EVOLUTION OF FISH SPECIES FLOCKS

EDITED BY

ANTHONY A. ECHELLE
OKLAHOMA STATE UNIVERSITY

IRV KORNFIELD
UNIVERSITY OF MAINE AT ORONO

University of Maine at Orono Press, Orono, Maine 1984

Oklahoma State University Museum of Cultural and Natural History,
Stillwater, Oklahoma

Migratory Fish Research Institute, Orono, Maine

The cover illustration is an untitled charcoal by Nina Sutcliff permanently housed in the Art Collection, the University of Maine at Orono.

EVOLUTION OF FISH SPECIES FLOCKS

University of Maine at Orono Press.

Manufactured in the United States of America.

9 8 7 6 5 4 3 2 1

Library of Congress Catalog Card Number
84-051502

ISBNO-89101-058-0 (cloth)
ISBNO-89101-057-2 (paper)

CLYDE D BARBOUR, Department of Biological Science, Wright State University. Dayton Ohio 45435 USA

PERETI BASASIBWAKI, Uganda Freshwater Fisheries Research Organization. P.O. Box 343 Jinja Uganda

KENT E CARPENTER, East-West Center and Department of Zoology, University of Hawaii. Honolulu Hawaii 96822 USA

BARRY CHERNOFF, Department of Ichthyology, Academy of Natural Sciences of Philadelphia. Philadelphia Pennsylvania 19103 USA

WALLACE J DOMINEY, Museum of Zoology and Division of Biological Sciences, University of Michigan. Ann Arbor Michigan 48109 USA

ALICE F ECHELLE, Department of Zoology, Oklahoma State University. Stillwater Oklahoma 74078 USA

ANTHONY A ECHELLE, Department of Zoology, Oklahoma State University. Stillwater Oklahoma 74078 USA

W NOEL GRAY, Department of Surveys. P.O. Box 349 Blantyre Malawi

P HUMPHRY GREENWOOD, Department of Zoology, British Museum (Natural History). Cromwell Road London SW7 England

JULIAN M HUMPHRIES, Museum of Zoology, University of Michigan. Ann Arbor Michigan 48109 USA

LESLIE S KAUFMAN, New England Aquarium. Central Wharf, Boston Massachusetts 02110 USA

IRV KORNFIELD, Migratory Fish Research Institute and Department of Zoology, University of Maine. Orono Maine 04469 USA

KAREL F LIEM, Museum of Comparative Zoology, Harvard University. Cambridge Massachusetts 02138 USA

PAUL V LOISELLE, 6707 North 77th Street No 6. Milwaukee Wisconsin 53223 USA

ERNST MAYR, Museum of Comparative Zoology, Harvard University. Cambridge Massachusetts 02138 USA

AMY R McCUNE, Section of Ecology and Systematics, Cornell University. Ithaca New York 14853 USA

KENNETH R McKAYE, Cape McClear Fisheries Research Station and Duke University Marine Laboratory. Pivers Island, Beaufort North Carolina 28516 USA

PAUL E OLSEN, Lamont-Doherty Geological Observatory, Columbia University. Palisades New York 10964 USA

LYNNE R PARENTI, Department of Ichthyology, American Museum of Natural History. Central Park West at 79th Street, New York New York 10024 USA

ANTHONY J RIBBINK, J.L.B. Smith Insititute of Ichthyology. Grahamstown 7140 South Africa

EXTRINSIC BARRIERS TO GENE FLOW IN ROCK-DWELLING CICHLIDS OF LAKE MALAWI: MACROHABITAT HETEROGENEITY AND REEF COLONIZATION

KENNETH R MCKAYE AND W NOEL GRAY

INTRODUCTION

Lake Malawi, southernmost of the rift valley lakes of East Africa, is the world's ninth largest lake at 22,480 km^2, 570 km long, 80 km wide, and 704 m maximum depth. Malawi, along with two other East African great lakes, Tanganyika and Victoria, has been the site of explosive speciation of cichlid fishes (Fryer, Iles 1972; Greenwood 1974; Barel et al. 1977). Icthyologists estimate that there are over 500 endemic species in the lake (Lewis, Ribbink pers. comm.; pers. obs.) . The mechanisms by which so many species have evolved and by which they coexist have evoked interest and controversy (Kosswig 1947, 1963; Lowe-McConnell 1959; Greenwood 1974; Fryer 1977; Fryer, Iles 1972; McKaye 1980).

Fryer's (1959; Fryer, Iles 1972) microallopatric model of speciation for the Lake Malawi cichlids hypothesizes that intralacustine speciation was due to habitat isolation followed by divergence of populations. The emphasis of the earliest ecological studies was on a group of rock-dwelling cichlids known by the local name *mbuna*. This group includes the genera *Pseudotropheus, Labeotropheus, Melanochromis, Cyathochromis, Genyochromis, Gephyrochromis,* and *Iodotropheus* which are probably of monophyletic origin (Fryer 1959; Lewis 1982, pers. comm.). Mbuna species are usually small, less than 20 cm long, and over 95 percent are confined to rock habitats. Fryer's (1959) research concentrated on the mbuna, which has turned out to be even more speciose than he realized (Lewis 1982; Marsh 1981; Ribbink et al. 1983). Fryer suggested that the lake shore is a mosaic of habitats, with alternating stretches of rock, sand, and weed environments. Significant habitat or patch discontinuity could serve to cluster and isolate fish populations such as the mbuna from each other. He also speculated that fluctuating lake levels would serve, 1) to isolate, and 2) to recombine fish populations from these patches (Figure 1).

However, neither the number, size and distribution of habitat patches in the lake, nor the effect of changing lake levels on the Lake Malawi shoreline have been examined. Some assume that sand habitat is scarce in Lake Malawi (Ostro 1979), and the idea that Lake Malawi is dominated by rocky shoreline may reflect the popularity of the mbuna in the aquarium trade. Our data suggest that habitat variation along Lake Malawi's western shoreline is significant, and that habitat isolation may be possible for some species.

We asked the following questions about the significance of isolated rock patches for cichlid occurrence: 1) Do rock-dwelling cichlids cross barriers and colonize new habitats? 2) Are the first rock-dwelling cichlids to colonize new habitats those that feed on zooplankton and are thus less dependent on rock habitats for food? 3) Does the size, structure or depth of a new habitat patch affect the species number or total number of fishes on the habitat? 4) How does species number and population density change over time? Movement of fishes between patches and colonization of new patches were examined by regular surveys of the fish on eight experimental reefs placed over sand 1 km from the nearest rock outcropping.

Our evidence shows that: 1) the Malawi lake shore is a mosaic of habitats with many rock patches isolated by large stretches of weed and sand areas, and 2) some of the rock-dwelling cichlid species colonize new habitats

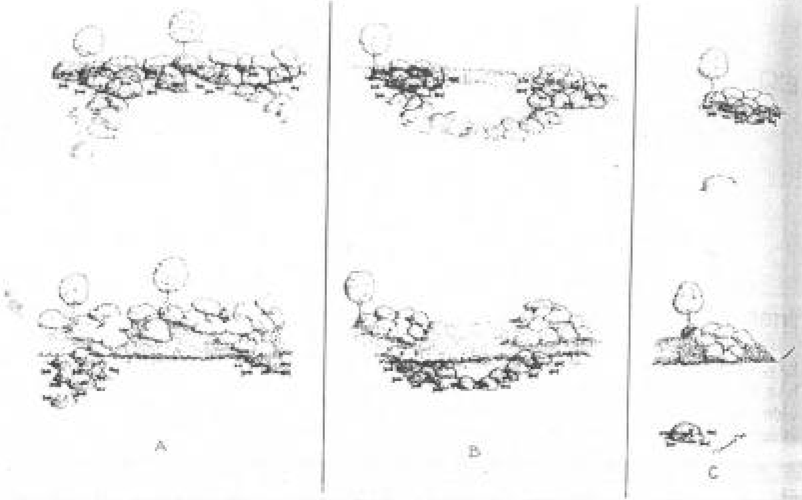

Figure 1: Effects of fluctuation in lake level and habitat utilization by cichlid fish. At A, a rise in lake level unites two populations. At B, a rise in lake level splits a single population into two. At C, a rise in lake level places a previously occupied rock habitat into water that is too deep, but opens up a new rocky shore habitat for colonization (Fryer 1977 modified).

within a short time. This assessment of the role of microhabitats isolating cichlid populations provides important baseline information for future studies on speciation and gene flow among cichlid populations.

METHODS AND MATERIALS

Aerial Shoreline Analysis.

To quantify the relative proportion of rock, sand, and weed habitat, we examined a series of 1972 aerial photos of the western shoreline of Lake Malawi. Four parameters were used to detail the pattern of habitat availability: 1) relative proportion of rock, sand and weed; 2) frequency of alteration of rock and sand-weed habitats along the shore; 3) patch size of each type of habitat; 4) distribution of rock and sand-weed habitats for four main regions along the western lake shore. We examined additional aerial photographs taken between 1966 and 1980 for the effect of increasing water level on shoreline configuration.

We divided the western lake shore into four main geographic regions from north to south: 1) Karonga to Chilumba (9°40'S to 10°15'S); 2) Chilumba to Nkhata Bay (10°15'S to 12°00'S); 3) Nkhata Bay to the Nankumba Peninsula; 4) from the Nankumba Peninsula to the Shire River (Figure 2). Habitat type was determined from 1972 aerial photographs and scored on survey maps 0933D2; 1034A3, A4, C1, C3; 1134A1, A3, A4, C1, C2, C3; 1234A3, C1, C3, C4; 1334A3, A4, C2, D1, D3; 1434B1, B3, B4; 1435A3 (Malawi Survey Dept).

The effect of rising lake level on shoreline topography was analyzed for two relatively flat regions, Sungu Point and Sungu Spit, for which we located a series of photographs that spanned 16 years. For these sites, which border the southwest edge of the lake, three sets of aerial photos were available and used (Figures 3 and 4). The scale of photographs taken in 1964 and 1966 for Sungu Point (13°35'S, 34°32'E) and Sungu Spit (12°55'S, 34°18'E) was 1/40,000, and the scale of photographs taken in these areas in 1972 and 1980 was 1/25,000. All figures were reduced to a common scale of 1/50,000, and area measurements were taken from the reduced diagrams with a Haff-315 planimeter.

Experimental Reefs.

Eight experimental reefs were placed offshore of the Cape Maclear Fisheries Research Station in May 1978 (McKaye 1981). Reefs were structured from cement blocks in two basic designs and two sizes (Figure 5). Four "homogeneous" reefs, two large and two small, were constructed with large interspaces. Four "heterogeneous" reefs, two large and two small, were constructed with blocks of medium square and round interspaces. The large (10 m) reefs consisted of 26 cement blocks. The small reefs consisted of 13 blocks. The height of all reefs was 80 cm. Four reefs, one of each type were placed at 6 m depth; actual depth varied between 5.5 and 7 m as lake levels changed during the course of this study. Four other reefs were placed at 9 m depth; actual depth varied between 8.5 and 10 m. The reefs were 50 m apart, and the ordering of the reefs at each depth, from west to east, was small homogeneous, large homogeneous, large heterogeneous, and small homogeneous. Otter Point, the nearest rock outcropping, was 1 km to the west (McKaye 1981).

Figure 2: Four main regions of Lake Malawi

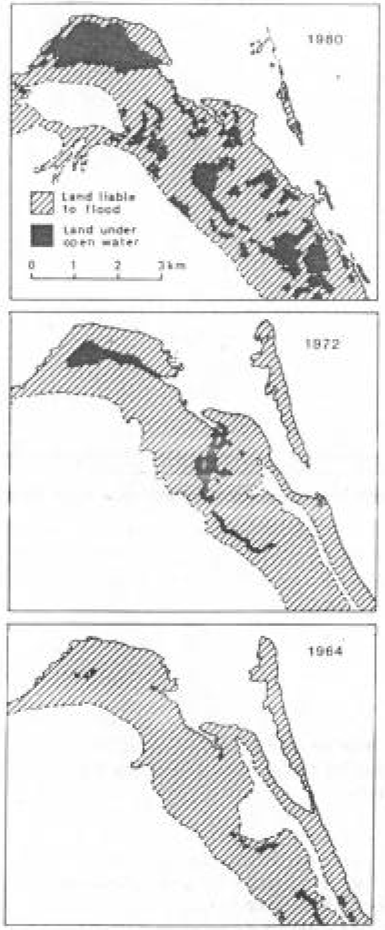

Figure 3: Sungu Point from 1964, 1972, and 1980 aerial photographs. White area on landward side, lower left, is not liable to flooding.

Census data exists for both the dry (June-November) and the wet (December-May) seasons for the 5-year period 1978-1983, except the 1982 wet season. The reefs were censused every 2-10 days. Sampling periods and number of censuses were: Dry-1978, 18; Wet-1979, 8; Dry-1979 13; Wet-1980, 7; Dry-1980, 21; Wet-1981, 10; Dry-1981, 18; Dry-1982, 12; Wet-1983, 12. The reefs were designed to allow divers to see completely through all holes. Therefore, all fish were easily counted. All fish which were in reef holes, feeding on the reef, or orienting to the reef within 2 m were included in the census.

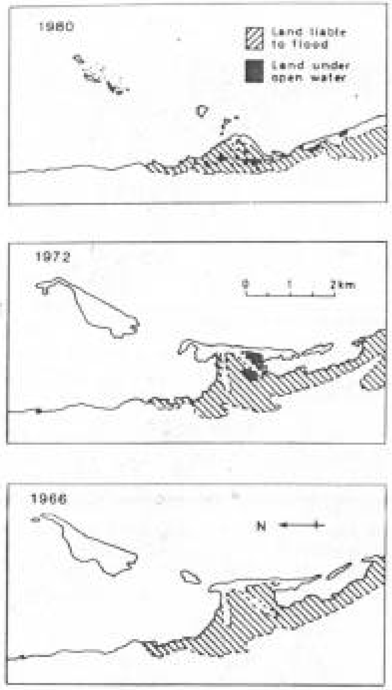

Figure 4: Sungu Spit from 1964, 1972, and 1978 aerial photographs. The shore of the lake is on the left side of the continuous line from left to right.

Excluded were cichlid species which occurred and fed only on the sand.

Water current velocities over the reefs were estimated in the dry season of 1980 by measuring the time suspended particulates in the water moved 30 cm. On the 21 reef censusing dates from June through August, 7 days had no current; 8 days had a slight current less than 2 cm/sec; and 6 days had a moderately strong current of 2-15 cm/sec, from east to west.

Zooplankton Availability.
Zooplankton samples were taken weekly from March 1978 to August 1980, 20 m offshore of the deeper set of experimental reefs, in 17 m water depth. Three samples were taken at depths of 5 and 10 m, which corresponded closely to the depths of nearby reefs. Samples were collected with a 9-liter Van Dorn bottle and concentrated through a 64 μm net. The three samples from each depth were combined for analysis. Mechanical breakdowns and bad weather caused the departure from weekly sampling. All plankters were identified to species (McKaye 1983), but we only report data for diaptomids and

Diphanosoma excisum. These are the primary plankters eaten by the rock-dwelling cichlids (McKaye, Marsh 1983) and by most other cichlids (McKaye 1983, unpubl. data).

RESULTS

Habitat Distribution and Availability.

As Fryer predicted (1959), Lake Malawi's shoreline was a distinct mosaic of alternating patches of sand, rock and weed habitats. In 1972, 61.0 percent of the western shoreline was sand, 20.9 percent weed, and 18.1 percent rock (Table 1). The lake level then was 474 m above sea level (Drayton 1979). The Region I shoreline of 86.6 km was a stretch of sand and weed, with no observable (►0.05 km) rock habitats (Table 1). The 222-km shoreline of Region II had the highest proportion, 44 percent, of rock habitats, among the four regions. Isolated patches of rock in this section ranged from 0.05 km to 6.3 km in length (Table 1, Figure 6). Region III was predominantly sand, with rock patches comprising less than 4 percent of this 369 km shoreline (Table 1). The longest continuous stretch of sand-weed habitat we observed, 99.5 km, was in this region between 13°02'S and 13°40'S. Region IV, which included the Nankumba Peninsula and Cape Maclear to the Shire River outlet of the lake, had about 27 percent rock along its shoreline. This southernmost region had the longest continuous stretch of rock we observed, 8.5 km

Figure 7 shows the frequency distribution of patch sizes of rock and of sand habitats in the four regions. Median patch length for rock was 300 m. Median patch length for combined sand-weed habitats was 400m. Though median patch size was similar, the rock habitats occur frequently as small islands, since rock predominates in patch sizes under 100 m. Sand and weed form the longest continuous stretches of habitat. Region II, with the greatest absolute amount of rock, had the highest number of rock patches: 43.2 per 100 km, vs. 9.2 for Region III and 23.6 for Region IV.

Shoreline Configuration over Time
Analysis of photographs taken between 1966-1980 demonstrated the creation and dissolution of isolated habitats over time. In 1966, Sungu Point consisted of a spit 4.2 km long pointing NNW that sheltered Domira bay to the west. On the landward side of the shoreline, about 17.5 ha were under water, and 1530 ha more were potentially flooded during the high rainy season (Figure 3).

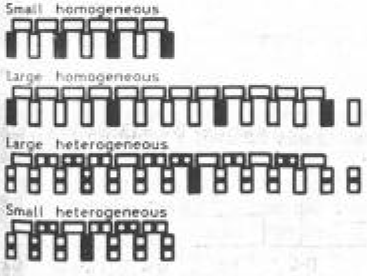

Figure 5: Structure of experimental reefs.

Table 1: Summed lengths (km) of three kinds of shoreline in four regions of western Lake Malawi, 1972 (See Figure 1)

	Sand	Marsh	Rock
Region I	76.9	9.7	0.17
Region II	116.5	9.5	97.0
Region III	235.7	119.1	14.5
Region IV	63.3	29.8	34.7
Total	491.4	168.1	146.2

Figure 6: Region II from Chilumba to Nkhata Bay showing longest stretch of uninterrupted rock in this region.

By 1972, following a slight increase of about 0.5 m in the lake level, the spit length shrank to 3.5 km. The landward extremity was separated from the mainland. An estimated 135 ha were under water with about 1500 ha liable to flood, and the shoreline had encroached noticeably onto the spit, to include some areas previously under water and usually isolated from the lake.

By 1980 the lake level increased 2 m and the spit had fragmented into a series of small islands separated by 1-2 km from the shore. Land under water had increased to an estimated 252 ha. Land not liable to flood had retreated, giving 1535 ha of flood plain (Figure 3).

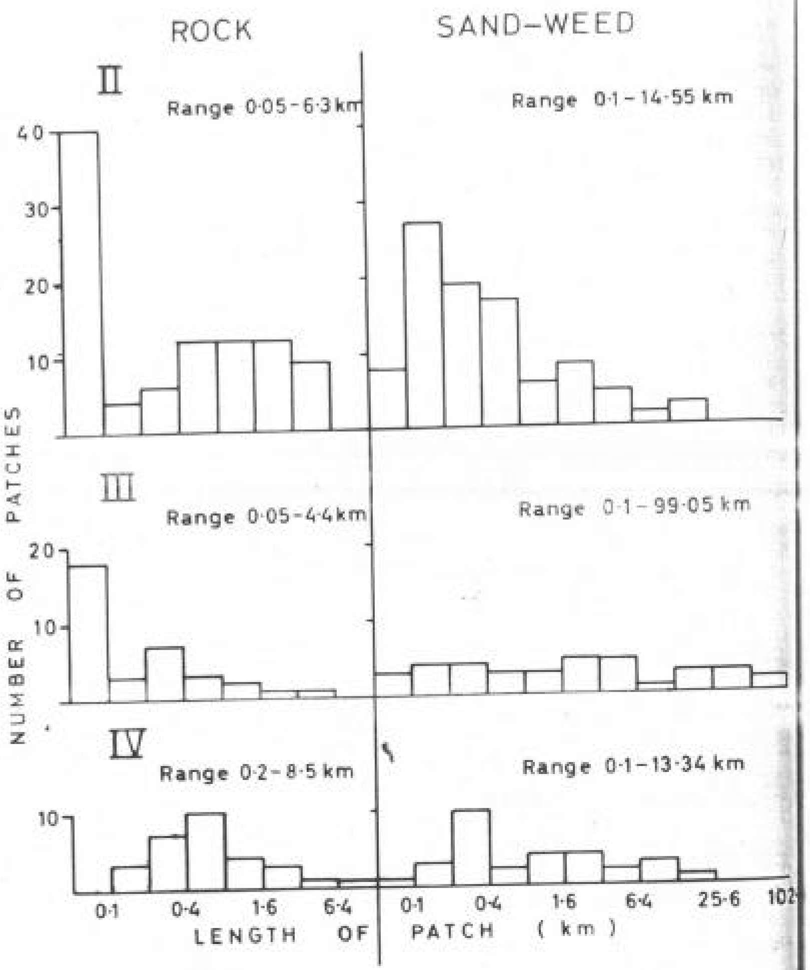

Figure 7: Distribution of habitat patch length in Lake Malawi: Regions II-IV. Horizontal axis is on log scale.

Another pattern of change is illustrated by Sungu Spit (Figure 4). In 1966 it was a detached spit 2.5 km long and 1 km from shore, pointing NNE. Probably it was attached earlier when the lake level was lower (Drayton 1979). To the south of the spit the shoreline contained a sheltered lagoon, 2.5 km x 0.5 km, or about 77.5 ha that was not completely isolated from the lake. Besides the lagoon, there was no open water on the landward side; however, 320 ha was near lake level and liable to flooding.

By 1972 there was a change in shape and size of the spit. On the landward side, sand had been deposited towards the spit. To the south, the lagoon remained about the same area, 77 ha, but an extra 5 ha of open water appeared to the north. The area liable to flood was reduced to 292.5 ha.

By 1980 a dramatic change had occurred, as with Sungu Point. The spit had been reduced to a few fragments. The landward extension had disappeared. The shoreline had retreated inland and eliminated the southern lagoon. Within the new shoreline, 12 ha was under open water, and only 200 ha remained liable to flood. Thus in only 16 years, land forms changed, islands appeared and disappeared, and shoreline continuity was significantly modified.

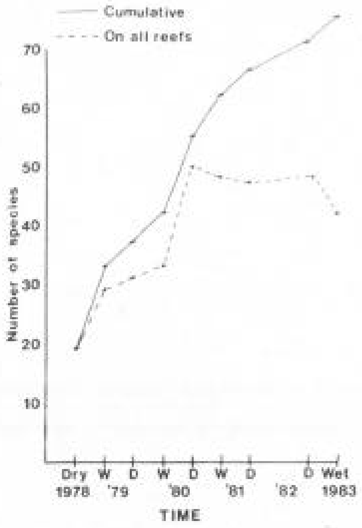

Figure 8: Pooled species numbers for all reefs, versus time. Solid line marks cumulative number of different species which ever visited the 8 reefs; dashed line marks the total number of different species on all eight reefs during any one season.

Reef Colonization: Rock-Dwelling Species

Data presented here for the five-year period, late 1978-early 1983, show the colonizing abilities of the rock-dwelling cichlids and the pattern in species diversity on the experimental reefs. Seventy-five different fish species have been recorded on the habitats since the reefs were established. New species which had never before been seen on the reefs continued to appear at a rate of about 5 per six months after 4.5 years. The rate of immigration of new species onto the reefs does not as yet appear to be diminishing (Figure 8). During the dry season of 1980 the maximum of 50 different species occurred on the eight reefs. At the wet season 1983 census, the number of different species on all habitats had dropped to 42. During this study, 18 species which have never been recorded over sand in the Cape Maclear region, either in 155 transects of 100 m^2 or 600 transects of 200 m^2 (McKaye 1983; McKaye, Reinthal unpubl. data), have occurred on the reefs (Table 2). Ten of these 18 species belong to the rock-dwelling mbuna complex (Fryer 1959; Lewis 1982) which includes the genera *Pseudotropheus* and *Petrotilapia*. All of these mbuna species except one undescribed *Pseudotropheus* sp. ("Yellow dorsal fin") were seen on the reefs every season, after their initial appearance. These nine resident mbuna species included individual territorial males or brooding females with young in their mouths. The other rock-dwelling cichlids did not remain consistently on the reefs from one season to the next.

Colonization Related to Reef Characteristics.

1. Large vs. Small. The four large reefs had both more species and greater numbers of fishes on them at all seasons than the comparable small reefs (Figures 9, 10). At 5 years the average large reef had 1.6 times as many species as did the average small reef.

2. Deep vs. Shallow. The four deeper reefs had both more species and a greater number of fishes on them during all seasons than the comparable shallower reefs (Figures 9, 10). At 5 years the average deep reef had 1.6 times as many species as did the average shallow reef.

3. Heterogeneous vs. Homogeneous. The four heterogeneous reefs had more species of fishes on them in 92 percent of the 36 censuses than the comparable homogeneous reefs (Figure 9, Sign test, $p < .01$); and 81 percent of the 36 censuses had greater numbers of fishes on the heterogeneous reefs (Figure 10, Sign test, $p < .05$). At 5 years the average heterogeneous reef had 1.3 times as

Table 2: Rock dwelling species appearing on experimental reefs.

Species Identification	1st Observation
**Pseudotropheus "macrophthalmus"* (Blue "tropheops")	1st season
**Pseudotropheus tropheops* (White with yellow fins)	1st season
**Pseudotropheus tropheops* (Orange head)	1st season
**Petrotilapia* spp. (Three species, females not distinguished)	1st season
Cyrtocara linni	½ year
**Pseudotropheus elongatus* (Species complex)	½ year
**Pseudotropheus tropheops* (Yellow)	2 years
Cyrtocara fenestratus / taeniolatus	2 years
Cyrtocara euchilis	2 years
**Pseudotropheus zebra* (Blue-black)	2½ years
**Pseudotropheus* sp. (Yellow dorsal fin)	2½ years
Alanocara sp. (nyassae)	2½ years
Labeo cylindricus	2½ years
Docimodus johnstoni	3 years
Trematocranus sp. (jacobfreibergi?)	4 years
Cyrtocara heterodon	4 years
**Pseudotropheus zebra* (Cobalt)	4½ years
**Pseudotropheus tropheops* (Dark)	4½ years

*Members of the mbuna complex.

many species as the average homogeneous reef.

Species and Total Fish Numbers through Time.

Each habitat has had a different pattern of species accumulation and population densities. Nevertheless, certain patterns emerge when the reefs are examined as a unit. The mean number of species per habitat peaked at 9 after 2 years, and has declined to 7 at 5 years. The mean number of individuals occurring on the reefs reached a peak within the first year, at 50 per reef, but declined steadily since the 1980 dry season. The last census in the 1983 wet season revealed an average of 22 fish.

Effect of Currents on Species Number and Population Densities

When currents were greater than 2 cm/sec, mean number of species and individuals on all eight reefs were greater than when currents were absent or less than 2 cm/sec (Figure 11). On average, there were 1.2 times more species, and 2.0 times more individuals on the reefs when the currents were running (Figures 11, 12). The increase in numbers of fish was 177 percent for the shallower reefs, and 43 percent for the deeper reefs.

Zooplankton Resources: Distribution and Seasonality

For the two years of sampling which corresponded with the beginning of the experiment, there was consistently less zooplankton in 5 m of water than in 10 m (Figure 13). Near the habitats, there appeared to be a bimodal peak of *Diaphanosoma* and diaptomids, one at the beginning of the rains in December-January, and one at the beginning of the *mwera*, or southerly winds, in June-July of 1979 and 1980. These results are consistent with observations on frequency of zooplankton feeding by fishes on the reefs (McKaye unpubl.).

DISCUSSION

The western shore of Lake Malawi is a heterogeneous environment of sand-weed and rock. Eighteen percent of the western shore is composed of 158 rock patches isolated by stretches of sand or weed. Such isolated rock sections provide the necessary physical situation for microallopatric speciation. Isolation would be possible if the movements of rock-dwelling cichlids are restricted, relative to the distances between rocks (Fryer 1959, 1977; Fryer, Iles 1972). Wide separation would minimize gene flow

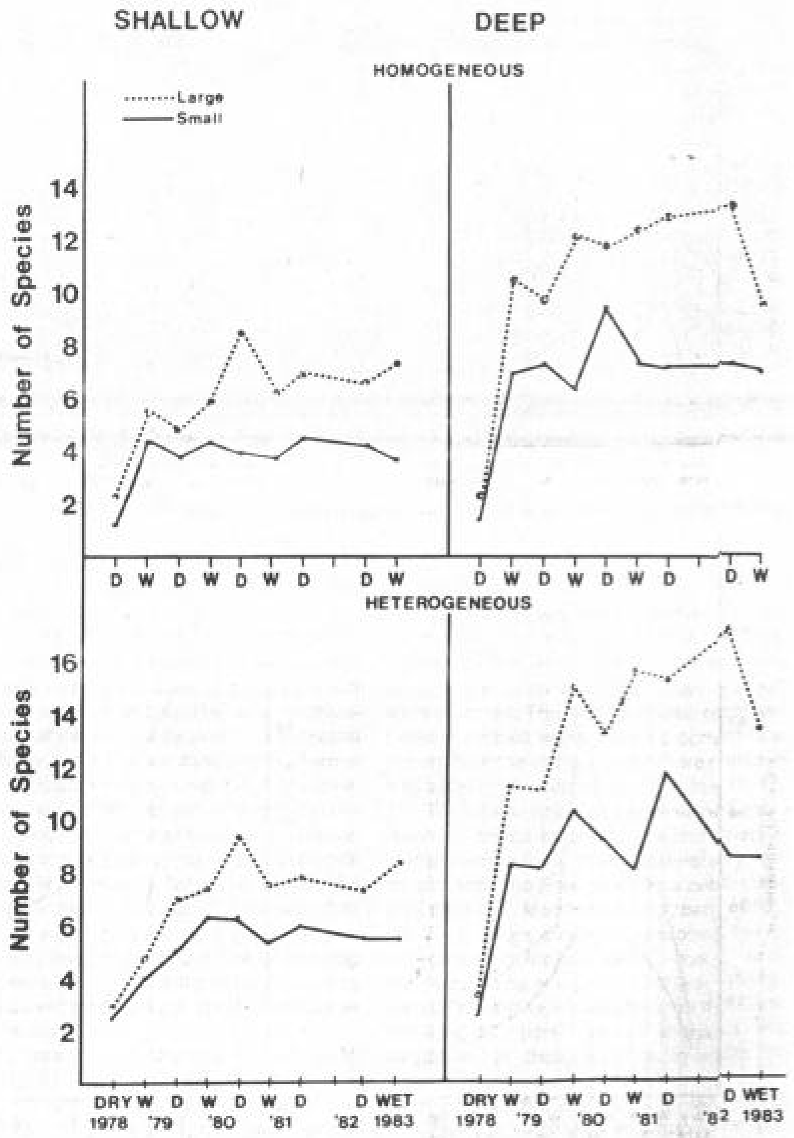

Figure 9: Mean number of species for each season on each of eight reefs.

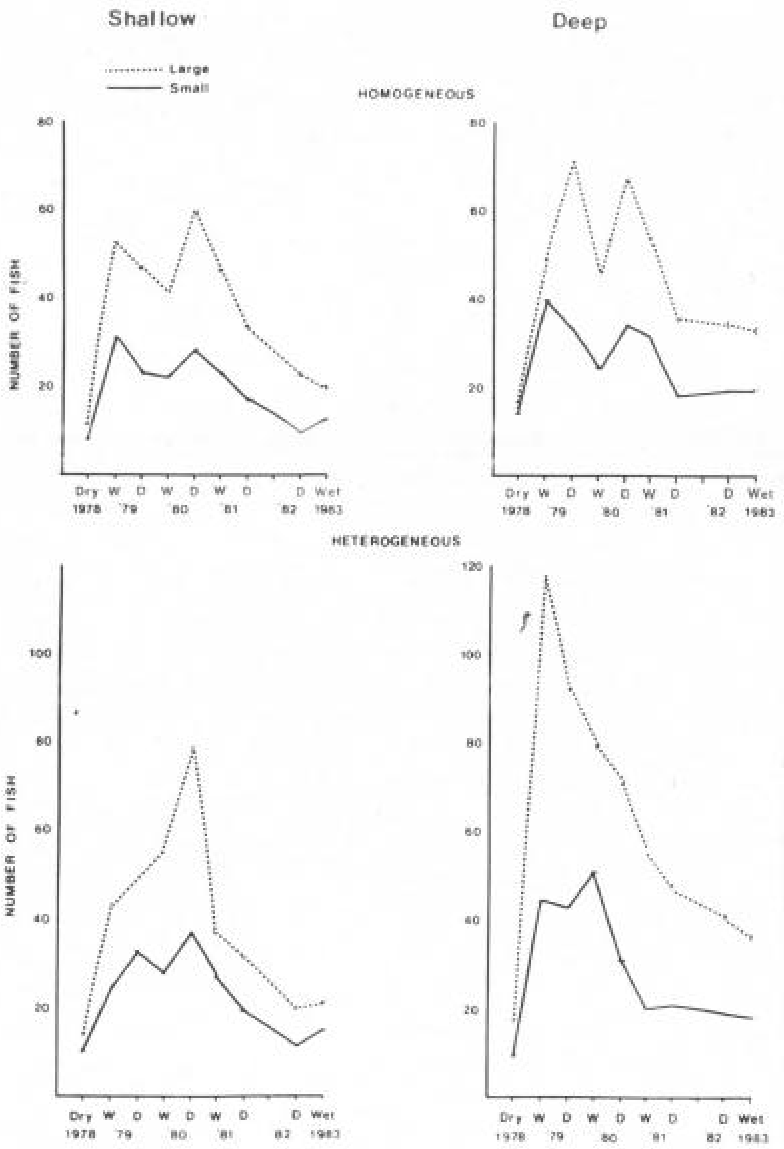

Figure 10: Mean number of individual fish for each season on each of the eight reefs.

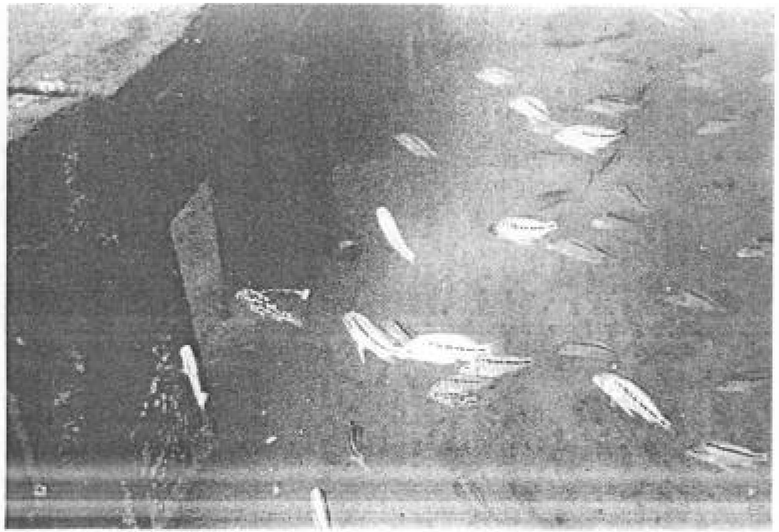

Figure 11: Cichlid fishes feeding on zooplankton in back of reef when strong current is flowing.

among populations and consequently would maximize the possibility of speciation due to geographic isolation.

The dynamics of the shoreline indicate that fragmentation of the lake into varying habitat can and does occur over surprisingly short timespans (Figures 3, 4). The rapid modification of habitat continuity along the mainland shoreline, plus the existence of numerous isolated islands and rock habitats in the lake, provide evidence that the physical discontinuity required for microallopatric isolation exists, and thus gives some support to Fryer's (1959, 1977) model for the evolution of cichlid species flocks in Lake Malawi. However, data from the experimental reefs suggest the process may be complex and differential among species subsets. Different groups, depending in part on trophic ecology, appear to disperse at different rates.

The results of the reef experiment specifically demonstrate this key point: that a subset of rock-dwelling cichlids will disperse over sand and colonize newly formed habitats. Further, fish species diversity and zooplankton productivity were correlated. Thus, food diversity and availability may contribute to determining species composition and successful colonization of new habitats. All of the species on the reefs were observed to feed on zooplankton at least some of the time. When currents were flowing, bringing more zooplankton onto the reefs, more species were counted. The most dramatic response in fish numbers with increased current flow occurred on the shallow reefs where plankton was at lower absolute density (Figures 11, 12, 13). The mbuna colonizers early in the 5-year research period belong to the four species complexes which feed extensively on zooplankton: the *Pseudotropheus zebra* complex (McKaye, Marsh 1983; Holzberg 1978), the *P. tropheops* complex (pers. obs.), the *P. elongatus* complex (pers. obs.), and the *Petrotilapia* complex (McKaye, Marsh 1983). These species are also ones that Liem (1978, 1980, pers. comm.) suggests are facultative in their feeding repertoire. It appears that the mbuna which fed extensively on zooplankton are the most vagile and thus, the most likely species to colonize a new habitat. These species groups may provide the founders for new populations and lead to rapid allopatric speciation (Mayr 1963). On

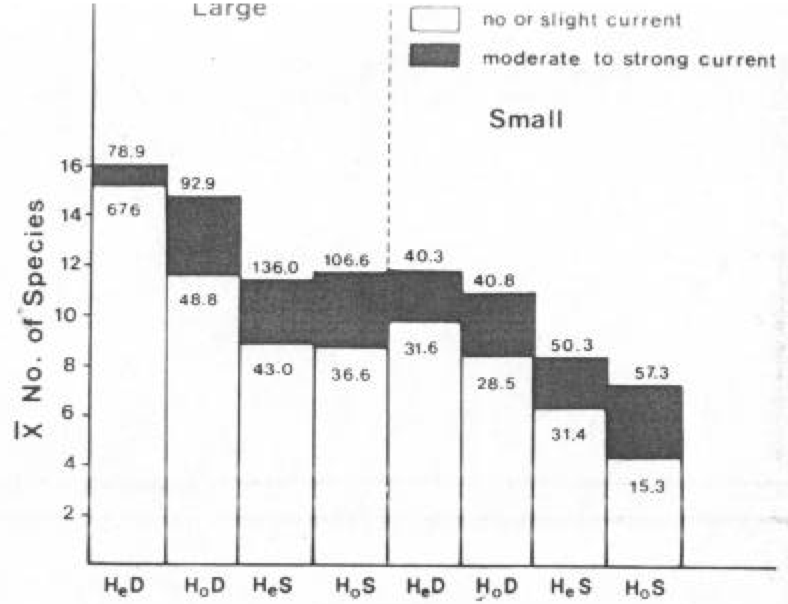

Figure 12: Effect of current on numbers of individual species occurring on reefs. On all eight reefs, numbers of individuals and species increased when currents were greater than 2 cm/sec. Lower numbers count fish on reef with little or no current; upper numbers count fish on reef with high current. Letters below bars signify heterogeneous (He) or homogeneous (Ho) reefs in deep (D) or shallow (S) water.

the other hand, increased gene flow between populations could retard allopatric speciation, and intrinsic isolating mechanisms could be more important than extrinsic ones in splitting species (McKaye 1980). More data are required to fully appreciate the implications of these observations.

The mapping data support the view that fragmentation of populations and subsequent reproductive isolation could occur both on a microgeographic scale, less than 20 km separation, for the less vagile species, and on a more macrogeographic scale. Along the western shore of the lake, the rock portions in the north were separated from those in the south by extensive sand-weed beaches. The longest single stretch was nearly 100 km. Northern mbuna species would have to traverse these large distances over sand in order to interbreed with southern conspecifics. Thus, the data lead to the prediction of distinctive northern and southern subsets of species occurring in each region. The available genetic data are consistent with this hypothesis. Electrophoretic analysis of isoenzymes of *Pseudotropheus zebra* show that Chilumba and Nkhata Bay populations in the north have gene frequencies that are not statistically different from each other, but do differ statistically from those of *P. zebra* populations at Mumbo and Domwe islands in the southern Cape Maclear region (McKaye et al. 1984). The longest sand-weed stretch between Chilumba and Nkhata Bay is 15.5 km; the longest sand beach between Nkhata Bay and Cape Maclear is close to 100 km. Thus, though *P. zebra* may feed on zooplankton while migrating, 100 km of sand appears to be a significant barrier while 15.5 km may not be. More data on migratory abilities of these fish are required before a definitive conclusion can be made about what constitutes a major barrier to gene flow between populations.

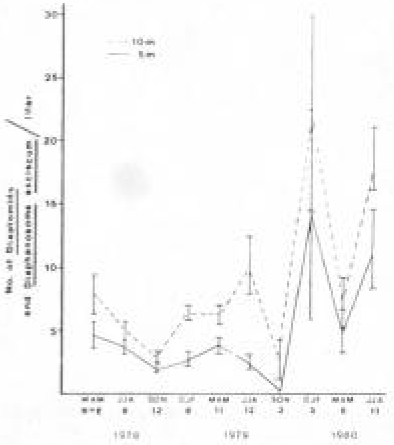

Figure 13: Density of zooplankton fed on by the majority of cichlids colonizing reefs at 5 and 10 m depths.

A related prediction to guide future research can be derived from the map data. We expect that the steep rocky shores in Region II should serve to isolate many of the obligate sand-dwelling cichlid populations in the northern Karonga area from those in the south. If so, the sand-dwelling fauna to the south of Nkhata Bay down to the outlet of the Shire River should be genetically differentiated from those in the northern sand portion of the lake.

Despite the limited extent of this survey regarding the history of the lake, these data should be useful in evaluating the contribution of island biogeography theory (MacArthur, Wilson 1967) to understanding cichlid species packing in communities. The isolated rock outcroppings in the lake, surrounded by sand, are islands of habitat. Species area curves, constructed for many groups of animals, predict the increase in number of species relative to increased habitat area. Barbour and Brown (1974) applied such analysis to fish faunas of many lakes throughout the world. In Lake Malawi we find rock outcroppings ranging in size from 0.05 to 8.5 km, with all intermediate sizes present (Figure 7). It should be possible in this diverse vertebrate assemblage, to test the applicability of the established species area relationship (MacArthur, Wilson 1967) for fishes on habitat patches within a large lake. Deviations from expected species diversities on given patches would focus attention on the processes determining community structure in this diverse fish assemblage. Our experimental data suggest that not only the size, but also spatial heterogeneity of the available habitat is important in determining how many species may ultimately find and inhabit a new region (Figure 10).

Greenwood's (1965) study of the endemic cichlids of Lake Nabugabo may also provide a relevant paradigm for the evolution and speciation of shore-bound cichlids in Lake Malawi. In Lake Nabugabo, which was separated from Lake Victoria for about 4000 years, five endemic cichlid species coexist. These species are each most closely related to cichlids in Lake Victoria, suggesting that they evolved allopatrically from those parent populations. The appearance and disappearance of lagoons in Lake Malawi, as indicated by the 16-year series of photographs (Figures 3, 4) could be analogous to the Lake Nabugabo situation. More detailed geological studies of Lake Malawi should allow us to begin to determine the age and continuity of isolation among various habitat patches or regions. With such information, we will be in a better position to determine the rate of evolution of the cichlid fishes in this lake, and to assess the degree of isolation and time necessary for new species to arise.

Interestingly, the mbuna species that feed extensively on zooplankton and colonized the experimental reefs would appear to be the groups least likely to have restricted gene flow. However, they are among the most species-rich groups of mbuna (Marsh 1982; Marsh et al. 1981; McKaye et al. 1982, 1983; Lewis, Marsh, Ribbink pers. comm.). Much further work is required before any definitive conclusions can be drawn concerning the evolutionary processes which caused this species-rich vertebrate flock to arise. We hope these data will stimulate research on the geololgy, history and fauna of Lake Malawi. This inland sea, with its habitat heterogeneity and highly diverse fauna, has the potential to provide further insight into the processes which mold the evolution and structure of complex communities.

SUMMARY

1. Aerial photos of the western shoreline of Lake Malawi support Fryer's view that Lake Malawi consists of a mosaic of alternating patches of sand (61%), weed (21%) and rock (18%).

2. Analysis of photographs taken between 1966-1980 documented the creation and dissolution of isolated habitats due to rising lake levels.

3. Data from eight experimental reefs placed on sand demonstrated that a subset of rock dwelling cichlids will move one kilometer from the nearest rock outcropping and colonize new habitats. These early colonizing species are facultative in their feeding repertoire and primarily exploit zooplankton.

4. Doubling the size of a reef resulted in a 60 percent increase in species number, and increasing the reef's spatial heterogeneity resulted in a 30 percent increase in species numbers. Deep reefs (9 m) had approximately 60 percent more species than did identical shallow reefs (6 m). This increase was due to the greater zooplankton densities at the greater depth. Zooplankton is the primary food of most cichlids.

5. The species groups most likely to colonize newly formed rock outcroppings are those which are among the most species rich. This anomaly suggests that in some circumstances intrinsic isolating mechanisms could be more important than extrinsic ones in splitting species. Processes of both allopatric intralacustrine speciation and sympatric speciation are probably occurring in the cichlid species flocks of the Great Lakes of Africa.

ACKNOWLEDGMENTS

We thank the Malawian Fisheries and Survey Departments for continuing assistance, J. Trendall and M. Salmon for reviewing the manuscript, and S. Louda for constant encouragement and patient review of the manuscript. The research was supported by the United States National Science Foundation.

REFERENCES

Barbour C D, J H Brown 1974 Fish species diversity in lakes. *Amer Nat* 108:473-489

Barel C D N, M J P van Oijen, F Witte, E L M Witte-Maas. 1977 An introduction to the taxonomy and morphology of the Haplochromine Cichlidae from Lake Victoria. *Neth J Zool* 27:381-389

Drayton R S 1979 A study of the causes of the abnormally high levels of Lake Malawi in 1979. Water Resources Division, Malawi WRD-NO. TP 5

Fryer G 1959 The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes and a discussion of the evolution of a group of rock-frequenting Cichlidae. *Proc Zool Soc Lond* 132: 153-281

——— 1977 Evolution of species flocks of cichlid fishes in African lakes. *Z Zool Syst Evolut-forsch* 15:141-165

Fryer G, T D Iles 1972 *The Cichlid Fishes of the Great Lakes of Africa.* Oliver, Boyd. Edinburg

Greenwood P H 1965 The cichlid fishes of Lake Nabugabo, Uganda. *Bull Br Mus Nat Hist (Zool)* 12:315-357

——— 1974 Cichlid fishes of Lake Victoria, East Africa: The biology and evolution of a species flock. *Bull Br Mus Nat Hist (Zool)* Suppl 6:1-134

Holzberg S 1978 A field and laboratory study of the behaviour and ecology of *Pseudotropheus zebra* (Boulenger): an endemic cichlid of Lake Malawi (Pisces: Cichlidae) *Z Zool Syst Evolut-forsch* 33:478-485

Kosswig C 1947 Selective mating as a factor for speciation in cichlid fish of East African lakes. *Nature* 159:604-605

——— 1963 Ways of speciation in fishes *Copeia* 1963:238-244

Lewis D S C 1982 A revision of the genus *Labidochromis* (Teleostei: Cichlidae) from Lake Malawi. *Zool Jour Linn Soc* 75:189-265

Liem K F 1978 Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. *J Morphol* 158:323-366

——— 1980 Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am Zool* 20:295-314

Lowe-McConnell R H 1959 Breeding behavior patterns and ecological differences between *Tilapia* species and their significance for evolution within the genus *Tilapia* (Pisces: Cichlidae). *Proc Zool Soc Lond* 132:1-30

MacArthur R, E O Wilson 1967 *The Theory of Island Biogeography.* Princeton Univ Press. Princeton NJ

Marsh A C 1981 A contribution to the ecology and systematics of the genus *Petrotilapia* (Pisces: Cichlidae) in Lake Malawi. MS Thesis, Rhodes Univ

Marsh AC, A J Ribbink, B A Marsh 1981 Sibling species complexes in sympatric populations of *Petrotilapia* Trewavas (Cichlidae, Lake Malawi). *Zool J Linn Soc* 71:253-264

Mayr E M 1963 *Animal Species and Evolution.* Belknap. Cambridge Mass

McKaye K R 1980 Seasonality in habitat selection by the gold color morph of *Cichlasoma citrinellum* and its relevance to sympatric speciation in the family Cichlidae. *Env Biol Fish* 5:75-78

McKaye K R 1981 Death feigning: A unique hunting behavior by the predatory cichlid, *Haplochromis livingstonii* of Lake Malawi. *Env Biol Fish* 6:361-365

——— 1983 Ecology and breeding behavior of a cichlid fish, *Cyrtocara eucinostomus*, on a large lek in Lake Malawi, Africa. *Env Biol Fish* 8:81-96

McKaye K R, A Marsh 1983 Food switching by two specialized algae-scraping cichlid fishes in Lake Malawi, Africa. *Oecologia* 56:245-248

McKaye K R, T Kocher, P Reinthal, I Kornfield 1982 A sympatric sibling species complex of *Petrotilapia* Trewavas from Lake Malawi analyzed by enzyme electrophoresis (Pisces: Cichlidae). *Zool J Linn Soc* 76:91-96

McKaye K R, T Kocher, P Reinthal, R Harrison, I Kornfield 1984 Genetic evidence for allopatric and sympatric differentiation among color morphs of a Lake Malawi cichlid fish. *Evolution* 38:215-219

Ostro M E 1979 *Tropical Fish Hobbyist* 27:71

Ribbink A J, B A March, A C Marsh, A C Ribbink, B J Sharp 1983 A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *S Afr J Zool* 18:1-180