Environmental Biology of Fishes **47**: 235–254, 1996.

Distribution and breeding biology of offshore cichlids in Lake Malawi/Niassa

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Received 4.4.1995 Accepted 2.2.1996

Key words: Great Lakes, Freshwater, Africa, *Copadichromis*, *Diplotaxodon*, *Rhamphochromis*, Gillnet, Trawl

Synopsis

Lake Malawi/Niassa is the second largest rift valley lake in Africa, with an area of 28 800 km^2, and an average and maximum depth of 292 m and >700 m, respectively. The lake is well known for the great diversity of fish occurring in the inshore zone. However, the offshore fish community is poorly documented. To rectify this, regular sampling was undertaken over two years, using trawl and gillnets at six offshore locations. This paper reports on the species composition, spatial distribution and breeding biology of the dominant cichlids species from the offshore pelagic zone. Cichlids formed approximately 88% of the offshore fish biomass. Most abundant were two species of zooplanktivores in the genus *Diplotaxodon* that made up 71% of the offshore fish biomass. An undescribed species, given the cheironym *D.* 'bigeye', was mainly found at a depth of 220 m during the day, but moved into near surface waters at night when the moon was full. This species was absent from the shallow regions of the lake. The most abundant offshore species was *D. limnothrissa*, which was distributed evenly throughout the lake to depths of 220 m. A less common offshore zooplanktivore was *Copadichromis quadrimaculatus* that formed 5% of the biomass and was confined to the upper 100 m of the water column. The main piscivores were in the genus *Rhamphochromis* and formed approximately 10% of the offshore fish biomass. The two dominant taxa were *R. longiceps* and the 'large *Rhamphochromis*' group, and both were more common in the southern half of the lake. The former occurred mainly in the upper 100 m of the water column and the latter mainly at depths of 100–150 m. The length at maturity and fecundity for the dominant offshore species were estimated and seasonal breeding cycles determined from gonad activity and gonado-somatic indices.

Introduction

Lake Malawi/Niassa lies at the western arm of the East African Rift Valley between 9°30′ S and 14°30′ S. This large freshwater lake, bordered by Malawi, Mozambique and Tanzania, is approximately 550 km long, has an average width of 55 km. The maximum depth is over 700 m and >80% of the lake area is over 200 m deep. The lake has a barrier to vertical mixing occurring at ca. 230 m depth, which also approximates to the oxic-anoxic boundary layer. There is a thermocline at a depth of 50–125 m that is strongly established in the hot wet season (November-February), but is weakened considerably during the cooler windier season (June-September) (Eccles 1974, Patterson & Kachinjika 1993). Primary production is highest in the shallow waters at the southern end of the lake, where deep nutrient-rich water upwells into the euphotic zone (Eccles 1974). The south-east arm of the lake supports productive fisheries, based largely on cichlids (Tweddle & Magasa 1989). These stocks are exploited by a variety of artisanal and semi-commercial fisheries, and by commercial trawlers, and are now believed to be fully- and probably over-exploited (FAO 1993). Other small scale inshore fisheries occur all around the lake, usually within 4 km of the shoreline, where a variety of methods are used to catch cichlids, cyprinids and catfish.

The fish inhabiting the offshore pelagic waters do not support an existing fishery and they have not been subject to detailed study. They belong to four families: the Cichlidae, Cyprinidae, Clariidae and Mochokidae. Notably absent are the Clupeidae and Centropomidae, that form the pelagic fishery in L. Tanganyika (Coulter 1991a).

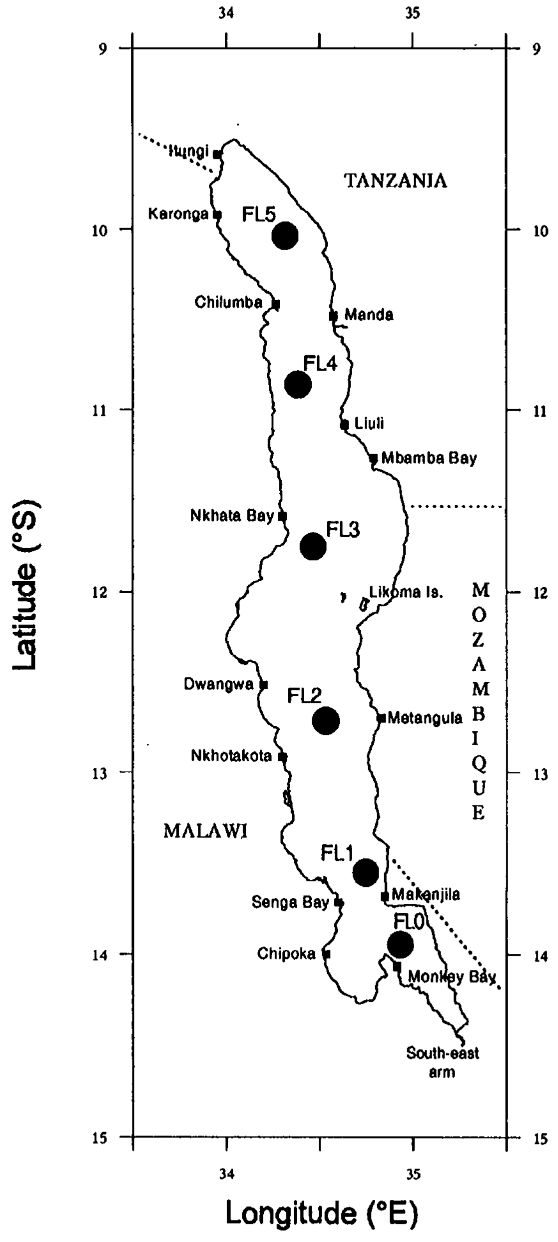

Fig. 1. Chart of Lake Malawi/Niassa showing main coastal towns in Malawi, Mozambique and Tanzania. Fishing locations are shown by closed circles.

A survey of the waters in central L. Malawi in 1978–1981 appeared to confirm that L. Malawi has few offshore pelagic cichlids. Turner[1] and Walczak[2] noted that total catches in a purse-seine net declined rapidly from 0.5–7.4 km offshore off Nkhata Bay, owing largely to a reduction in catches of *Copadichromis* spp. This reduction in fish catches probably occurred within 3.7 km of the shore, as Rufli[3] found no difference in overall fish abundance off Nkhata Bay in acoustic transects and gillnet samples taken from 3.7–25.9 km offshore. Catches in a purse-seine that sampled the upper 55 m of the water column were comprised, by weight, of *Copadichromis (= Haplochromis) quadrimaculatus* (72.1%), *Opsaridium* spp. (Cyprinidae) (10.5%), *Rhamphochromis* spp. (8.2%), *Engraulicypris sardella* (Cyprinidae) (7.6%), and catfish (1.5%). The

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[1] Turner, J.L. 1982. Analysis of purse seine and gillnet catch data off Nkhata Bay, Lake Malawi, from March 1980 to April 1981. pp. 154–162. *In*: Biological Studies on the Pelagic Ecosystem of Lake Malawi, FI:DP/MLW/75/019, Tech. Rep. 1, FAO, Rome.

[2] Walczak, P.S. 1982. Feeding habits and daily food consumption rates of the major pelagic fish species of Lake Malawi. FI:DP/MLW/75/019, Field Doc. 25: 1–19, FAO, Rome.

[3] Rufli, H. 1982. Seasonal abundance and depth distribution of pelagic fish off Nkhata Bay. pp. 117–137. *In*: Biological Studies on the Pelagic Ecosystem of Lake Malawi, FI:DP/MLW/75/019, Tech. Rep. 1, FAO, Rome.

catch composition by weight in night-set gillnets set vertically from the surface to 160 m, was *Rhamphochromis* spp. (35.9%), *Bathyclarias* spp. (Clariidae) (17.5%), *Diplotaxodon argenteus* (16.9%), *Copadichromis* spp. (11.2%), *Opsaridium* spp. (7.9%), and others (10.6%) (Turner[1]). Vertical distribution studies by Rufli[3] showed that fish were fairly evenly distributed over the 20–120 m depth range in gillnet atches, and that fish were observed on acoustic traces down to 230 m with the highest concentrations in the 30–180 m depth range. However, Turner[1] and Walczak[2] observed a decline in gillnet catches with depth, with highest catches in the top 30 m, decreasing steadily down to 160 m; the maximum depth sampled. Rufli[3] found acoustic traces of fish down to the limits of dissolved oxygen at ca. 230 m, which suggests that netting to this depth would be necessary to study the offshore fish community.

This paper reports the results of trawl and gillnet surveys carried out over two years at six offshore locations distributed along the north-south axis of the lake. The abundance and size-range of offshore cichlid species from near surface to 220 m during the day and night is presented. Breeding cycles are examined for common offshore species and fecundities of major species determined.

Materials and methods

Sampling gear

A small 100 HP four-panel semi-pelagic trawl was deployed from the project's 15 m catamaran research vessel, *R/V Usipa*, at 1.5–2 m s^{-1}. All four panels of the trawl were identical, with a headline length and vertical height of 6 m. The mouth opening during operation was approximately 4 × 3.5 m. Mesh sizes ranged from 150 mm stretched in the wings to 38 mm stretched in the main body of the net, with an 18 mm mesh cod end and a 4 mm mesh liner. A cover of 36 mm mesh protected the cod end. Two 1 m^2 doors were attached to the net with 20 m bridles, with 30 kg of weights hung from either end of the foot rope. 700 m of 12 mm wire cable was wound on to each of the two main winches.

Mono-filament nylon gillnets of 50 m length by 6 m deep were used, with floating headlines and leaded foot-ropes giving slight negative buoyancy. Each net consisted of six randomly arranged 8.15 × 6.00 m panels of mesh sizes 20, 32, 50, 86, 134 and 180 mm stretched (Regier & Robson 1966). A 50% hanging ratio was used to give square-shaped meshes. The nets were fished as a fleet and connected by hanging ropes. Six nets were set at most fishing locations, giving a total net area of 1800 m^2, with net headlines at 3, 30, 60, 100, 150, and 220 m to cover the depth range of the pelagic fish (Allison et al. 1994). There was sufficient depth of water to set only five nets at FL1 and four nets at FL0 (Fig. 1). The nets drifted upto 2 km over a 6–12 h set, as nets were not anchored.

Survey design

Fish were sampled at five deep water fishing locations along the north-south axis of the lake, with a

Table 1. Details of fishing cruises undertaken by *R/V Usipa* with the number of locations sampled by the trawl and gillnets.

Cruise dates	Cruise name	Trawl samples	Gillnet samples
31.3.92–7.4.92	April 1992	3	5
15.6.92–30.6.92	June 1992	5	5
26.8.92–2.9.92	August 1992	5	5
10.11.92–17.11.92	November 1992	5	5
3.2.93–9.2.93	February 1993[a]	6	6
18.5.93–25.5.93	May 1993[a]	6	5
4.8.93–11.8.93	August 1993[a]	6	6
28.10.93–3.11.93	October 1993[a]	5	6

[a] Includes an additional fishing location in the south-east arm.

sixth location in the south-east arm added for the 1993 cruises. The fishing cruises were undertaken from the *R/V Usipa* and required about 8–10 days for completion. The same fishing locations were sampled on each cruise: these were 13°57′ S 34°56′ E (FL0), 13°33′ S 34°45′ E (FL1), 12°43′ S 34°32′ E (FL2), 11°45′ S 34°28′ E (FL3), 10°52′ S 34°23′ E (FL4), and 10°02′ S 34°19′ E (FL5) (Fig. 1). The water depth at each location was 110, 170, 310, 430, 580, and 460 m, respectively. Eight fishing cruises were completed during 1992 and 1993, with fish being sampled at each location using trawl and gillnets. Occasionally, due to poor weather or logistic constraints, some sampling could not be undertaken (Table 1). Additional sampling to determine breeding cycles was undertaken at 12°50′ S 34°28′ E on 4–6 February 1992, at 13°32′ S 34°38′ E on 26–27 March 1992, at 13°13′ S 34°38′ E on 15–17 September 1992, at 12°42′ S 34°32′ E on 27–29 October 1992, and at 13°35′ S 34°50′ E on 24–27 August 1993.

The mid-water trawl was fished during the night between 18:00 and 5:00 h. Generally, a deep tow was undertaken at 100–140 m depth followed by a shallower tow at 10–80 m depth. The depth of the net was usually adjusted once or twice during each deployment to sample the depth range more fully. This gave an approximately integrated sample of the fish in the water column. It was only possible to sample to a depth of 30 m for FL0, FL4 and FL5 during the October 1993 cruise, owing to damaged warps. The duration of each tow was approximately one hour for the first few cruises, which gave low total catches. A tow duration of 4–5 h was used for later cruises.

Gillnets were deployed on all eight fishing cruises, with five fishing locations (FL1–FL5) sampled on the initial four cruises, and an additional location in the south-east arm (FL0) added on the final four cruises. Nets were set during daylight hours between 8:00 and 16:00 h on the first five cruises, and at night on the last three cruises, when the nets were set at dusk (ca. 18:00 h) and hauled just after dawn (ca. 5:30 h). Nets set during the day and night were fished for 6–9 h and 10–12 h, respectively. It was likely that night-set nets also caught fish that were active at dawn. The procedure was slightly different for the initial two cruises, as the method of setting gillnets as a single gang was being developed. This resulted in some lost nets and data from the initial two cruises. No nets were set at FL5 on the May 1993 cruise due to the presence of river-borne debris.

All fish caught in trawl and gillnets were identified and the total length (TL) measured to the nearest 1 cm below. Larger fish were weighed on board; whereas others were sealed in plastic bags and deep-frozen, and weighed within one week of returning from cruises. Occasionally length-weight regression equations were used to estimate catch weights when, for some reason, fish were not weighed.

Monthly samples, from the south-east arm south of 14°15′ S, of *Diplotaxodon limnothrissa* and *Rhamphochromis longiceps*, were obtained from the Maldeco Fishing Company, Mangochi. These fish were caught by the *M/V Crystal Lake* using a pelagic trawl with a 38 mm stretched mesh cod end. *D. limnothrissa* were collected throughout 1992 and 1993, whereas collections of *R. longiceps* commenced in October 1992 owing to earlier difficulties in identification.

Taxonomy

The majority of offshore cichlids belonged to the three genera, *Copadichromis* Eccles & Trewavas, *Diplotaxodon* Trewavas, and *Rhamphochromis* Regan. Brief descriptions of known species in these genera are given in Eccles & Trewavas (1989), but many undescribed species exist. Offshore specimens of *Copadichromis* caught in this study fitted the description of *Copadichromis quadrimaculatus* (Regan) in almost all cases. Occasionally, individuals were assigned to other species, but these identifications were uncertain and are not considered further. The most abundant offshore species was *D. limnothrissa* Turner 1994. It is possible that a second species of *Diplotaxodon* exists that superficially resembles *D. limnothrissa* in appearance but inhabits the deeper offshore zone. These were not separated from *D. limnothrissa* in this study. A second very common undescribed species (or species group?) was given the cheironym *Diplotaxodon* 'bigeye'.

Morphometric studies indicated that most *D.* 'bigeye' occurring in offshore samples belonged to a single species, however, individuals were occasionally found that could not be assigned to this or any described species (Allison et al. 1995b). Specimens of *D.* 'bigeye' are held at the Monkey Bay Research Laboratory, Malawi.

Difficulties were experienced in specific identification of *Rhamphochromis*. Our identification was again based on Eccles & Trewavas (1989), however, Stiassny (1981) and G.F. Turner (personal communication 1994) both believe that there are several undescribed species. The most common *Rhamphochromis* found offshore were small (max. length 25 cm) and slender-bodied, with small, closely-spaced teeth. They resembled Eccles & Trewavas' (1989) description of *R. longiceps* (Günther). A second group of large (max. length 50 cm) deeper-bodied large-toothed *Rhamphochromis* were assigned to the 'large *Rhamphochromis*' group. This group was highly variable, and contained several species, including *R. ferox* Regan, *R. woodi* Regan and *R. lucius* Ahl. These three species could not always be separated by the key in Eccles & Trewavas (1989). A third group of slender, cylindrical-bodied species, with a maximum total length of 30–40 cm, were assigned either to *R. esox* (Boulanger) or *R. leptosoma* Regan.

Analytical methods

Comparisons of catch weights were made with ANOVA tests on $\ln(X + 1)$ transformed data using the multi-variate General Linear Modelling program module in SYSTAT (Wilkinson 1990), which allowed for unbalanced designs. Tukey multiple comparisons tests were used to identify where significant differences lay.

A three-way Model I ANOVA was fitted separately to day-set and night-set gillnet catches. All factors were treated as fixed level categorical variables. The full model for the catch of species s (X_s) at

Table 2. Length (cm) of fish, by species, caught by trawl and gillnet surveys on the *R/V Usipa* for the eight main fishing cruises.

Species		Trawl net	Gillnet
		Mean (range)	Mean (range)
Copadichromis quadrimaculatus		18 (13–20)	18 (16–19)
Diplotaxodon argenteus	>10 cm	15 (10–22)	20 (12–28)
D. argenteus[a]	<10 cm	3 (2–9)	
D. 'bigeye'	>10 cm	15 (10–18)	15 (10–18)
D. 'bigeye'	<10 cm	6 (2–9)	
D. limnothrissa	>10 cm	15 (10–19)	16 (10–18)
D. limnothrissa	<10 cm	3 (2–9)	
D. greenwoodi		24 (22–36)	24 (14–35)
Diplotaxodon spp.[b]		16 (6–22)	21 (16–24)
Oreochromis lidole[c]		28 (21–33)	
Rhamphochromis brevis		31 (29–32)	
R. esox			40 (19–49)
'Large *Rhamphochromis*'		35 (9–50)	41 (16–49)
R. leptosoma			31 (22–36)
R. longiceps[d]	>10 cm	18 (10–31)	18 (10–34)
R. longiceps	<10 cm	7 (2–9)	9
R. lucius[c]		22 (13–38)	41 (38–46)
R. macrophthalmus[c]		14	

[a] Includes a catch of 2387 from one haul in the south-east arm.

[b] Excludes 264 unidentified *Diplotaxodon* juveniles.

[c] Caught at the southern two most fishing locations only.

[d] Specimens above 25 cm were probably not *R. longiceps*.

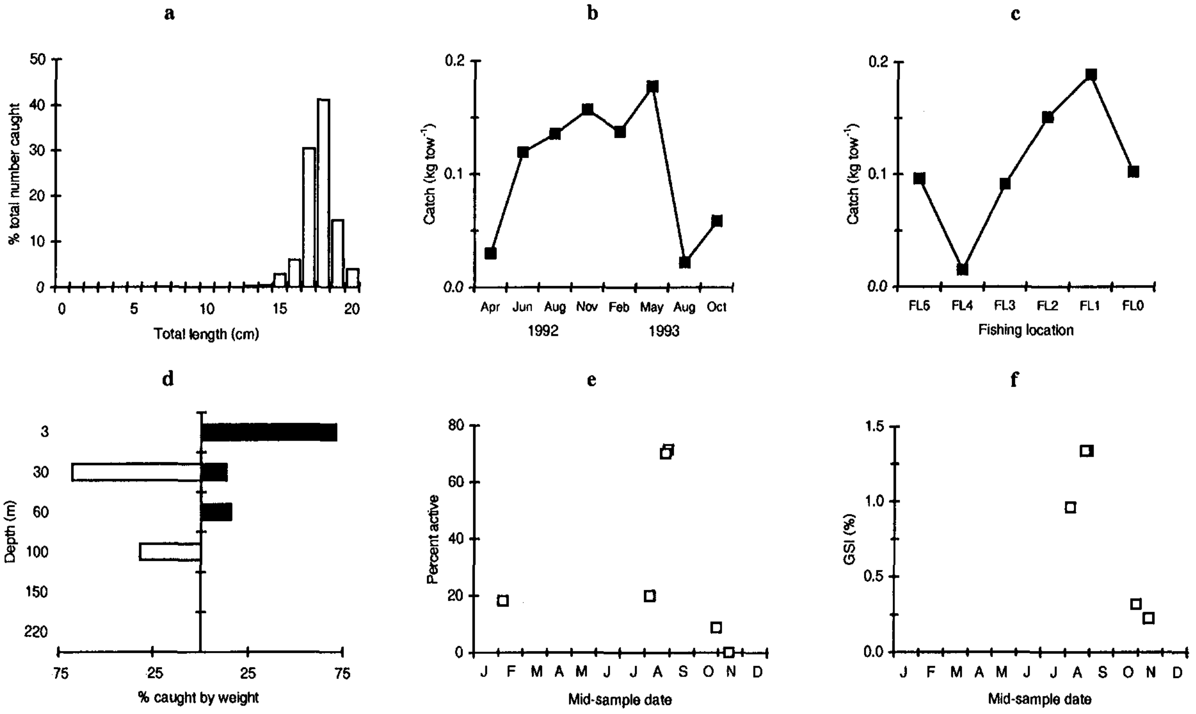

Fig. 2. Statistics for offshore *Copadichromis quadrimaculatus*: a – size range caught by all trawls combined, b – average trawl catch for each cruise combined over all fishing locations, c – average trawl catch at each fishing location combined over all fishing cruises, d – depth distribution during day (open) and night (closed) gillnet catches, e – monthly changes in percent of active gonads from mature females taken from offshore fishing locations, f – monthly changes in the gonado-somatic index from mature females taken from offshore fishing locations.

each depth (A_i), fishing location (B_j), and cruise (C_l) was

$$\ln(X_s + 1) = aA_i + bB_j + cC_l + dA_iB_j + eA_iC_l + fB_jC_l + \varepsilon.$$

FL0 was excluded from the day-set gillnet analyses, as nets were only set there on only one of the five cruises. Estimates of missing values in the three-way tables were made using the method of Shearer (1973). Error degrees of freedom were adjusted to account for missing data.

Trawl catches were standardised to 10 km tow distance and given as kg tow^{-1}. Gillnet catches were combined over all meshes and standardised to a 10 h set and 1 000 m^2 of net area and given as kg set^{-1}.

The vertical distribution of fish in the water column was determined from gillnet catches at the deep fishing locations FL2–FL5 only. Data from the two southern fishing locations FL0 and FL1 were not included as the water depth was less than 220 m. Catches were combined over all sampling dates, locations, and meshes, and expressed as the percentage of the total catch, by weight, in the 3, 30, 60, 100, 150 and 220 m depth nets for either day-set or night-set gillnets.

Breeding biology

Female fish were frozen on board and examined in the laboratory within a few weeks of capture. Gonad maturity of female fish was assessed on the 5-point scale of immature (Stage I), maturing virgin and recovering spent (Stage II), ripening (Stage III), ripe (Stage IV), and spent (Stage V), as detailed by Holden & Raitt (1974). An index of breeding activity was determined by expressing the number of female fish considered to be actively breeding (Stages III and IV) as a percentage of the total

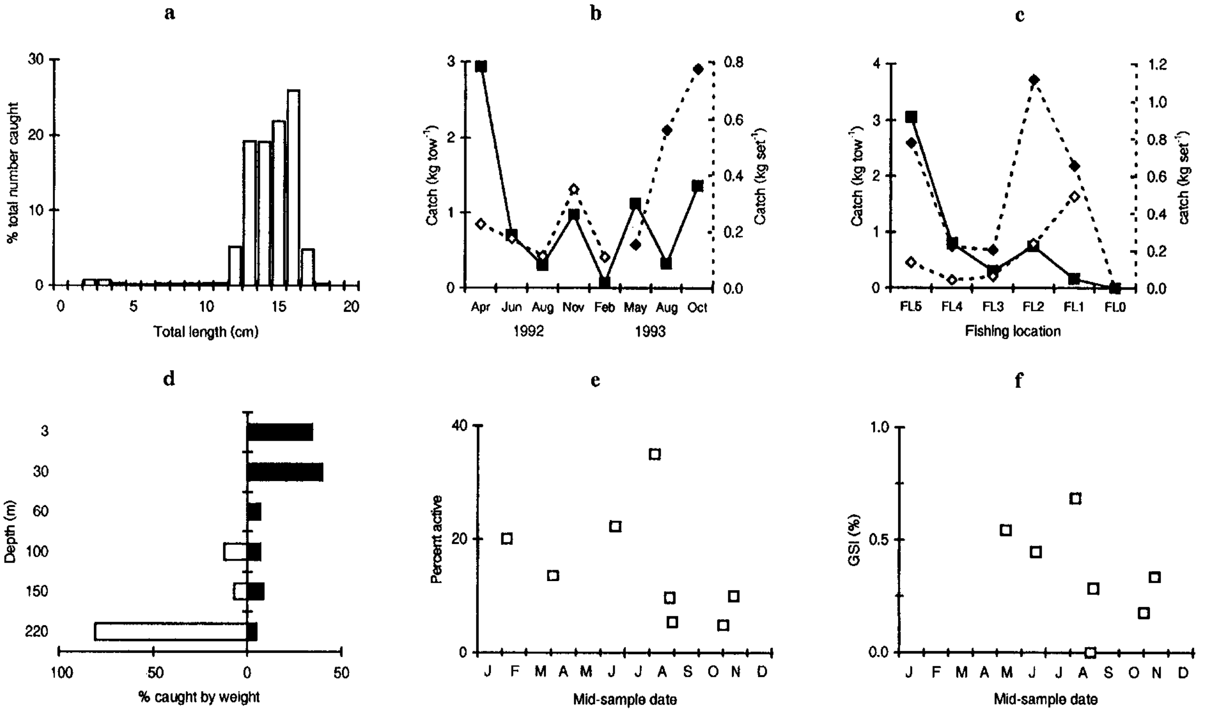

Fig. 3. Statistics for offshore *Diplotaxodon* 'bigeye': a – size range caught by all trawls combined, b – average trawl (closed squares) and day-set (open diamonds) and night-set (closed diamonds) gillnet catches for each cruise combined over all fishing locations, c – average trawl (closed squares) and day-set (open diamonds) and night-set (closed diamonds) gillnet catches at each fishing location combined over all fishing cruises, d – depth distribution during day (open) and night (closed) gillnet catches, e – monthly changes in percent of active gonads from mature females taken from offshore fishing locations, f – monthly changes in the gonado-somatic index from mature females taken from offshore fishing locations.

number of mature female fish caught (Stages II–V) greater or equal to the maximum length of first maturity. Gonads were weighed to the nearest 0.01 g. Total egg counts were made from Stage IV gonads fixed in 4% formalin. Absolute fecundity was the number of eggs in Stage IV female fish, and relative fecundity was the number of eggs kg^{-1} of body tissue. The gonado-somatic index (GSI) of maturation was calculated as the percentage gonad weight relative to body weight excluding the gonads. The indices of breeding activity and GSI were only calculated when ten or more individuals were collected from samples combined over all fishing locations.

The average length at first maturity was estimated graphically, as there was no simple way of assigning Stage II fish to either immature or mature categories. A plot was made of the percentage of fish known to be mature or very nearly mature (Stages III–V), of fish that were definitely immature (Stage I), and of those that could fall into either of the above (Stage II), for each length class. The smallest size at maturity was taken as the minimum size at which a mature fish was found in the population. The maximum size at first maturity was less easy to define, but was taken to be that point when the proportion of Stage II to Stages III–V fish became constant. This assumed that the proportions in each stage reached a constant only when all fish above a certain size were mature.

Results

Catch composition

The species composition of offshore trawl and gillnet catches from FL1–FL5 differed markedly (Ta-

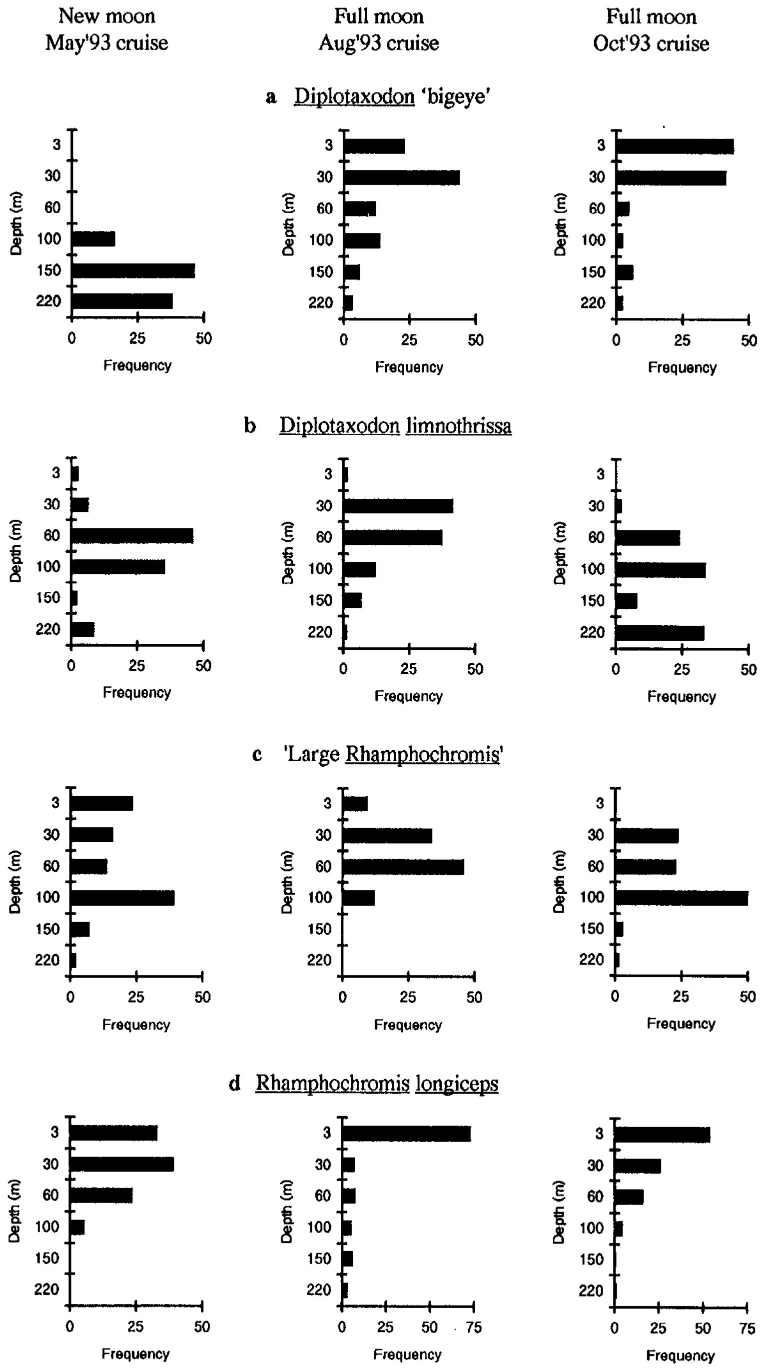

Fig. 4. The depth distribution by percent weight caught of: a – *Diplotaxodon* 'bigeye', b – *D. limnothrissa*, c – 'large *Rhamphochromis*', d – *R. longiceps*; during a cruise coinciding with the new moon and two cruises coinciding with the full moon.

ble 2). Cichlids comprised 88% and 93% of the total catch weight of the trawl and gillnets, respectively, with cyprinids and catfish forming the balance. *Diplotaxodon* formed 71% the trawl catch weight, whereas *Rhamphochromis* formed 85% of the day-set gillnet catch weight. *Copadichromis quadrimaculatus* formed only 5% of the trawl catch weight. *D. limnothrissa* and *D.* 'bigeye' comprised 63% and

31% by weight, respectively, of all trawl caught *Diplotaxodon*. The 'large *Rhamphochromis*' and *R. longiceps* formed 54% and 43% by weight, respectively, of all trawl caught *Rhamphochromis*. The size range of cichlids caught by trawl and gillnets are given in Table 2.

Copadichromis quadrimaculatus

Copadichromis quadrimaculatus ranged in size from 13–20 cm TL with a mean of 18 cm TL (Fig. 2a). Catches were insufficient to allow any analysis of spatial or temporal differences in length distributions. No juveniles were caught in the pelagic waters.

Trawl catches averaged 0.1 kg tow^{-1}, and only a few individuals were caught by gillnets. No significant differences were found in mean trawl catches among cruises ($p > 0.05$) or among fishing locations ($p > 0.05$) (Fig. 2b,c). Gillnet catches were too poor for detailed analysis of vertical distribution, but it is reasonable to conclude that *C. quadrimaculatus* occurred in the upper 100 m of the water column during both day and night (Fig. 2d).

A total of 186 female *C. quadrimaculatus* was available for an analysis of breeding status with numbers from each cruise ranging from 8 to 77. Only a few Stage I females were caught and all were 15 cm TL or less. The average size at first maturity was estimated at 15 cm TL and it is likely that fish above 16 cm TL were all mature. The proportion of females larger than 16 cm in active spawning condition (Stages III and IV) ranged from zero to 70% (Fig. 2e). The GSI reached a maximum of 5% in individual fish, with an average value of 2.9% body weight for Stage IV females. The low offshore abundance often resulted in too few individuals being available to give reliable breeding indices in some months. However, there appeared to be a peak of breeding around August and September when both the percent active females and GSI were high (Fig. 2f). The sex ratio of adults did not differ significantly from unity ($p > 0.05$). The fecundity of ten fish of 17–20 cm total length averaged 50 eggs per fish with a relative fecundity of 650 eggs kg^{-1}.

Diplotaxodon 'bigeye'

Diplotaxodon 'bigeye' in the trawl catch were divided into 2–9 cm and 10–18 cm total length groups. Mouth-brooded juveniles of 2–4 cm TL were identified as *D.* 'bigeye' only during the second year of sampling (Fig. 3a), and occurred throughout the deep waters of the lake north of FL1. Unidentified *Diplotaxodon* juveniles were caught during 1992 and many could have been *D.* 'bigeye'. The adults grew to a maximum of 18 cm TL with a mean of 15 cm TL.

D. 'bigeye' was distributed throughout the offshore waters, with an average trawl catch of 0.8 kg tow^{-1}, and 0.2 and 0.5 kg set^{-1} for day-set and night-set gillnets, respectively (Fig. 3b). Significant differences in trawl catches occurred among cruises ($p < 0.05$) and among fishing locations ($p < 0.01$). Catches of *D.* 'bigeye' were high in the April 1992 cruise and low in the February 1993 cruise, but were similar in other cruises. Gillnet catches differed significantly among cruises for night-sets only ($p < 0.01$),

Table 3. The effect of the phase of the moon on trawl catches of *Diplotaxodon* 'bigeye' from the upper 50 m and upper 80 m of the water column. Catch data were apportioned into nights that were 0–6 days either side of the full moon and nights that were 11–15 days either side of the full moon. The latter category represented the new moon period.

Depth zone fished (m)	Days from full moon	Catch (kg per 10 km trawlline)			Statistics
		n	$\bar{x}$	se	
10–50	0–6	25	0.51	0.28	$t = 2.0$
	11–15	9	0.04	0.03	$p = 0.05$
10–80	0–6	30	0.65	0.31	$t = 1.3$
	11–15	20	0.80	0.47	$p > 0.05$

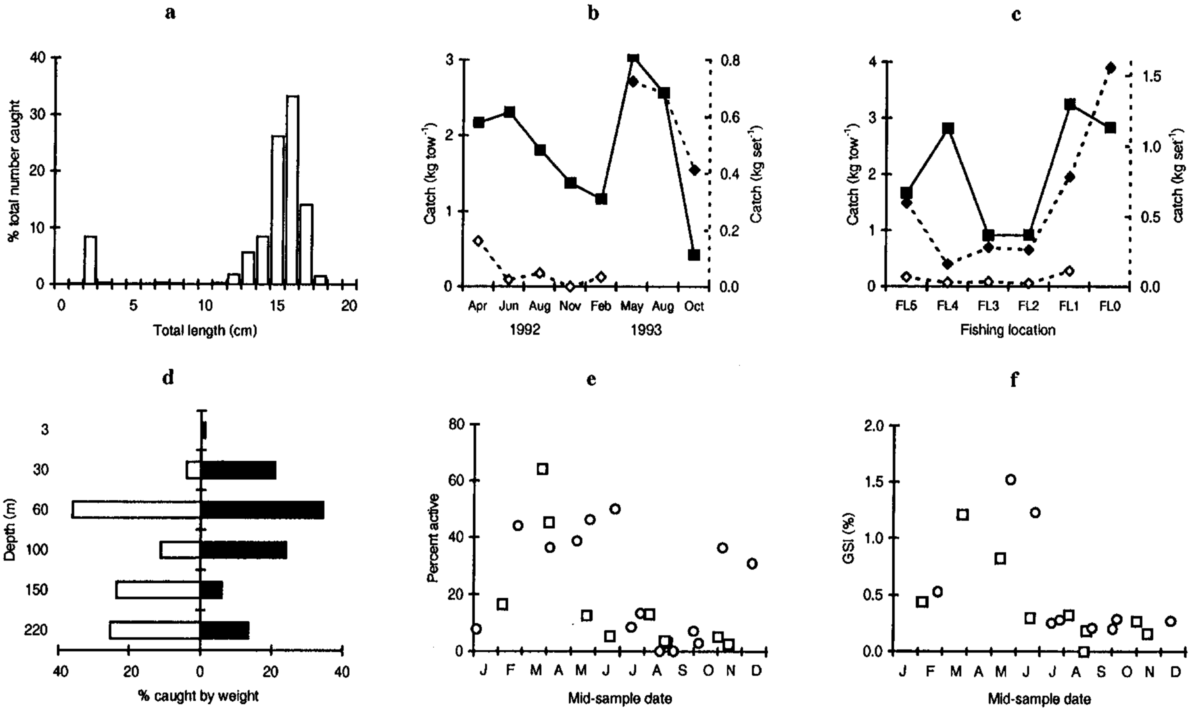

Fig. 5. Statistics for *Diplotaxodon limnothrissa*: a – size range caught by all offshore trawls combined, b – average trawl (closed squares) and day-set (open diamonds) and night-set (closed diamonds) gillnet catches for each cruise combined over all fishing locations, c – average trawl (closed squares) and day-set (open diamonds) and night-set (closed diamonds) gillnet catches at each fishing location combined over all fishing cruises, d – depth distribution during day (open) and night (closed) gillnet catches, e – monthly changes in percent of active gonads from mature females taken from offshore fishing locations (squares) and an inshore location in the south-east arm (circles), f – monthly changes in the gonado-somatic index from mature females taken from offshore fishing locations (squares) and an inshore location in the south-east arm (circles).

and were due to movements of fish into near surface waters when there was a full moon, as reported below, rather than any real temporal changes in abundance. Both day-set and night-set gillnets showed a significant difference in catches among fishing locations ($p < 0.001$ and $p < 0.01$, respectively, Fig. 3c). Catches in the trawl and day-set gillnets indicated a low abundance in the central region. Trawl catches were highest in the north at FL5, and lowest in the south at FL1. Day-set gillnet catches were highest at FL1 and FL2 in the south, and lower in central and northern areas. No *D.* 'bigeye' were caught in the south-east arm at FL0. It is not known why gillnet catches showed a marked increase at FL1 and FL2, whereas trawl catches in this region showed no similar increase. There were no records of *D.* 'bigeye' from samples collected south of 14°15′ S by the Maldeco Fishing Company.

The vertical distribution of *D.* 'bigeye' was studied using gillnets set at FL2–FL5. Day-set catches from 25 sets between April 1992 and February 1993 showed that *D.* 'bigeye' were always deep during the day at 100–220 m, with 81% being caught in the net set at 220 m (Fig. 3d). Night-set gillnets for the May 1993 cruise were set approximately two days before a new moon and caught *D.* 'bigeye' from 100–220 m only. The August 1993 and October 1993 cruises were both within a few days of the full moon and caught 78% of *D.* 'bigeye' in nets set at 3 and 30 m below the surface (Fig. 4a). Support for *D.* 'bigeye' occuring in the surface waters at night was obtained from trawl net catches (Table 3). Average trawl catches in the upper 50 m of the water column were significantly different for full and new moon phases ($p = 0.05$), but not from catches in the upper 80 m ($p > 0.05$). Therefore, *D.* 'bigeye' was always

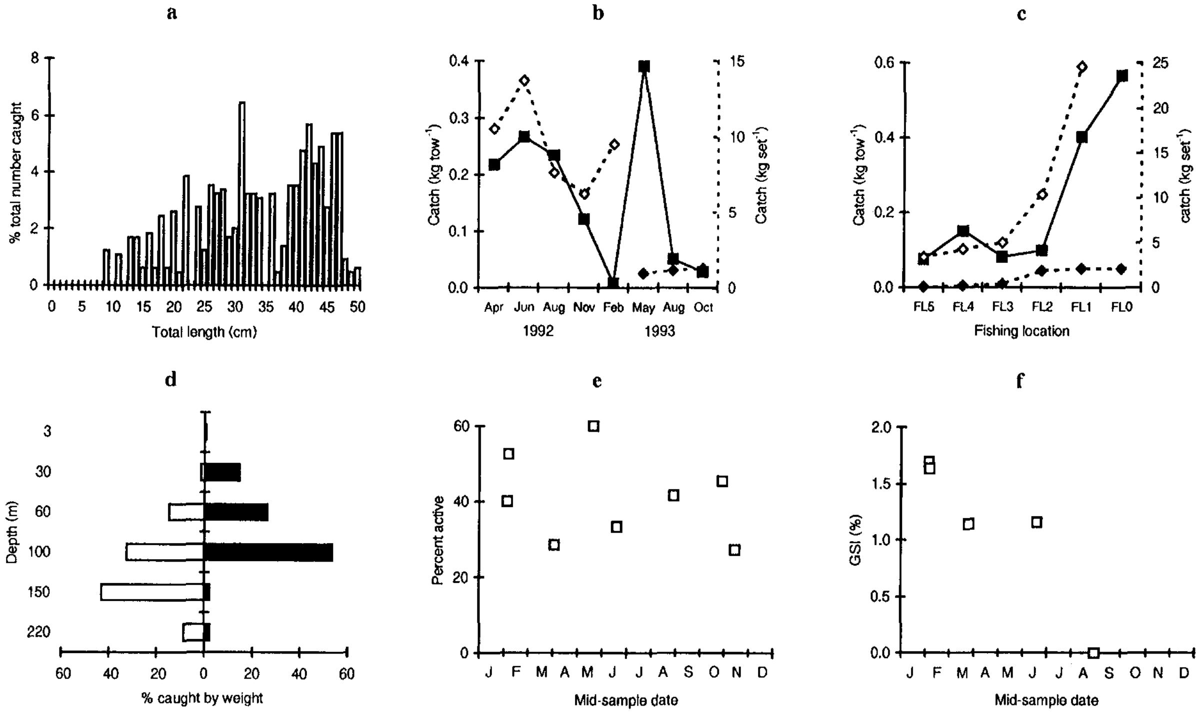

Fig. 6. Statistics for offshore 'large *Rhamphochromis*': a – size range caught by all trawls combined, b – average trawl (closed squares) and day-set (open diamonds) and night-set (closed diamonds) gillnet catches for each cruise combined over all fishing locations, c – average trawl (closed squares) and day-set (open diamonds) and night-set (closed diamonds) gillnet catches at each fishing location combined over all fishing cruises, d – depth distribution during day (open) and night (closed) gillnet catches, e – monthly changes in percent of active gonads from mature females taken from offshore fishing locations, f – monthly changes in the gonado-somatic index from mature females taken from offshore fishing locations.

found deep during the day and relatively deep at night when there was a new moon, but was deep in the day and near surface at night during full moon periods.

All maturity stages of *D.* 'bigeye' were found in 948 females analysed from offshore waters. Mature fish were first seen at 11 cm TL, and by 15 cm TL all females were mature. The average length at first maturity was estimated at 13 cm TL. An average of 14% of female *D.* 'bigeye', above 15 cm TL, were in active breeding condition, and male fish in breeding colours were also recorded. There were no offshore records of *D.* 'bigeye' mouth-brooding eggs, but small numbers of mouth-brooded juveniles were found throughout the year. The GSI for Stage IV ripe females averaged 2.6% body weight, but reached 5% body weight in some individuals. No distinct breeding seasonality was noted in either percent of active females or GSI, although slight increases occurred from July to August. The percentage of active females and average GSI was low, indicating that spawning occurs throughout the year with no distinct synchrony among individuals (Fig. 3e,f). There were, on average, slightly more females than males giving rise to a sex ratio of 1.1:1 ($p < 0.05$). The average fecundity of 17 fish 13–17 cm long was only 24 eggs per fish with a relative fecundity of 602 eggs kg^{-1}.

Diplotaxodon limnothrissa

The average size of adult *D. limnothrissa* caught in the trawls was 15 cm TL, with a range of 10–19 cm TL. Juveniles of 2 cm TL were identified in trawls taken from south of FL2, often in large numbers, with a few tentative records occurring in the central

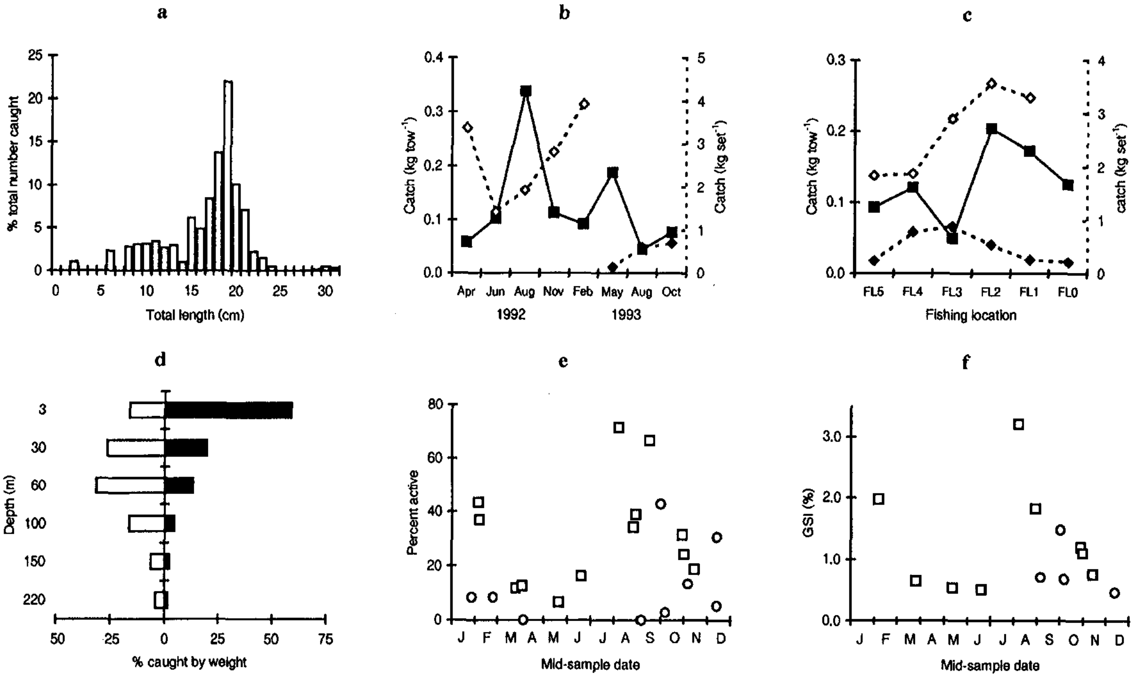

Fig. 7. Statistics for *Rhamphochromis longiceps*: a – size range caught by all offshore trawls combined, b – average trawl (closed squares) and day-set (open diamonds) and night-set (closed diamonds) gillnet catches for each cruise combined over all fishing locations, c – average trawl (closed squares) and day-set (open diamonds) and night-set (closed diamonds) gillnet catches at each fishing location combined over all fishing cruises, d – depth distribution during day (open) and night (closed) gillnet catches, e – monthly changes in percent of active gonads from mature females taken from offshore fishing locations (squares) and an inshore location in the south-east arm (circles), f – monthly changes in the gonado-somatic index from mature females taken from offshore fishing locations (squares) and an inshore location in the south-east arm (circles).

area of the lake. Very few individuals of 4–10 cm TL were caught offshore (Fig. 5a).

D. limnothrissa was the most abundant fish in the trawl with an average catch of 2.0 kg tow^{-1} (Fig. 5b). Trawl catches at the northern and southern two fishing locations averaged 1.7–3.2 kg tow^{-1} whereas catches at the two central locations were around 0.9 kg tow^{-1}. However, there was no significant differences in trawl catches among cruises ($p > 0.05$) or fishing locations ($p > 0.05$). Night-set gillnets caught approximately 13 times more than day-set gillnets (Fig. 5c). Visual examination of both trawl and gillnet catches indicated a slightly higher abundance in the north, lower in the central region and highest in the south and south-east arm.

D. limnothrissa occurred throughout the depth range sampled of 3–220 m, but showed peak catches in gillnets set at 60 m and 220 m (Fig. 5d). There was an upwards movement of approximately 30 m at night, which was not related to the presence of a full or new moon (Fig. 4b). Our impression was that *D. limnothrissa* occupied mainly the upper 100 m of the water column, whereas a probable second species similar in appearance to *D. limnothrissa*, was represented in the gillnet catches at 150–220 m depth. Difficulties in identification, prior to publication of the description of *D. limnothrissa* by Turner (1994), precluded the possibility of separating these two species.

Samples of 1097 and 408 female *D. limnothrissa* were collected from offshore fishing cruises and from inshore sampling in the south-east arm, respectively, for analysis of breeding condition. Immature females were found to 14 cm TL in both areas. The average size at first maturity was 14 cm TL and all females above 15 cm TL were probably mature. There was no difference in average size at maturity for the two regions. Adult female *D. limnothrissa* mouth-brooding juveniles were observed in the south of the lake and into the south-east arm, and females mouth-brooding eggs were occassionally observed in May and September 1992 from FL1 and FL2. The GSI for each maturity stage was also similar for offshore and inshore regions with Stage IV females having an average value of 1.7% body weight, with extreme values reaching 4% body weight. The percentage of females with active overies (Stage III and IV) peaked from May to June at 40–60% and declined to less than 20% from July to October (Fig. 5e). The average GSI in the mature female population showed a similar pattern, with an increase during February and March, through to a peak in June, and followed by a sharp decline to low levels in July (Fig. 5f). This suggests that *D. limnothrissa* spawns around June, which was confirmed by the presence of small juveniles in commercial catches in the south-east arm at this time (Thompson et al. 1995). No difference in the sex ratio was recorded ($p > 0.05$). The fecundity of 49 Stage IV *D. limnothrissa* of 14–18 cm TL averaged 15 eggs per fish with a relative fecundity of 861 eggs kg^{-1}.

'Large Rhamphochromis*' group*

The mean size for the 30 'large *Rhamphochromis*' caught in the trawl was 36 cm TL, with a range of 9–50 cm TL. The majority of these were towards the upper end of the size range, showing an accumulation of older fish in the population (Fig. 6a). *Rhamphochromis* were difficult to identify but most 'large *Rhamphochromis*' could be separated from *R. longiceps* by body shape and size of teeth. Embryo and small juvenile 'large *Rhamphochromis*' could only be identified if in the buccal cavity of mouth-brooding adults and this was rare.

'Large *Rhamphochromis*' were caught in only 21 of 87 trawls undertaken in the routine fishing surveys, and had an overall average abundance of only 0.2 kg tow^{-1} (Fig. 6b). Catches of 'large *Rhamphochromis*' in day-set gillnets were relatively high at 3.4–24.6 kg set^{-1}, according to fishing location, and averaged 9.5 kg set^{-1}. Average catches in night-set gillnets were lower at 1.1 kg set^{-1} and indicated that this large visually feeding piscivore is more active in the day. Day-set and night-set gillnet catches of 'large *Rhamphochromis*' did not differ significantly among cruises, indicating that this group was present in the offshore waters in similar quantity throughout the year. Day-set gillnet catches of 'large *Rhamphochromis*' were significantly higher at FL1 than at the other fishing locations ($p < 0.001$), with night catches also tending to be higher in the southern part of the lake. This was supported by trawl catches, which were also significantly higher at the southern fishing locations FL0 and FL1 ($p < 0.05$). Trawl and gillnet catches showed that 'large *Rhamphochromis*' were three to five times more abundant in the south compared with the northern and central areas (Fig. 6c).

The day and night vertical distribution was determined from gillnet catches for FL2–FL5 combined (Fig. 6d). 'Large *Rhamphochromis*' were deep during the day with 75% of the catch coming from nets set at 100 m and 150 m depth. There was an upwards movement of 30–50 m during the night, with the majority being caught at 60 m and 100 m depth. There was no indication that the night-time vertical distribution of 'large *Rhamphochromis*' was related to the phase of the moon (Fig. 4c).

The length at first maturity was determined from 148 adult females, and 14 unsexed juveniles. No Stage I females were identified. The size at first maturity was 20–25 cm TL. Two males were caught in the trawl with eggs and small juveniles in the mouth, but it was unknown if this was a natural phenomenon. A single record of a female mouth-brooding eggs was recorded from a gillnet set at FL3. The average GSI of Stage IV females was 4% body weight, and reached 6% in some individuals. The percentage of females in active spawning condition was 29–60%, and spawning probably occurred throughout the year (Fig. 6e). Only five GSI were calculated and these were from the first half of the year, and no seasonal spawning pattern could be inferred (Fig. 6f). The fecundity of 18 'large *Rhamphochromis*' of 29–49 cm TL was size dependent and ranged from 130 to 550 eggs per fish. The relative fecundity was 461 eggs kg^{-1}.

Rhamphochromis longiceps

Rhamphochromis longiceps was more commonly caught in trawl and gillnets than 'large *Rhamphochromis*'. The average size in the trawl was 17 cm TL with a range of 2–24 cm TL (Fig. 7a). A few morphologically similar individuals up to 34 cm TL were caught, and probably represent an undescribed species. Small numbers of females mouth-brooding juveniles were caught, but were too uncommon to comment on seasonal occurrence.

The average catch of *R. longiceps* in the trawl was 0.1 kg tow^{-1}, and in the day-set and night-set gillnets was 2.7 and 0.5 kg set^{-1}, respectively (Fig. 7b). There were some conflicting results in the analyses of abundance for trawl and gillnet catches. Trawl catches showed a significant difference among cruises ($p < 0.025$), due to a high catch in the August 1992 cruise, although a high catch was not observed in the August 1993 cruise. There was a significant difference among cruises for day-set gillnets ($p < 0.001$) and for night-set gillnets ($p < 0.01$), however none of the observed differences could be matched with similar changes in abundance seen in the trawl net for the same sampling periods. No significant difference in catch rate among fishing locations was observed in the trawl catches ($p > 0.05$) or in day-set gillnet catches ($p > 0.05$) (Fig. 7c). Catches in night-set gillnets showed that significantly more fish were caught in the central region of the lake ($p < 0.001$). However, night-set gillnet catches overall were low and probably do not reflect abundances as accurately as the other two methods.

The vertical distribution of *R. longiceps* differed during day and night periods (Fig. 7d). The distribution from the surface to 100 m was fairly even, with a slight preference for the 60 m depth zone. There was an upwards movement during the night, with 59% of the biomass being caught in the surface gillnet. Small numbers of *R. longiceps* were recorded to 220 m during both day and night periods. These upward movements were more apparent when there was a full moon (Fig. 4d).

A total of 1333 and 261 *R. longiceps* were collected, respectively, from the offshore fishing cruises and from the inshore sampling in the south-east arm. The minimum, average and maximum estimates of size at first maturity were 14, 17 and 19 cm TL, respectively. The average GSI of Stage IV females was approximately 4.5% in both regions, but some offshore fish had a GSI of nearly 7% body weight. The percentage of females in active spawning condition was slightly lower for fish from the south-east arm and ranged from 0–42%, compared to offshore fish that ranged from 7–71%. There was a higher percentage of mature female individuals with active gonads around August to December for most of the samples taken from both offshore and the south-east arm. Two offshore samples taken in February also had 37% and 43% of females with active gonads, but this was not observed in the south-east arm samples taken around the same period. A period of inactivity occurred from March to June (Fig. 7e). The same pattern also occurred in the GSI (Fig. 7f). It was not possible to see if the GSI of fish from the south-east arm was, on average, lower than the offshore *R. longiceps*, owing to GSI being determined for only four of the south-east arm samples. However, the majority of these south-east arm fish were in an inactive spawning state. Females from offshore had GSI values reaching 1.8–3.2% in January-February and July-August for 1992 and 1993. It appeared that there were two peaks of spawning activity in the offshore waters, but this requires confirmation by more frequent sampling. The fecundity from a sample of 70 fish of 16–25 cm TL was size-dependent. The mean number of eggs was 30–75 per fish with a relative fecundity of 861 eggs kg^{-1}.

Other cichlids

Two other described species of *Diplotaxodon* were caught offshore, as well as several undescribed species. A total of two and 13 individual *D. greenwoodi* were caught offshore in trawl and gillnets, respectively, over two years of sampling. The sizes ranged from 14–36 cm TL, and the gillnet catches were from 100–220 m south of FL3. *D. argenteus* was caught, occasionally in large numbers, south of FL2, with the exception of a singe individual caught at FL5. The size range was 2–28 cm TL, with large numbers of juveniles <5 cm TL caught at FL0 during the May and August 1993 fishing cruises. *D. argenteus* appears to be a semi-demersal fish of the south-east arm. Small numbers of female *D. argenteus* were collected from the south-east arm, and the size at first maturity was 14–19 cm TL. The fecundity of 14 *D. argenteus* of 16–22 cm TL was correlated with fish size, and ranged from 15 to 75 eggs. The relative fecundity was 730 eggs kg^{-1}. There were other *Diplotaxodon* specimens caught, not usually in significant quantity, that could not be assigned to any described species.

Other cichlids were caught sporadically and in small numbers in gillnets and trawl. *R. leptosoma* and *R. esox* were caught at night south of FL3 at 30–100 m and 0–60 m depth, respectively. *R. lucius* was caught south of FL2 only. *Oreochromis* spp. and *Lethrinops* spp. were caught at FL0 in the south-east arm, but not elsewhere and were not considered to form part of the offshore pelagic fish community.

There were other families of fish inhabiting the offshore pelagic zone. Catfish were common and formed upwards of 8% of the biomass. They comprised of the mochokid *Synodontis njassae* that lives deep during the day and moves to the surface at night, and large mainly filter-feeding clariid catfish of the genus *Bathyclarias* that inhabit the upper layers. The cyprinids were represented mainly by *Engraulicypris sardella* that formed an average of only 3% of the offshore pelagic fish biomass during the two years studied, although this species shows high variability in abundance (Tweddle & Lewis 1990). Other cyprinids caught uncommonly offshore were *Opsaridium microcephalum* and *Opsaridium microlepis*. The distribution and breeding biology of the offshore cyprinids and catfish is discussed by Thompson et al. (1996).

Discussion

Cichlid fish in the offshore pelagic zone of L. Malawi form a simple structured community. The number of species is low, with six species, or species groups, forming 88% of the total fish biomass. This contrasts with the inshore littoral and shallow-water cichlid communities of L. Malawi, which are among the most diverse fish faunas in the world with over 500 described species (Ribbink 1987). This relates to the pelagic zone having a more homogenous environment, with depth, distance from shore, and seasonal productivity providing the main gradients. The lack of horizontal boundaries offshore reduces reproductive isolation.

The most significant finding reported here is the extent to which zooplanktivorous cichlids, mainly *Diplotaxodon* species, have adapted to a pelagic mode of life. Previous workers considered cichlids to be confined to near-shore habitats by their reproductive biology, and by their inefficiency as zooplanktivores (Fryer & Iles 1972, FAO[4]). However, in L. Malawi the cichlids occupy most of the pelagic niches, although their low reproductive output prevents them from rapidly increasing their numbers to take advantage of high productivity. This niche is occupied by the pelagic cyprinid *Engraulicypris sardella* (Thompson et al. 1996). Most remarkable is the depth range that cichlids inhabit, with the importance of *D.* 'bigeye' as a major grazer of *Chaoborus edulis* (lakefly) larvae and pupae just above the oxy-anoxic boundary being realised (Allison et al. 1995a). Cichlids have closed swim-bladders, and normally undergo relatively minor vertical movements, whereas cyprinids and catfish have open swim-bladders and their upward vertical movements are less constrained (Thompson et al. 1996). Ribbink (1981) and Marsh & Ribbink (1981) showed that some species of cichlids that normally live in the upper 50 m of the water column can survive a maximum pressure change of 40% in either a negative or positive direction over a period of 12 h. The 'large *Rhamphochromis*' and *D. limnothrissa* move upwards by 50–100 m, experience a pressure difference of less than 50%, and probably within the above tolerance limits. However, our studies on the depth distribution of *D.* 'bigeye' appears to contradict these findings. *D.* 'bigeye' was always recorded from deeper than 150 m and usually at 220 m during the day. However, on two cruises coinciding with the full moon, *D.* 'bigeye' were recorded in the 3 m

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[4] FAO. 1982. Biological studies on the pelagic ecosystem of Lake Malawi. FI:DP/MLW/75/019, Tech. Rep. 1, FAO, Rome. 182 pp.

and 30 m gillnets set at night. The conclusion from this observation is that this species, with a closed swim-bladder, was able to move from around 220 m to within a few metres of the surface, probably within a few hours and vice versa. The predicted change in gas volume for a fish moving from 220 m to, say, 10 m, is 22 times, with the greatest change occurring near to the surface. Arnold & Greer Walker (1992) working on cod *Gadus morhua*, found evidence for fish being negatively buoyant at depth, which allowed them to ascend at a quicker rate that would be predicted if they had been neutrally buoyant. It is still difficult to imagine that *D.* 'bigeye' were neutrally buoyant at about 30 m and yet spent a good proportion of their day at 220 m. An alternative hypothesis, that *D.* 'bigeye' slowly adapts over a full lunar cycle, so that the upward movements would be much reduced when there was a full moon, is rejected; as gillnet catches of *D.* 'bigeye' during the June 1992, November 1992 and February 1993 cruises were all near to a full moon and their mean daytime depth was ca. 210 m. The adaptive advantage of this upward movement coinciding with the full moon allows this visual predator of *C. edulis* to extend its feeding period. Walczak[2] also records evidence for a nightly upwards movement of *D.* 'bigeye' (= '*D. macropthalmus*' nomen nudum of Walczak[2]); which was caught in a purse seine fishing to 55 m below the surface at night, but none were caught during the day. No explanation can be suggested to account for the apparent ability of *D.* 'bigeye' to survive the pressure changes experienced during these vertical movements.

Depth distribution patterns of other cichlid species can also be interpreted in terms of their feeding ecology. *D. limnothrissa* feeds mainly on crustacean zooplankton, and is found mainly at depths of 30–100 m, where prey densities are highest. *R. longiceps* feeds mainly on *E. sardella* larvae, and both inhabit the 0–100 m depth range. The piscivorous 'large *Rhamphochromis*' eat both *D. limnothrissa* and *E. sardella* in the top 100 m of the water column and *D.* 'bigeye' deeper down, and occurred in the 60–150 m depth range.

The abundance of cichlids was not uniform over the lake. Most species had a low biomass in the central zone of the lake around FL3, with a slight increase in the north at FL5, and usually a marked increase in the south at FL1 and the south-east arm at FL0. The higher abundance in the south may be a result of the higher primary production in this area due to the upwelling of nutrient rich water (Eccles 1974). The absence of *D.* 'bigeye' from the shallow regions of the lake, particularly from the south-east arm, is probably due to the distribution of *C. edulis*, which are concentrated at or just below the oxic-anoxic boundary at 200–230 m. High predation by the demersal fish community may confine *C. edulis* to this low-oxygen refuge. *R. longiceps* mainly feeds on crustacea and *E. sardella* larvae when young, but becomes more piscivorous when older and feeds on adult *E. sardella*. The 'large *Rhamphochromis*' are the main piscivorous predators in the lake and feed on adult *E. sardella* and *Diplotaxodon* (Allison et al. 1995a). The particularly marked increase in *Rhamphochromis* in the south of the lake is probably a result of higher concentrations of *E. sardella* in this region (Thompson et al. 1996).

D. 'bigeye' was the most offshore species of cichlid encountered, and with its large eye, is clearly adapted to feed at the low light intensities encountered at 150–220 m depth. Mouth-brooded juveniles of this species were found offshore feeding on *C. edulis* larvae, hence they seem well adapted to a completely offshore existence. The absence of all sizes of *D.* 'bigeye' from the south-east arm suggests this species spawns in water deeper than 100 m, but whether in the deep benthic or bathypelagic zone remains unknown.

D. limnothrissa lacks the large eye characteristic of deeper-water cichlids, and occurred shallower in the water column than *D.* 'bigeye'. It is likely that its preferred spawning location is also in shallower water, but probably still at depths greater than 40 m. Mouth-brooded juvenile *D. limnothrissa* were mostly found south of 12°43′ S in water with a total depth of 50–100 m, with a few tentative records from the deep central zone of the lake. Small juveniles were common in the Maldeco trawl fishery from the south-east arm (Thompson et al. 1995), but are not caught by inshore Kambuzi beach seines (FAO 1993). No aggregation of breeding males were found in demersal trawl surveys, so it is unlikely that this species forms demersal spawning arenas (Turner 1994). *D. limnothrissa* of 10–12 cm TL must return to the offshore pelagic habitat to spend their adult life, presumably to avoid competition for food with inshore cichlids.

The life-history of *Rhamphochromis* species remains more of a mystery. However, the following seems probable for *R. longiceps*. Adults are pelagic and are ripe during January/February and July/September. Small juveniles were rarely caught offshore or by the Maldeco trawl fishery in the south-east arm, but are caught close inshore by Kambuzi beach seines (FAO 1993, personal observations). The evidence suggests that breeding occurs offshore in the pelagic or deep benthic zones, and that the juveniles either swim inshore or are deposited inshore by the female. It appears that once they reach 8–10 cm TL they move into the deeper waters of the offshore pelagic zone to mature.

These studies, and the observations of Turner (1994) on *D. limnothrissa*, suggest that some of the pelagic cichlid species may be able to spawn independently of the bottom of the lake. This is unusual in African cichlids. There appears to be a requirement for most cichlids to be associated with the substrate during breeding (Lowe-McConnell 1987).

The cichlids in the offshore waters, mainly *Copadichromis*, *Diplotaxodon* and *Rhamphochromis*, produce relatively few eggs per female and care for their young in the first few weeks of life by mouth-brooding (Eccles & Lewis 1981). Initially it was thought that all cichlids in L. Malawi were maternal mouth-brooders that spawned on the substrate around a 'nest' that was defended by the male (Fryer & Iles 1972, Eccles & Trewavas 1989), however, it is now realised that some species may be able to spawn in open water (Balon 1977, 1978). Eccles & Lewis (1981) observed, from the jetty at Monkey Bay, males of *Copadichromis* (= '*Haplochromis*') *chrysonotus* in full breeding colours displaying to females in mid-water. The total water depth was less than 10 m and fish could have used a visual cue to a fixed point on the substrate. Males were observed to hold 'mobile' territories within a moving shoal, which they aggressively defended against other males in breeding colours suggesting that substrate cues were transient. The same species was reported by Fryer & Iles (1972) to establish substrate spawning arenas, but Eccles & Lewis (1981) noted that it was unlikely that the same species had contrasting spawning styles and suggested that an erroneous identification may have occurred. Mating in open water 10–30 cm above a rocky substrate has been observed in *Labeotropheus* sp. in L. Malawi (Balon 1977). Another exception in L. Malawi is the non-endemic tilapiine, *Tilapia rendalli*, which is a substrate spawner with eggs and young tended by both parents, but without buccal incubation (Trewavas 1983, Lewis et al. 1986).

Comparisons with cichlid spawning behaviour in other African Great Lakes are instructive. The cichlids of L. Tanganyika represent two main breeding styles (Balon 1975, 1981): substrate tenders or nesters with maternal or biparental guarding of eggs and young at a nest site, and mouth-brooders with buccal incubation by the female and no close association with the substrate although males usually exhibit territorial behaviour (Kuwamura 1986, Coulter 1991b). Coulter (1991b, p. 189) suggests that 'epibenthic spawning' occurs in certain benthic cichlids as spawning takes place above, but probably not very far from, the bottom. In L. Tanganyika, off-bottom spawning has been reported for only three species of cichlid, *Tropheus moorii* (Fryer & Iles 1972), and *Cryprichromis nigripinnis* and *C. leptosoma* (Scheuermann 1976). Four of the seven species of *Bathybates*, which are large-mouthed predatory pelagic or bathypelagic cichlids from L. Tanganyika and occupy a similar niche to *Rhamphochromis* in L. Malawi, have been found with a distended buccal cavity containing mouth-brooded eggs and juveniles (Coulter 1991b). Brichard (1978) believes that there may have been a gradual evolution in L. Tanganyika from substrate tenders to mouth-brooders. This would allow for open-water spawning, but their is no evidence to suggest that mouth-brooding is an adaptation for spawning in deeper water. Kuwamura (1987) found that more than half of the mouth-brooders restricted their distribution to water <5 m deep, whereas substrate tenders had a wider depth preference.

The parallels between the adaptations to an offshore life style in cichlids from L. Malawi and L. Tanganyika are not surprising. However, whereas cichlids of the genus *Rhamphochromis* are the only significant pelagic piscivores in L. Malawi, L. Tanganyika cichlids such as *Bathybates*, morphologically similar to *Rhamphochromis*, have not invaded the pelagic zone to the same extent. The presence of the four predatory *Lates* spp. (including *Lates* (= '*Luciolates*') *stappersi*) is probably the reason why *Bathybates* and zooplanktivorous cichlids have not invaded the pelagic zone in L. Tanganyika to the same extent as cichlids in L. Malawi. It is now well known, from studies in L. Victoria, that cichlid populations are vulnerable to predation and can be annihilated by *Lates niloticus* (Barel et al. 1985, Bruton 1990), with this introduced piscivore having a profound effect on the entire ecosystem through the 'trophic cascade' (Goldschmidt et al. 1993). The 'large *Rhamphochromis*' are the only offshore piscivores in L. Malawi that can feed on adult *Diplotaxodon* and on smaller *Rhamphochromis*, but exert only moderate predation pressure on these groups (Allison et al. 1995a).

Some cichlid fish in L. Malawi show distinct breeding seasons, and these include *C.* (= '*H.*') *quadrimaculatus* (Jackson et al. 1963) and three *Oreochromis* spp. (FAO 1993), many are capable of breeding throughout the year, in which case one or two seasonal peaks are often noted (Marsh et al. 1986, Lewis & Tweddle 1990). Lowe-McConnell (1987) and Coulter (1991b) cite studies that indicate the inshore substrate nesting cichlids of L. Tanganyika have a protracted spawning season, whereas the more pelagic or bathypelagic mouth-brooding cichlids tend to have a short well-defined spawning season. This generalisation does not appear to hold for L. Malawi. The most pelagic of the cichlids, *D.* 'bigeye', shows evidence of spawning activity throughout the year, while the more inshore *C. quadrimaculatus*, *D. limnothrissa* and *R. longiceps* all have distinct breeding peaks. These peaks were around the February-March and August-September periods, but exact details were species dependent.

The dependence on the substrate for reproduction and the perceived inefficiency of the precocious cichlids as pelagic zooplanktivores have been viewed as major barriers to their colonisation of the pelagic zone of L. Malawi (Fryer & Iles 1972, FAO[4], Hecky 1984). However, evidence of open-water spawning in cichlids has come to light, as has the existence of pelagic zooplanktivorous haplochromines in L. Victoria (Goldschmidt et al. 1990) – many species of which may now be extinct due to the pressure of predation by introduced *Lates niloticus* in that lake (Goldschmidt et al. 1993). Some species of *Copadichromis* in L. Malawi are also offshore zooplanktivores (Iles 1971), although most are associated with submerged reefs, where they are able to feed on current-borne zooplankton. However, *D. limnothrissa* and *D.* 'bigeye' are specialised offshore zooplanktivores (Allison et al. 1995a). In the light of data presented here, we must reject Hecky's (1984, p. 439) assertion, refering to L. Malawi, that 'Even the prodigiously speciating Cichlidae have not exploited the deep water pelagic'. The abundance and lakewide distribution of many *Diplotaxodon* and *Rhamphochromis* species provide contrary evidence. Pelagic cichlids exist in L. Malawi.

Acknowledgements

This work was funded by the Overseas Development Administration, U.K., and undertaken in cooperation with the Southern African Development Community states of Malawi, Mozambique and Tanzania. We would particularly like to thank T. Kadzombe from Malawi, F. Amido from Mozambique, and G. Kitila, B. Maige and K. Shindika, from Tanzania, for their assistance with every aspect of this study. We also thank R. Lowe-McConnell for helpful discussions on cichlid breeding styles.

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