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Seasonal and Spatial Patterns of Experimental Trawl Catches in the Southwest Arm of Lake Malawi

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ABSTRACT. *Experimental demersal trawl samples were collected in the same manner at the same sites on a monthly basis over an annual cycle in the southwest arm (SWA) of Lake Malawi. Catch composition in terms of species representation and mass was compared over time and depth (10, 30, 50, 75, 100 and 125 m). The average catch per unit effort was calculated per species and depth. Haplochromine cichlids dominated the catches at every depth, making up 75 to 92% of the biomass. The remainder was made almost exclusively of catfishes. Despite catching more than 140 species in the trawls, 60 to 80% of the catches consisted of ten or fewer species, including three catfishes. About twenty species accounted for 90 to 95% of the catches at any depth, suggesting that many species are uncommon or rare. Previous authors reported dramatic changes in species composition at 50 m in the southwest arm. Data presented here suggest that this might be due to a change in the nature of the substratum at 50 m. The greatest diversity of species is in shallow waters, but the highest catches in terms of biomass were recorded between 50 and 125 m and peaked at 75 and 100 m. As catches in the deep waters were dominated by fishes with favorable life history characteristics and which are large relative to species in the shallow waters (though the largest species of cichlid occur in the shallow water, the catches are dominated by small species), it is recommended that the possibility for increased exploitation of the SWA deep demersal stocks should be explored by encouraging controlled development of a demersal commercial fishery in the SWA .*

INDEX WORDS: *Lake Malawi, cichlids, trawl catches, SWA, catfish.*

INTRODUCTION

African Great Lakes Victoria, Tanganyika, and Malawi are best known in biological disciplines for the species richness of their endemic fishes, most of which belong to the family Cichlidae (Fryer and Iles 1972, Ribbink *et al.* 1983, Ribbink and Eccles 1988, Ribbink 1991, Eccles and Trewavas 1989, Turner 1996). Set in the Western Rift Valley, Lake Malawi/Niassa/Nyasa is the southernmost of these great lakes. Three countries, Malawi (Lake Malawi), Mozambique (Lago Niassa), and Tanzania (Lake Nyasa), share the responsibility for the lake's fisheries resources. As the work to be described here was confined to Malawi waters only, the lake will be referred to as Lake Malawi. Lake Malawi supports more fish species than any other lake in the world, between 500 and 1,000 cichlid species (Konings 1995, van Oppen *et al.* 1998). These fishes have fascinated evolutionary biologists, who are intrigued that so many species could have evolved within the lake in the relatively short time of a few million years (Stiassny and Meyer 1999), and possibly during the last 200 to 300 years for some species (Owen *et al.* 1990). To fisheries biologists also, the lake offers great challenges as they have to manage what is arguably the world's most diverse multispecies fisheries. Fisheries biologists have to strive to conserve the fishes and ensure sustainability of providing good quality animal protein

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to the human population of the region. Part of the challenge stems from the fact that many species are habitat restricted and have an entire distribution range that can be limited to a small part of the lake (Eccles and Trewavas 1989). Perhaps the greatest constraint to management of the fisheries is that too little is known about the biology and ecology of the fishes for well-informed decisions to be made. Many of the species are not yet systematically described and little is known about their distribution, ecology, breeding behavior, life history, interrelationships within communities, and population density (Lowe-McConnell *et al.* 1994, Worthington and Lowe-McConnell 1994, Turner 1995).

Since the closing of trawling activities between Domira Bay and Nkhotakota in 1993, the trawl fisheries occur almost exclusively in the southeast arm (SEA) and southwest arm (SWA) of the lake (Fig. 1; Tweddle and Magasa 1989, Banda *et al.* 1996, Banda and Tómasson 1996). Several reports have indicated that overexploitation of fish communities by trawling has led to changes in size structure, species composition and a decline in catches in the SEA, which is the most heavily fished region of the lake (Turner 1977a, Turner 1977b, Turner 1995, Turner *et al.* 1995, Banda *et al.* 1996). In contrast, the SWA is lightly fished by trawlers. An artisanal fishery operates in the nearshore area, with production comparable to that of the SEA in the shallow waters exploited nearshore (Tómasson and Banda 1996), but the SWA has a very lightly exploited deeper, offshore zone. A single pair-trawler operates in the SWA and only in the shallower southern zone of the arm (Tómasson and Banda 1996; A. Bulirani, Director of Fisheries Research Unit, Malawi, pers. com.). The only other fishing in the SWA was for research purposes at no more than quarterly sampling (Tweddle 1991, Banda and Tómasson 1996, Tómasson and Banda 1996). The offshore part of the northern SWA can therefore be considered as almost unexploited, particularly in the northern region. This region appeared to be an ideal area to conduct a program designed to assess the spatio-temporal trends in species distribution, diversity, abundance, and life histories of the most important fish species caught by trawling (Duponchelle and Ribbink 2000). The unexploited nature of the fish stocks was particularly favorable for the estimation of growth and natural mortality of the major species which are essential information for fisheries management (Turner 1995, Duponchelle and Ribbink 2000). The unexploited fishery also allows for the study of seasonal fluctuations and depth variations in catch composition under natural conditions. In this paper the spatio-temporal patterns of trawl catches taken at exactly the same sites and depths on a monthly basis in the northwestern part of the SWA are followed over an annual cycle with the purpose of recommending possible strategies for expanding and managing the Lake Malawi fishery.

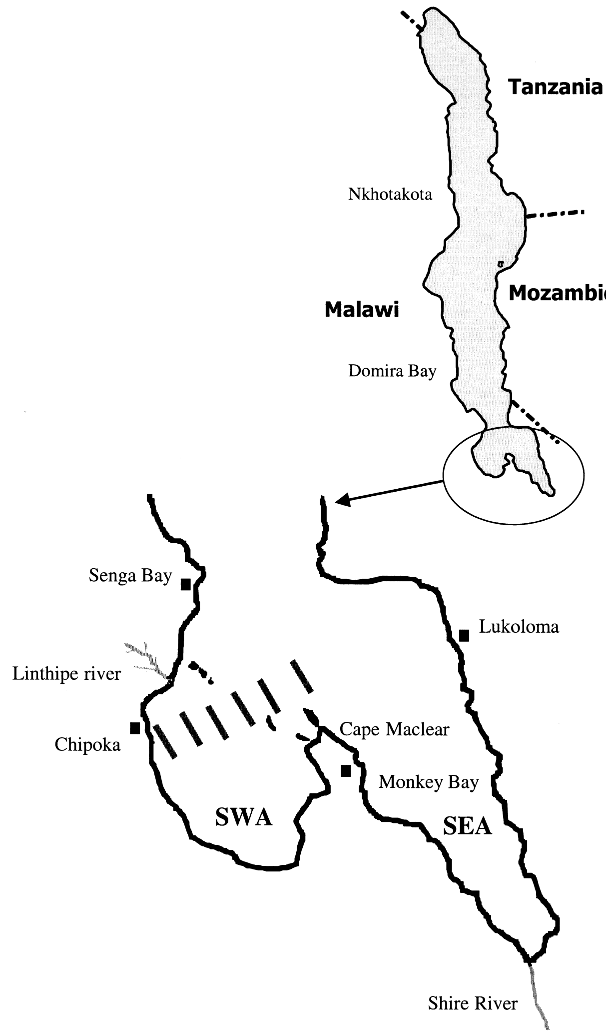

FIG. 1. Detail of the southern part of Lake Malawi. The gray bars represent monthly sampled areas at 10, 30, 50, 75, 100, and 125 m depths.

MATERIAL AND METHODS

Trawl Surveys

July 1998 to May 1999. Two research vessels were used. R/V *Usipa* was used for all surveys except for the months of July and August 1998, when the R/V *Ndunduma* was used. No sample was collected in September 1998, as neither research vessel was available. The *Ndunduma* is a 17.5 m long trawler propelled by a 380 HP engine. R/V *Usipa* is a 15 m steel catamaran powered by twin 135 HP engines. The bottom trawl had approximately a 40 m footrope and 35 mm stretched cod end mesh. Morgère semi oval doors of 135 kg each spread the trawl. Actual opening of the trawl was observed using a Scanmar height sensor, CT 150, which was displayed on a color graphic monitor. The trawl opening varied between 4.1 and 4.3 m.

Each tow was for duration of 20 minutes at a speed of ± 4,630 m/h (2.5 knots, range 2.3–2.7). On average the distance covered by each tow was 1,540 m. The monthly tows were made at 10, 30, 50, 75, 100, and 125 m depth at the same sites along a line between Chipoka and Lukoloma (Fig. 1). The exact positions of every tow are given in Duponchelle and Ribbink (2000).

The depth ranges used in the text are defined as follows, according to the depths of the tows: shallow waters (10 and 30 m tows), intermediate waters (50 m), deep waters (75 and 100 m), and very deep waters (125 m). However, the following categorization of depth ranges will sometimes be simplified for discussion with the covered depths under brackets: shallow waters (10 to 50 m) and deep waters (75 to 125 m).

Perhaps the biggest problem with fish identification in this very diverse community is the lack of consistency between different projects. To resolve this problem one of the authors (Mr. D. Mandere), who has been responsible for field identification for the Malawi Fisheries Department as well as its donor-funded projects over a number of years, supervised the fish identifications on board. In addition, during the first two cruises, Mr. M. Hanssens, a taxonomist of the SADC/GEF, Lake Malawi/ Nyasa Biodiversity Conservation Project, assisted with species identification in order to ensure the consistency of names used by the Fisheries Department and the SADC/GEF Project. Further advice was provided by G. Turner (an expert in demersal Malawi fishes), who was present on the August 1998 cruise. For more information see Duponchelle and Ribbink (2000). The spelling of species names used is that given in Turner (1996).

Catch Analysis

For each tow, the catfishes *Bathyclarias* spp. and *Bagrus meridionalis* were separated from the main catch, counted, and weighed. The rest of the catch was then randomly distributed in 50 kg boxes and the weight recorded. The total catch weight (kg) was recorded as the sum of *Bathyclarias* spp., *Bagrus meridionalis,* and the remaining catch.

A 50 kg filled box was taken as a representative sample of the whole catch and analyzed. Large and medium sized fish, as well as rare species were sorted out of this sample and classified according to their taxonomic status. The weight of the remaining "small fish" (< 5 to 8 cm TL) from the catch was measured and a random sub-sample of about 3 kg was removed from the sample and placed in the deep freeze for later examination. When the large, medium, and rare species were processed, the sub-sample of small fishes were processed following the same protocol.

For each species, the number of specimens and their total weight were recorded to the nearest gram. The standard length (SL) of each specimen was recorded to the nearest mm for analysis of length frequencies. When the number of specimens for a given species was too large, a sub-sample (in proportion to the weight of the main sample was recorded) comprising at least 100 specimens was taken. This procedure was mainly used for the large schools of males of identical size.

Environmental Data

After each tow, a CTD profile and a sediment grab sample were taken in the middle of the transect. The CTD (SeaBird Sea Cat 19) measurements included depth (m), temperature (ºC), oxygen concentration (mg/L), conductivity (mS/cm), water clarity (% transmission), and fluorescence (relative unit). A 24 cm mouth width benthic Ponar grab was used to collect sediment samples. The grab digs about 10 cm into the sediment in such a way that the upper layers form more of the sample than the lower layers. The sample was used to qualitatively estimate the sediment particle size. Each sediment sample was placed in a bucket. A sub-sample was taken, placed in a 250 mL plastic bottle, and frozen for later determination of sediment particle size. To determine sediment particle size, the frozen sub-sample was thawed, mixed by hand, and a sub-sample of 200 cc was placed in a 1 liter measuring cylinder topped up to 1,000 cc with water. The cylinder was shaken to suspend the sediment, which was then passed through a series of sieves (2 mm, 1 mm, 500 µm, 250 µm, 125 µm, 63 µm) starting at the largest aperture. The volume of sediment re-

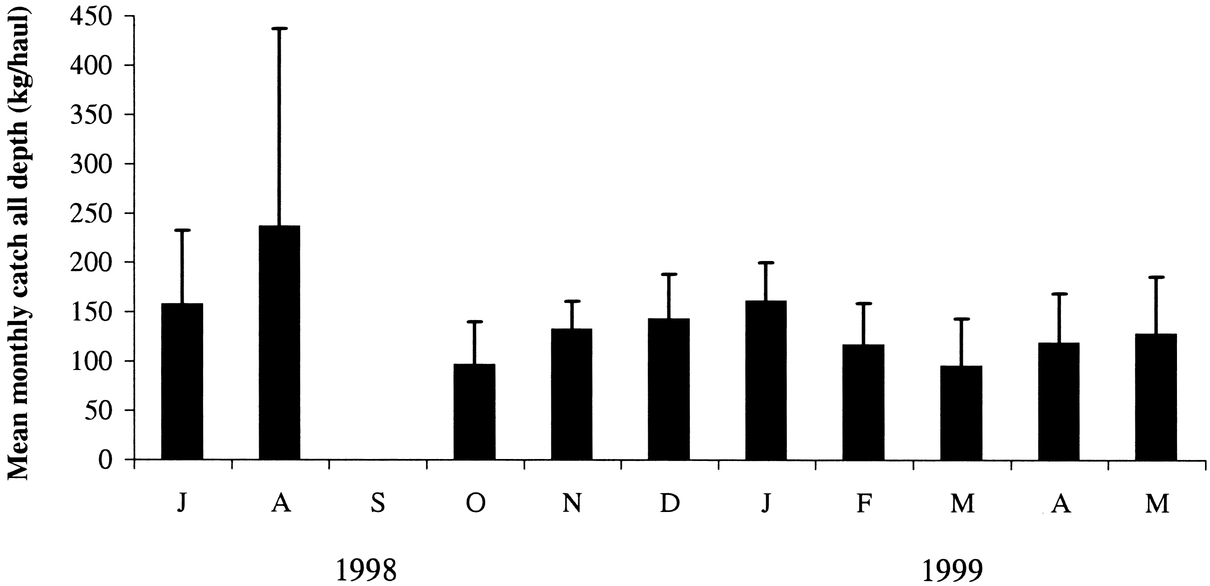

FIG. 2. Mean monthly catches all depths pooled (and standard deviation) over the full sampling period (July 1998 to May1999).

tained in each sieve was determined using a measuring cylinder filled with water. Size class boundaries were as follows: > 4 mm = pebbles, 2 to 4 mm granules, 1 to 2 mm = very coarse sand, 500 µm to 1 mm = coarse sand, 63 µm to 500 µm = fine sand, < 63 µm = silt and clay (mud). According to the proportions of the different components, the sample was then roughly categorized as "coarse sand" (> 1 mm), "medium sand" (250 µm to 1 mm), "fine sand" (63 µm to 250 µm), and "mud"(<63µm).

RESULTS

Catches Per Month and Depth

The mean monthly catches when depths were pooled fluctuated between 94 kg and about 236 kg for 20-minute pulls (Fig. 2). The high value of 626 kg recorded in August 1998 was due to an exceptional catch of *Bathyclarias* spp. at 50 m: 42 specimens giving a total of 400 kg (Fig. 3). Individual catches fluctuated between 30.5 kg at 100 m in October and 283 kg at 75 m in July, excluding the 626 kg recorded in August (Fig. 3). Temporal fluctuation was observed in the catches. The lowest were recorded in October 1998 and March 1999 and the highest in July and August 1998 and January 1999 (Fig. 2). This temporal fluctuation was observed for each depth (Fig. 3). The mean CPUE per depth, all months pooled (Fig. 4a), showed that the highest catches were recorded at 50 m and the lowest at 30 m. Catches were generally higher in the deep zone (50 to 125 m) than in the shallows (10 to 30 m). Almost the same results were obtained when the exceptional catch of *Bathyclarias* spp. in August 1998 was removed, except that the highest catches were recorded at 75 m (Fig. 4b). However, differences of catch were significant neither between depths nor months, respectively with (Two-way ANOVA: $F_{month} = 1.763$, 9 df, $p = 0.103$, $F_{depth} = 1.556$, 5 df, $p = 0.192$) or without the exceptional August *Bathyclarias* spp. catch (Two-way ANOVA: $F_{month} = 1.625$, 9 df, $p = 0.137$, $F_{depth} = 1.899$, 5 df, $p = 0.113$).

Proportions of Cichlids and Catfishes

Although cyprinids and mormyrids were sometimes caught, their occurrence was so rare and their contribution to the catches so weak that they were negligible. Therefore only the catches of cichlids and catfishes are analyzed below. The catfishes (*Bagrus meridionalis*, *Bathyclarias* spp., and *Synodontis njassae*) constituted between 2 and 9% of the catches in number from July to December 1998 and less than 0.5% between January and May 1999 (Fig. 5a). However, catfishes represented consistently 8 to 25% of the catches in weight during the whole sampling period (Fig. 5b).

The proportion of catfishes per depth varied from 2% at 75 and 100 m to 5% at 125 m, in number (Fig. 6a) and from 15.3% at 10 m to 22% at 100 m,

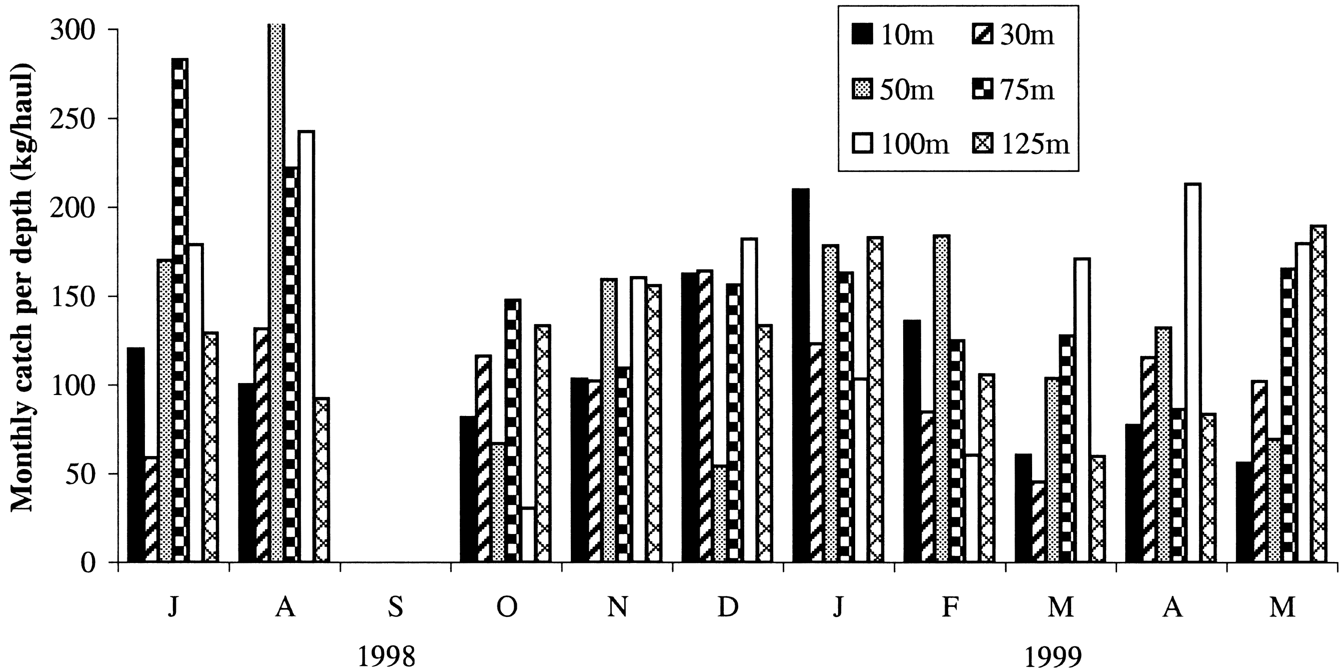

FIG. 3. CPUE per depth over the full sampling period (July 1998 to May 1999).

in weight (Fig. 6b). However, there was no significant difference in the overall abundance (F = 0.324, 5df, p = 0.896) and biomass (F = 1.076, 5df, p = 0.384) of catfish between depths over the sampling period.

Catch Composition

Fishes representing the major part of the catches are presented in Figures 7a and 7b for the depths of 10 m, 30 m, 50 m, and 75 m, 100 m, 125 m respectively.

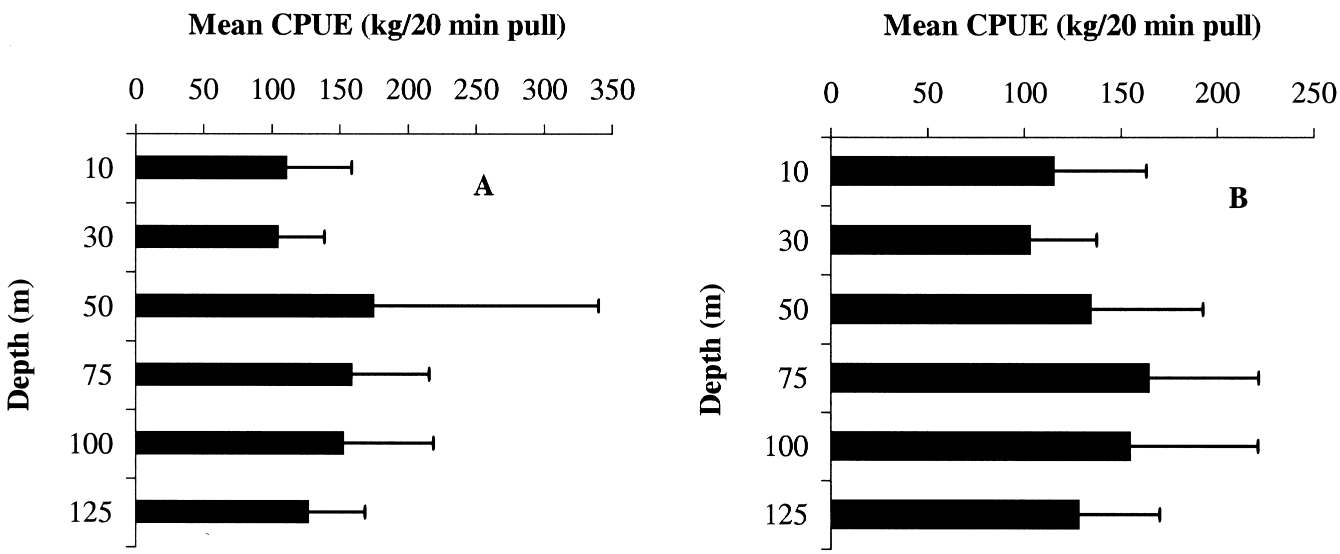

FIG. 4. Mean CPUE (kg/20 min pull) per depth (± standard deviation) over the full sampling period in the SWA (July 98 to May 99) (a) and with the exceptional Bathyclarias *spp. catch removed (b). The high value recorded in August 1998 was due to an exceptional catch of* Bathyclarias *spp. at 50 m, 42 specimens giving a total of 400 kg, with a total catch of 626 kg.*

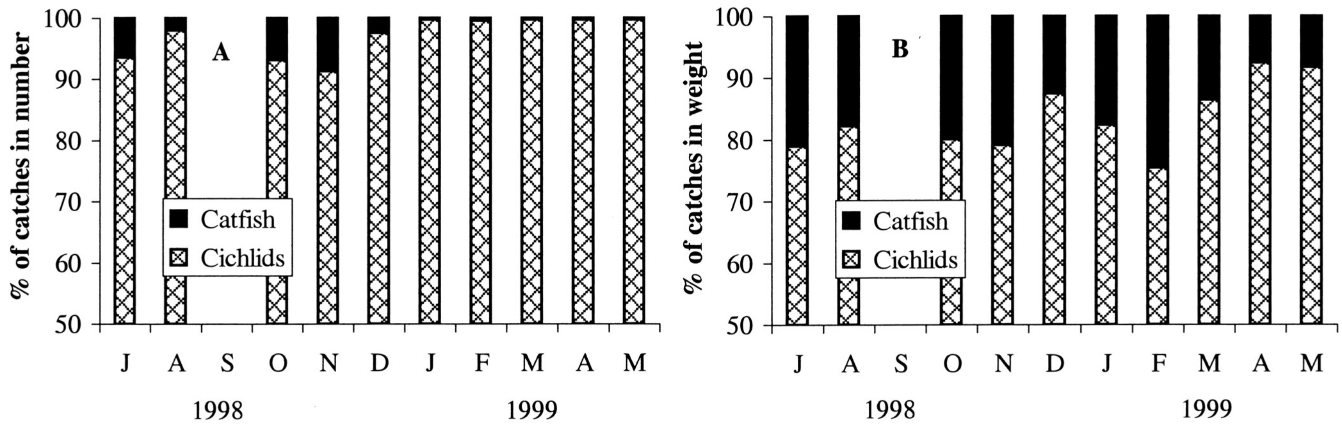

FIG. 5. Proportions of cichlids and catfishes in the catches over the sampling period (July 98 to May 99) in number (a) and weight (b).

The catfish species (*Bathyclarias* spp., *Bagrus meridionalis,* and *Synodontis njassae*) were consistently amongst the most abundant species (by weight) at each depth, averaging 15.3% of the catches at 10 m, 19.3% at 30 m, 21% at 50 m, 18.9% at 75 m, 21.6% at 100 m and 17.6% at 125 m (Figs. 7a and 7b). Owing to their large sizes, the proportional representation of *Bathyclarias* spp. (Fig. 8a) and *Bagrus meridionalis* (Fig. 9a) by number was less than by weight. *B. meridionalis* accounted for a larger proportion of the catches in the shallow waters (10 to 50 m) while *Bathyclarias* spp. was better represented in the deep waters (75 to 125 m). The smaller *S. njassae* was more evenly represented in number and weight and accounted for a larger proportion of the catches in the very deep zone (100 to 125 m, Fig. 10a).

The abundance and biomass of *Bathyclarias* spp. (Fig. 8b) were on average greater in medium-deep waters (50 to 100 m). However, differences in biomass or abundance between depths were not significant, either with or without the exceptional catch at 50 m. There were on average significantly more *B. meridionalis* at 30, 50, and 75 m depths (Kruskal-Wallis one way Anova on ranks, $H = 17.898$, 5df, $p = 0.003$; Multiple comparison test of Student-New-

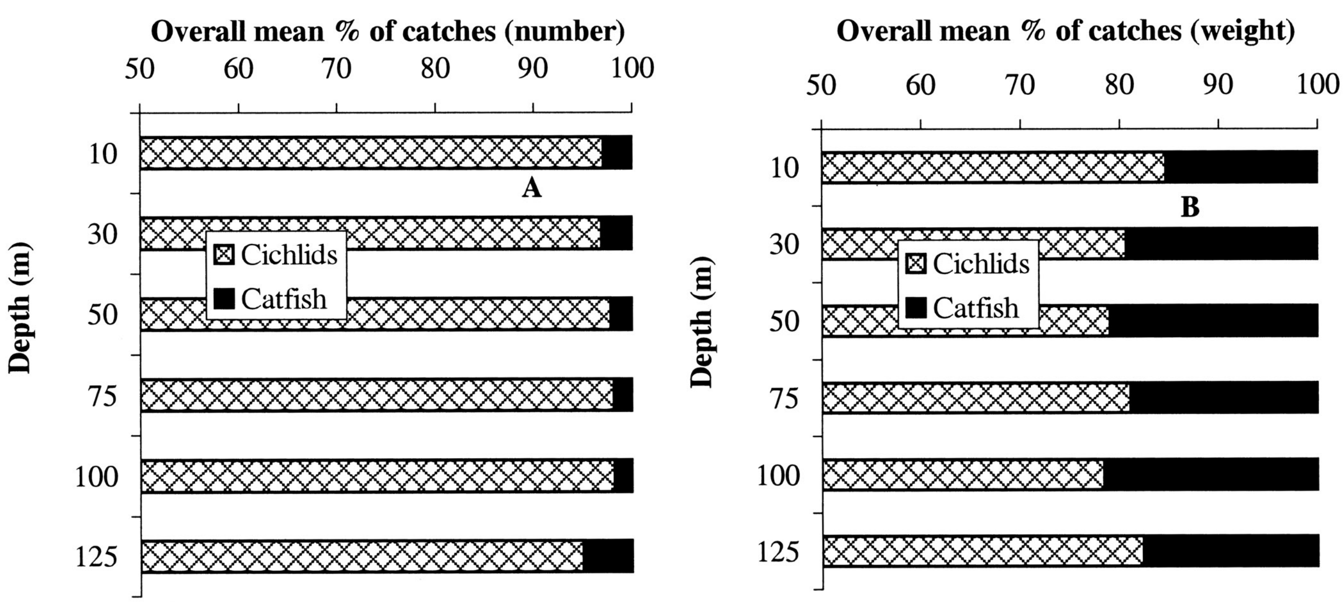

FIG. 6. Proportions of cichlids and catfishes in the catches per depth all months pooled, in number (a) and weight (b).

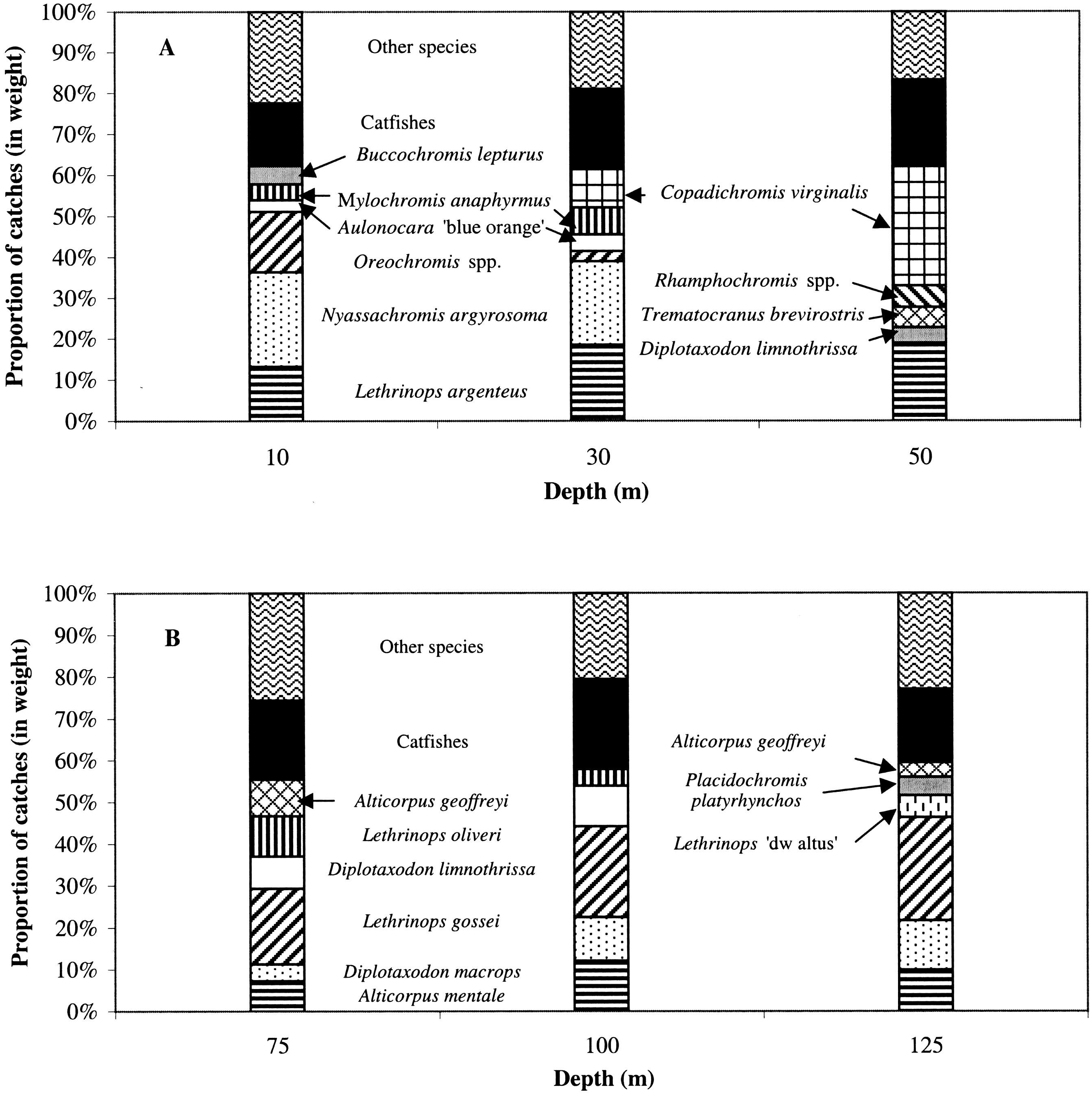

FIG. 7. Mean proportion in weight of the main demersal species trawled in the SWA over the sampling period (a) at 10, 30, 50 m depth, and (b) at 75, 100, and 125 m depth. Catfishes are **Bathyclarias** ***spp.,*** **Bagrus meridionalis,** ***and*** **Synodontis njassae.**

man-Keuls). Their biomass was also greater at these depths (Fig. 9b), although differences were significant only between 50 m and 100 to 125 m ($H = 13.440$, 5df, $p = 0.02$; Multiple comparison test of Student-Newman-Keuls). Abundance and biomass of *S. njassae* tended to increase with depth (Fig. 10b), the differences being significant (Multiple comparison test of Student-Newman-Keuls) between 10 m and 50, 100, 125 m ($H = 12.388$, 5df, $p = 0.03$ and $H = 18.775$, 5df, $p = 0.002$ for abundance and biomass, respectively).

A minimum of 139 different species was caught

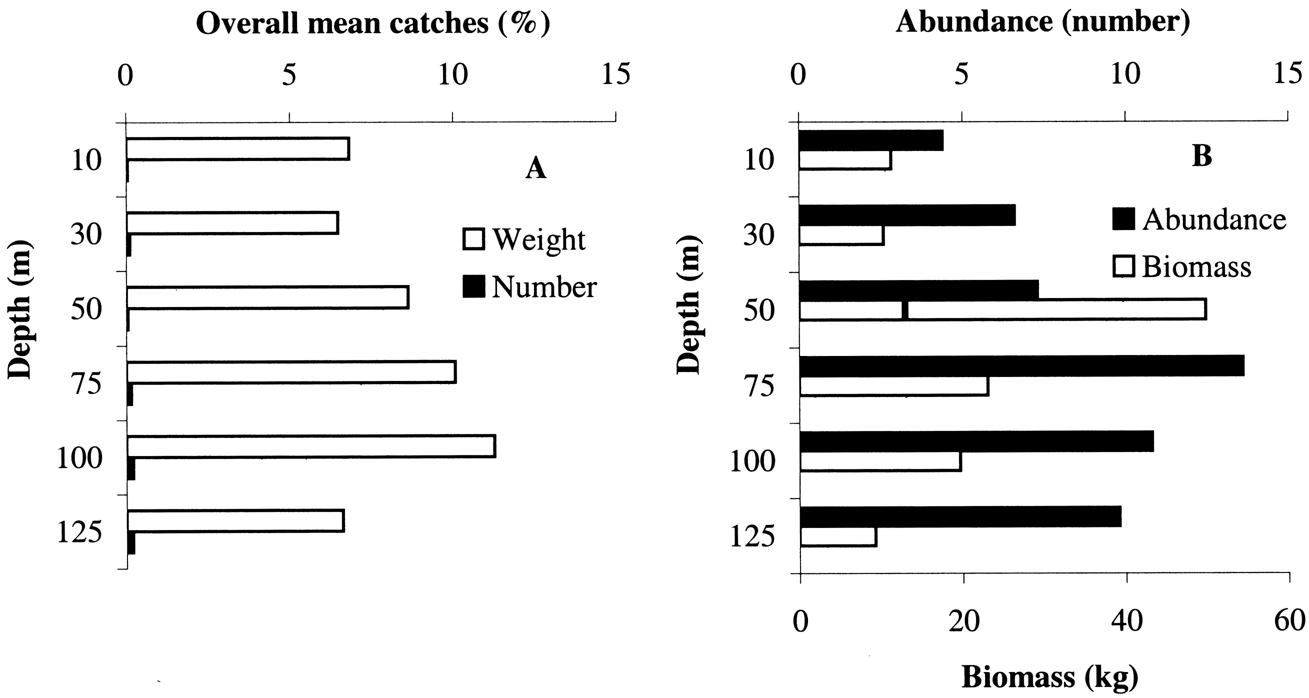

FIG. 8. **Bathyclarias** *spp. (a) Mean proportion (in weight and number) of the total catches at each depth over the sampling period (July 98 to May 99). (b) Mean abundance and biomass at each depth over the sampling period. The vertical line in the biomass histogram at 50 m indicates the mean biomass at 50 m (13.8 kg) when the exceptional* **Bathyclarias** *catch is not taken into account.*

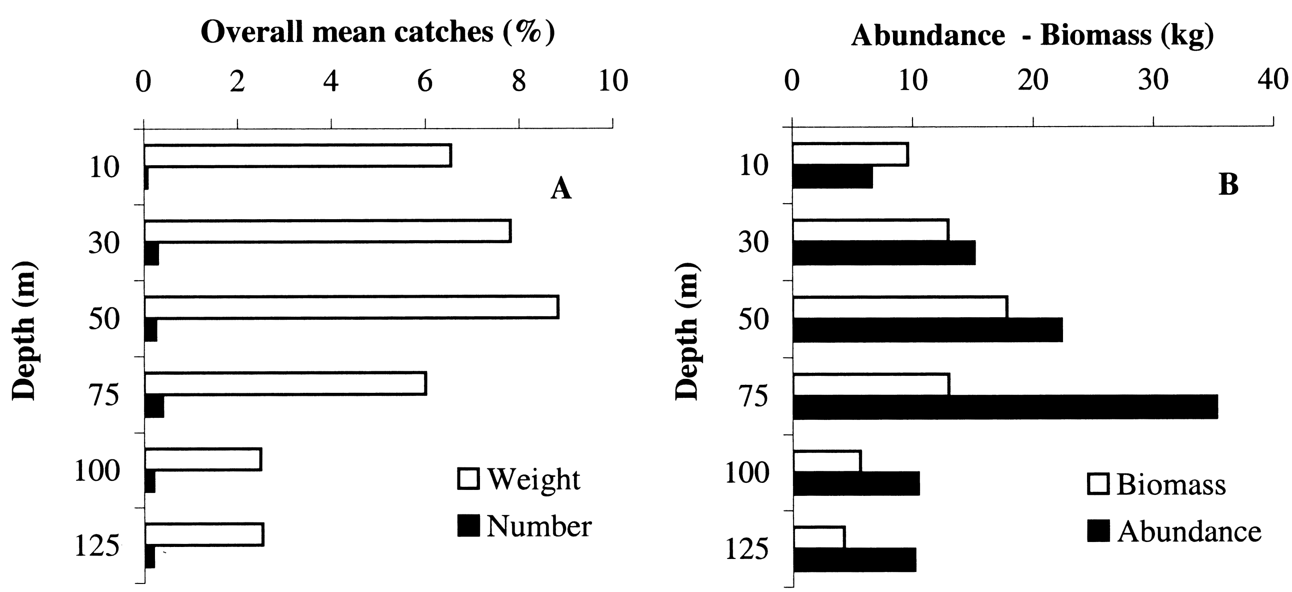

FIG. 9. **Bagrus meridionalis.** *(a) Mean proportion (in weight and number) of the total catches at each depth over the sampling period (July 98 to May 99). (b) Mean abundance and biomass at each depth over the sampling period.*

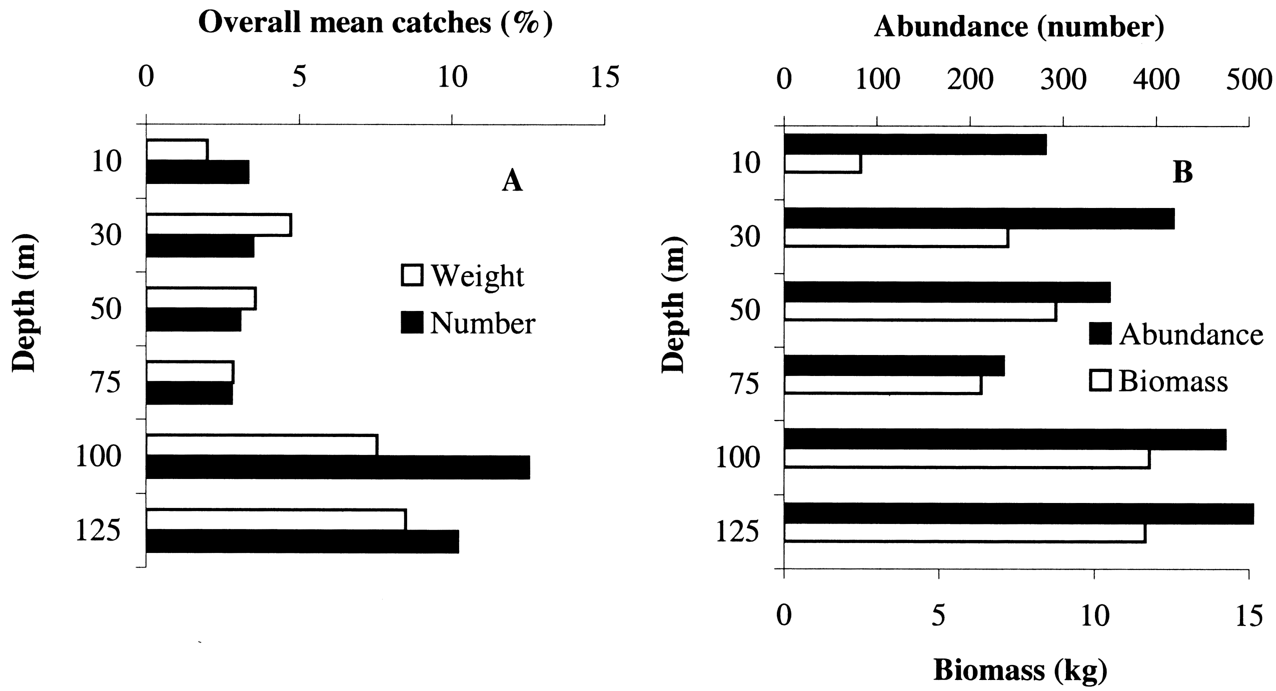

FIG. 10. **Synodontis njassae.** ***(a) Mean proportion (in weight and number) of the total catches at each depth over the sampling period (July 98 to May 99). (b) Mean abundance and biomass at each depth over the sampling period.***

from June 1998 to May 1999, to which must be added the several species lumped together under their generic names, such as the *Aulonocara* spp., *Bathyclarias* spp., *Copadichromis* spp., *Lethrinops* spp., *Mylochromis* spp., *Nyassachromis* spp., *Oreochromis* spp., *Otopharynx* spp., *Placidochromis* spp., *Rhamphochromis* spp., *Sciaenochromis* spp. (Appendix 1). However, despite this high number of sampled species, relatively few cichlid species accounted for more than 50% of the catches in weight at all depths, i.e., about 3 species = 51% at 10 m (*Lethrinops argenteus*, *Nyassachromis argyrosoma,* and *Oreochromis* spp. Fig. 7a), 4 species = 55.2% at 30 m (*Copadichromis virginalis*, *L. argenteus, Mylochromis anaphyrmus,* and *N. argyrosoma* Fig. 7a), 4 species = 56.9% at 50 m (*C. virginalis*, *Diplotaxodon limnothrissa*, *L. argenteus*, and *Trematocranus brevirostris* Fig. 7a), 6 species = 55.5% at 75 m (*Alticorpus geoffreyi*, *Alticorpus mentale*, *Diplotaxodon macrops*, *D. limnothrissa*, *Lethrinops gossei,* and *Lethrinops oliveri* Fig. 7b), 4 species = 53.9% at 100 m (*A. mentale*, *D. macrops*, *D. limnothrissa*, *L. gossei* Fig. 7b) and 4 species = 51.6% at 125 m (*A. mentale*, *D. macrops*, *Lethrinops "deep water altus"* and *L. gossei* Fig. 7b). Some of these species were dominant over two to three depths (Figs. 7a, b, Appendix 1), such as *L. argenteus*, *C. virginalis,* and *N. argyrosoma* in the shallows (10 to 50 m), *A. mentale*, *D. macrops*, *D. limnothrissa,* and *L. gossei* in the deeper waters (75 to 125 m). Considering catfish and cichlids together, about 10 species only accounted for 70 to 80% of the catches in weight at each depth over the sampling period (Figs. 7a, b).

A clear change in species composition appeared after 50 m, the "shallow-water" species being encountered down to 50 m whereas the characteristic "deep-water" species appeared from 75 m downward (Figs. 7a, b).

The results of catch per unit effort (kg/20 minute pull) for each species according to depth are summarized in Appendix 1. The total number of species caught over the sampling period decreased with increasing depth from 80 species at 10 m to 48 at 125 m (Appendix 1). Again, species richness is underestimated because several species were lumped together under their generic names. However, the difference in the mean monthly number of species caught per depth was significant only between 10 m and all the other depths (Kruskal-Wallis one way Anova on ranks, H = 14.758, 5df, p = 0.011; Multiple comparison test of Student-Newman-Keuls). Unlike the three catfish species, which were consistently caught at any depth, very few cichlid species had depth distribution covering all the sampled depths (Appendix 1). Only 12 out of the 139 + cichlid species, or species groups, covered all (or at least 5 of) the sampled depths. Most of the others were restricted to three or four depths and some species were confined to one or two depths only (Appendix 1).

DISCUSSION

During the whole sampling period, no other trawler was encountered in the sampled area, from Chipoka to just north of Cape Maclear (Fig. 1). The only trawler (one pair trawler) active in the SWA fishes in the southern part of the arm only. The R/V *Ndunduma* occasionally trawls for research purposes in the northern part of the SWA (A. Bulirani, pers. com.). Therefore, the sampled area in this study is very lightly used by commercial trawlers, and it is considered to be occupied by virgin stocks.

In terms of biomass, the highest catches were recorded at 75 and 100 m, and the catches were higher at 125 m than at 10 and 30 m. This is confirmed by overall bottom trawling operations conducted during the course of the SADC/GEF Lake Malawi Biodiversity Conservation Project (Day 1999), but is in contradiction with the results of previous work where the reported CPUE was higher in the shallower zones (Turner 1977a, Tómasson and Banda 1996). This might be a consequence of the light exploitation of the deep zone by commercial fisheries whereas the shallow zones in SWA appear as heavily exploited by artisanal fishermen as in the SEA (Tómasson and Banda 1996).

Temporal fluctuations of the total catches per month (when all depths pooled; Fig. 2) were seen at every depth, suggesting that the representativeness of the sampling was good, despite a potential inter-haul variability. Tweddle and Magasa (1989) also reported seasonal trends in the catch rates in the SEA with usually a peak in August and September, which is supported by our results in the SWA.

The catches were dominated by cichlids both in number and weight. However, the catfishes, represented by only three genera (*Bathyclarias*, *Bagrus,* and *Synodontis*) of which two have a single species (*Bagrus meridionalis* and *Synodontis njassae*), consistently constituted a significant part of the catches. Owing to the large size of *Bathyclarias* spp. and *Bagrus meridionalis*, their contribution to the catches in terms of biomass was greater than their contribution in terms of numerical abundance. They consistently represented between 10 and 25% of the catches. Tómasson and Banda (1996) found that in the SWA, *B. meridionalis* was more abundant in the deep waters (50 to 100 m) but bigger in the shallows (0 to 50 m). In these samples, *B. meridionalis* was more abundant at 50 and 75 m, and large specimens were evenly distributed according to depth. *Bathyclarias* spp. tended to be better represented in the deep waters from 50 m downward whereas their maximum catch was previously observed at 40 to 60 m by Turner (1977a). As observed by Tómasson and Banda (1996), *Synodontis njassae* was common at all depths and displayed an increasing occurrence and abundance with depth, becoming much more abundant in the very deep zone (100 and 125 m). Although specimens of *Synodontis* from 50 to 200 mm (standard length) were recorded, most individuals caught were of uniform size, between 90 and 110 mm SL, which corresponded to previous observations of 10 to 14 cm TL (Tómasson and Banda 1996, Thompson *et al.* 1996a).

In Lake Malawi, demersal (this study, Tómasson and Banda 1996, Turner 1996) as well as pelagic (Thompson *et al.* 1996a, b) catches are almost exclusively made of cichlids and catfishes, with a strong predominance of cichlids. This is in sharp contrast with the situation in the other two great lakes. In Lake Tanganyika, the pelagic community is composed of six endemic clupeids and centropomids and only a few cichlid species, referred to as bathypelagic, occasionally occur in the pelagic zone (Coulter 1991). The demersal community in Tanganyika is much more diverse with cichlids, catfishes (bagrids, mochokids, malapterurids, clarids), centropomids, cyprinids, cyprinodontids, and mastacembelids. The relative proportions of these families in the catches are also more evenly distributed than in Lake Malawi (Coulter 1991). The situation in the much shallower Lake Victoria requires a cautious distinction between before and after the Nile perch (*Lates niloticus*) upsurge. The offshore zone is now mainly occupied by the native cyprinid *Rastrineobola argentea* and the introduced Nile perch, (Goldschmidt *et al.* 1993, Witte and van Densen 1995, Wanink and Witte 2000) although zooplanktivorous haplochromines were believed to also occupy this niche (Goldschmidt and Witte 1990, Goldschmidt *et al.* 1990, Witte and van Oijen 1990, Wanink and Witte 2000) before the Nile Perch upsurge (Goldschmidt *et al.* 1993, Witte *et al.* 1992). Apparently, a few of these zooplanktivorous haplochromine species are now abundant offshore in

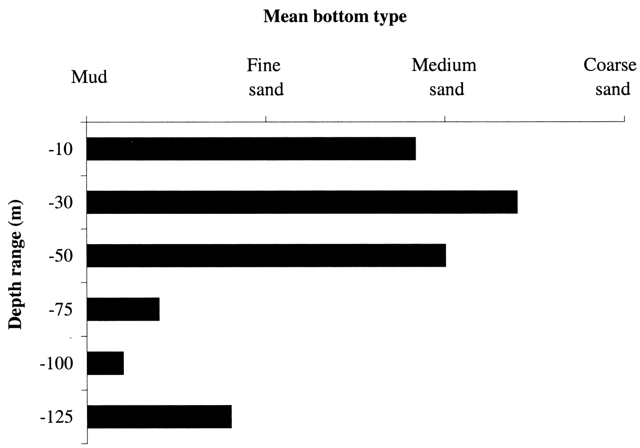

FIG. 11. Modification of bottom type with depth in the SWA. Each bottom type category was given an arbitrary value for graphic representation: 15 for "coarse sand," 10 for "medium sand," 5 for "fine sand," and 0 for "mud." The values are the means over five months (June to December 1998).

Lake Victoria (R. Hecky, D. Tweddle, Y. Fermont, pers. coms.). Haplochromine cichlids, which used to make up more than 80% of the demersal fish biomass in the 1960s (Kudhongania and Cordone 1974), have now become negligible in the catches compared to the Nile perch and the Nile tilapia (Witte *et al.* 1992). However, it must be emphasized that the haplochromine demersal fishery in Lake Victoria has also been severely constrained by eutrophication and deoxygenetation (Hecky *et al.* 1994).

The CPUE per species and depth category (Appendix 1) were not always consistent with those obtained in the SWA by Tómasson and Banda (1996) when adjusted for a 30 min pull, and are discussed in detail elsewhere (Duponchelle and Ribbink 2000). However, reasons for these differences may lie in differences in the design of these studies: Tómasson and Banda's study covered all the SWA, whereas this study was restricted to the northern part and always harvested the same sites, and their sampling frequency was quarterly whereas this study was monthly. Also, their towing speed (3.7 knots) was about 1 knot faster than in this study (2.5 knots).

A marked change in species composition was observed between 50 and 75 m in the SWA. This species change was already reported by Tómasson and Banda (1996), who suggested that it was related to the position of the thermocline or the substrate type. However, the position of the thermocline does not seem to be the best explanation for that pattern because it fluctuates significantly from about 50 to > 125 m with season (Eccles 1974, Patterson and Kachinjika 1995, Duponchelle and Ribbink 2000), whereas the species distribution pattern is stable over time in this study which had monthly sampling. Most of these exploited species are demersal fish (Eccles and Trewavas 1989, Tómasson and Banda 1996, Turner 1996). A few species were observed with pelagic tendencies such as *Copadichromis* spp. (Fryer and Iles 1972) and some *Diplotaxodon* spp. (Thompson *et al.* 1996b; Turner *et al.* 2001a, b) as well as a few truly pelagic species, such as *Copadichromis quadrimaculatus*, *Diplotaxodon limnothrissa*, and *Rhamphochromis* spp. (Thompson *et al.* 1996b; Turner *et al.* 2001a, b). Most of the trawled species are therefore closely associated with the bottom, and the sediment quality might constitute a better explanation for the break in the depth distribution of species at approximately 50 m. The grab sample analyses revealed a gradient in bottom type composition from the shallows to the deep waters (Fig. 11). A clear change in bottom composition from coarse and medium sand to fine sand and mud appears after 50 m and is more likely to be a controlling factor in species distribution with depth than the thermocline. A similar species shift is known to occur in the SEA, but around 60 m (Tómasson and Banda 1996). A bottom composition analysis along the depth gradient in the SEA would test this hypothesis of dependency on sediment grain size composition.

A notable observation was that, throughout the year, the bulk of the catches by weight was constituted by a few common cichlid and catfish species. At any given depth, despite the large number of species regularly recorded, 60 to 80% of the catches were made of no more than ten species including the three catfishes. And about twenty species only accounted for 90 to 95% of the catches at each depth, with some species being dominant in two or three of the sampled depths. This indicates that many species are uncommon or rare. The occurrence in the catches of some of the rarest species might simply reflect a coincidental appearance in the sampled areas of species that normally do not occur there. Another potential explanation might be that the samples were restricted to uniform habitats and did not collect fishes from other, more diverse habitats, though this hypothesis is very unlikely given the surface covered by a 20 min pull. It seems, therefore, that many species have a small population size and/or have patchy distributions either because of their high specialization to specific type of habitats or because of the narrowness of their trophic niche (Eccles and Trewavas 1989). Such species are likely to be endangered by intensive exploitation, given the typically precocial (*sensu* Balon 1990) life history characteristics of Malawi cichlids (Fryer and Iles 1972, Turner 1996, Duponchelle and Ribbink 2000).

The decreasing number of species caught with increasing depth reported by previous authors (Turner 1977a, Tómasson and Banda 1996) was confirmed by this study (Appendix 1). The finding that demersal cichlids usually have restricted depth distributions (Eccles and Trewavas 1989, Banda and Tómasson 1996, Tómasson and Banda 1996, Turner 1996) was also supported by the results, as was the trend for decreasing occurrence of large cichlid species with depth (Turner 1977a). Even though there was a higher number of large species in the shallows (*Buccochromis* spp., *Taeniolethrinops* spp., *Serranochromis robustus*) their numerical abundance is low with the exception of *Oreochromis* spp. Shallow-water catches were dominated by small species such as *Aulonocara* spp., *Nyassachromis* spp., or *Copadichromis virginalis* and a few larger species such as *Lethrinops argenteus* and *Mylochromis anaphyrmus* (Fig. 7a). On the other hand, the dominant species of the deep zone were, on average, larger fish such as *Lethrinops gossei*, the *Alticorpus* spp. and *mentale* particularly, the *Diplotaxodon* spp. (Fig. 7b). The decreased occurrence of large and medium-sized species from the shallow waters of the SEA (Turner 1977b, Turner *et al.* 1995) seems to be true of the shallow waters of the SWA too. However, in the almost unexploited deep zone in the SWA, larger fish predominate. Over the year, the highest catches were recorded from 50 m downward, where the dominant species are relatively large and possess life history characteristics (higher relative fecundities, extended breeding seasons, Duponchelle and Ribbink 2000) that should make them more resilient to fishing pressure (Adams 1980, Pitcher and Hart 1982, Garrod and Horwood 1984, King 1995 for reviews) than many of the less prolific and more seasonally-spawning species currently overexploited in the shallower waters. Exploiting the deep zones might relieve excessive fishing efforts currently applied to the shallower zones of the southern arms of the lake (Turner 1995, Turner *et al.* 1995). The results suggest that increased harvesting of fishes of deeper waters should be explored with appropriate incentive schemes to encourage nearshore effort to move to deeper waters while maintaining surveillance and biological monitoring of the offshore stocks to guard against excessive exploitation.

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APPENDIX 1. Mean CPUE (kg/20minute pull) per depth for each species over the sampling period (July-1998 to May-1999). – means absent or negligible. 0.0 means < 0.05 kg/20 minute pull.

Species / Depth (m)	10	30	50	75	100	125
Alticorpus spp.	—	0.2	0.1	1.0	0.9	1.2
Alticorpus 'geoffreyi'	—	—	0.3	21.4	3.5	6.1
Alticorpus macrocleithrum	—	—	—	0.9	2.5	0.4
Alticorpus mentale	—	0.0	0.7	12.2	21.9	13.4
Alticorpus pectinatum	—	—	—	2.8	2.8	1.7
Aristochromis christyi	0.1	0.0	—	—	—	—
Aulonocara 'cf. macrochir'	0.0	0.1	1.7	—	—	—
Aulonocara spp.	0.2	—	0.2	0.5	0.0	1.1
Aulonocara 'blue orange'	5.6	5.6	0.5	—	—	—
Aulonocara 'copper'	—	—	—	0.4	—	—
Aulonocara guentheri	0.9	0.1	—	—	—	—
Aulonocara 'long'	0.0	—	0.0	0.2	0.1	0.2
Aulonocara 'minutus'	—	—	—	1.4	0.9	1.7
Aulonocara rostratum	0.0	—	—	—	—	—
Aulonocara 'rostratum deep'	—	—	0.1	1.0	0.1	0.3
Bagrus meridionalis	9.6	12.9	17.8	13.0	5.6	4.3
Barbus eurystomus	0.0	0.1	—	—	—	—
Barbus johnstonii	—	0.2	—	—	—	—
Barbus litamba	—	—	0.1	—	—	—
Bathyclarias spp.	11.3	10.4	49.8	23.1	19.7	9.3
Buccochromis lepturus	3.7	0.6	—	—	—	—
Buccochromis nototaenia	1.0	2.3	0.1	—	—	—
Buccochromis rhoadesi	0.5	0.1	—	—	—	—
Buccochromis 'small'	0.0	—	—	—	—	
Caprichromis liemi	—	0.0	0.0	—	—	—
Champsochromis caeruleus	0.1	0.1	—	—	—	—
Chilotilapia rhoadesi	1.4	1.1	—	—	—	—
Copadichromis inornatus	0.1	—	—	—	—	—
Copadichromis quadrimaculatus	0.9	2.6	1.1	0.1	—	—
Copadichromis spp.	0.1	0.0	—	—	—	—
Copadichromis trimaculatus	—	—	—	—	—	0.0

(Continued)

APPENDIX 1. Continued.

Species / Depth (m)	10	30	50	75	100	125
Copadichromis virginalis	0.7	16.7	47.7	—	0.1	—
Corematodus taeniatus	0.0	0.0	0.0	0.0	—	—
Ctenopharynx nitidus	0.2	0.1	—	—	—	—
Ctenopharynx pictus	—	—	0.1	—	—	—
Dimidiochromis sp.	0.0	—	—	—	—	—
Diplotaxodon apogon	—	—	—	5.0	5.4	4.0
Diplotaxodon argenteus	—	—	1.0	4.4	2.9	2.2
Diplotaxodon spp.	—	—	—	0.3	0.5	0.5
Diplotaxodon 'brevimaxillaris'	—	—	0.0	0.1	0.2	0.6
Diplotaxodon greenwoodi	—	—	—	0.1	0.3	0.2
Diplotaxodon limnothrissa	0.1	—	9.7	13.4	9.3	2.7
Diplotaxodon macrops	—	—	—	7.3	18.9	16.0
Diplotaxodon 'similis'	—	—	—	0.0	—	0.1
Docimodus johnstonii	0.1	0.0	0.3	—	—	—
Engraulicypris sardella	0.0	0.0	—	0.0	0.0	—
Exocochromis anagenis	—	—	0.0	—	—	—
Haplochromis 'sp.'	—	—	0.0	—	—	—
Hemitaeniochromis 'insignis'	—	—	0.0	0.1	0.0	0.1
Hemitaeniochromis urotaenia	0.1	—	0.0	—	—	—
Hemitilapia oxyrhynchus	—	—	—	—	—	—
Lethrinops christyi	0.3	0.0	1.0	—	—	—
Lethrinops 'matumbae'	—	1.0	0.0	—	—	—
Lethrinops 'deep water albus'	—	—	1.4	3.5	0.0	4.8
Lethrinops albus	—	—	0.2	0.0	—	0.6
Lethrinops altus	0.2	2.6	2.1	1.8	1.4	4.6
Lethrinops spp.	1.0	0.1	2.0	0.5	0.1	0.4
Lethrinops 'blue orange'	—	0.6	—	—	—	—
Lethrinops 'cf. auritus'	0.0	—	—	—	—	—
Lethrinops dark	2.6	0.3	4.1	0.3	0.3	1.5
Lethrinops 'deep water altus'	—	—	—	1.0	4.7	2.2
Lethrinops 'cf. furcifer'	1.1	0.1	—	—	—	—
Lethrinops gossei	—	—	0.2	32.0	40.0	34.4
Lethrinops 'grey'	—	—	—	—	1.0	—
Lethrinops lethrinus	0.2	—	—	—	—	—
Lethrinops longimanus	—	0.5	7.3	0.2	1.1	0.1
Lethrinops argenteus	20.3	23.9	40.7	0.1	0.0	0.2
Lethrinops macrochir	3.5	—	—	—	—	—
Lethrinops 'macrostoma'	—	—	—	0.0	—	—
Lethrinops microdon	1.0	—	0.1	0.0	0.0	—
Lethrinops 'minutus'	0.0	—	3.5	—	—	—
Lethrinops mylodon	—	0.2	0.1	—	0.2	—
Lethrinops 'oliveri'	—	—	—	18.2	8.3	3.6
Lethrinops 'cf. parvidens'	0.4	0.0	0.1	—	—	—
Lethrinops 'pink head'	0.2	—	—	—	—	—
Lethrinops polli	—	—	—	7.0	1.2	0.2
Lethrinops stridei	—	—	—	—	0.0	—
Lethrinops 'yellow chin'	—	—	0.9	—	—	—
Mormyrus longirostris	—	—	—	—	—	0.1
Mylochromis anaphyrmus	4.6	8.6	2.3	0.0	—	—
Mylochromis formosus	0.1	0.1	0.2	—	—	—
Mylochromis gracilis	—	0.2	0.2	0.5	—	—
Mylochromis spp.	0.2	0.1	—	—	—	—
Mylochromis melanonotus	0.3	0.2	—	—	—	—
Mylochromis sphaerodon	0.0	0.0	—	—	—	—

(Continued)

APPENDIX 1. Continued.

Species / Depth (m)	10	30	50	75	100	125
Mylochromis spilostichus	0.4	0.5	7.4	—	—	—
Mylochromis 'torpedo'	0.0	—	—	—	—	—
Nevochromis chrysogaster	0.0	—	—	—	—	—
Nimbochromis livingstonii	0.1	0.0	0.2	0.1	—	—
Nimbochromis venustus	0.0	—	—	—	—	—
Nyassachromis argyrosoma	28.6	31.7	0.9	—	—	—
Nyassachromis spp.	0.5	0.3	—	—	—	—
Nyassachromis eucynostomus	0.5	0.1	—	—	—	—
Nimbochromis polystigma	0.0	—	—	—	—	—
Opsaridium microcephallus	—	0.0	—	—	—	—
Opsaridium microlepis	—	0.0	0.7	0.2	—	—
Oreochromis spp.	27.7	1.1	7.8	0.1	—	—
Otopharynx argyrosoma	2.2	2.2	0.1	—	—	—
Otopharynx auromarginatus	—	—	—	—	—	—
Otopharynx brooksi	—	—	—	0.5	0.0	0.0
Otopharynx 'productus'	0.7	0.0	—	—	—	—
Otopharynx decorus	0.4	0.4	—	—	—	—
Otopharynx spp.	0.2	—	—	—	—	0.0
Otopharynx speciosus	—	0.8	2.1	0.1	—	—
Pallidochromis tokolosh	—	—	0.1	1.8	0.6	2.9
Placidochromis 'acuticeps'	—	—	—	—	—	0.1
Placidochromis "flatjaws"	—	—	—	0.0	1.3	0.3
Placidochromis spp.	—	—	0.0	0.3	0.0	—
Placidochromis 'macrognathus'	—	0.0	0.0	0.0	0.0	0.1
Placidochromis 'hennydaviesae III'	—	—	—	—	—	0.1
Placidochromis 'hennydaviesae IV'	—	—	—	—	—	0.1
Placidochromis johnstonii	—	0.0	—	—	—	—
Placidochromis 'long'	—	0.4	1.7	—	—	—
Placidochromis 'platyrhynchos'	—	—	—	0.0	1.1	4.1
Placidochromis 'cf. subocularis'	0.1	0.0	—	—	—	—
Protomelas spilopterus	0.0	0.0	—	—	—	—
Protomelas triaenodon	0.0	—	—	—	—	—
Pseudotropheus elegans	0.1	0.1	—	—	—	—
Pseudotropheus lanisticola	—	—	—	—	—	—
Pseudotropheus livingstonii	1.1	0.1	—	—	—	—
Pseudotropheus spp.	—	0.0	—	—	—	—
Rhamphochromis spp.	0.6	3.9	8.5	4.2	0.7	0.6
Sciaenochromis spp.	0.1	0.0	0.0	—	—	—
Sciaenochromis alhi	0.4	0.1	0.1	0.3	0.2	0.2
Sciaenochromis benthicola	0.1	0.5	3.1	1.4	0.2	0.0
Sciaenochromis psammophilus	—	—	—	0.1	—	—
Serranochromis robustus	0.1	—	—	—	—	—
Stigmatochromis pholidophorus	0.0	—	—	—	—	—
Stigmatochromis woodi	0.0	0.0	0.1	0.0	—	0.0
Stigmatochromis 'guttatus'	0.0	—	0.5	0.3	0.0	0.0
Synodontis njassae	2.5	7.2	8.8	6.4	11.8	11.7
Taeniochromis holotaenia	0.0	0.0	—	—	—	—
Taeniolethrinops furcicauda	1.3	0.0	—	—	—	—
Taeniolethrinops laticeps	—	0.2	—	—	—	—
Taeniolethrinops praeorbitalis	1.1	0.3	—	—	—	—
Tramitichromis lituris	0.8	—	—	—	—	—
Trematocranus brevirostris	—	0.0	6.6	—	—	—
Trematocranus macrostoma	0.0	—	—	—	—	—
Trematocranus placodon	1.3	—	—	—	—	—
Minimum number of species per depth	**80**	**71**	**66**	**58**	**47**	**48**