

Floating Islands: A Means of Fish Dispersal in Lake Malawi, Africa

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Floating masses of vegetation are commonly seen in the southern region of Lake Malawi. These floating islands disperse littoral fishes across deep portions of the lake. Six islands were sampled and all yielded fishes. The 129 individuals collected belong to ten species, including one mormyrid, one cyprinid, two clariids, one cyprinodontid, four cichlids and one mastacembelid. Most of the species are characteristic of lakeshore swamps and are not endemic to Lake Malawi. Dispersal by floating islands may increase gene flow between disjunct populations of widespread species, particularly those inhabiting swamps. Such dispersal, theoretically, could also serve to establish founder populations of geographically isolated species.

LAKE Malawi, the southernmost of the African Great Rift Lakes, contains the world's largest lacustrine fish fauna. At least 400 species of fishes are now known from the lake. More than 90% are cichlids, 99% of which are endemic to the Lake Malawi system, including Lake Malawi itself, the upper Shire River and Lake Malombe.

The shoreline of Lake Malawi consists of three main types of habitat: sandy beach, rocky shore and swamp. Alternating stretches of sandy beach and rocky shore predominate. River mouths and parts of the lakeshore are fringed with swamp vegetation, dominated by papyrus (*Cyperus papyrus*) and reeds (*Phragmites communis* and *Typha* sp.). Swamp is particularly extensive in the southwest arm, but reeds, at least, occur throughout Lake Malawi in suitable habitats (Ricardo Bertram et al., 1942). Each of the three shoreline habitats has a distinctive fish community, in part because many of the cichlid and other species are markedly stenotopic (Fryer and Iles, 1972). However, the fish community of the river mouths and lakeshore swamps owes its distinctive character to nonendemic forms, including several mormyrids, a number of cyprinids, a characid, three clariids, a cyprinodontid, several cichlids and a mastacembelid (Jackson, 1961, and pers. obs.). Indeed, the lakeshore swamp is unique among the three types of shoreline in lacking any lacustrine endemics, either cichlid or noncichlid, that are characteristic of this habitat. Collections made in the swamp at Chembe, Cape Maclear, Lake Malawi contain several hundred fishes, but include only a few individuals of endemic lacus-

trine cichlids. All were probably incidental visitors from the adjacent sandy shore.

The shape of the boundaries between swamps and the lake is constantly changing. The combined actions of wind and waves can loosen swamp vegetation and cause it to drift into the open waters of Lake Malawi as floating islands (Ricardo Bertram et al., 1942). The existence of these drifting masses of vegetation is well known to both African and European boatmen. A chart of the southwest arm of the lake carries the warning that "towards the end of the rainy season large floating islands of reeds and sudd occur in this vicinity" (Southern Rhodesia Federal Government, 1958). Islands are seen at all times of the year, but they are most abundant during the rainy season (Jan.-March). During Feb. as many as 20 floating islands per day drift within sight of Cape Maclear Research Station.

Fishes are associated with these floating islands. This is not surprising, since it is reasonable to expect that small fishes should remain with, or be attracted to, floating vegetation that is dislodged from lakeshore swamps.

The association of fishes with floating islands is not unique to Lake Malawi. In the Amazon many fish species, from minute characids to the giant *Arapaima gigas*, regularly swim beneath or near the "floating meadows" of aquatic grasses that drift downriver (Junk, 1970). More than 1,000 fishes were caught beneath a 25 m² piece of this vegetation (Junk, 1973).

The floating islands in Lake Malawi regularly shelter several species of swamp-dwelling fishes, and occasionally even endemic lacustrine cichlids, among their submerged parts. Littoral

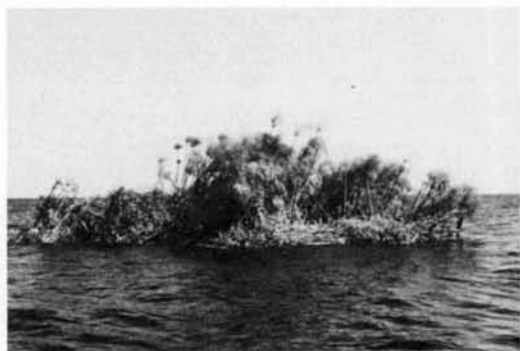


Fig. 1. Floating island 1, length 14 m, composed mainly of *Cyperus papyrus*. 1 Aug. 1980.

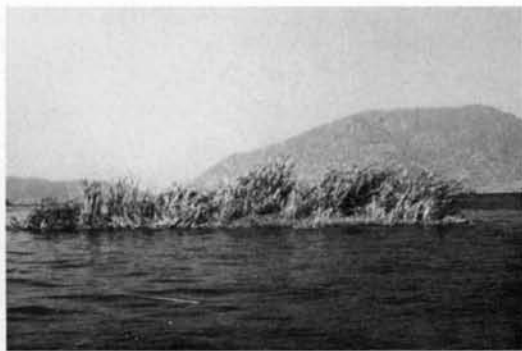


Fig. 2. Floating island 2, length 21 m, composed mainly of reeds. 13 Aug. 1980.

fishes have been collected from these islands as far as 8 km from the nearest land. Thus, the vegetation may serve to transport these fishes across several kilometers of deep water—a long distance to territorial, philopatric animals such as cichlids. This intralacustrine dispersal may be of importance to the evolution and speciation of fishes in Lake Malawi. We will summarize the collections from the six floating islands sampled, and then attempt a preliminary assessment of the significance of this dispersal mode.

METHODS

During the first exploration of a floating island (island 1) only SCUBA and a dipnet were available for fish collecting. Inspection beneath the island failed to reveal any fishes, but several were caught by scooping the dipnet along an arbitrarily chosen 2-m section of the island's perimeter from an inflatable Zodiac boat. These fishes undoubtedly represent only a small fraction of the total number in the vegetation. Each of the other islands (2–6) was sampled using 2–3 liters Noxfish emulsified rotenone, SCUBA and hand nets. Even these ichthyocide collections seriously underestimate the numbers of fishes actually present. Most floating islands are too large for effective overall coverage by rotenone. Some fishes were seen to escape collection by swimming into unpoisoned areas of the vegetation.

The collections were made while the islands were 0.3–8.0 km from land and over water 10–100 m deep. All fishes are deposited in the US National Museum of Natural History.

Our use of cichlid generic names requires

some explanation. Greenwood (1979) restricted the genus *Haplochromis* to five East African species and suggested resurrecting *Cyrtocara* (not used since 1935) from synonymy with *Haplochromis* for all endemic Malawian species allocated to *Haplochromis* by Trewavas (1935). However, the senior author is revising the generic nomenclature of many Malawian cichlids. For the sake of continuity, therefore, we prefer to employ "*Haplochromis*" for species of *Haplochromis* sensu Trewavas (1935). We follow Greenwood (1979) in referring to the nonendemic species *H. callipterus* as *Astatotilapia calliptera*.

RESULTS

Floating islands are composed primarily of either papyrus (Fig. 1) or reeds (Fig. 2). The submerged parts of this vegetation (Fig. 3) comprise a complex framework of closely spaced,

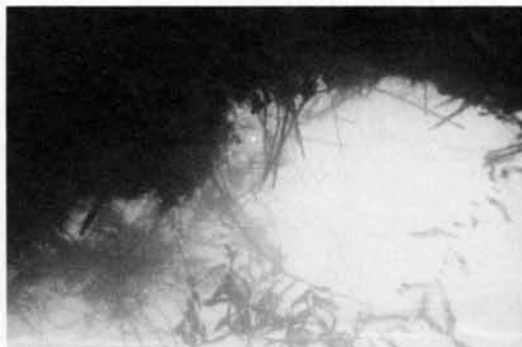


Fig. 3. Underwater view of floating island 2, looking obliquely upward, to show densely tangled submerged vegetation. 13 Aug. 1980.

TABLE 1. DATE OF FISH COLLECTION, DIMENSIONS AND DOMINANT PLANT TYPE FOR FLOATING ISLANDS IN LAKE MALAWI.

	Floating island					
	1	2	3	4	5	6
Collection date	1 Aug. 80	13 Aug. 80	19 Feb. 81	19 Feb. 81	20 Feb. 81	20 Feb. 81
Length × width (m)	14 × 7	21 × 6	50 × 25	10 × 5	20 × 8	10 × 5
Circumference at waterline (m)	35	46	170	30	65	33
Maximum height above water (m)	3.7	2.4	2.5	2	2	2
Maximum depth below water (m)	2.1	1.8	—	—	—	—
Dominant plant	Papyrus	Reeds	Reeds	Reeds	Reeds	Reeds

densely tangled roots, providing many crevices in which small fishes can hide from larger, predatory fishes. The roots also provide substrata or shelter for edible organisms. Epiphytic algae were noted, and dragonfly and damselfly larvae, water scorpions (Hemiptera: Nepidae), atyid prawns (*Caridina nilotica*) and postlarval fishes were collected beneath floating islands.

The collection date, measurements, and dominant plant type of the six floating islands sampled are given in Table 1. The places of origin of these islands are unknown, but we suspect that they came from the extensive swamps of the southwest arm of the lake. The locations of the islands when sampled are shown in Fig. 4. Every island had fishes beneath it. A total of

129 fishes belonging to 6 families and 10 species was collected (Table 2). Except for young of two species of predatory cichlids, all the fishes belong to littoral, demersal or paludal species not previously reported from epipelagic waters. Both the habitat preferences of these species and the observed absence of small fishes from the open water around the islands indicate that all the fishes collected were traveling among the submerged plant parts.

DISCUSSION

Several characteristics of the collections are immediately noteworthy.

1) Most of the species are inhabitants of the

TABLE 2. FISHES COLLECTED BENEATH FLOATING ISLANDS IN LAKE MALAWI [number of specimens (SL in mm)].

Species	Floating island					
	1	2	3	4	5	6
Mormyridae						
<i>Marcusenius nyasensis</i> (Worthington)	—	—	—	1 (140)	—	—
Cyprinidae						
<i>Barbus macrotaenia</i> Worthington	—	1 (18)	1 (30)	—	—	—
Clariidae						
<i>Clarias theodora</i> Weber	—	2 (70–157)	—	5 (79–117)	2 (78–111)	17 (60–161)
<i>C. mossambicus</i> Peters	—	1 (56)	—	—	—	3 (54–90)
Cyprinodontidae						
<i>Aplocheilichthys johnstoni</i> (Günther)	5 (10–12)	17 (11–36)	—	—	—	—
Cichlidae						
<i>Sarotherodon</i> cf. <i>squamipinnis</i> (Günther)	—	1 (34)	—	—	—	5 (14–18)
<i>Astatotilapia calliptera</i> (Günther)	—	18 (24–75)	2 (40–78)	—	2 (42–48)	36 (15–54)
" <i>Haplochromis</i> " cf. <i>kiwinge</i> Ahl	1 (25)	3 (23–27)	—	—	—	—
<i>Rhamphochromis</i> sp.	—	—	—	—	—	3 (15–19)
Mastacembelidae						
<i>Mastacembelus shiranus</i> Günther	—	—	—	—	1 (138)	2 (126–185)

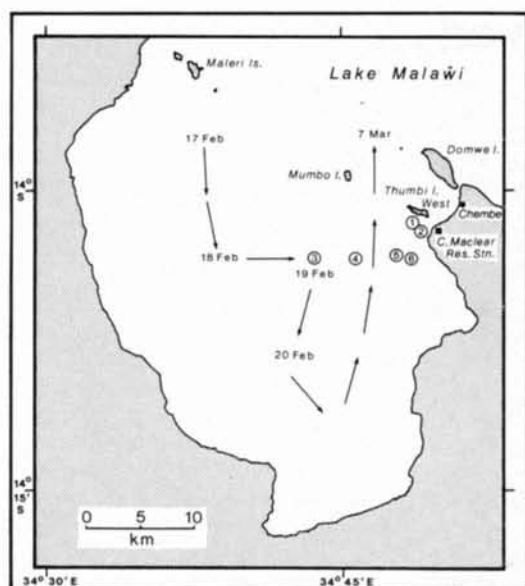


Fig. 4. Approximate locations of floating islands (numbered circles) at time of fish collecting. Island numbers correspond to those in Tables 1 and 2. Estimated drift of island 3, as observed from vicinity of Cape Maclear Research Station, is indicated by arrows and dates in Feb.–March 1981.

lakeshore swamps and river mouths. This includes the only cichlid common on the floating islands, *Astatotilapia calliptera* and both clariids known from the islands. [Trewavas (1949) suggested that *Astatotilapia calliptera* "may very well represent the ancestor of many species" of haplochromine cichlids in Lake Malawi. It might, therefore, seem tempting to suspect that the dispersal of this species by floating islands, documented here, had special significance in the formation of the Malawian cichlid species fauna. But there is no evidence in the form of synapomorphic characters shared by *A. calliptera* and the Malawian endemic cichlids to substantiate a close cladistic relationship between them. The cladistic relationship of *A. calliptera* to other species outside Lake Malawi is equally unknown, and the genus *Astatotilapia* has no defining synapomorphies (Greenwood, 1979). Unless *A. calliptera* is indeed related to all or some of the Malawian endemic species, the significance of its dispersal to their speciation is probably limited to any role it may have in competition with them. It is thought to be trophically generalized (Trewavas, 1949), but too little is known of the biology of *A. calliptera*—and of most Malawian endemics—to permit assess-

ment of even that possibility], [Like two cichlids the clariid catfishes have produced an endemic species flock in Lake Malawi (Jackson, 1959; Greenwood, 1961). However, the two clariid species known from floating islands (Table 2) are both nonendemic. Their cladistic relationships are unknown. Perhaps the dispersal of these clariids by floating islands played a role in promoting clariid speciation in Lake Malawi. This hypothesis could be refuted by showing that neither of the species known to disperse is most closely related to the endemic Malawian clariids].

2) The species diversity of the collections is rather low, but 8 of the 10 species collected were represented on two or more of the floating islands. Two species, *Clarias theodorae* and *Astatotilapia calliptera*, were collected on four of the six islands. Several species were abundant on at least one island.

3) Few lake cichlids are present under floating islands. Only three species of endemic lacustrine cichlids occur in the collections, and each of these is represented by only a few juvenile individuals. One species, *Sarotherodon* cf. *squamipinnis*, mouthbroods its young in weedy or reedy areas (Lowe, 1953), which might explain the presence of some of these young on floating islands. However, the other two species, "*Haplochromis*" cf. *kiwinge* and *Rhamphochromis* sp., are not known to occur in swampy habitats. They are two of the commonest species of predatory cichlid found in more open water off rocky and sandy shores (Jackson, 1961). The presence of young of these species on floating islands is discussed further in the next paragraph.

4) Most fishes in the collections are small. Many are juvenile or subadult; the only adult fishes actually collected belong to species with a small adult size. This size distribution is probably not an artifact of sampling with ichthyocide. Inspection beneath the floating islands during collecting showed that the only large (>200 mm SL) fishes present were predatory cichlids (*Rhamphochromis* sp. and "*Haplochromis*" *kiwinge*) which sometimes appeared from open water after smaller fishes began emerging from the rotenone cloud. These adult predators were not collected. Perhaps some of them were females that were mouthbrooding their young and lost some in the vegetation while feeding on the emerging swamp fishes. Alternatively, these young may have been free-swimming fishes that joined the islands closer to shore; in this case,

the presence of conspecific adults of these common species at the islands would be coincidental. Unfortunately, no data are available concerning the frequency and feeding behavior of these two species at undisturbed floating islands.

Hypothetical dispersal patterns.—Four hypothetical patterns of dispersal by floating islands can be distinguished from the standpoint of the number of contacts an island makes with land subsequent to its formation, and the types of habitat occurring at the source and destination of the dispersing fishes. Although successful dispersal may never occur, this classification of possible patterns is helpful in organizing a discussion of the potential effects of dispersal.

The pattern perhaps most likely to favor survival of the dispersers and subsequent gene flow or colonization is dispersal from one patch of lakeshore swamp to another, similar patch. Dispersal of this type would have little or no importance for the speciation of lacustrine endemics, since they do not inhabit swamps, but would be important in maintaining gene flow among disjunct populations of swamp species.

More interesting than the former, but perhaps less likely to occur, is successful dispersal from a patch of lakeshore swamp to a different habitat. On several occasions islands were observed to float against a sandy beach or a rocky permanent island. The floating islands remained lodged against the shore for days and eventually broke up there. It is uncertain whether a fish species usually occurring in swamps could survive and reproduce in an area of rock or bare sand. However, on 3 June 1980 we collected a single adult of *Astatotilapia calliptera* in a rocky bay with sandy bottom on the north shore of Mumbo Island. This swamp-dwelling cichlid species has never previously been reported from any permanent island in Lake Malawi, but it occurs commonly on floating islands. Mumbo Island is within the area in which floating islands are frequently seen (Fig. 4). The individual caught on Mumbo may have arrived by floating island, but this speculation is, of course, untestable. Also, on 28 Feb. 1981 we observed more than 100 individuals of *A. calliptera*, including males in breeding coloration and females mouthbrooding young, beneath a floating island that was lodged against the rocky south shore of Thumbi I. West. When this floating island broke up after 8 days, the fishes on it are presumed to have moved onto

Thumbi I. West. Whether this species will become established there remains to be seen.

The third hypothetical pattern of dispersal by floating islands is from one patch of non-swamp habitat to another. For this to be possible, an island would have to make two encounters with land after leaving its swamp of origin. This would be the most interesting pattern because of its implications for the possibility of speciation by founder effect in the endemic cichlid fauna (see "Floating islands and speciation," below). But, for dispersal to occur, stenotopic cichlids would have to leave their preferred habitat for the very different habitat offered by floating vegetation. The limited collecting done under floating islands to date does not disclose enough dispersing cichlids of endemic lacustrine species to substantiate the occurrence of this dispersal pattern.

Rock-dwelling species of the genera *Petrotilapia* and *Pseudotropheus*, and also "*Haplochromis*" *euchilus*, were seen feeding among the roots underneath an island that landed against Thumbi I. West. When approached by a diver these cichlids left the floating island for the protection of the rocks. Also, one nonendemic predatory cichlid, *Serranochromis robustus* (150 mm SL), was observed stalking prey among the roots. We observed the behavior of the fishes underneath this island on 4 of the 8 days that elapsed before it broke up. From these observations it appears that rock-dwelling adult cichlids will feed among the roots but probably leave the floating island if a shift in the wind or current causes it to move away from the rocks.

It is possible that mouthbrooding female cichlids occasionally lose some of their young among this floating vegetation while feeding under it. These young could then be transported to new localities. The collection of post-larvae of obligate rock-dwelling cichlids from floating islands away from shore would provide evidence to substantiate this speculation.

A floating island could transport lacustrine species from a patch of nonswamp habitat to a lakeshore swamp. Such dispersal seems unlikely for the reasons discussed in the preceding, and in any case would probably be unimportant for speciation.

Floating islands and speciation.—To explain the existence of cichlid species flocks, both intralacustrine allopatric (Fryer and Iles, 1972) and sympatric modes of speciation (Kosswig, 1947, 1963) have been discussed. For the intralacus-

trine allopatric mode, Fryer and Iles (1972) suggested two different models. First, since littoral cichlids are restricted to isolated patches of suitable habitat, the separated populations could diverge and become reproductively isolated (Type 1a of Bush, 1975: allopatric speciation by subdivision). Alternatively, speciation could occur following colonization of a new isolated site (Type 1b of Bush, 1975: allopatric speciation by founder effect).

Testing these and other hypotheses concerning the geographic patterns of fish speciation requires detailed knowledge of the cladistic relationships and distribution of fishes within the lake. The methods of vicariance biogeography (Platnick and Nelson, 1978; Rosen, 1978) should permit the unique pattern (estimated by a unique area cladogram) formed when speciation occurs following an individual dispersal event to be distinguished from the repeated pattern (estimated by multiple, concordant area cladograms) formed when speciation takes place in several groups of organisms in a biota subjected to a common series of vicariance events. [The history of the present Lake Malawi basin (Banister and Clarke, 1980) appears to involve the consecutive north-south faulting and filling of three or four subbasins now weakly delimited by submerged ridges (Yairi, 1977). The northernmost and oldest subbasin is at most 2.5 my old; the southernmost may be less than 1 my old (R. Crossley, pers. comm.). It is unknown whether these subbasins have ever existed as a series of isolated lakes. If so, one might predict that, for a monophyletic group (X) of organisms with diagnosable representatives (X_1, X_2, X_3, X_4) in each subbasin (B_1, B_2, B_3, B_4), each representative is the sister group of all those to the south: ($X_1, (X_2, (X_3, X_4))$). Indeed, if conspecific cichlid populations in Lake Malawi can be effectively isolated by distance, as Fryer and Iles (1972) suggest, this repeated cladistic pattern might occur even if the subbasins were merely formed and filled sequentially but never isolated from one another. Thus, the postulated north-south extension of Lake Malawi provides a hypothetical series of vicariance events that can be compared with the cladograms of Malawian organisms. Deep coring on the ridges between the subbasins could yield estimates of the absolute dates of formation and filling of the subbasins.] Regrettably, the necessary cladistic and distributional data on Malawian fishes are still too scarce for effective tests of this kind to be made.

Two conflicting influences of dispersal on speciation processes are possible. Dispersal by floating islands could either 1) promote allopatric speciation by establishing founder populations in new areas, or 2) inhibit allopatric speciation by increasing gene exchange between isolated populations. The result of any particular dispersal event would depend on the distribution and ecology of the fish species involved. A localized Malawian species, such as a cichlid endemic to a particular rocky island (Iles, 1960; Oliver and Loiselle, 1972; Lewis, 1980), might undergo allopatric speciation following successful dispersal. Conversely, a widespread Malawian species would be more likely to encounter a conspecific population upon dispersing, and gene flow might occur.

At present, no persuasive evidence exists to suggest that dispersal by floating islands has led to the successful colonization of a new locality by any species, or even to suggest that such dispersal has enhanced gene flow between preexisting disjunct populations. We suspect, however, that the latter process may take place, since hundreds of floating islands and many thousands of associated fishes are drifting between dozens of disjunct habitat patches in southern Lake Malawi each year. Gene flow between disjunct populations of swamp fishes seems the most probable significant effect of such dispersal.

The occurrence of colonization or gene flow following dispersal by floating islands is potentially testable. The geographic distribution of rare electromorphs, direct observation of the behavior of dispersing fishes when floating islands form and when they contact land, and experimental manipulations of floating islands and their faunas would contribute to such tests.

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