Parental behaviour and mixed broods among cichlid fish of Lake Malawi

A.J. Ribbink, A.C. Marsh, B. Marsh and B.J. Sharp
JLB Smith Institute of Ichthyology, Rhodes University, Grahamstown

The number of species of cichlid found to host foreign offspring in mixed broods in Lake Malawi is much greater than originally supposed. It is suggested that all species which show well developed parental behaviour may have foreign fry mix with their broods on occasion. A variety of species of fry were found in mixed broods. These come from two categories of fish: those which apparently do not guard their free swimming fry; and those which have a well entrenched phase of protective care. Although substrate spawners may encourage other fry to join their broods it is argued that foreign young are unwelcome guests of mouthbrooders.
S. Afr. J. Zool. 1980, 15: 1–6

Die aantal spesies van die Cichlidae in die Malawi-meer wat vreemde kleintjies in gemengde skole beskerm is baie meer as wat aanvanklik veronderstel is. Daar word voorgestel dat alle spesies met goed ontwikkelde ouersorg by tye vreemde kleintjies tussen hul eie sal hê. Hierdie vreemde kleintjies is afkomstig van twee kategorië van visse: die wat nie hul vryswemmende nageslag klein vissies oppas nie; en die wat 'n goed gevestigde tydperk van beskerming het. Alhoewel visse wat op die bodem kuitskiet ander klein vissies kan aanmoedig om by hulle kleintjies aan te sluit is dit twyfelagtig of vreemde kleintjies welkom sou wees by mondbroeiers.
S.-Afr. Tydskr. Dierk. 1980, 15: 1–6

One of the most remarkable features of cichlid fish is the manner in which they care for their progeny. It is usual for one or both parents to aerate, cleanse and protect developing eggs and fry. Cichlidae have developed two principal modes of parental behaviour; substrate spawners lay their eggs on the substratum and guard these, whereas mouthbrooders take the eggs into their mouths where they are held and protected throughout their development. These forms of parental behaviour were described in some detail by Baerends and Baerends-Van Roon (1950) as well as by Fryer and Iles (1972). Substrate spawners form strong pair-bonds and both parents care for the eggs, larvae and fry, whereas mouthbrooders form extremely tenuous pair-bonds and only one parent cares for the progeny (Fryer & Iles 1972). The majority of the cichlids in the African Great Lakes are maternal mouthbrooders; as far as is known, all but one species (*Tilapia rendalli* Dumeril) of Lake Malawi cichlids are of this category.

Protective behaviour is important among cichlid fish communities as eggs and young are often subjected to heavy predation. Though progeny may be lost to other groups of fish it is the Cichlidae themselves which provide much of the predatory pressure as they are opportunists which readily devour the offspring of their own and other species when they can. Even specialized herbivores will consume eggs and fry of other fish (Fryer 1959a; Fryer & Iles 1972; Greenwood 1974; Ward & Wyman 1975; McKaye & McKaye 1977; Zaret 1977). Indeed, in the Great Lakes of Africa where cichlids dominate the fauna in an ecological and taxonomic sense there is evidence that specialized paedophages may have developed (Greenwood 1974; Fryer 1977). It is necessary therefore that cichlids which lay relatively few eggs should invest in protective parental care, and this has become a striking feature of cichlid behaviour in Africa, Asia and the Americas.

Usually parental fish protect their own fry only, but communal care of several different conspecific broods has been reported among substrate spawners (Ward & Wyman 1975; McKaye & McKaye 1977). Some substrate spawners of Lake Jiloa, Nicaragua, have been found caring for mixed broods composed of two species (McKaye & McKaye 1977; McKaye 1977). This latter phenomenon is not limited to substrate spawners, however, as Ribbink (1977) found mouthbrooders in Lake Malawi caring for mixed broods, and suggested that the foreign fry may be exhibiting a form of cuckoo behaviour. Further observations during 1977/78

A.J. Ribbink*, A.C. Marsh, B. Marsh and B.J. Sharp
JLB Smith Institute of Ichthyology, Rhodes University,
P.O. Box 94, Grahamstown 6140, South Africa
A.J. Ribbink*
Present address: Fisheries Research Centre,
P.O. Box 27, Monkey Bay, Malawi
*To whom all correspondence should be addressed

Received 28 March 1979; accepted 21 September 1979

have shown that mixed broods occur on a much wider scale in Lake Malawi than initially supposed. These additional observations are reported below and an argument is developed in which it is suggested that, while substrate spawners may derive benefit from the presence of foreign fry in their mixed broods (McKaye & McKaye 1977), this is not the case among mouthbrooders. Accordingly, substrate spawners might actively encourage foreign fry to mingle with their progeny, but mouthbrooders would tend to discourage such mixing.

Methods

Data presented below were collected while diving (SCUBA) in Lake Malawi. Observations were recorded on plastic slates and transcribed after each dive. Whenever a fish guarding a mixed brood was found, its behaviour was recorded and the ratio of foreign fry to native fry was estimated. Normal guarding behaviour was observed by divers who maintained their distance so that the parent and fry were apparently undisturbed by their presence. On other occasions divers actively interfered with broods in order to stimulate recall behaviour. When the parent is chased away the fry prepare themselves for collection by grouping together in a school which awaits the mother's return. Once the divers retreat the parent returns to gather her brood. This recall behaviour was recorded as well as the facility with which foreign fry entered the foster parent's mouth. Responses of fry to hand movements which simulated the parent's recall behaviour were also noted.

Observations of mixed broods in Lake Malawi

Ribbink (1977) reported that a number of predatory species of Lake Malawi cichlids were found caring for mixed broods consisting of their own offspring, easily recognized because they have adult coloration and markings from the outset, and fry of another species differing in coloration and sometimes in size. In those instances the foreign fry appeared to belong to a single species, *Haplochromis chrysonotus* Boulenger which is a zooplanktivore found in surface waters (Iles 1960). The foster parents, *Haplochromis polystigma* Regan, *Haplochromis macrostoma* Regan, and *Serranochromis robustus* Regan are all bottom-dwelling predators usually found in water less than 30 m deep. Since the initial discovery of mixed broods in Lake Malawi further diving observations have resulted in the number of species found to act as foster parents increasing from 3 — 13 (Table 1).

It will be noted from Table 1 that a number of species are unidentified and others are considered together. The reason for this is that about 270 species of cichlid have evolved in Lake Malawi, many of which are undescribed and a great number are extremely similar in coloration, markings, general morphology and size, so that positive identification of fish underwater is sometimes impossible. An indication of the taxonomic complexities and problems of identification of Lake Malawi cichlids is given in a number of papers (Eccles & Lewis 1977, 1978; Stock 1976; Balon 1977). Accordingly, we have indicated (Table 1) where identifications are uncertain. Of these, *Haplochromis fenestratus* Trewavas and *Haplochromis taeniolatus* Trewavas are virtually indistinguishable when in the lake, since they are morphologically and behaviourally similar, and appear to have almost identical ecological requirements. As a result these two species have been considered together. There is also some doubt whether *H. macrostoma* and *H. maculiceps* Ahl are in fact two distinct species (Eccles *pers. comm.*). In the field one can distinguish two colour forms, but there is some evidence that this fish can change its markings from one form to that of the other (*pers. observ.*). Ecologically and morphologically these fish appear indistinguishable and consequently they are also considered together.

Table 1 shows that not all foster parents are predatory, as omnivores, herbivores and sand-dwellers which forage for benthic infauna, as well as those which feed on microorganisms in the sand, are represented. Common to all species, however, is well-developed parental behaviour during which the parents care for free-swimming fry.

Although *H. chrysonotus* was the only species originally found in mixed broods (Ribbink 1977) a number of other species have since been found intermingled with fry of foster parents. At least 15 different species of fry may occur in mixed broods, but *H. chrysonotus*-like fry appear to be the foreign species found most often. This identification is pre-

Table 1 The species of fish which have been found to host foreign fry, and what they eat. *H. polystigma* and *H. livingstonii* are ambush predators which also consume plant material. The number of mixed and pure broods found with each species is indicated

Host species	Diet	No. of pure broods	No. of mixed broods
Haplochromis kiwinge	Piscivore	8	5
H. macrostoma/maculiceps	Piscivore	25	12
H. fuscotaeniatus	Piscivore	4	3
H. polyodon	Piscivore	—	3
Serranochromis robustus	Piscivore	11	5
H. polystigma	Piscivore/omnivore	14	10
H. livingstonii	Piscivore/omnivore	5	1
H. fenestratus/taeniolatus	Epilithic/omnivore	31	9
H. sphaerodon	Infauna of sand	—	1
H. rostratus	Infauna of sand	9	3
H. pictus-like?	Sand-dweller, food uncertain	3	4
H. simulus-like?	Sand-dweller, food uncertain	—	1
H. annectens-like?	Sand-dweller, food uncertain	1	1

sented with caution as one cannot be certain that fry identified as *H. chrysonotus* in the field were indeed this species on every occasion. Other species of closely related zooplanktivores collectively referred to as utaka (Iles 1960) such as *Haplochromis quadrimaculatus* Regan, *H. likomae* Iles, *H. jacksoni* Iles, *H. nkhatae* Iles and *H. trimaculatus* Iles are very similar to *H. chrysonotus* and may behave in the same way. So far those utaka fry reared in the laboratory for identification were *H. chrysonotus*, but frequently we were unable to catch members of a mixed brood and relied upon underwater identifications. Several other species of fry found intermingled among host progeny have been identified. Of these, *H. macrostoma/maculiceps* has been found among native broods of *H. kiwinge, H. fuscotaeniatus, H. polystigma* and *S. robustus. H. kiwinge* fry have been found among broods of *H. macrostoma/maculiceps*. Then, *H. fenestratus/taeniolatus* fry appeared among broods of *H. kiwinge, H. macrostoma/maculiceps, H. polystigma* and *S. robustus*. An interesting feature of these species is that the adults may host foreign fry while offspring of their own species may be found with surrogate parents. Consequently, it is possible that a parent may guard her own offspring and those of a conspecific and this may account for some of the size differences of fry observed in broods which were homogeneous regarding species composition.

Mixed broods of more than two species are also found in Lake Malawi. On one occasion an *H. macrostoma/maculiceps* was discovered caring for its own fry and those of three other species. On five other occasions parents guarding mixed broods containing two foreign species were observed. Usually very few foreign fry were found in mixed broods. Most frequently they comprised less than 5% of a brood, but occasionally as many as 50% were intruders (Fig. 1).

A parent cichlid chased from its brood usually returns promptly, chases off those fish which are attempting to eat the unguarded brood and then retrieves the fry which have gathered together. As fry are not usually taken into the mouth at once, but are collected in several batches it is possible to see whether foreign fry are among the first or last to enter the mouth. It was found that native fry were usually

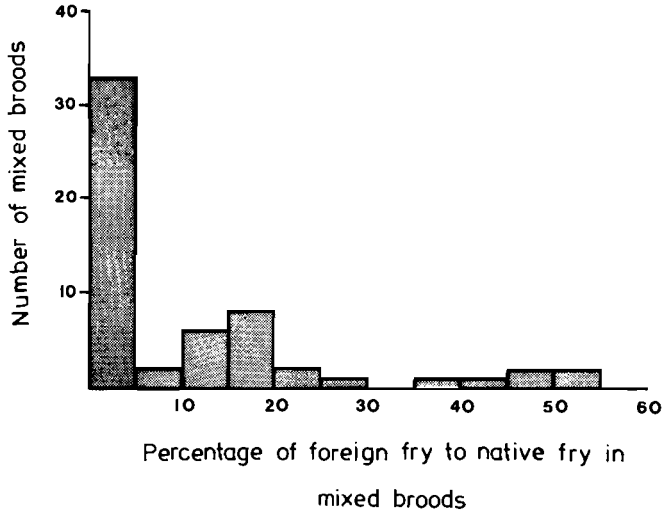

Fig. 1 The number of occurrences of a particular ratio of foreign fry to native fry in mixed broods, expressed as a percentage of the total brood (n = 58 mixed broods).

the first to gain protection within the mouth while foreign fry were among the stragglers. This is not a general rule, however, as a group of unidentified darkly blotched fry mixed with a brood of *H. polyodon* found at Nkhata Bay, were the leaders of the school and among the first to enter the parent's mouth when recalled.

Under conditions of stress imposed by divers who disturb broods so that they might observe recall behaviour, it is not possible to tell whether the parent is able to distinguish between her own and foreign fry. Her response is to take as many fry into her mouth as quickly as she can. On one occasion in which foreign fry were introduced into a brood by a diver they were apparently recognized by the *H. fenestratus/taeniolatus* parent and shepherded away from the native brood. The introduced fry, which were not identified, were light in colour and without markings, whereas the native fry were blotched like their parent and readily distinguishable.

Young fry appear unspecific about the recall stimulus to which they respond (Baerends & Baerends-Van Roon 1950; Ribbink 1971), so much so that divers are able to induce broods to clump together and enter a cupped hand which is moved in a manner which simulates the parent's recall movements. Such a lack of specificity in very young fry suggests that at that early age they will readily accept any parent which summons them. As fry become older they apparently learn to recognize their parent to which they respond with alacrity and may even swim some distance to meet her. Concomitantly one finds that their response to simulated recall movements becomes weaker.

In general, different species of parental fish show characteristic preferences for different types of site in which to release their broods. *H. taeniolatus/fenestratus* and *H. kiwinge* normally select fairly exposed areas on or near the top of rocks. *H. macrostoma/maculiceps, H. polystigma, H. polyodon, H. fuscotaeniatus, H. livingstonii* and *S. robustus* are usually found in areas sheltered by a rock wall on at least one side, while *H. polystigma* and *H. rostratus* may be found with broods over both sand and rock. When over sand (three sightings) parental *H. polystigma* were found to use deserted *Sarotherodon* nests in which to guard their young. *S. robustus* were also found guarding fry among *Vallisneria* weed on two occasions. All of the remaining species listed in Table 1 were found in the intermediate zone (sand mixed with rock: Fryer 1959a) where they chose areas with rocky cover.

Although a full history of parental care from the first release of fry to the eventual disintegration of the parent-offspring bond has not yet been observed in any species in Lake Malawi, it is possible to piece together evidence to produce a picture which may have general applicability. Parents select a site from which they chase all other fish and once established in their defended area (territory) they release the fry.

It appears that once a locus is selected the parent and fry remain at that site for a long time, probably the entire period of parental care. On a number of occasions groups of fry were discovered in the care of their parent at exactly the same site for a week or longer (*H. macrostoma/maculiceps* 11 days, *H. kiwinge* nine days, *H. rostratus* and *H. taeniolatus/fenestratus* seven days). As these various observations were of offspring at different stages of growth

it is suggested that the tendency to stay at a particular site is a feature of the parental behaviour of all species of Lake Malawi mouthbrooders which care for their fry. In the case of *H. macrostoma/maculiceps* parental duties may continue for about a month by which time the offspring are about 35 mm S L.

It seems particularly important that young fry should remain near the centre of the defended area if they are to gain the protection afforded by its sanctuary. Fry which remain in or return to predetermined areas when scattered will be found easily and rescued rapidly by their mother. Indeed, on every occasion that fry were disturbed by divers they formed schools which showed a powerful tendency to return to the defended area where their parent would gather them. Thus, both parent and progeny need to acquire a knowledge of the locality and it is possible that young fry learn to recognize their immediate environment before they learn to recognize their parent. In their early free-swimming days, survival of the fry is dependent on their ability to recognize and stay on the selected site, especially when the parent chases away intruders, grouping together when the mother is defending the site so that they are prepared for collection, and responding with immediacy to the recall movements. At this stage recognition of the parent is not essential as the chance of any fish other than the parent performing a recall within the protected area is remote. It is suggested that early imprinting may be on features of the locality rather than on a parent. Later, as fry grow and become more mobile, they are better able to recognize their parent and are less responsive to artificial recall stimuli as presented by divers.

All parental fish studied in Lake Malawi to date appear to stay at a preselected site with their broods but *Pseudocrenilabrus philander* Weber, a cichlid found in many fresh waters of Southern Africa, carries its fry from one site to another in order to remain in warm water (Ribbink 1975). Water temperatures in Lake Malawi are both warmer and more constant (Eccles 1974) than those in which *P. philander* were studied and therefore migratory response to temperature gradients may be unnecessary.

Origin of mixed broods in Lake Malawi

There are probably several ways in which broods might become mixed. It is believed that these are largely accidental or chance occurrences and that the fry which acquire foster parents are adapted to take advantage of opportunities which enable them to join other broods. There seems little doubt that foreign fry benefit from associations with the foster parents. It seems probable that fry of species which apparently do not guard their young (e.g. *H. chrysonotus*) and fry of species which show strong parental behaviour (e.g. *H. taeniolatus/fenestratus*) will become incorporated into mixed broods in different ways.

Introduction of non-protected fry

It appears that when *H. chrysonotus* fry are ready to be released the parent carries them away from the shoals of brooding females in surface waters down to the substrate. Although brooding fish have been followed on eight occasions when they left the surface schools, and although *H. chrysonotus* and other similar species of utaka, carrying well-developed fry in their mouths, have been observed on innumerable occasions among rock, over sand and in weedbeds, we have never found any utaka caring for a brood of free-swimming fry. Furthermore, unattended schools of utaka fry have been found frequently among rocks. This evidence suggests that *H. chrysonotus* and related utaka take their young to the bottom where they release them to fend for themselves.

An examination of eggs and fry taken from several species of utaka caught at Likoma Island showed that they are extremely large; indeed eggs from an undescribed species referred to as *Nguwa* by fishermen at Likoma Island had a mean length of 6,1 mm and a mean diameter of 4,6 mm (n = 31). (Specimens of *Nguwa* have been lodged in the JLB Smith Institute of Ichthyology, Rhodes University, Grahamstown.) These are the largest eggs laid by any cichlid in Lake Malawi. The next largest are those laid by *Labeotropheus fuelleborni* Ahl (6,0 × 4,0 mm: Fryer 1959a) and *H. chrysonotus* (5,8 × 4,4 mm). The size of these eggs is particularly noteworthy as *L. fuelleborni* and the utaka species are relatively small fish with females that seldom exceeds 12 cm S L. Many larger species of cichlid, including species of *Sarotherodon* (= *Tilapia* which are mouthbrooders: Trewavas 1973), lay eggs which are considerably smaller (Fryer & Iles 1972 p.107). Large eggs produce large fry and those of *Nguwa* taken from the parent's mouth shortly before they were ready to be released measured 17,6 mm S L (n = 36), while those of *H. chrysonotus* were 13,7 mm S L (n = 28). It is argued (Fryer 1959b; Fryer & Iles 1972) that cichlids which lay a few large eggs do so in order to produce young which are better able to care for themselves under conditions where predatory pressure is high as it is on the rocky shores of Lake Malawi.

After being released among the rocks the fry move around in small groups, avoiding predators and feeding independently. They may find their way into protected broods as a result of a tendency to school. Many young cichlids, including most species of *Haplochromis*, form schools when groups of different species but of similar size come together. This behaviour which results in fry of one species, such as *H. chrysonotus*, mingling with other groups of similar size regardless of species, could enable them to mix with a brood in the care of its parent and accordingly gain protection from foster parents. If this surmise is correct, then those *H. chrysonotus* fry which do not find a surrogate parent would remain unprotected and have reduced chances of survival. Clearly, evolutionary selection pressures would favour large well-developed fry which found foster parents and responded correctly to their signals.

The merging of two broods was observed on an artificial reef at Khuyu Bay, Likoma Island in August 1978. A group of 21 unattended, unidentified fry joined a brood of about 40 *H. fenestratus/taeniolatus*. The mixed brood was guarded by the parent which attempted to retrieve all individuals when divers disturbed her. But she was unable to accommodate all fry so that about 14 individuals were omitted, of which 6 − 8 were native fry. Both species of fry tried to squeeze into the parent's mouth. After a period of seven minutes all fry were released again and the mixed brood was still together about 90 min after this release. The following day the brood was still mixed but the number of individuals was reduced to about 40, of which seven

belonged to the foreign species. The missing fry may have moved elsewhere or they may have been lost to predators during the night when they may not have found shelter in the parent's mouth.

Introduction of protected fry

The fry of *H. chrysonotus* and other closely related utaka may enter broods of surrogate parents as a consequence of a tendency to school. Such a mechanism could account for the way in which *H. fenestratus/taeniolatus, H. macrostoma/maculiceps* and *H. kiwinge* join other broods but it does not explain how they become divorced from their parents originally. Unlike *H. chrysonotus* these other species are known to have a well-developed phase of protective behaviour. Accordingly their fry stay in discrete groups which are localized in prescribed sites and which respond with alacrity to parental recall. With the exception of *H. fenestratus/taeniolatus* all the other species are large enough to defend their broods against almost all other cichlids in the lake, so chances of desertion are remote, especially as parental behaviour is strongly entrenched in these species. McKaye and Mckaye (1977) found that pairs of substrate spawners in Lake Jiloa, Nicaragua, were close enough to have their broods intermingle. In Lake Malawi, however, we never found broods that were close enough to become mixed due to overlapping of the areas occupied by respective broods. Indeed it is unlikely that parents would tolerate neighbours which are close enough for such a mixing of broods to occur. Thus the formation of these mixed broods remains largely unexplained.

An incident in which *H. kiwinge* fry were separated from their parent may give a clue to the origin of mixed broods of this type. A homogeneous brood of approximately 80 young *H. kiwinge* fry estimated to be 15 mm S L were found in the care of their parent. In order to gauge the response of the fry to artificial recalls, the parent was chased off by a diver. When the diver eventually backed away, but before the parent returned, the brood was attacked by three *Melanochromis* (*Pseudotropheus*) *auratus*, two *Melanochromis melanopterus*, three *Pseudotropheus tropheops*, a *Pseudotropheus elongatus*, a *H. macrostoma/maculiceps* and two other *Haplochromis* spp.

This attack fragmented the brood so that small groups of fry were chased in a number of different directions while other adult mbuna and *Haplochromis* joined in the chase. Under these circumstances it appeared impossible for the fry to dodge back to the protected site which was on top of a large exposed rock. One group of fry was seen to flee for about 6 m before it was lost to view. Many of the young were caught and eaten. The parent arrived back rather too late to rescue its young. This particular brood fragmentation was the direct result of interference by a diver in the normal guarding behaviour of a parent. It is possible, however, that a simultaneous attack from a number of predators while the parent is away chasing an intruder could cleave a small group of fry from a brood and chase it from the protected site. Many of these young would be lost, but a few might survive to find their way into the broods of foster parents. This would be consistent with the observation that the majority of mixed broods contain a very small proportion of foreign fry (Fig. 1). It is also possible that native fry which would normally remain with their parent are displaced by foreign individuals and while unable to find shelter in the parent's mouth they are forced to go elsewhere by predators which separate them from their parent. These may eventually attach themselves to another brood.

Nature of mixed brood relationships

It was suggested that *H. chrysonotus* might be cichlid cuckoos in the sense that foster parents guard their young (Ribbink 1977). Although a complete parallel between avian cuckoos and those cichlids whose young are cared for by surrogate parents is not possible, a number of parallels exist which justify the retention of the term cichlid cuckoo. Adult cichlids have never been observed to deposit their young with foster parents. Indeed it is unlikely that a brooding adult would be allowed near enough to a guarding parent to mix the broods. It is more likely that foreign fry find their own way into mixed broods and in this manner become social parasites. Cichlid cuckoos have not been found to actively destroy the host's offspring, which is the practice of bird cuckoos, but foreign fry might be directly responsible for the loss of host fry which they displace and leave unprotected. Clearly if foreign fry scramble into the limited space of a protective mouth before native offspring, then the chances of the foster parent losing some of her young to a predator are increased. Thus foreign fry of maternal mouthbrooders in Lake Malawi are cuckoos in the sense that they gain protection from the foster parent and in doing so they may exclude host offspring at some cost to the parent.

While foreign fry are probably unwelcome guests of mouthbrooders, this is apparently not the case among certain substrate spawners in Lake Jiloa, Nicaragua. McKaye and McKaye (1977) found that *Cichlasoma citrinellum* readily adopted broods of conspecifics and on occasion appeared to kidnap fry to add to their broods. Broods of mixed species were also commonly defended by pairs of substrate spawners in Lake Jiloa and it was suggested that additions of foreign individuals to these broods may be advantageous to the host as adopted fry may be eaten before their own. This would be especially true if the additional fry are sufficiently different from those of the host to be singled out more easily by a predator.

Also in Lake Nicaragua, McKaye (1977) found a herbivorous fish, *Cichlasoma nicaraguense*, which cared for the progeny of one of its predators, *Cichlasoma dovii*. It was suggested that this altruistic behaviour may be repaid at a later date when *C. dovii* preyed upon another species of herbivorous cichlid which competed with *C. nicaraguense* for the same natural resources.

Mixed broods occur far more commonly than was originally supposed and have been reported from Sri Lanka (Ward & Wyman 1975), from Africa (Burchard 1967; Ribbink 1977) and from Nicaragua (McKaye & McKaye 1977; McKaye 1977). In Lake Malawi mixed broods containing two or more species are found more frequently than initially expected. Indeed, it is possible that all species of cichlid which guard their broods in Lake Malawi may occasionally have foreign fry mingle with their native offspring. Similarly the tendency for fry of many species to school with other fish, regardless of species, suggests that further research might add substantially to the list of species known to contribute to mixed broods.

Acknowledgement

The support given this work by the Governments of South African and Malawi is gratefully acknowledged. We are also appreciative of the hospitality and facilities afforded us by the Department of Fisheries, Malawi.

References

BAERENDS, G.P. & BAERENDS-VAN ROON, J.M. 1950. An introduction to the study of cichlid fishes. *Behaviour* Suppl. 1: 1–242.

BALON, E.K. 1977. Early ontogeny of *Labeotropheus* Ahl, 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and development. *Envir. Biol. Fish.* 2: 147–176.

BURCHARD, J.E. 1967. The family Cichlidae. In: Fish and Fisheries of northern Nigeria, (ed.) Reed, W., pp. 123–144. Min. Agricult. northern Nigeria.

ECCLES, D.H. 1974. An outline of the physical limnology of Lake Malawi (Lake Nyasa). *Limnol. Oceanogr.* 19: 730–742.

ECCLES, D.H. & LEWIS, D.S.C. 1977. A taxonomic study of the genus *Lethrinops* Regan (Pisces:Cichlidae) from Lake Malawi. Part I. *Ichthyol. Bull. Rhodes Univ.* 36: 1–12.

ECCLES, D.H. & LEWIS, D.S.C. 1978. A taxonomic study of the genus *Lethrinops* Regan (Pisces:Cichlidae) from Lake Malawi. Part II. *Ichthyol. Bull. Rhodes Univ.* 37: 1–12.

FRYER, G. 1959a. The trophic interrelationships and ecology of some littoral communities in 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.

FRYER, G. 1959b. Some aspects of evolution in Lake Nyasa. *Evolution,* 13: 440–451.

FRYER, G. 1977. Evolution of species flocks of cichlid fishes in African lakes. *Z. zool. Syst. Evol. Forsch.* 15: 141–165.

FRYER, G. & ILES, T.D. 1972. The cichlid fishes of the Great Lakes of Africa: Their biology and evolution. Oliver & Boyd, Edinburgh.

GREENWOOD, P.H. 1974. The 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.

ILES, T.D. 1960. A group of zooplankton feeders of the genus *Haplochromis* (Cichlidae) in Lake Nyasa. *Ann. Mag. nat. Hist.* (13) 2: 257–280.

McKAYE, K.R. 1977. Defence of a predator's young by a herbivorous fish:An unusual strategy. *Am. Nat.* 3: 301–315.

McKAYE, K.R. & McKAYE, N.M. 1977. Communal care and kidnapping of young by parental cichlids. *Evolution,* 31: 674–681.

RIBBINK, A.J. 1971. The behaviour of *Hemihaplochromis philander,* a South African cichlid fish. *Zool. Afr.* 6: 263–288.

RIBBINK, A.J. 1975. A contribution to the understanding of the ethology of the cichlids of Southern Africa. Ph.D. Thesis, Rhodes University, Grahamstown, South Africa.

RIBBINK, A.J. 1977. Cuckoo among Lake Malawi cichlid fish. *Nature, Lond.* 267: 243–244.

STOCK, A.D. 1976. The taxonomic status of *Labidochromis joanjohnsonae* Johnson, *Labidochromis fryeri* Oliver and *Melanochromis exasperatus* Burgess. *Buntbarsche Bull.* 55: 14–19.

TREWAVAS, E. 1973. I. On the cichlid fishes of the genus *Pelmatochromis* with proposal of a new genus for *P. congicus:* On the relationship between *Pelmatochromis* and *Tilapia* and the recognition of *Sarotherodon* as a distinct genus. *Bull. Br. Mus. nat. Hist. (Zool.)* 25: 1.

WARD, J.A. & WYMAN, R.A. 1975. The cichlids of the Resplendent Isle. *Oceans Mag.* 8: 42–47.

ZARET, T.M. 1977. Inhibition of cannibalism in *Cichla ocellaris* and hypothesis of predator mimicry among South American fishes. *Evolution,* 31: 421–437.