et al., 1983). This report shows that *Tropheops* species differ quantitatively in the shape of their lower jaws. Two morphotypes are recognized. The first is a shallow-water form characterized by short, stout jaws with high mechanical advantage. This form is clearly adapted to feeding on attached filamentous algae in areas clear of sediments. The second form is characteristic of species that live in deep, sediment-rich areas and possess longer jaws with low mechanical advantage used to sift sediments, suck plankton, and nip algae from the substrate. These species appear to be more generalized feeders. While all *Tropheops* species forage from the rocky substrate, differences in the epilithic community at different depths have likely contributed to the evolution of distinct foraging strategies and divergent jaw morphologies in species with restricted vertical distributions.

Shallow- and deep-water forms exhibit other stereotypical differences in trophic morphology. Shallow-water forms, for example, possess relatively steep craniofacial profiles and narrow, beak-shaped mouths. Deep-water forms, on the other hand, are characterized by more gently sloping heads and broader mouths (e.g., *Tropheops* 'broad mouth'). Comprehensive differences in craniofacial morphology among *Tropheops* species will be published elsewhere. While two forms can be described, trophic diversity among all *Tropheops* species appears to be a continuum between deep- and shallow-water forms, and likely reflects a balance between competition for food resources and adaptation to a local environment. In other words, differences in trophic morphology at each site are discrete (i.e., Mumbo Island), whereas differences across all *Tropheops* species are relative. Linear regression analysis supports this proposition (Fig. 4). A broad correlation between depth distribution (derived from Ribbink et al., 1983) and jaw shape was observed among 11 *Tropheops* species in southern Lake Malawi ($r^2 = 0.5323$, $P = 0.011$). These data are consistent with the idea that depth distribution is an important factor in maintaining species diversity in Lake Malawi's rock-dwelling cichlid community.

The importance of depth and other microhabitat variables.—At nearly every rocky habitat throughout Lake Malawi there are discrete vertical groupings of mbuna species (Ribbink et al., 1983; Genner et al., 2004). For example, RC and LIL always occupy the shallows, whereas *T. gracilior* is most abundant below 15 m. At many localities OC has a peak distribution at

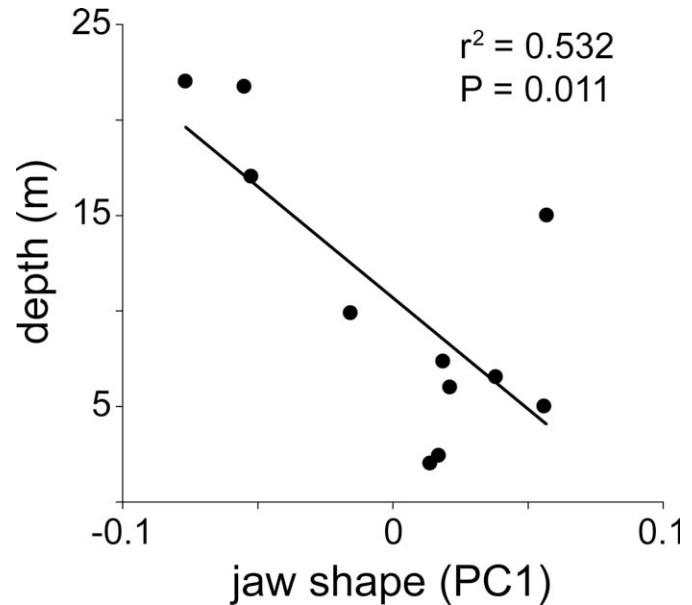


Fig. 4. Morphology predicts depth distribution of *Tropheops* species in southern Lake Malawi. Results of a Pearson's correlation are shown between mean jaw shape (scores on PC1) and mean peak depth distributions for each *Tropheops* species.

an intermediate depth, between the ranges of deep and shallow water species. Perhaps most striking is the observation that wherever more than one *Tropheops* species occurs, one occupies the deep-water habitat and the other inhabits the shallow-water habitat (Ribbink et al., 1983; Albertson, pers. obs.).

In a survey of food resource use, Genner et al. (1999) did not detect foraging-niche partitioning among mbuna species at Nkhata Bay (150 km north of Mitande Cove). In particular, no differences were observed in the foraging behavior of two *Metriaclima* species, *M. zebra* and *M. callainos*. Genner et al. (1999) concluded that alternatives to niche theory should be considered to explain this coexistence. However, species can afford to have the same foraging behavior if they have distinct spatial (i.e., depth) distributions (Reinthal, 1990a). For example, *M. zebra* and *M. callainos* also co-occur at Thumbi West Island where they have distinct vertical distributions (Trendall, 1988; Albertson, pers. obs.). Thus, *M. zebra* and *M. callainos* may indeed have identical feeding strategies, but at Thumbi West Island they still partition their habitat according to depth. It would be interesting to know whether *M. zebra* and *M. callainos* at Thumbi West Island also possess distinct trophic morphologies.

Is there a preferred depth distribution for different mbuna species? This is an important, but as-of-yet unresolved question. Anecdotally, it could be argued that the shallow-water habitat and its associated epilithic community are largely preferred by most species. For instance, mbuna species diversity is generally greater in the shallow-water habitat (Ribbink et al., 1983). It is also apparent that when particular species coexist, the distribution of one is shifted to deeper water. When *M. zebra* occurs with *M. callainos*, it is restricted to deeper waters, but where *M. zebra* occurs by itself, its peak depth distribution is shallower (Ribbink et al., 1983; Albertson, pers. obs.). The depth distribution of OC also appears to depend on the presence or absence of other *Tropheops* species, with its distribution being shifted to

shallower waters when no other shallow-water *Tropheops* species is present.

Because the substrate in deeper habitats tends to be covered with a thick layer of organic sediments, it is not surprising that deep-water species tended to feed from sediment-covered rocks more often than shallow-water species. Depth, however, is not always a reliable predictor of whether a species will forage from sediment-covered or sediment-free substrate. For example, *T. gracilior* is typically restricted to deeper, sediment-rich substrates, but will also enter the shallows in sheltered regions where sediments have accumulated (Ribbink et al., 1983). In this study several species were also observed to employ a foraging behavior that effectively altered their foraging niche in terms of sedimentation. At Thumbi West, OC fed from sediment-free rocks almost to the same extent as the shallow-water species, and within the shallow-water assemblage, sedimentation was the only variable in which RC and LIL differed. *Tropheops* RC and OC, along with another shallow-water species, *Labeotropheus fuelleborni*, were often observed foraging adjacent to heterospecifics with different feeding modes. All three of these species forage on attached filamentous algae and possess lower jaws with mechanical advantages among the highest in Lake Malawi (Albertson, pers. obs.). Both RC and OC feed with a nip, twist, and jerking motion, while *L. fuelleborni* has a wide, flat mouth that it uses to crop algae while swimming parallel to the substrate. These filamentous algae specialists were often observed feeding along side members of the genus *Petrotilapia*, which possess a unique trophic morphology characterized by a thick brush of long, slender teeth on both the upper and lower jaws used to comb edible material from between strands of attached algae (Ribbink et al., 1983). This 'combing' motion served to clean the underlying algal mat on which RC, OC, and *L. fuelleborni* feed, and these species would wait for a *Petrotilapia* individual to 'clean' an area of settled material before picking at the freshly exposed strands of algae. Even territorial males tolerated the presence of these heterospecifics within their territories, which they vigorously defended from other fish. This behavior allowed species to feed more exclusively on clean filamentous algae.

Results presented in this study are consistent with the hypothesis that depth shapes the vertical distribution of mbuna species along the rocky substrate (Hill and Ribbink, 1978; Marsh and Ribbink, 1981; Ribbink et al., 1983), but they also underscore the idea that species distributions are influenced by habitat fidelity as well (Ribbink et al., 1983). When the rocky habitat is unsuitable, species are absent from their typical depth distribution (Ribbink et al., 1983). It is therefore noteworthy that all other microhabitat variables measured in this study exhibited significant differences between at least two species (Table 2). Many of these differences in habitat reflect differences in the underwater topography of the study site, and were associated with depth (e.g., differences in slope at Thumbi West). In other cases, differences in habitat indicated a clear preference for a distinct foraging niche, independent of depth (e.g., slope at Mumbo Island, surface area, and shelter).

Diversity and coexistence within a complex community.—Fryer (1959) viewed the cichlid rock-dwelling community as a "peaceful condominium" that violates the Gaussian principle of competitive exclusion. In contrast, recent data suggest that competition for resources does exist among mbuna

(Bouton et al., 1998; Genner et al., 1999), that competition manifests itself as foraging-habitat partitioning and morphological divergence (Reinthal, 1990a, 1990b; present study), and that variation in trophic morphology results in different feeding efficiencies on a common food source (Bouton et al., 1997). Contrary to Liem's paradox (Liem, 1980), these findings suggest that variation in cichlid feeding morphology is adaptive.

Two general conclusions can be drawn from this study. First, depth and sedimentation are correlated microhabitat variables that collectively explain the majority of variance along a major axis of habitat partitioning among *Tropheops* species. Second, variation in trophic morphology is broadly assorted by depth distribution. Recent phylogenetic work supports the monophyly of *Tropheops*, and suggests that deep- and shallow-water forms have diverged several times during the evolution history of the *Tropheops* species complex (Kidd, 2006). These data are consistent with the hypothesis that the cichlid lower jaw is an evolutionarily labile character complex that responds quickly to divergent natural selection (Ruber et al., 1999; Albertson et al., 2003a, 2003b). Quantitative genetic analyses have further demonstrated that functionally related aspects of the cichlid jaw are genetically modular (Albertson et al., 2005) and that patterns of morphological integration of the jaw match patterns of variation and covariation among *Tropheops* species (Albertson and Kocher, 2006; Albertson, pers. obs.). These data suggest that a conserved set of genetic loci are segregating among Lake Malawi cichlid fishes and may underlie certain patterns of trophic divergence.

Future work will focus on testing this hypothesis through the use of complementation crosses between independently evolved shallow- and deep-water species. If, for example, two unrelated, but morphologically similar, *Tropheops* species produce hybrids with jaw morphologies that are similar to both parents, then the traits complement, and it can be concluded that the same genetic loci are involved in the evolution of the trait. If, on the other hand, hybrids possess novel morphologies, then it can be concluded that a different combination of loci underlie the evolution of convergent jaw morphologies in *Tropheops*. These data will facilitate an understanding of whether the evolution of recurrent phenotypes in Lake Malawi cichlids involves changes in the same or distinct genetic loci. Genetic crosses between deep- and shallow-water forms can also be used to reveal the specific genetic loci involved in the ecomorphological divergence of *Tropheops* species. These efforts will provide insights into the genetic basis of phenotypic divergence in the context of habitat partitioning and the maintenance of biodiversity within Lake Malawi.

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whose experience and knowledge of Lake Malawi's animal fauna was unsurpassed; he will be missed.

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