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The feeding habits of a group of herbivorous rock-dwelling cichlid fishes (Cichlidae: Perciformes) from Lake Malawi, Africa

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Synopsis

The feeding habits of a group of tropical herbivorous rock-dwelling cichlid fishes from Lake Malawi, Africa, are investigated using stomach content analyses. The various species fed selectively on the periphyton of the rocky shores. Blue-green alga of the genus *Calothrix* was the most common item ingested by the group. Diatoms (Chrysophyta) also were abundant food items. Discriminant analysis showed that dietary items were good variables to identify species. Interspecific dietary differences showed a continuum from those species feeding primarily on *Calothrix* to those feeding primarily on diatoms. Algal resources exhibit distinct patterns of spatial variation. Diet was correlated with foraging behavior and trophic morphology. Interspecific differences in diet could possibly facilitate ecological coexistence among various species. Such coexistence would contribute to the maintenance of the high diversity fish faunas characteristic of the Great Rift Lakes of Africa.

Introduction

The cichlid fishes of the Great Lakes of Africa are well known for their ‘explosive’ speciation and adaptive radiation (Fryer & Iles 1972, Greenwood 1974, Lewis et al. 1986). One group which exemplifies the evolutionary capabilities of the family, notably with specializations in feeding morphology and behavior, belong to an apparently monophyletic subset of Lake Malawi cichlids (Fryer & Iles 1972, Ribbink et al. 1983, Marsh & Ribbink 1985). Commonly referred to by their Chitonga name ‘mbuna’, ten genera and about 200 species of these rock-dwelling fishes have been identified (Trewavas 1935, Ribbink et al. 1983). In his classic work, Fryer (1959) suggested that the mbuna community

is a ‘peaceful condominium’ which violates the Gaussian principle of competitive exclusion. To Fryer, an apparent superabundance of algae allowed these fishes to eat the same items of food and to circumvent competition for food. He considered that the differences in trophic morphology and behavior, which characterize many groups within the mbuna species flock, were indicative of different feeding specializations for eating the same resource.

The primary food resource of most mbuna is epilithic algae but knowledge of specific food components taken by different species is lacking. Fryer (1959) recognized the importance of algae in diets and viewed the resource as a homogeneous algal mat dominated by *Calothrix*. Ribbink et al. (1983)

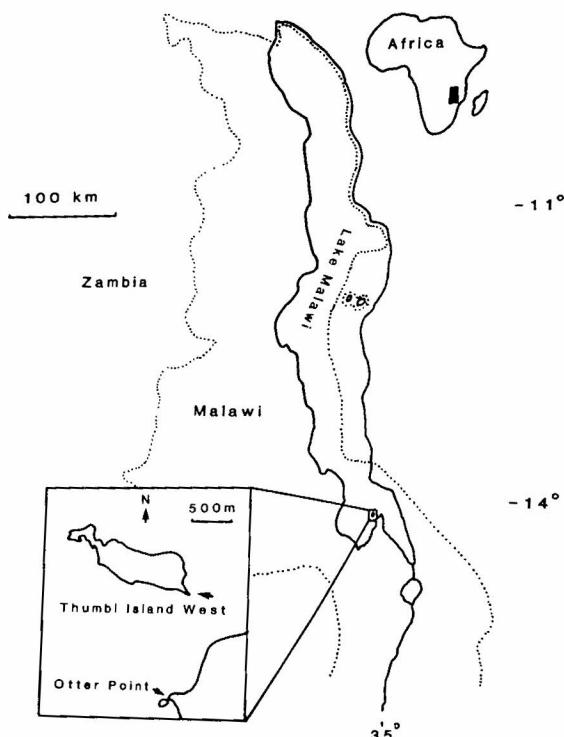


Fig. 1. The Cape Maclear region of Lake Malawi. Inset and arrows show study site locations of Otter Point and Thumbi Island West.

reported stomach analyses of various mbuna and classified algal components into filamentous algae, loose Aufwuchs, and phytoplankton. Types of filamentous algae described were: (1) *Cladophora* sp. and a co-dominant, *Calothrix parietina* in shallow water, (2) reddish-brown tufts, and (3) a coarse green algal mat in deeper water dominated by a different species of *Cladophora*. Loose Aufwuchs refers to components of the mat of algae that adhere loosely to or live among filamentous algae. Little evidence of food partitioning was apparent from these studies.

Here I present the results of a series of stomach content analyses on a representative group of herbivorous mbuna and quantitative analyses of the algal mat resource. The stomach contents are discussed relative to the morphology and ecology found within the group and the distribution patterns of algal resources. The results presented will help answer two important questions concerning

the evolution of this species assemblage of herbivorous fishes. First, what fine scale resource partitioning, if any, exists which would allow this diverse fish assemblage to coexist as a stable ecological community? Second, are there relationships between the ecological divergence and the behavioral and morphological trophic specializations in this group of fish?

Materials and methods

Seven mbuna species, all of which are common indigenous members of the community at Cape Maclear in southern Lake Malawi ($14^{\circ}0' S$, $34^{\circ}50' E$, Fig. 1) are treated in this study (Table 1). In addition, five mbuna species were examined which were introduced into the Cape Maclear region from other parts of Lake Malawi in the early 1970s by a fish exporter. These species are considered exemplary of most mbuna genera and the foraging strategies employed by herbivores in the group (Ribbink et al. 1983). Because most mbuna species are not formally described, all names used here are taken from Ribbink et al. (1983) and the informal nomenclature is maintained. To determine if diet varied intraspecifically between localities, individuals of *Pseudotropheus tropheops* 'orange-chest' were examined from two allopatric sites, Otter Point and Thumbi Island West (Fig. 1). A planktivorous species, *Cynotilapia afra*, was sampled at a six-month interval to determine if there is seasonal variation of plankton in the diet.

Fish were collected by SCUBA diving and monofilament block nets between May and July 1985 from either Otter Point or Thumbi Island West. Stomachs were immediately injected with formalin (10%) and removed from the fish. Algal types were counted in wet slide mounts of haphazardly sampled stomach contents with a Wild M11 compound microscope at $600\times$ magnification.

Lake Malawi algae are poorly known and were identified mostly to genus using Van Meel (1954) and Bold & Wynne (1984). A minimum of 150 individual algal items (individual cells, colonies or filaments) were counted from at least eight individual fish of the seven species (Table 1). For the five

introduced species, 50 items in at least five individuals were counted. A field of view was counted and then a new field was haphazardly selected.

Estimating quantities of algal food items in fish stomach contents can be problematic. Different sizes of algal cells result in an increased importance of cyanophytes in abundance estimates while calculations of volume may over emphasize chlorophytes. Both percent abundance and percent volume of various food items are presented here. Percent volume of each algal type was calculated from abundance, cell size, and average number of cells per filament data.

To determine algal distributions in the field, I separated epilithic algae by eye into *Calothrix*, smooth and slippery brown patches with filaments rarely greater than 2 mm in length, and *Cladophora*, coarse green felt-like patches that grow submerged to lengths of 5 to 20 mm or more. At Thunbi Island West, distribution patterns of attached algae were determined using five transects, 25 m in length laid parallel to the shore line at 1, 3, 5, 10 and 15 m depths. Five points perpendicular to the transect were classified by each of two SCUBA divers at 1 m intervals along the transect as *Cladophora*-dominated, *Calothrix*-dominated, or bare rock or sand.

Differences in algal cover on horizontal and vertical surfaces were determined at Otter Point using a 0.25 m² piece of plexiglass as a template to measure algae on the rock surfaces. The plate was divided into one hundred uniformly distributed points and placed flat on the rock surfaces. *Cladophora*, *Calothrix*, and bare rock could be distinguished at points through the plate. Replicates were conducted on horizontal and vertical surfaces at 1.5 m and 7 m water depths.

It was necessary to use the different methods at the two sites because of differences in topology. Otter Point is dominated by large boulders and rock slabs with little relief. The algal mat is a fine mosaic of inter-mixed patches of *Calothrix* and *Cladophora*. At Thunbi Island West, rocks are smaller and broken up with virtually uniform stands of *Calothrix*-dominated or *Cladophora*-dominated patches.

Analyses of feeding data

Principal component analysis

Principal component analyses using covariance matrices were conducted on both abundance and

Table 1. Species on which stomach analyses were conducted, location at which the fish were collected, the number of fish examined, and average number of algal cells counted per individual. Species names from Ribbink et al. (1983) except for *Pseudotropheus elongatus* 'green-back' which represents a previously undescribed species.

Species	Location	Number of fish	Average count per stomach
Endemic species			
<i>Pseudotropheus tropheops</i> 'orange-chest'	Otter Point	8	154
<i>Pseudotropheus tropheops</i> 'orange-chest'	Thunbi Island West	17	77
<i>Pseudotropheus gracilior</i>	Otter Point	8	154
<i>Pseudotropheus zebra</i>	Thunbi Island West	10	140
<i>Pseudotropheus elongatus</i> 'green-back'	Otter Point	8	166
<i>Petrotilapia nigra</i>	Otter Point	8	157
<i>Labeotropheus fuelleborni</i>	Otter Point	8	156
<i>Melanochromis auratus</i>	Thunbi Island West	8	161
Introduced species			
<i>Melanochromis</i> 'black-white johanni'	Thunbi Island West	5	50
<i>Pseudotropheus aurora</i>	Otter Point	10	50
<i>Pseudotropheus zebra</i> 'cobalt'	Thunbi Island West	10	51
<i>Melanochromis joanjohnstonae</i>	Thunbi Island West	6	50
<i>Cynotilapia afra</i> November, 1984	Thunbi Island West	8	116
<i>Cynotilapia afra</i> July, 1985	Thunbi Island West	5	100

volume of the specific algal components which were represented by more than 1% in any stomach. The data were square-root arcsine transformed. The covariance matrix was used because units are comparable allowing for direct interpretation of eigenvectors. Scheffe's multiple range tests were conducted on the scores of the first three principal components for both volume and abundance.

Discriminant analysis

Discriminant analysis using a generalized squared distance function was used to determine the extent of individual and species variation in diets. For this analysis, only the top twelve food items that accounted for greater than one percent mean abundance in all species were used (see Results for algae used). This makes the test more conservative and indicative of the extent of individual variation.

Niche breadth and overlap

Feeding relationships in terms of dietary breadth and overlap of species were determined using the following indices. Dietary breadth was calculated for both abundance and volume data using Levins' index (Levins 1968):

$$\text{Resource breadth} = 1 / \sum_i P_i^2,$$

where P_i = the percent abundance or volume of food item i to a species. Dietary overlap between species was calculated using both abundance and volume data with Schoener's index (Linton et al. 1981):

$$\text{Resource overlap} = 1 - 1/2 \sum |P_{ij} - P_{ik}|,$$

where P_{ij} equals the percent of food item i in diets of species j and P_{ik} equals percent of food item i to species k . Overlap values are arbitrarily considered high (>0.6), intermediate ($0.4 - 0.6$) or low (<0.4) (Grossman 1986).

These indices assume prey to be equally available to all predators. In this study, the percent cover of periphyton and availability of diatoms was heterogeneous among microhabitats. Because fish are mobile herbivores, I assume they can use vari-

ous microhabitats and that the indices provide an indication of dietary relationships. Also, Schoener's index is more sensitive to changes in rare prey items than to changes in common prey (Shulman 1983). Recalculation of overlap deleting all percentages of less than 1% revealed a systematic lowering of overlap values. However, this did not result in reclassification of any species interactions as high, intermediate, or low. Hence, inclusion of rare dietary items did not bias results and original calculations are retained.

Results

Algal cover

At Thunbi Island West, *Calothrix* was the most common epilithic alga at all depths except 1 m where *Cladophora* dominated (Fig. 2). Less than 1% of total substrate was bare rock. At Otter Point, both types were equally common on shallow (1 m) horizontal surfaces but *Cladophora* dominated on shallow vertical faces (Fig. 3). At 7 m, both algal types were equally abundant on both substrates.

During November and December 1985, large patches of *Oscillatoria* were found growing on rocky substrates below 5 m. During this period, the hot, dry season, *Oscillatoria* accounted for about 12% of total cover.

Stomach analysis

Most algae were identified to genus and a total of 41 different taxonomic categories of algae were recognized in stomach contents (Table 2). The algae are being described in detail elsewhere (Haberyan & Mhone personal communication). Three orders of algae accounted for all algal stomach items: Cyanophyta (blue-greens), Chlorophyta (greens), and Chrysophyta (diatoms).

The most common food item in the stomach contents of the endemic mbuna, in terms of both abundance and volume, was the blue-green alga, *Calothrix* (Table 3). Two species of the blue-green algae genus *Oscillatoria* were also prominent food items. The green alga *Cladophora* was found in the stomachs of all species and contributed considerably to volume. Diatoms were relatively abun-

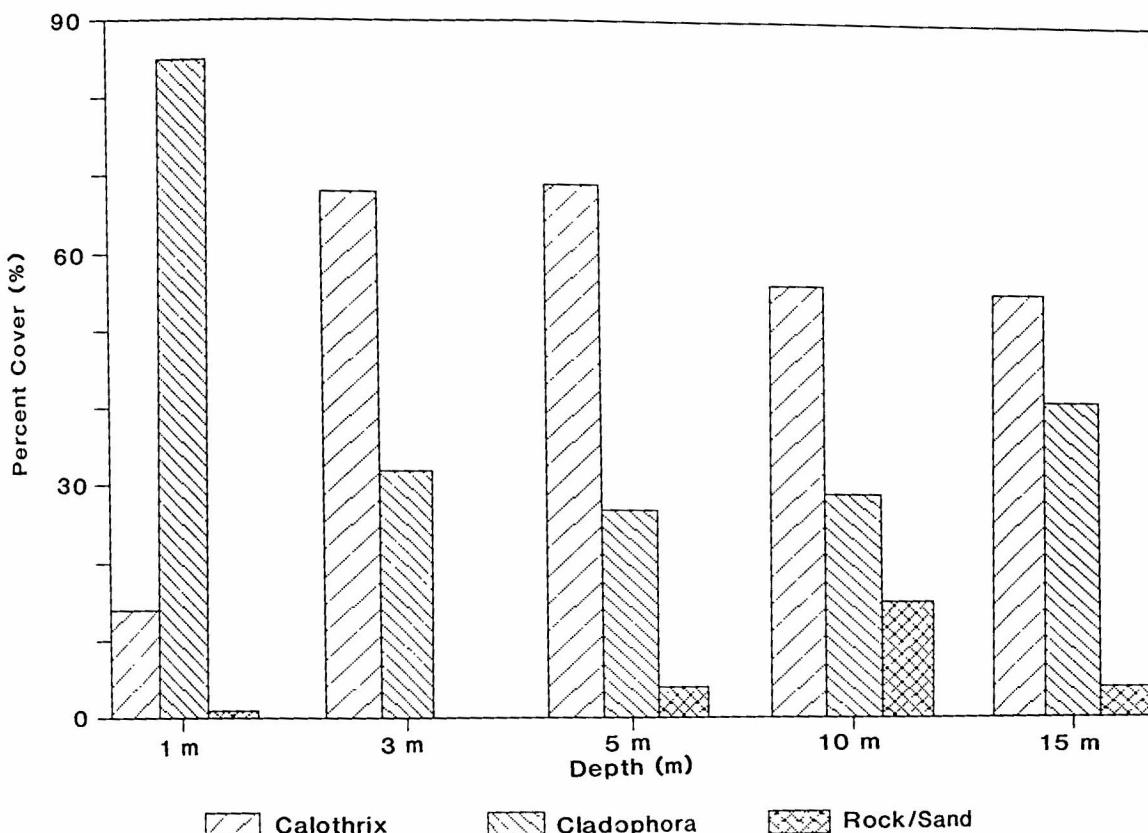


Fig. 2. Percentage cover of the two major attached algal species and bare rock or sand at five water depths at Thumbi Island West, Lake Malawi. Cover was determined through a series of transects along the various (1, 3, 5, 10 and 15 m) depths. Each depth represents the percentage of 250 points at each depth counted by two divers.

dant in the stomach contents of the fish and contributed substantially to both abundance and volume calculations. Both epiphytic and pelagic diatoms were found in the diets.

Species specific characteristics

Pseudotropheus tropheops 'orange-chest' (P.T. in Table 3, Fig. 4). Cyanophytes dominated the diet of this species and *Calothrix* was the most common food item in both abundance and volume. If an individual specimen had little *Calothrix* in its stomach, the most prevalent food items were one of two species of *Oscillatoria*. A few individual fish had many small diatoms in their stomach contents and the most numerous diatoms, *Gomphonema* and

Navicula, are epiphytic on attached algae.

Fish from Otter Point and Thumbi Island West, compared for geographical variation in diet, showed a difference in the amount of *Calothrix* (Table 4). At Thumbi Island West, almost 50% of all food items were *Calothrix* as opposed to only 17% at Otter Point. In stomachs of fish from Otter Point, *Oscillatoria* was more abundant and dominated the volume. Dense stands of *Oscillatoria* were found in crevices and cracks at Otter Point. At Thumbi Island West, *Oscillatoria* was primarily found near sand surfaces and away from areas where these fish were observed feeding.

Labeotropheus fuelleborni (L.F. in Table 3, Fig. 4). The two most common dietary items, for both abundance and volume, were *Calothrix* and *Oscil-*

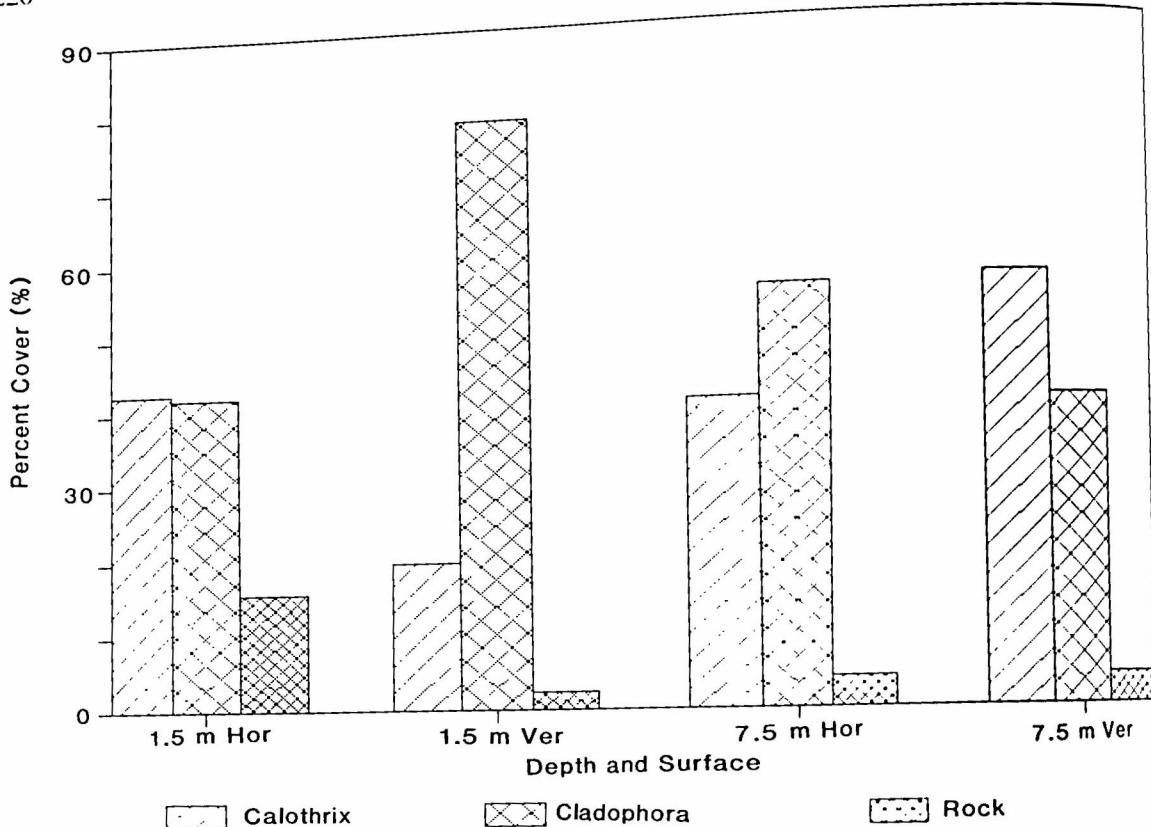


Fig. 3. Percentage cover of *Calothrix* and *Cladophora* from 1.5 and 7 meters depth on horizontal (0°) and vertical (90°) surfaces at Otter Point, Lake Malawi. Rock indicates areas with no discernible algal cover.

latoria. *Cladophora* was the only chlorophyte represented by greater than 1% in either volume or abundance. The two abundant diatoms found in stomachs, *Gomphonema* and *Navicula*, are epiphytic. Diatoms accounted for 48.3% of the abundance but were small and represented only 7.7% of the volume. The only other contents found were sponge spicules.

Melanochromis auratus (M.A. in Table 3, Fig. 4). The most abundant food items found in the stomach contents were *Navicula*, *Calothrix*, and *Oscillatoria*. *Calothrix* and *Cladophora* were most numerous in volume calculations. *Eucapsis*, a planktonic cyanophyte, was the fourth most abundant alga found but was present in only three of nine individuals. Other items found were fish, sponge spicules, and cyclopoid copepods. This omnivorous species

showed the widest range of non-algal dietary items of all species examined.

Pseudotropheus gracilior (P.G. in Table 3, Fig. 4). The diet of this species was dominated by diatoms. Over 71% of the algae were diatoms that accounted for 42.3% by volume. The three most abundant food items were the diatoms *Rhopolodia*, *Melosira*, and *Nitzschia epiphyticoides*. The most abundant items for volume were *Calothrix* followed by *Melosira*. Other items occasionally recorded were copepods, ostracods, sponge spicules and an unidentified crustacean.

Pseudotropheus elongatus 'green-back' (P.E. in Table 3, Fig. 4). The most abundant food items were *Calothrix* and *Rhopolodia* and, in terms of volume, *Cladophora* and *Calothrix*. This species

ate large numbers of diatoms, but they comprised only 15.4% of the volume. Of the two abundant diatoms found in the stomach contents, *Rhopolodia* is epiphytic but *Stephanodiscus* is planktonic. Sponge spicules were the only other contents found.

Petrotilapia nigra (P.N. in Table 3, Fig. 4). The diet of this species was dominated by diatoms (over 70% by abundance and 37.5% by volume), and loose *Calothrix* and *Oscillatoria*. One individual had the diatom *Cocconeis* in its stomach contents which is found growing primarily on the aquatic vascular plant *Vallisneria*. Limited amounts of copepods and sponge spicules were also found in stomachs.

Pseudotropheus zebra (P.Z. in Table 3, Fig. 4). Diatoms dominated the stomach contents in abundance and volume. The most abundant diatoms were *Melosira* and *Nitzschia epiphyticoides*. The

only other mbuna found to have such a high proportion of *Melosira*, a planktonic diatom, in its diet was *Cynotilapia afra* which is well known for its plankton feeding habits (Ribbink et al. 1983). Cladocerans, copepods, an unidentified larva, and a chironomid were found in limited amounts in stomachs.

Introduced species

Melanochromis 'black-white johanni' (M.B. in Table 5). The most abundant food in the diet of this fish were the diatoms *Nitzschia epiphyticoides* and *Melosira*. *Melosira* was also the most abundant food item for volume followed by *Cladophora*.

Pseudotropheus aurora (P.A. in Table 5). Again the diatoms *Nitzschia epiphyticoides* and *Melosira* were the most abundant food items. The planktonic diatoms *Melosira* and *Stephanodiscus* dominated the volume.

Pseudotropheus zebra 'cobalt' (P.C. in Table 5). This species fed upon a wide range of food items with no individual item having a greater abundance than 16%. As with the two previous species, the most abundant items were *Melosira* and *Nitzschia epiphyticoides*. Volume was dominated by *Oscillatoria*, *Melosira*, and *Calothrix*.

Melanochromis joanjohnsonae (M.J. in Table 5). *Nitzschia spiculum*, *Oscillatoria*, and *Rhopolodia*, all relatively small algae, were the most abundant food items. The volume of the diet was dominated by *Cladophora* and *Calothrix*. This was the greatest proportion of *Cladophora* found for any species. This fish is found in shallow (< 2 m) water where *Cladophora* is the dominant attached alga (Fig. 2).

Cynotilapia afra. Seasonal variation of zooplankton and phytoplankton eaten was determined by analyzing stomachs in November 1984 and again in July 1985 (Table 6). The results from the two time periods showed that the diet was dominated for both volume and abundance by the pelagic diatom, *Melosira*. The green alga, *Coelastrum*, was also

Table 2. The Cyanophytes (blue-green algae), Chlorophytes (green algae) and Chrysophytes (diatoms) found in the mbuna examined.

Algal divisions

Cyanophyta	Chlorophyta	Chrysophyta
<i>Anabaena</i>	<i>Bulbochaeta</i>	<i>Acanthales</i>
<i>Calothrix</i>	<i>Chlorella</i>	<i>Amphora</i>
<i>Eucapsis</i>	<i>Cladophora</i>	<i>Cocconeis</i>
<i>Lyngbya</i>	<i>Coelastrum</i>	<i>Cymbella</i>
<i>Microcystis</i>	<i>Cosmarium</i>	<i>Diploneis</i>
<i>Oscillatoria thick</i>	<i>Dimorphococcus</i>	<i>Epithemia</i>
<i>Oscillatoria thin</i>	<i>Oedogonium</i>	<i>Eunotia</i>
<i>Spirulina</i>	<i>Pediastrum</i>	<i>Fragillaria</i>
	<i>Scenedesmus</i>	<i>Gomphocymbella</i>
	<i>Selenastrum</i>	<i>Gomphonema</i>
	<i>Sirogonium</i>	<i>Melosira</i>
	<i>Spirogyra</i>	<i>Navicula</i>
	<i>Staurastrum</i>	<i>Nitzschia accommodata</i>
		<i>Nitzschia epiphyticoides</i>
		<i>Nitzschia spiculum</i>
		<i>Pinnularia</i>
		<i>Pleurosigma</i>
		<i>Rhopolodia</i>
		<i>Stephanodiscus</i>
		<i>Surirella</i>

relatively abundant in the July 1985 samples. This was not noted for other species and *Cynotilapia afra* may have been feeding in a patch of *Coe-*

lastrum rich water. While zooplankton is found in the stomachs, this fish fed primarily on phytoplankton.

Table 3. Average percent abundance (% A) and volume (% V) of algal food items found in the stomachs of mbuna. Trace (t) indicates <1%. Species abbreviations given in the text.

ALGAE	P.T.		L.F.		M.A.		P.G.		P.E.		P.N.		P.Z.	
	% A	% V	% A	% V	% A	% V	% A	% V	% A	% V	% A	% V	% A	% V
CYANOPHYTA														
Anabaena	t	t	—	—	—	—	t	t	—	—	—	—	1.9	1.2
Calothrix	39.6	49.4	23.1	35.3	15.8	42.8	8.5	26.0	18.8	35.0	10.2	34.6	t	1.2
Eucapsis	—	—	—	—	8.7	t	t	t	—	—	1.4	t	t	t
Lyngbya	4.5	7.5	t	t	—	—	t	1.6	t	t	t	t	t	1.6
Microcystis	t	t	t	t	—	—	t	t	—	—	—	—	t	t
Oscillatoria														
O. 'thick'	8.6	22.5	9.0	28.8	1.2	6.8	1.1	7.1	1.5	5.9	3.0	21.3	t	2.5
O. 'thin'	10.0	t	13.5	t	9.2	t	2.9	t	9.5	t	11.8	t	3.8	t
Spirulina	—	—	—	—	—	—	t	t	—	—	—	—	—	—
CHLOROPHYTA														
Bulbochaeta	—	—	—	—	—	—	—	—	—	—	—	—	t	t
Chlorella	t	t	2.0	t	1.1	t	10.4	t	3.5	t	2.1	t	t	t
Cladophora	1.8	15.0	2.7	27.5	2.0	36.1	t	8.2	3.4	42.2	t	4.5	t	7.9
Coelastrum	—	—	—	—	—	—	t	14.0	—	—	—	—	—	—
Cosmarium	—	—	t	t	—	—	—	—	—	—	—	—	t	t
Dimorphococcus	t	—	—	—	—	—	—	—	—	—	—	—	t	t
Oedogonium	t	t	1.0	t	1.1	t	1.0	t	3.9	t	1.0	t	4.7	1.6
Pediastrum	t	t	—	—	t	t	—	—	—	—	—	—	—	—
Scenedesmus	—	—	—	—	—	—	t	t	t	t	—	—	—	—
Selenastrum	—	—	—	—	—	—	—	—	—	—	—	—	—	t
Sirogonium	t	1.9	—	—	—	—	—	—	—	—	—	—	—	—
Spirogyra	—	—	—	—	—	—	—	—	—	—	—	—	t	9.0
Staurastrum	—	—	t	t	—	—	—	—	t	t	—	—	t	t
CHRYSOPHYTA														
Acanthales	—	—	—	—	—	—	t	t	—	—	t	t	—	—
Amphora	t	t	t	t	—	—	t	t	—	—	t	t	t	t
Cocconeis	—	—	—	—	t	t	t	t	t	t	3.7	2.4	t	t
Cymbella	2.9	t	5.1	t	4.9	t	6.7	t	5.4	t	6.6	t	2.6	t
Diploneis	t	t	—	—	—	—	—	—	t	t	t	t	—	—
Epithemia	—	—	—	—	t	t	t	t	t	t	t	t	—	—
Eunotia	—	—	—	—	—	—	—	—	t	t	t	t	—	—
Fragillaria	t	t	t	t	t	t	1.6	t	1.0	t	t	t	t	t
Gomphocymbella	t	t	2.4	t	—	—	t	t	1.4	t	t	t	t	t
Gomphonema	7.5	t	12.6	t	6.6	t	6.2	t	8.6	t	7.5	t	1.3	t
Melosira	1.0	t	1.7	1.1	1.0	1.2	13.3	17.5	2.9	2.3	5.2	7.6	34.5	58.2
Navicula	7.2	t	9.5	t	29.9	3.9	4.7	t	9.1	t	7.3	1.2	2.6	t
Nitzschia														
N. accommodata	t	t	—	—	—	—	—	—	—	—	—	—	—	—
N. epiphyticoides	5.3	t	2.1	t	1.0	t	9.2	t	2.4	t	3.2	t	32.9	1.2
N. spiculum	2.4	t	5.7	t	6.8	2.0	6.7	2.2	2.0	t	13.1	4.8	1.2	t
Pinnularia	t	t	—	—	—	—	—	—	—	—	—	—	—	—
Pleurosigma	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhopolodia	5.1	1.1	5.7	1.5	8.7	4.0	16.9	8.9	21.1	6.7	16.1	9.4	6.5	4.4
Stephanodiscus	1.1	t	3.1	2.7	1.2	1.9	3.4	6.0	4.3	4.6	5.8	11.3	1.7	3.8
Surirella	—	—	—	—	—	—	t	5.8	—	—	—	t	5.6	—

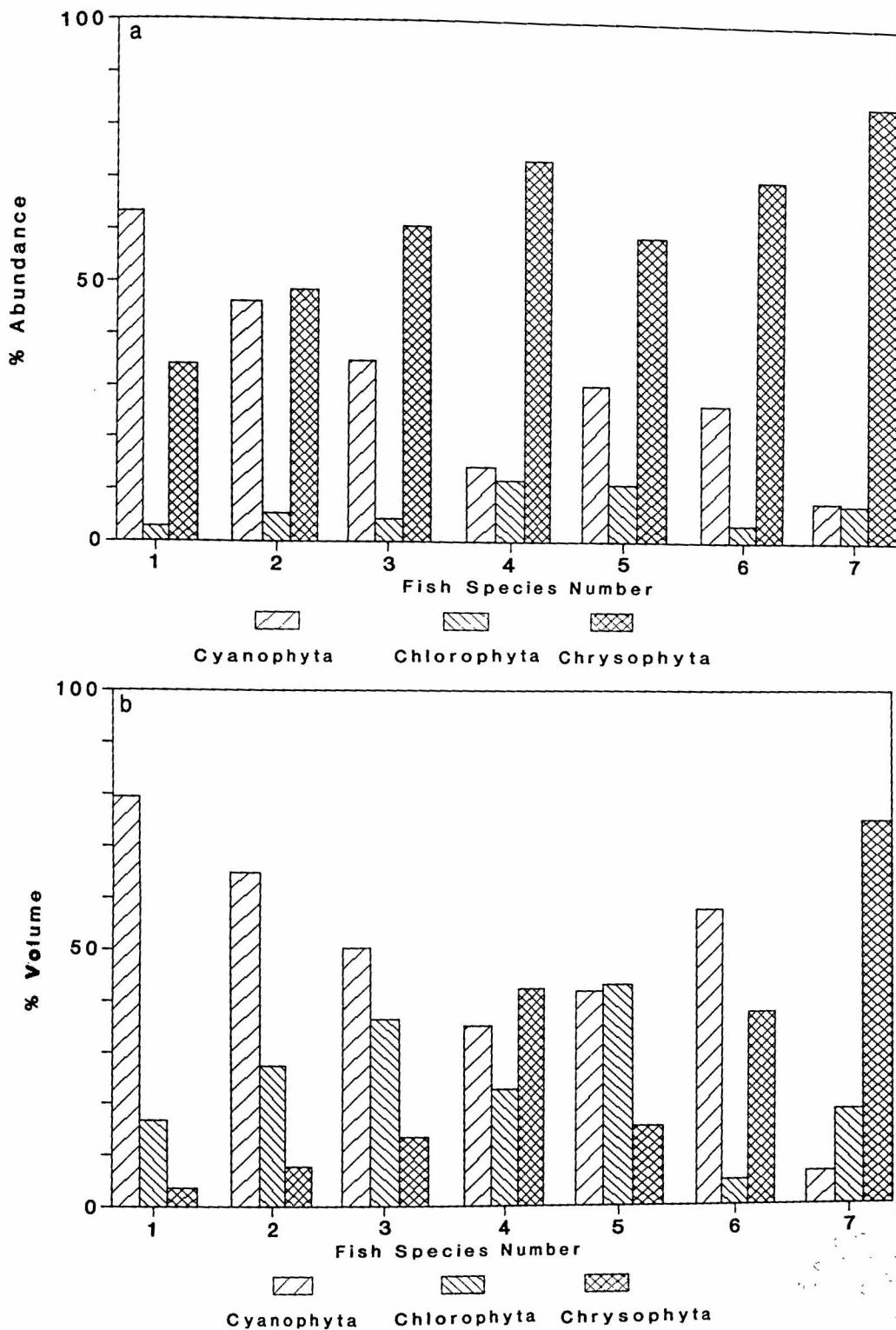


Fig. 4. The percentage abundance (a) and percentage volume (b) of the three major algal divisions, Cyanophyta, Chlorophyta, and Chrysophyta found in the stomachs of the seven endemic species. The species numbers correspond to the following: 1 = *Pseudotropheus tropheops* 'orange-chest', 2 = *Labeotropheus fuelleborni*, 3 = *Melanochromis auratus*, 4 = *Pseudotropheus gracilior*, 5 = *Pseudotropheus elongatus* 'green-back', 6 = *Petrotilapia nigra*, 7 = *Pseudotropheus zebra*.

Discriminant analysis

The discriminant analysis with the endemics showed 71 of 76 individual fish correctly classified into the correct species. All misclassifications (one *Pseudotropheus tropheops* 'orange-chest' from Otter Point, one *Labeotropheus fuelleborni*, one *Petrotilapia nigra* and two *Melanochromis auratus*) were placed into the *Pseudotropheus gracilior* category and were the result of individuals with large amounts of diatoms in the stomach contents.

Dietary indices

The smallest dietary breadths of the endemics, for both abundance and volume, were shown by *Pseu-*

dotropheus zebra and *P. tropheops* 'orange-chest' respectively (Table 7). The principal components analysis, together with Figure 4a-b, showed these two species as the end points of a resource utilization gradient. They are the mbuna most specialized in feeding habits for diatoms and attached algae. The greatest breadths were found for *P. gracilior* and *Petrotilapia nigra*. The only ranking differences between the abundance and volume breadths were in the order of the third, fourth and fifth species: *Labeotropheus fuelleborni*, *Pseudotropheus elongatus* 'green-back' and *Melanochromis auratus*.

In general, interspecific dietary overlap was high

Table 4. Food items found in the stomach contents of two allopatric populations of *Pseudotropheus tropheops* 'orange-chest' from Otter Point and Thumbi Island West. Trace (t) indicates <1%.

ALGAE	Thumbi Island West		Otter Point	
	Percent abundance	Percent volume	Percent abundance	Percent volume
CYANOPHYTA				
Anabaena	t	t	t	t
Calothrix	49.0	57.6	16.7	24.9
Lynbya	3.9	6.1	6.0	11.9
Microcystis	-	-	1.5	t
Oscillatoria 'thick'	5.4	13.3	15.6	48.7
Oscillatoria 'thin'	9.9	t	10.1	t
CHLOROPHYTA				
Chlorella	t	t	t	t
Cladophora	2.5	19.6	t	4.0
Dimorphococcus	t	t	t	t
Oedogonium	t	t	1.0	t
Sirogonium	-	-	t	4.5
CHRYSOPHYTA				
Amphora	t	t	t	t
Cymbella	2.0	t	4.9	t
Diploneis	-	-	t	t
Fragillaria	t	t	t	t
Gomphocymbella	t	t	t	t
Gomphonema	4.9	t	2.0	t
Melosira	1.1	t	13.2	t
Navicula	5.6	t	1.0	t
Nitzschia				
N. accommodata	t	t	10.5	t
N. epiphyticoides	6.4	t	-	-
N. spiculum	1.2	t	3.2	t
Pinnularia	-	t	4.9	t
Rhopolodia	5.9	-	t	t
Stephanodiscus	t	1.2	3.4	t
		t	1.6	1.4

(Table 8). These values ranged from 0.167 (volume, *Pseudotropheus tropheops* 'orange-chest' / *P. zebra*) to 0.863 (volume, *Melanochromis auratus* / *P. elongatus* 'green-back'). Of the 42 different abundance and volume pairwise comparisons, ten were arbitrarily low values (< 0.4, all involving *P. zebra*), 13 were medium (> 0.4 and < 0.6) and 19 were high (> 0.6). The species showing highest average overlap was *P. elongatus* 'green-back' for abundance data and the lowest average overlap was *P. zebra* for volume data. *P. zebra* showed low overlap values (< 0.400) with all species except *P. gracilior*.

The greatest difference between volume and abundance overlap values was for *Melanochromis auratus* and *Pseudotropheus elongatus* 'green-back'. This was due to many of the small diatoms, *Navicula* and *Rhopolodia*, influencing abundance data. For both volume and abundance, the overlap between the two species was high. The endemic species with the lowest breadth values, *P. zebra*, also had the lowest average overlap values.

The dietary breadth indices for the introduced species were on the average smaller than those found for the endemics (Table 7). There were only

Table 5. Average percent abundance (% A) and volume (% V) of algal food items found in the stomachs of four herbivorous mbuna introduced to Thunbi Island West. Trace (t) indicates <1%. Species abbreviations given in the text.

ALGAE	M.B.		P.A.		P.C.		M.J.	
	% A	% V	% A	% V	% A	% V	% A	% V
CYANOPHYTA								
Anabaena	1.2	t	—	—	t	21.8	5.7	13.7
Calothrix	—	—	—	—	6.4	—	—	—
Lyngbya	—	—	—	—	t	2.7	—	—
Microcystis	—	—	t	t	—	—	—	—
Oscillatoriaria								
O. 'thick'	1.2	10.0	—	—	3.3	23.5	t	3.4
O. 'thin'	4.4	t	t	t	8.3	t	15.3	t
CHLOROPHYTA								
Chlorella	—	—	t	t	1.0	1.0	t	t
Cladophora	1.0	21.2	—	—	t	9.1	4.0	64.5
Oedogonium	t	t	1.0	t	1.2	t	t	t
Scenedesmus	—	—	—	—	t	t	t	t
Staurastrum	—	—	—	—	—	—	t	t
CHRYSOPHYTA								
Amphora	t	t	—	—	t	t	t	t
Cocconeis	t	t	—	—	—	—	2.0	t
Cymbella	1.6	t	2.4	t	3.6	t	10.0	t
Diploneis	—	—	—	—	—	—	—	—
Epithemia	—	—	—	—	t	t	—	—
Fragillaria	8.0	t	1.6	t	t	t	3.0	t
Gomphocymbella	t	t	—	—	2.6	t	10.3	t
Gomphonema	1.6	t	t	t	8.6	t	3.0	3.1
Melosira	28.4	48.5	29.2	69.0	15.6	22.7	6.0	t
Navicula	4.4	t	1.8	t	8.2	1.3	—	—
Nitzschia								
N. accommodata	—	—	—	—	6.0	1.7	8.0	t
N. epiphyticoides	30.4	1.2	44.8	2.4	15.4	t	16.7	4.3
N. spiculum	7.2	3.1	6.0	3.7	2.4	t	10.7	4.4
Rhopolodia	4.8	3.3	3.6	3.5	9.0	5.2	2.0	2.8
Stephanodiscus	4.4	10.0	6.0	19.6	4.6	8.9	—	—

Table 6. Seasonal variation in algal food items found in the stomachs of the introduced species *Cynotilapia afra* caught at Thimbi Island West during November 1984 and July 1985. Trace (t) indicates < 1%.

ALGAE	November 1984		July 1985	
	Percent abundance	Percent volume	Percent abundance	Percent volume
CYANOPHYTA				
Anabaena	-	-	1.6	t
Calothrix	-	-	t	1.2
Microcystis	t	t	-	-
Oscillatoria 'thick'	-	-	t	t
Oscillatoria 'thin'	7.2	t	t	t
CHLOROPHYTA				
Chlorella	-	-	t	t
Cladophora	-	-	1.6	14.2
Coelastrum	-	-	2.5	36.4
Oedogonium	t	t	3.6	t
Scenedesmus	-	-	t	t
Spirogyra	-	-	t	t
CHRYSOPHYTA				
Cocconeis	t	t	t	t
Cymbella	-	-	t	t
Gomphonema	t	t	-	-
Melosira	54.6	79.0	46.9	38.0
Navicula	-	-	t	t
Nitzschia				
N. accommodata	-	-	t	t
N. epiphyticoides	23.0	1.0	27.7	t
N. spiculum	6.0	2.4	3.5	t
Rhopalodia	t	t	t	t
Stephanodiscus	6.8	16.0	9.0	6.8

Table 7. Resource breadth values for mbuna species based on stomach content analyses. Breadth values are presented for both abundance and volume data.

Species	Abundance	resource breadth	Volume	resource breadth
Endemics (mean \pm S.D.)				
<i>Pseudotropheus tropheops</i> 'orange-chest'	7.79 \pm 3.2		3.95 \pm 1.5	
<i>Pseudotropheus gracilior</i>	5.14		3.09	
<i>Pseudotropheus zebra</i>	13.06		6.89	
<i>Pseudotropheus elongatus</i> 'green-back'	4.21		2.77	
<i>Petrotilapia nigra</i>	8.67		3.21	
<i>Labeotropheus fuelleborni</i>	10.77		5.06	
<i>Melanochromis auratus</i>	6.05		3.52	
Introduced (mean \pm S.D.)				
<i>Melanochromis b-w johanni</i>	6.65		3.10	
<i>Pseudotropheus aurora</i>	6.48 \pm 3.8		3.30 \pm 1.5	
<i>Pseudotropheus</i> 'cobalt'	5.16		3.31	
<i>Melanochromis joanjohnsonae</i>	3.54		1.93	
<i>Cynotilapia afra</i> June	11.02		5.73	
November	9.92		2.27	
	2.74		3.24	
	1.54		3.31	

minor non-significant differences in the overlap values of the endemic and introduced species (Table 9).

principal components analysis

The results of the Scheffe's multiple range test on species scores of the first three principal components (PCI-PCIII) for both abundance and volume data show that many species were included in more than one statistical grouping on the basis of dietary variation (Table 10). The only species forming exclusive groups were *Pseudotropheus tropheops* 'orange-chest' from Thambi Island West for abundance PCI and *P. zebra* for abundance PCII. *Pseudotropheus elongatus* 'green-back' and *Petrotilapia nigra* shared all abundance PC groups. Abundance PCIII showed no differences between species.

The first three PC's accounted for 63% of the abundance variation and 79% of the volume varia-

tion. The rank order of volume PCI was the same as abundance PCI for all species except for the order of *Pseudotropheus elongatus* 'green-back' and *Petrotilapia nigra*. However, groupings were different.

Eigenvectors defining the major axes included two high elements of the 25 items. The highest elements for abundance PCI, PCII and PCIII were those of *Calothrix* and *Melosira*, *Melosira* and *Navicula*, and *Oscillatoria* spp. and *Calothrix* respec-

Table 9. Mean (\pm S.D.) resource overlap values for endemic and introduced mbuna species.

	Abundance overlap	Volume overlap
Endemic/Endemic	0.54 ± 0.17	0.53 ± 0.21
Endemic/Introduced	0.49 ± 0.17	0.43 ± 0.20
Introduced/Introduced	0.55 ± 0.14	0.43 ± 0.15

Table 8. Resource overlap values for mbuna species based on stomach content data. Overlap values are presented for both algal abundance (upper right) and volume (lower left) data.

tively. The highest elements for volume PCI, PCII, and PCIII were those of *Calothrix* and *Melosira*, *Cladophora* and *Oscillatoria*, and *Oscillatoria* and *Melosira*.

In general, the principal components indicate a continuum of algal utilization by various fish species (Fig. 4a-b, Table 10). The extremes are fish that feed primarily on *Calothrix*, e.g. *Pseudotropheus tropheops* 'orange-chest', and those that feed primarily on diatoms, e.g. *Pseudotropheus zebra*. The two most abundant attached algae, *Calothrix* and *Cladophora*, and the most abundant diatom, *Melosira*, were the major sources of variation in the diets.

Discussion

Algal resources

The results of the algae transects revealed that epilithic periphyton is heterogeneous in its distribution; hence, the algae do not represent a homogeneous food resource. Distinct patterns of spatial variation, corresponding to depth and substrate inclination, are found in percent cover of attached algae. Spatial heterogeneity in periphyton is common. For example, Power (1983) demonstrated that standing crop of periphyton varied with depth and substrate in tropical streams. Sharp (1981) also showed spatial variation in epilithic algal abundance at Monkey Bay, Lake Malawi, which corresponded to territories of various male mbuna. Phytoplankton (Reinthal 1987) and epiphytic algae are

Table 10. Mean principal component scores for the seven endemic species. Principal components analyses were conducted on square root arcsine transformed abundance and volume data. Lines indicate groups not considered significantly different ($p < 0.05$) by Scheffé's multiple range test. The species represented are: PT1 = *Pseudotropheus tropheops* 'orange-chest' from Otter Point, PT2 = *Pseudotropheus tropheops* 'orange-chest' from Thumbi Island West, PZ = *Pseudotropheus zebra*, PG = *Pseudotropheus gracilis*, PE = *Pseudotropheus elongatus* 'green-back', PN = *Petrotilapia nigra*, MA = *Melanochromis auratus*, and LF = *Labeotropheus fuelleborni*.

Abundance

Mean PCI	0.46 PZ	~0.26 PG	~0.14 MA	~ 0.12 PN	~ 0.03 PE	~-0.12 LF	~-0.14 PT1	~-0.74 PT2
Mean PCII	0.32 MA	~0.15 LF	~0.12 PE	~ 0.07 PT1	~ 0.06 PN	~-0.07 PG	~-0.13 PT2	~-0.52 PZ
Mean PCIII	0.46 PZ	~0.26 PG	~0.14 MA	~ 0.12 PN	~ 0.03 PE	~-0.12 LF	~-0.14 PT1	~-0.74 PT2
Volume								
Mean PCI	0.67 PZ	~0.20 PG	~0.10 MA	~ 0.05 PE	~ 0.01 PN	~-0.06 LF	~-0.22 PT1	~-0.76 PT2
Mean PCII	0.48 MA	~0.36 PE	~0.06 LF	~-0.06 PT2	~-0.07 PG	~-0.18 PT1	~-0.20 PN	~-0.36 PZ
Mean PCIII	0.14 LF	~0.14 PT1	~0.12 MA	~ 0.08 PN	~ 0.00 PE	~-0.04 PG	~-0.07 PZ	~-0.27 PT2

also factors that influence resource heterogeneity.

The three 'species' of *Cladophora* discussed by Ribbink et al. (1983) could not be discerned. One may represent a species of the cyanophyte *Oscillatoria* and the other two may be ecophenotypes of shallow and deep water *Cladophora*. *Oscillatoria* showed seasonal variability and was relatively abundant during the hot season. The reddish-brown tufts, termed C2 by Ribbink et al. (1983), most likely correspond to *Calothrix* here. Detailed descriptions of the algae of the Cape Maclear region of Lake Malawi are discussed elsewhere (Haberyan & Mhone manuscript).

Feeding habits

The data presented here show that the mbuna use most algal resources available to them. Forty-one different types of algae were ingested by the species examined here and these represent most of the algae available. *Calothrix* sp., the dominant epilithic species, is the most abundant and voluminous component of mbuna diet. These results concur with those of Fryer (1959) and Ribbink et al. (1983) who found *Calothrix* to be prominent in gut contents of many species. Diatoms were also a major component in the diets of many mbuna and *Melosira* was the diatom most commonly found. The importance of phytoplankton in the mbuna diet had not been previously emphasized.

Three different methods of feeding on diatoms are found in the mbuna. Species in the *Cynotilapia* group pluck plankton out of the water column and are considered true planktivores. Members of the *Pseudotropheus zebra* and *Petrotilapia* complexes feed primarily by brushing settled phytoplankton and loose algae from the substrate. The third group of fishes feeding on diatoms are those that do not have specialized trophic mechanisms but are eating them because of microhabitats they forage in. For example, feeding experiments with *Pseudotropheus gracilior* show that attached algae are preferred feeding resources (Reinthal 1987) but the diet is dominated by diatoms. The trophic morphology of this species is also characteristic of species feeding on attached algae. However, high sedimentation rates in deeper waters make diatoms the only available resource because they cover the at-

tached algae. Stomach contents were similar for other species found in the sediment-rich intermediate zone (e.g. *Melanochromis* 'black-white johanni' or *Pseudotropheus aurora*).

Items found in the diets were good indicators of species. Using only the top twelve dietary items, 71 of 75 individuals are correctly classified by discriminant analysis into the proper species category. All misclassified individuals are placed in *Pseudotropheus gracilior*, the species with the largest abundance and volume dietary breadth values of any species examined. It was only individual fish with large amounts of diatoms in their stomachs who were misclassified.

In this monophyletic group of fish, the species differ in diets and present a continuum in the various algae ingested. This resource continuum ranges from those species feeding primarily on attached algae, especially *Calothrix* and *Cladophora*, to those feeding primarily on diatoms, especially *Melosira*. The species at the ends of the continuum, *Pseudotropheus tropheops* 'orange-chest' and *Pseudotropheus zebra*, showed the smallest dietary breadths.

Introduced species

Of the five introduced species examined here, three were primarily diatom/sediment and loose aufwuchs feeders, one a *Cladophora* feeder and one a pelagic diatom feeder. *Melanochromis johnsonae* is found only in very shallow water (<1 m) where *Cladophora*, but not other mbuna, is common. *Cynotilapia afra* is the only mbuna consistently found feeding in the water column. Thus, the successfully established species examined here were either sediment feeders or foraged in non-exploited habitats.

Digestion

Fryer (1959) and Ribbink et al. (1983) were unsure of the nutritional value of *Calothrix*. They suggested either the mucilage sheath prevents cell digestion, the mucus is digested (Fryer and Iles 1972), or fish ingest algal strands for epiphytes. Examination of algal cells along the digestive tract and in fecal material showed that algal material is digested. Inferences concerning blue-green algae digestion

from other studies on the digestive capabilities of members in the Cichlidae are useful corollaries until mbuna physiological capabilities are studied. In *Tilapia nilotica*, high concentrations of acid in stomachs lyse blue-green algae cells, and contents are digested in the intestine (Moriarty 1973). Also, the presence of a true stomach, a dilatation in the anterior part of the alimentary tract, allows *T. nilotica* and *Haplochromis nigripinnis* to digest blue-green algae (Moriarty 1973). The mbuna possess true stomachs and, given the similarity of stomach contents of some mbuna and *Oreochromis* spp. (formerly *Tilapia* in Lake Malawi), there is no evidence to suggest the mbuna cannot digest blue-green algae. Furthermore, it does not appear as if the mbuna ingest *Calothrix* for epiphytes. Few diatoms grow epiphytically on *Calothrix* and it sheds detritus. *Nitzschia accommodata* was one of the few diatoms found to be epiphytic on *Calothrix* and only a trace was found in the stomachs of any species.

Pelagic foraging

Cynotilapia afra frequently feeds on plankton in the water column (personal observation, Ribbink et al. 1983). Other mbuna, especially members of *Pseudotropheus* and *Petrotilapia* species complexes, also feed on plankton (Ribbink et al. 1983, McKaye & Marsh 1983). The stomach contents of *Cynotilapia afra* were dominated by the pelagic diatom *Melosira*. A preponderance of pelagic *Melosira* was also in the diets of *Pseudotropheus zebra* and *Petrotilapia nigra*. All three species are reported to eat zooplankton (Ribbink et al. 1983, McKaye & Marsh 1985) but the results here indicate that water column feeding is primarily for phytoplankton. Whereas zooplankton are eaten, it is pelagic forms of algae that are important food items. Caution must be taken in extrapolating observations of feeding in the water column to feeding on zooplankton. Individuals of all three species feeding in the water column were caught using SCUBA and nets. Two species of pelagic algae, *Melosira* and *Anabaena*, but no zooplankton, were found in full stomachs. *Anabaena*, a floating blue-green alga with patchy seasonal and spatial distributions, drifts over rocky habitats. Many *Pseu-*

dotropheus zebra and *Petrotilapia* spp. individuals feed on it in the water column. Thus, these species are facultative feeders (Liem 1980) but the primary switching mainly occurs between the same food item (e.g. *Melosira* or other pelagic alga) found in different habitats (settled on substrates vs. pelagic). There is seasonal variation in zooplankton (Twombly 1983), phytoplankton (Haberyan & Mhone manuscript), and attached algal abundances and distributions. Mbuna will opportunistically use whatever resources are seasonally or spatially available.

Ecological coexistence

Distinct dietary differences were found between most mbuna studied and these fish do not all eat the same algal resource. Thus, differential resource utilization, along with specific spatial requirements (Ribbink et al. 1983), could be a mechanism of ecological coexistence in this high diversity community. In cases of species pair-wise comparisons where high dietary overlap was found, other ecological factors may explain coexistence. An example is *Pseudotropheus tropheops* 'orange-chest' and *P. elongatus* 'green-back'. These two species feed primarily on attached algae. Trophic morphology and behavior are also similar. However, these fish use rock faces with different slopes. *P. tropheops* 'orange-chest' individuals are found on horizontal surfaces, while *P. elongatus* 'green-back' individuals are found on vertical surfaces. Another example is three sibling species of *Petrotilapia* in which Marsh & Ribbink (1985) found differences in feeding site utilization regulated by a social dominance hierarchy in three *Petrotilapia* sibling species.

In this trophically defined community, the species differ in diets and present a continuum in the various algae ingested from those feeding primarily on attached algae to those feeding primarily on diatoms. The herbivorous members do not share the same algal food items as originally suggested. Nor is there a superabundance of food which would permit ecological coexistence; in fact, algal resources appear to be limited (Sharp 1981, Reinthal 1987). While bare rock forms a small percent of the actual cover, the algal mat is cropped and fish grazing prevents luxuriant growth. If food, primarily

ily the algal mat, is in limited supply, resource partitioning and competition is to be expected. Food availability would then be important in selecting for morphologically specialized trophic apparatuses.

Diet, foraging behavior, trophic morphology and phylogeny

Strong correlates of diet are found in foraging behavior, trophic morphology and phylogenetic relationships. The species examined here show four basic types of feeding behavior (Reinthal 1987). Members of the *Pseudotropheus tropheops* group, *Pseudotropheus elongatus* 'green-back', and *Melanochromis auratus* all feed by taking single bites with a 'nipping' motion. In contrast, *Pseudotropheus zebra* and *Petrotilapia nigra* feed with short 'brushing' bites. *Labeotropheus fuelleborni* feeds by 'mowing' and *Cynotilapia afra* is a pelagic forager. The species that feed with a 'nipping' or 'mowing' behavior mainly eat attached algae. The species using the 'brushing' and 'pelagic' behaviors eat more diatoms. However, there are exceptions and habitat utilization is sufficient to explain these differences.

Pseudotropheus tropheops 'orange-chest' and *P. gracilior* show the same foraging behavior but have disjunct depth distributions. The deeper zone, occupied by *P. gracilior*, was sediment-laden and the fish ate more diatoms. However, this species showed distinct preferences for attached algae in paired choice feeding experiments (Reinthal 1987). Thus, the diet of *P. gracilior* is a result of fish feeding in a sub-optimal habitat where preferred resources, attached algae, are unavailable due to sediment cover. The diets of other fish are also impacted by habitat use. Both *Labeotropheus fuelleborni* and *P. elongatus* 'green-back', that forage primarily on vertical surfaces, had a greater proportion of *Cladophora* in their diets than *P. tropheops* 'orange-chest', that forages on adjacent horizontal surfaces. In shallower, sediment-free depths, *Cladophora* dominated the vertical surfaces. *Melanochromis auratus* and *M. 'black-white johanni'* show similar morphologies but *M. 'black-white johanni'* occupies a sediment rich habitat and showed a diet dominated by diatoms. *M. joan-*

johsonae is restricted to shallow (< 2 m) waters. This zone was dominated by *Cladophora* on all substrates and this fish showed the highest percent volume of *Cladophora*.

Distinct groupings based on neurocranial ethmovomer shape have been identified within the mbuna (Reinthal 1989). This structural variation is associated with variation in buccal jaws and other oral morphology (e.g. teeth). Therefore, it is not surprising that diet is correlated with these features. Those species that feed primarily on diatoms and loose algae with the brushing behavior (e.g. *Pseudotropheus zebra* and *Petrotilapia nigra*) have enlarged, horizontally directed vomers, terminal mouths and long, slender, flexible teeth. Alternatively, those species that feed primarily on attached algae (e.g. *Pseudotropheus tropheops* 'orange-chest' and *Pseudotropheus elongatus* 'green-back') have down-turned, thin vomers and more inferior mouths. Intestine length is also correlated with diet (Reinthal 1987). Those species feeding on diatoms in sediment rich habitats have longer intestines than those feeding primarily on attached algae in sediment free environments. An exception is *Cynotilapia afra* which, because of its pelagic foraging habits, has a short intestine.

Given the morphological and behavioral specializations that correlate with diet, there do appear to be adaptive characteristics associated with foraging strategies. Unfortunately, nothing is known about the feeding efficiencies of these fish on the various algal prey types.

An important question concerning the initiation of speciation and trophic adaptive radiation in mbuna are the relative roles of ecological and behavioral diversification versus morphological differentiation. Morphology, ecology and behavior all influence dietary habits. The data and interpretations presented here are of interest given the debate of whether 'differences in habits and behavior can precede and initiate morphological differences' and 'produce... changes in function which themselves lead to changes in structures...' (Fryer & Iles 1972, quotes cited from Greenwood 1974: p. 109, Fryer 1977). Greenwood (1974) regards the evolution of behavior and morphology as 'to say the least equivocal'. Fryer (1977) insists that they

are 'far from being equivocal' and 'on the one hand changes in habits can initiate speciation and, at another level, how persistent habits have been a major factor in long term evolutionary trends' (p. 142).

Species with strikingly similar morphology (e.g. *Pseudotropheus tropheops* 'orange-chest' and *P. gracilior*) can use different algal resources. In addition, Ribbink et al. (1983) found individuals of *P. gracilior* with their stomachs 'crammed to capacity with benthic invertebrates'. This shows similar trophic morphologies being used to feed on different resources both within a resource level (e.g. algae) and between levels (invertebrates were not found in the diet of *P. tropheops* 'orange-chest'). *Pseudotropheus zebra* feeds primarily by scraping rock surfaces for settled diatoms, but also feeds in the water column on pelagic food items. This is an example of change in behavior without corresponding structural change but the question of behavioral homology remains problematic.

The feeding habits are useful in assessing the phylogeny of the group. For example, phylogenetic relationships proposed by Lewis & Reinthal (unpublished) consider *Petrotilapia* and the monotypic genus *Cyathochromis* as sister taxa. *Cyathochromis* feeds primarily by scraping algae from the leaves of macrophytes. A diatom found in the diet of *P. nigra*, *Cocconeis*, is known only to occur on macrophytes (Haberyan & Mhone unpublished). Another *Petrotilapia* species, *P. genalutea* was observed feeding by scraping the macrophyte *Vallisneria* at Mumbo Island and Otter Point. The similarity in feeding and shared unique behavior between the *Petrotilapia* spp. and *C. obliquidens* support this hypothesized relationship.

Many of the dietary differences between species may be mainly due to the species' phylogenetic histories. The results indicate that the more closely related genera have more similar diets. Dietary similarities may be considered synapomorphies and are correlated, either causally or subsequent to, cladogenic events. Trophic polymorphism is often invoked as a necessary precursory step to speciation in cichlids (Sage & Selander 1975, Meyer 1989). Different algal prey types may function in an analogous manner to soft and hard prey

in molluscivore and papilliform morphs. Thus, specializations for feeding on particular algal types may occur during ecological bottlenecks in food resources (Wiens 1977) where specializations permit the exploitation of alternate, less preferred food resources (Liem 1980, McKaye & Marsh 1983, Meyer 1989). However, this is only true if the derived morph is the one feeding on the less preferred resource and the plesiomorphic morph is the one feeding on the preferred resource. Alternatively, these specializations may permit more efficient utilization of preferred prey types and this appears to be the case in the herbivores discussed here.

The results of this study should by no means be taken to describe completely the dietary habits of these herbivorous mbuna. Fish species exhibit fluctuations in both dietary items consumed and dietary relationships to other species relative to resource availability and predictability. Examined here are a small number of individuals from a limited area and season. Further long term sampling is needed to determine the ecological consequences of herbivory in a high diversity community that has undergone such a spectacular adaptive radiation.

The extent of the cichlid adaptive radiation is well defined at a broad scale of trophic differentiation (e.g. piscivores vs. herbivores vs. molluscivores, etc.). However, distinctions within a trophic group had not been previously described. Distinct differences in diet are noted for various herbivorous mbuna examined here. Furthermore, correlations of diet with trophic morphology and behavior are identified. Resource partitioning, regulated through differences in trophic behavior and morphology, is important for the ecological coexistence of this high diversity community. The differentiation of diets on algal resources may represent an important step in the adaptive radiation of this group of fish.

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