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Changes in fish species diversity, size structure and distribution in the trawlable demersal zones of Lake Malawi, Malawi

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Abstract
A study was conducted to assess temporal and spatial changes in the trawlable demersal zones of Lake Malawi. Data from surveys conducted in 1998 and 2020 targeting 120 stations covering a surface area of 9647.97 km^2 was used. Trawling speed of *Research Vessel Ndunduma* was restricted to 4.6 km/hr. Length frequency distribution was modelled with the probability density function for determining the likelihoods in the gamma distribution. Parameters for modal length and logistic modelling were guessed and Solver in Microsoft Excel 2021 was used to generate the best of fit values through iteration with GRG Nonlinear approach. The study determined fish diversity using the Shannon and Weiner relationship. The recent survey recorded fewer fish species (149) against 158 sampled in the previous survey. The overall catch rates in 2020 and 1998 ranged from 3.8 kg/0.5 h to 2003.8 kg/0.5 h and 28.7 kg/0.5 to 1,884.3 kg/0.5 h, respectively. Overall fish density in the 2020 and 1998 surveys was calculated at 11.7 tons/km^2 and 7.5 tons/km^2, respectively representing a 35.6% drop. The study has revealed temporal and spatial shifts in the fish stock composition, distribution and abundance which necessitates urgent management interventions to prevent further fisheries resource losses. Efforts to regulate mesh sizes of the codends of trawlers are encouraged just like the initiative of introducing a closed season for the commercial operators.

Keywords Lake Malawi fisheries · Trawling · Cichlids · Sexual maturity · Management measures

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1 Introduction

Lake Malawi with over 800 fish species has the greatest diversity of freshwater fishes in the world (Stauffer et al., 2018) and still counting! The latest addition to this species rich waterbody was made by Stauffer et al., (2018) where two deep-water *Diplotaxodon* fish species were described. Lake Malawi fisheries provide essential socio-economic and ecosystem services to the country (Weyl et al., 2010). Fish and fisheries products contribute 4% to the gross domestic product (GDP) while nutritionally about 70% of the animal protein and 40% of the total protein are derived from fish (Government, 2021). With the current annual fish landings of 170,844 metric tons having an average "beach" value of US$1.3/kg, fisheries of Malawi are estimated at a landed value of MK184 billion or US$ 230 million. The fishery directly employs over 80,000 people as gear owners and crew members while over 500,000 are employed in ancillary activities like fish processing, marketing, trading, boat building, repairing, net mending and fishing gear supply business (Government, 2021).

Lake Malawi fisheries are mainly distinguished by their level of mechanisation hence, are classified into small-scale/artisanal and commercial (aquarist and trawlers) components, (Banda, 2001). The traditional fishery is known for its low investment cost, low production per unit effort, labour intensive and wide spreading across all waterbodies (Kolding et al., 2019). Aquarist or ornamental fishery in Malawi dates back to the early 1970 and is primarily appreciated for the foreign exchange earnings through global export of wild-caught cichlid fishes (Msukwa et al., 2020). The fishery takes advantage of the robust fish diversity particularly the colourful rock-dwelling species commonly known as *Mbuna*. A total of MK141 million or US$176,250 was generated in 2020 after exporting 23, 985 pieces of live fish (Government, 2021). The total revenue was significantly reduced (more than 100%) when compared to 2019 and this was attributed to the Covid-19 cross boarder restrictions. The commercial trawl fishery on the other hand was introduced in 1968 after successful trawl trials in 1965 in the southern part of Lake Malawi (Banda, 2001; Weyl et al., 2010). Globally, bottom trawling dates back to as early as 1376 (Roberts, 2008). In Lake Victoria, the very first lake wide experimental bottom trawling was conducted from 1969 to 1970 (Mbuga et al., 1998) while a midwater experimental trawling in Lake Tanganyika was conducted in 1998 (Sarvala et al., 1999). The western African coastal (Guinea-Bissau, Guinea, Sierra Leone and Liberia) started bottom trawling as early as 1950 (Virdin et al., 2019). Lake Malawi trawl fishery is mainly categorised based on the number of trawl units hauling the net (Banda, 2001), they are stern (single boat) and pair trawlers (paired boats). Kanyerere et al. (2018) identified the current trawling techniques in Lake Malawi as semi-pelagic stern trawling; demersal stern trawling and semi-pelagic pair trawling. Entry into the commercial trawl fishery is controlled by area specific permits issued by the Department of Fisheries.

A substantial change in the species composition as a result of the introduction of trawl fishing was observed in Lake Malawi fish stocks (Banda & Tomasson, 1997; Weyl et al., 2010). It was particularly noted that large demersal fish species were being replaced by smaller haplochromine species. A significant decline in one of the commercially important fish, *Oreochromis spp* locally known as *chambo* was particularly noted Weyl et al., (2010). The decline in the bigger fish was attributed to a number of factors but the paramount reason was the increased fishing effort and non-compliance to set out management regulations (Turner et al., 2005). It was observed that vessels particularly pair trawlers routinely fish within one nautical mile (1.8 km) from the shore or in less than 18 m water depth, whichever comes first; mesh sizes have been reduced from the legal minimum size of 38 mm to less than 20 mm. Furthermore, the fishery was characterised by increasing engine horse power and the trawl nets while fishing hauls lasting more than the recommended aggregated duration of 8 h per day (Turner et al., 2005).

Efforts to assess the status of the fish stocks of the lake have partially been there with no distinct pattern and technical consistency. The last comprehensive demersal trawl survey was conducted in 1998 by the Department of Fisheries. Kanyerere and M'balaka (Unpublished Data) assessed the demersal zone of the central part of Lake Malawi and made some investment recommendations for trawlers. The study attempted to bring solutions to decongest the over-capacitated southern part of the lake as earlier observed by Turner et al., (2005). Kanyerere et al., (2018) recently assessed the status of commercial trawl fisheries in southern Lake Malawi using time series data. Latest attempts to assess the fish stocks in the demersal zones were made by M'balaka et al., (2019) in the southeast arm of Lake Malawi. Based on the recent efforts, it is clear that Lake Malawi has not been comprehensively covered to assess the status of its stocks since the 1998 survey. It is imperative therefore that an assessment of the status of fish stocks was conducted in 2020 to generate new information for renewed perspectives of the fisheries resources in Lake Malawi. Findings of this study culminate into a number of recommendations for sustainable management of the demersal fish stocks in Lake Malawi.

2 Materials and methods

2.1 Study area

The study made use of data from biomass assessment surveys that were conducted in 2020 and 1998 in the demersal zones of Lake Malawi. The two surveys covered the following districts which were categorised in regions as follows; Karonga, Nkhata Bay, central (Nkhotakota and Salima), Southwest Arm (SWA) covering Dedza and Mangochi and the Southeast Arm (SEA) in Mangochi district (Fig. 1).

2.2 Survey equipment

Research vessel Ndunduma, a 17.5 m stern trawl, powered by a 386 Hp Caterpillar engine, was used in carrying out the surveys. The vessel used a 38 mm mesh-sized codend Guttorpur bottom trawl net with horizontal and vertical openings of about 14 m and 4 m, respectively. An on-board global positioning system (GPS) receiver was used to locate the stations. The trawling speed was restricted to 2.5 knots/hour (4.6 km/hour). Since catchability of species and their respective sizes depend on the trawling duration, hauls were standardised to an interval of 30 min. The research team from the Research Division of the Department of Fisheries was involved in both designing and implementation of the surveys.

2.3 Sampling procedure

Once the fish were moved from the net into the receiving bin, a 30% sample was randomly collected from the landed catch. Where the sample was too big for handling, a sub-sample was drawn from the sample. The procedure was done following protocols recommended by Sparre and Venema (1989). The total catch was determined by a summation of all the

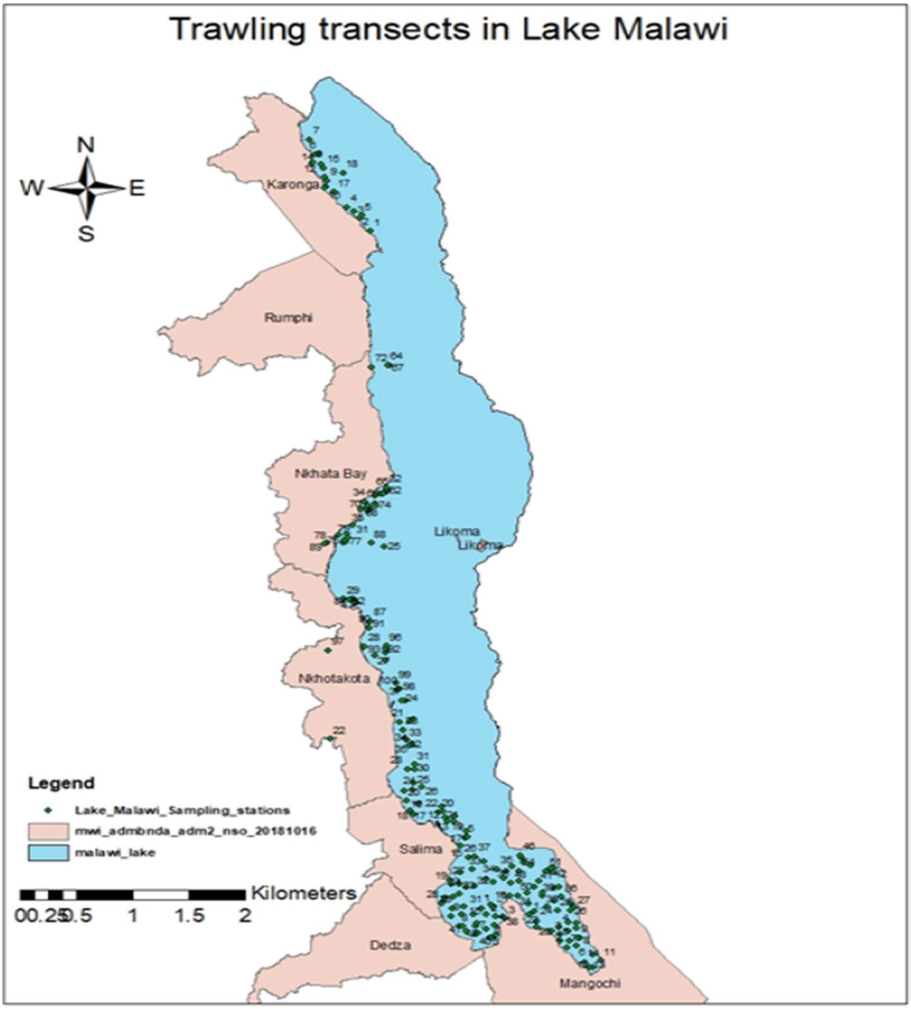

Fig. 1 Sampling points used in the 2020 and 1998 demersal trawl surveys in Lake Malawi

number of fish containers (with predetermined weight) filled with fish. The fish sample was then sorted by species by taxonomists while making references to Fish Taxonomy Field Guides by Turner (1996) and Ad Konings (2016). Individual total length (TL) in mm and weight in g using stainless ruler and digital weighing scale respectively were measured. Data collection form was designed and used in capturing both metadata and the catch data.

2.4 Data source and processing

Data for the two surveys was collected at Monkey Bay Capture Fisheries Research Station under the Department of Fisheries. Technical Assistants of the station were engaged in the data entry in Microsoft Excel package. Fish catch composition for the two surveys was compared through cross-tabulation using pivot tables in Microsoft Excel. Graphs of the catch composition at family and genus levels were produced in SigmaPlot 12.5 upon importing the dataset from the Microsoft Excel.

2.4.1 Size structure and distribution

To determine size structure, length frequency distribution data was modelled with probability density function for determining the likelihoods for the gamma distribution (Hastings & Peacock, 1975) as shown;

$$L\{x|c,b\} = \frac{\left(\frac{x}{b}\right)^{(c-1)\frac{-x}{e^{b}}}}{\mathrm{b}\Gamma(c)}$$

where x is the value of the variate, b is the scale parameter, c is the shape parameter, and $\Gamma(c)$ is the gamma function for the c parameter. The values for b and c were guessed and the solver in Microsoft Excel 2021 was applied to generate the values for the best fit through iteration with GRG Nonlinear approach which only uses smooth nonlinear data. The set objective for the solver was to minimise the residual sum of squares (RSS) by adjusting the variables, b and c. The results from the solver were then imported in SigmaPlot 12.5 for production of the modelled length frequency graphs.

The choice of gamma distribution function was based on the flexibility of the function as it follows the behaviour of the size distribution hence, most biological scientists working with size structure data (Sullivan, 1992; Sullivan et al., 1990) prefer to use it. It is therefore one of the most powerful simulation tools in fisheries science (Punt et al., 2016).

Unlike in previous studies where weight-based assessments were widely preferred to determine the importance of fish species in the catch (Banda & Tomasson, 1997; M'balaka & Kanyerere, 2019), this study used their numerical importance as adopted by Turan (2022). The advantage of this approach is that it considers conservation-related aspects of smaller fishes that might otherwise not significantly contribute to the total catches. Lake Malawi is dominated by cichlids, most of which are smaller in sizes. It was therefore imperative that this assessment approach was selected for realistic fisheries diversity conservation recommendations.

Length frequency distributions for the top five fish species were modelled using the logistic model (Holt, 1963). The logistic model shown below was used to determine the probability of a fish being retained by the trawl net.

$$P_{(L)} = \frac{1}{1 + e^{-k(L-L_{50})}}$$

where P is the probability of capture of the gear on a fish of size L, L_{50} is the size-at-50% which is the mean length at which 50% of the fish encountered by the trawl net is retained in the cod-end (mean length at first capture), and k is a parameter related to the size range which changes from values between 0 and 1. Again, the values for L_{50} and k were guessed and solver in Microsoft Excel 2021 was used to generate the best fit values through iteration with GRG Nonlinear approach. The set objective for the solver was to minimise the residual sum of squares (RSS) by adjusting the variables, L_{50} and k. The results from the solver were then imported in SigmaPlot 12.5 for production of the sigmoid shaped graphs.

2.5 Fish species diversity

Fish species richness and abundance have been used broadly to describe and assess the status of fisheries ecosystems (Van Oppen et al., 1998). This study determined fish diversity in two ways; Species richness (number of species in the study area) and species abundance as a relative number of species (Gorman et al., 1978). Species diversity indices for the two time periods were calculated and compared using the Shannon and Weaver (1949) relationship.

$$H = -\sum_{i=1}^{n} \left(\frac{n_i}{N} [\log_2] \left(\frac{n_i}{N} \right) \right)$$

where H stands for the Shannon and Weaver index of diversity; n_{i} is the total number of individuals of a species and N is the total number of individuals of all species

To estimate the real diversity, effective number of species (ENS) was estimated by getting the exponential of the Shannon and Weaver Index ('H) (Van Oppen et al., 1998) as shown below.

$$ENS = Exp('H)$$

3 Results

3.1 Catches sampled

Table 1 provides a summary of the total recorded catches by region for both 2020 and 1998 biomass assessment surveys. The 2020 biomass assessment survey recorded 27,261.6 kg of fish against 37,853.2 kg registered in the 1998 survey thereby representing a decrease of 28%. At regional level, the recent survey recorded 713.3 kg of fish in Karonga which represented a drop of 58.1% from 1700.6 kg reported in 1998. Another big decline was recorded in the SEA where catches of 9,233.1 kg were registered in 2020 against 17,912 kg recorded in the previous survey translating into a 48.5% drop. The central part and the SWA reported declines of 13.4% and 4.6%, respectively. Nkhata Bay was the only site that reported an increase of 12.3% between the two surveys.

Table 1 Comparative results of total fish catch and mean catch rates between 2020 and 1998 surveys

Region	2020			1998		
	No of stations	Total catch (kg)	Mean catch rates (kg/0.5Hr)	Total catch (kg)	Mean catch rates (kg/0.5Hr)	Change (%)
Karonga	7	713.3	101.9 ± 53.8	1700.6	242.9 ± 148.3	− 58.1
Nkhata Bay	14	4,267.7	304.8 ± 46.6	3800.9	271.5 ± 44.2	12.3
Central	29	7,130.0	245.9 ± 28.3	8234.0	283.9 ± 37.2	− 13.4
SWA	27	5,917.5	219.2 ± 28.4	6205.6	229.8 ± 25.1	− 4.6
SEA	39	9,233.1	236.7 ± 52.6	17,912.0	459.3 ± 67.8	− 48.5

3.2 Fish species composition

The 2020 survey recorded fishes comprising 7 families, 45 genera and 149 species. The catch from the former survey on the other hand consisted of 7 families, 45 genera and 158 species. The family Cichlidae that contributed 86% in 2020 and 83% in 1998 survey was dominant in both surveys (Fig. 2). The Cichlidae dominance in the recent survey, was followed by Clariidae, Bagridae, Mormyridae and Mochokidae with 7.1%, 3.4%, 1.4% and 1.2%, respectively. The family Cyprinidae had smaller contribution of less than 1%. In the former survey, family Bagridae Clariidae, Mochokidae and Cyprinidae with 6%, 5%, 5% and 1%, respectively followed the dominant display of the Cichlids. Family Mastacembelidae and Mormyridae had insignificant contributions of less than 1% each in the earlier survey.

At genus level, Fig. 3 shows fish that contributed to more than 1% of the total sampled catches. The recent survey recorded *Lethrinops* (23%) *Copadichromis* (9%), *Placidochromis* (9%), *Aulonocara* (8%), *Otopharynx* (7%) and *Diplotaxodon* (7%), as the most common with a combined contribution of more than 60%. In the former survey, *Lethrinops* (22%) *Otopharynx* (10%), *Copadichromis* (9%), *Aulonocara* (8%), *Diplotaxodon* (7%), *Rhamphochromis* (6%) *Alticorpus* (5%) and *Bagrus* (4%) were the most important genera in the sampled catches. The genera *Taeniolethrinops*, *Stigmatochromis* and *Placidochromis* were the least in the 1998 survey.

In the category of fish genus that contributed less than 1% in the recent survey, the genera *Synodontis* (0.71%) and *Sciaenochromis* (0.57%) contributed more than 0.5% each (Fig. 4). The least were the genera *Barbus, Corematodus, Docimodus* and *Labeo* with 0.013%, 0.011%, 0.011 and 0.002%, respectively. The 1998 survey recorded *Pallidochromis* (0.86%), *Chilotilapia* (0.84%), *Engraulicypris* (0.79%), *Ctenopharynx* (0.74%),

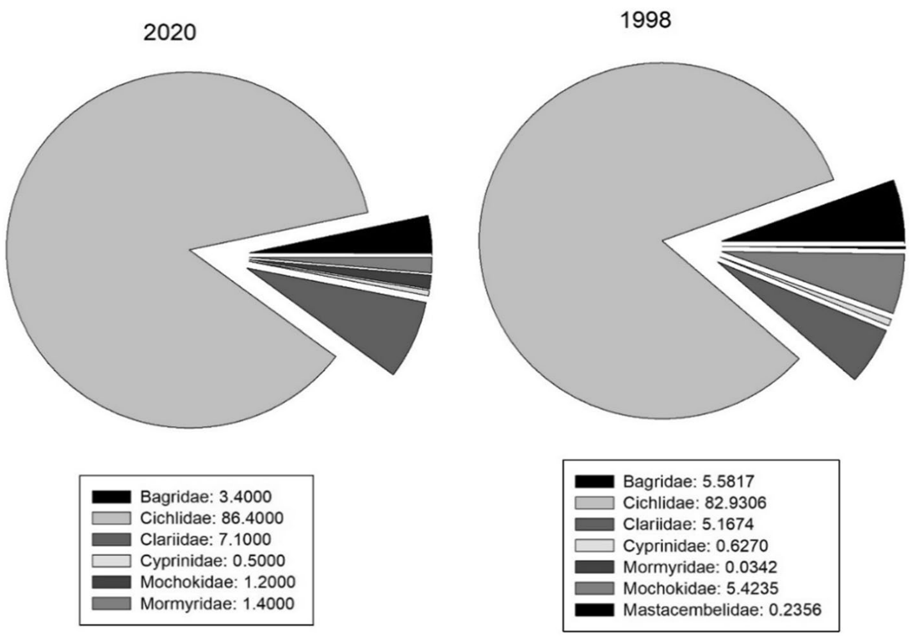

Fig. 2 Catch composition at family level between 2020 and 1998 biomass assessment survey

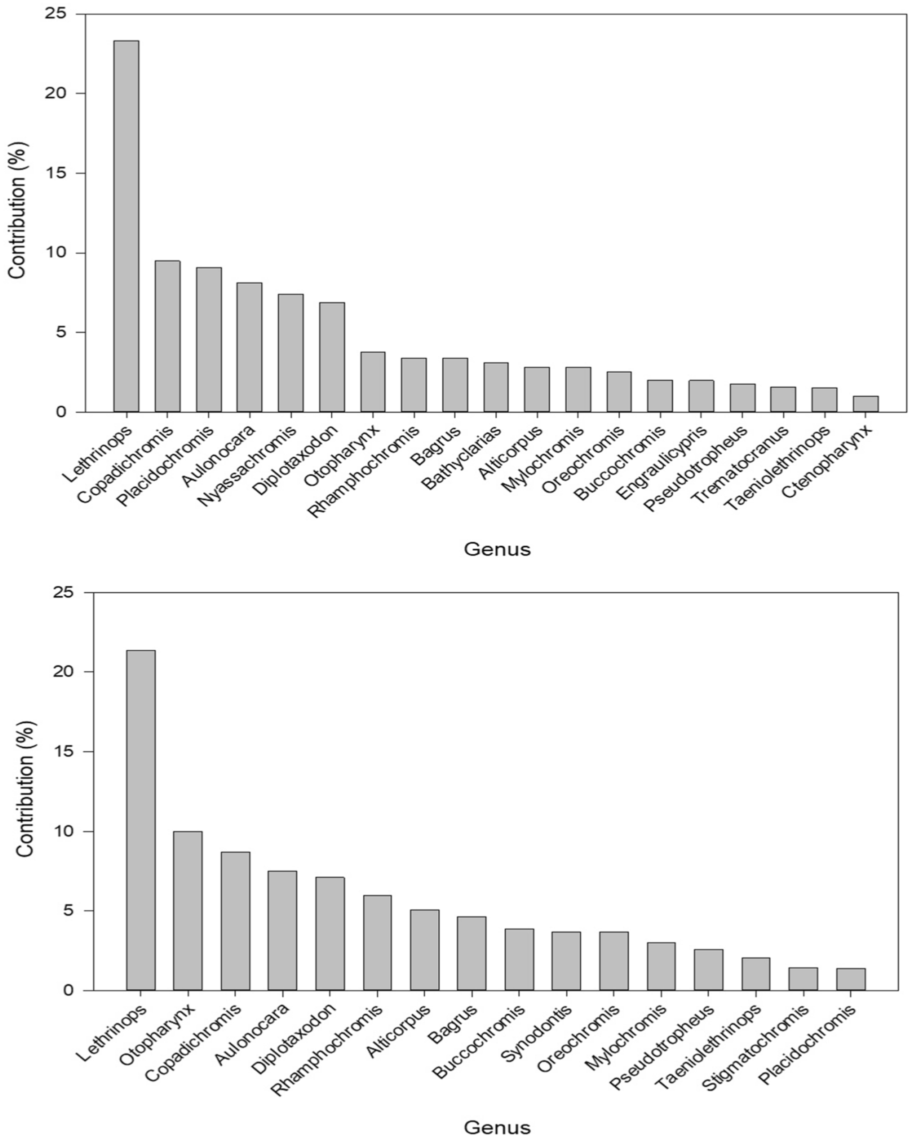

Fig. 3 Catch composition by dominant fish genera that contributed more than 1% in the 2020 (Top) and 1998 (Below) surveys

Nimbochromis (0.65%) and *Hemitaeniochromis* (0.62%) having contributions of more than 0.5% each. The genera *Labeo, Lichnochromis* and *Clarias* with 0.01%, 0.002% and 0.002%, respectively were the least.

From the 149 fish species recorded in the recent survey, the SEA dominated with 119 species followed by central with 113 species. The trend was similar to the one reported in 1998 survey. The third highest number of fish species (92) was also registered in SWA while Nkhata Bay and Karonga on the other hand recorded 62 and 46 species, respectively.

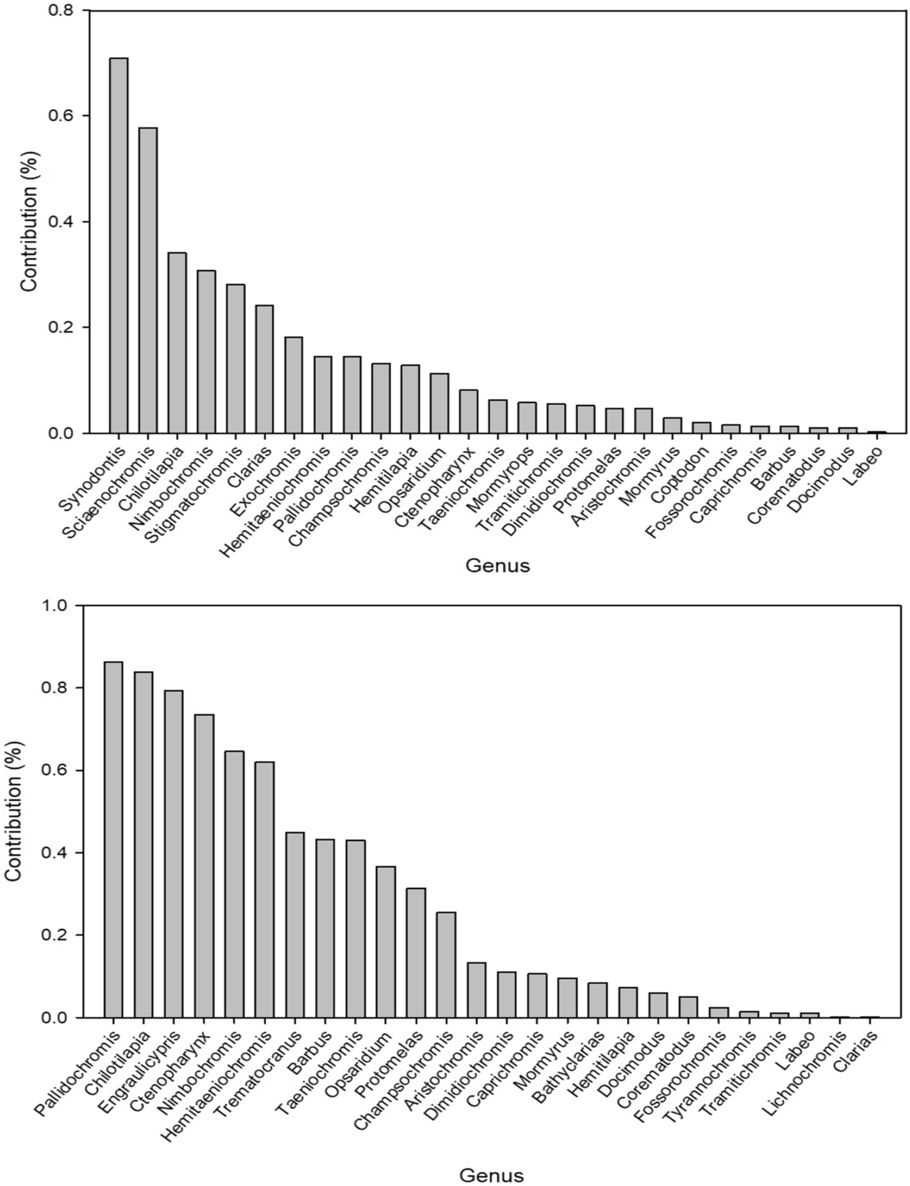

Fig. 4 Catch composition by fish genera with less than 1% contributions in 2020 (top) and 1998 (below) surveys

In terms of number of sampled specimens recorded in the recent survey, SEA with 14,890 was again dominant followed by SWA and central with 10,075 and 8,713 individuals, respectively. Nkhata Bay and Karonga were the last two with 3,305 and 1104, respectively. A further assessment of the 38,037 spacemen indicated that *Otopharynx argyrosoma* (2,541), *Copadichromis virginalis* (2051), *Lethrinops oliveri* (2011), *Aulonocara minutus* (1675) and *Placidochromis longimanus* (1607) had a numerical advantage from the rest.

Hence, the five top most abundant fish species were subjected to length-based analyses and Table 2 provides a summary of the parameters used.

The 1998 survey reported a total of 49,223 specimens which comprised 2170 in Karonga, 5882 in Nkhata Bay, 10,244 in the central, 13,987 in the SWA and 16,940 in the SEA. At regional level, the highest number of fish species was recorded in the SEA with 125 which was closely followed by the central part with 120. The third highest was SWA with 110 species whereas Nkhata Bay and Karonga were the last two with 70 and 43 species, respectively. A numerical assessment of the 158 fish species indicated that *Otopharynx argyrosoma* (3,899), *Bagrus meridionalis* (2282), *Copadichromis virginalis* (2136), *Diplotaxodon limnothrissa* (1984) and *Synodontis njassae* (1812) were among the top five fish species.

3.3 Size structure and selectivity of selected fish species

The top five dominant fish species were subjected to further length-based analyses to determine their size structure. The fishes were analysed at two levels; using the gamma distribution function and logistic model for gear selectivity. Table 2 shows the solver fitted parameters that this study used to plot length frequency graphs and selection ogive.

Figure 5 and Table 2 show modelled size structure for *O. argyrosoma, C. virginalis, L.* 'sp oliveri'*, A. minutus* and *P. longimanus* sampledin the recently survey. The study registered the smallest *O. argyrosoma* of 51 mm and the largest being 121 mm with a mean total length of 83.3 ± 0.25 mm. The model predicted a modal length of 85 mm for the fish. The smallest *C. virginalis* measured 40 mm and the largest was 160 mm with a mean total length of 97 ± 1.02 mm. The model estimated a value of 108 mm as the modal length for the fish. The 2020 survey recorded sizes of *L.* 'sp oliveri' that ranged from 32 mm to 155 mm with an average total length of 83.9 ± 0.35 mm. The predicted modal length was estimated at 83 mm. Length for *A. minutus* ranged from 40 mm to 80 mm with a mean total length of 67.7 ± 1.08 mm. The sampled fish had a length distribution estimate of 72 mm as modal length. The sizes of *P. longimanus* ranged from 42 mm to 135 mm with an average total length of 75.6 ± 0.85 mm. The predicted modal length of *P. longimanus* was 77 mm.

Table 2 Solver fitted parameters for Gamma distribution and Logistic Models for the top 5 fish species

	Fish species	Sample (*n*)	Gamma model parameters			Logistic model	
			Phi	Sigma	Modal length (mm)	L_{50}	Sigma
2020	*Otopharynx argyrosoma*	2541	0.81	105.30	85	81	0.14
	Copadichromis virginalis	2051	0.95	115.38	109	97	0.08
	Lethrinops 'sp oliveri'	2011	0.80	105.44	83	81	0.13
	Aulonocara minutus	1675	0.72	100.40	72	67	0.20
	Placidochromis longimanus	1607	0.83	93.45	77	74	0.20
1998	*Otopharynx argyrosoma*	3899	0.70	118.59	82	85	0.14
	Bagrus meridionalis	2282	2.95	101.97	298	290	0.014
	Copadichromis virginalis	2136	1.02	118.46	120	114	0.08
	Diplotaxodon limnothrissa	1984	0.98	93.40	90	132	0.04
			2.06	78.65	160		
	Synodontis njassae	1812	1.1	118.54	130	122	0.11

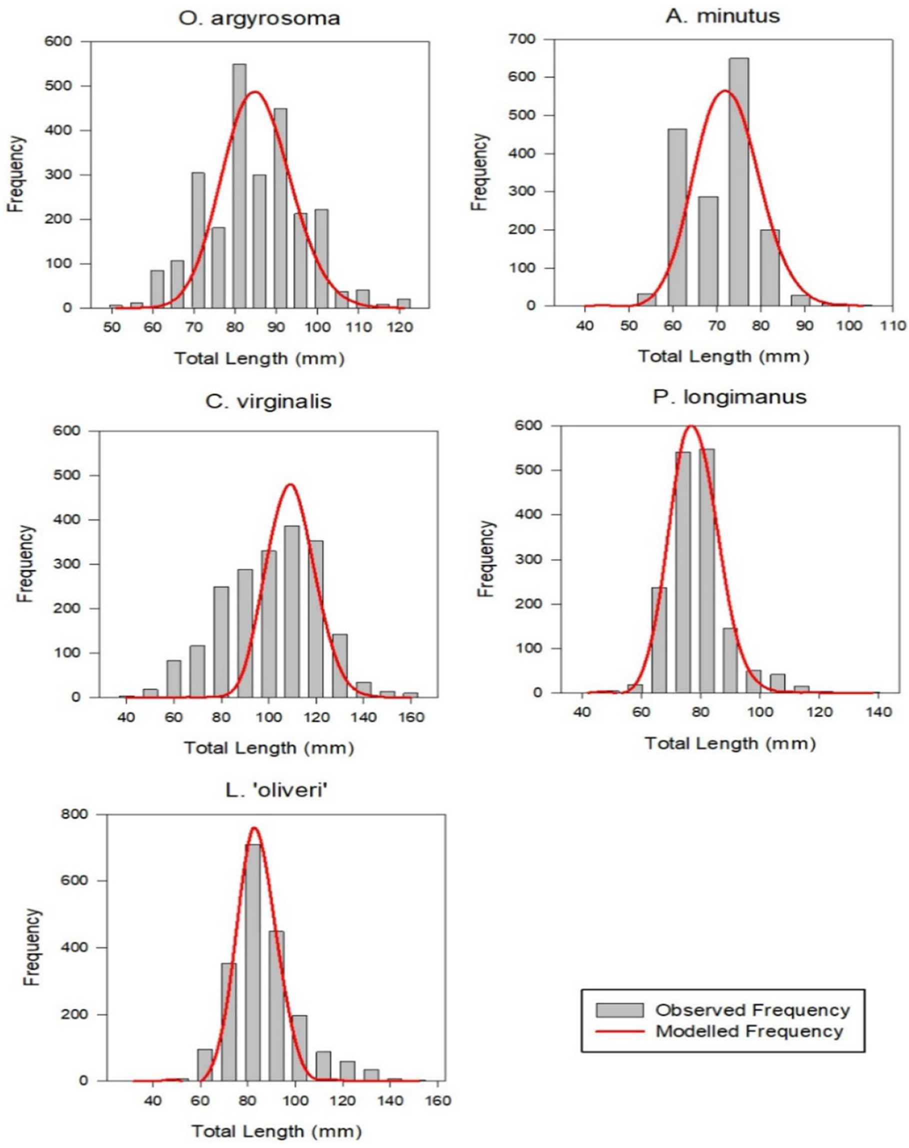

Fig. 5 Modelled size structure for top 5 fish species sampled during the 2020 survey

Table 2 and Fig. 6 show the selection ogive of the five fish species. The length at which *O. argyrosoma* had 50% chance of being retained by the 38 mm cod-end meshes was 81 mm. The values of L_{50} for *C. virginalis, L.* 'sp oliveri', *A. minutus* and *P. longimanus* were estimated as 97 mm, 81 mm, 67 mm and 74 mm, respectively.

The modelled size structures for *Otopharynx argyrosoma, Bagrus meridionalis, Copadichromis virginalis, Diplotaxodon limnothrissa* and *Synodontis njassae* for the former survey are shown in Fig. 7. The survey registered the smallest *O. argyrosoma* of 35 mm and the largest being 155 mm. The modelled length frequency distribution

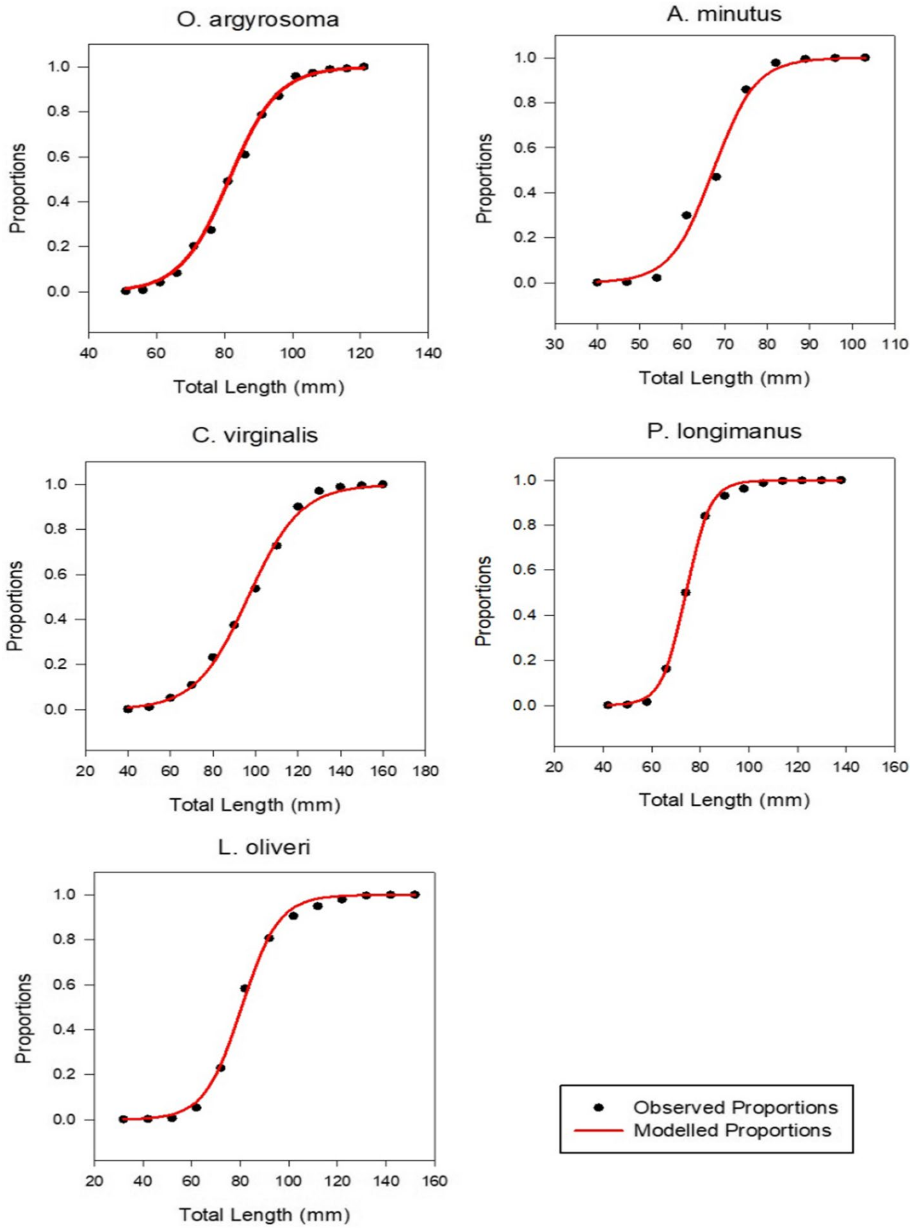

Fig. 6 Selective ogive for top 5 fish species sampled during the 2020 survey

clearly indicated that the study sampled most of the fish species with a total length ranging from 75 mm to 115 mm having a mean total length of 88 ± 1.01 mm. The model predicted a modal length value of 82 mm for the fish. According to this study that recorded a total of 2,282 individual *B. meridionalis*, the smallest fish measured 50 mm and the largest was 980 mm. The modal length of the fish species was estimated at 298 mm with

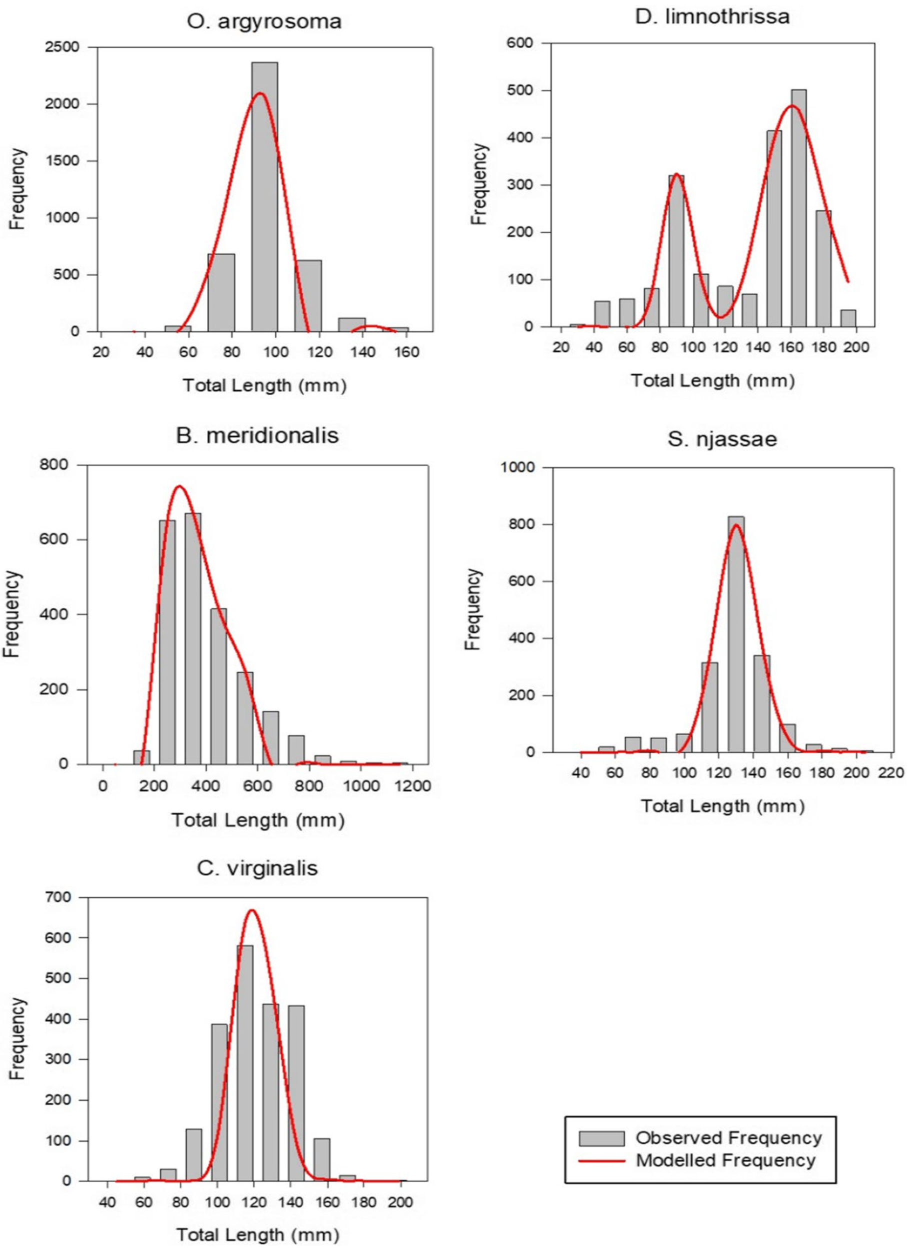

Fig. 7 A modelled size structure for top 5 five species sampled during the 1998 survey

a mean total length of 306.7 ± 2.11 mm. The smallest *C. virginalis* measured 45 mm and the largest was 195 mm having a mean total length of 114.6 ± 0.89 mm. The sampled fish had a modal length estimate of 120 mm. The study that registered a total of 1,984 *D. limnothrissa* specimens reported the smallest fish of 30 mm and the largest being 195 mm. The modelled length frequency distribution showed that the sampled fish belonged to two length peaks; the first one was at 90 mm while the second one was at 165 mm. Because of this, the model generated two separate parameters with the first modal length at 90.2 mm followed by another one at 160.2 mm. The sizes of *S. njasse* ranged from 40 mm to 205 mm with an average total length of 123.3 ± 1.11 mm. The predicted modal length from the model was 129.8 mm.

Figure 8 and Table 2 show the L_{50} values for *O. argyrosoma, B. meridionalis, C. virginalis, D. limnothrissa* and *S. njassae*. The length at which *O. argyrosoma* had 50% chance of being retained by the 38 mm cod-end meshes was 85 mm. The value for L_{50} for *B. meridionalis* was estimated at 290 mm while for *C. virginalis, D. limnothrissa* and *S. njassae* were 114 mm, 131.8 mm and 122 mm, respectively.

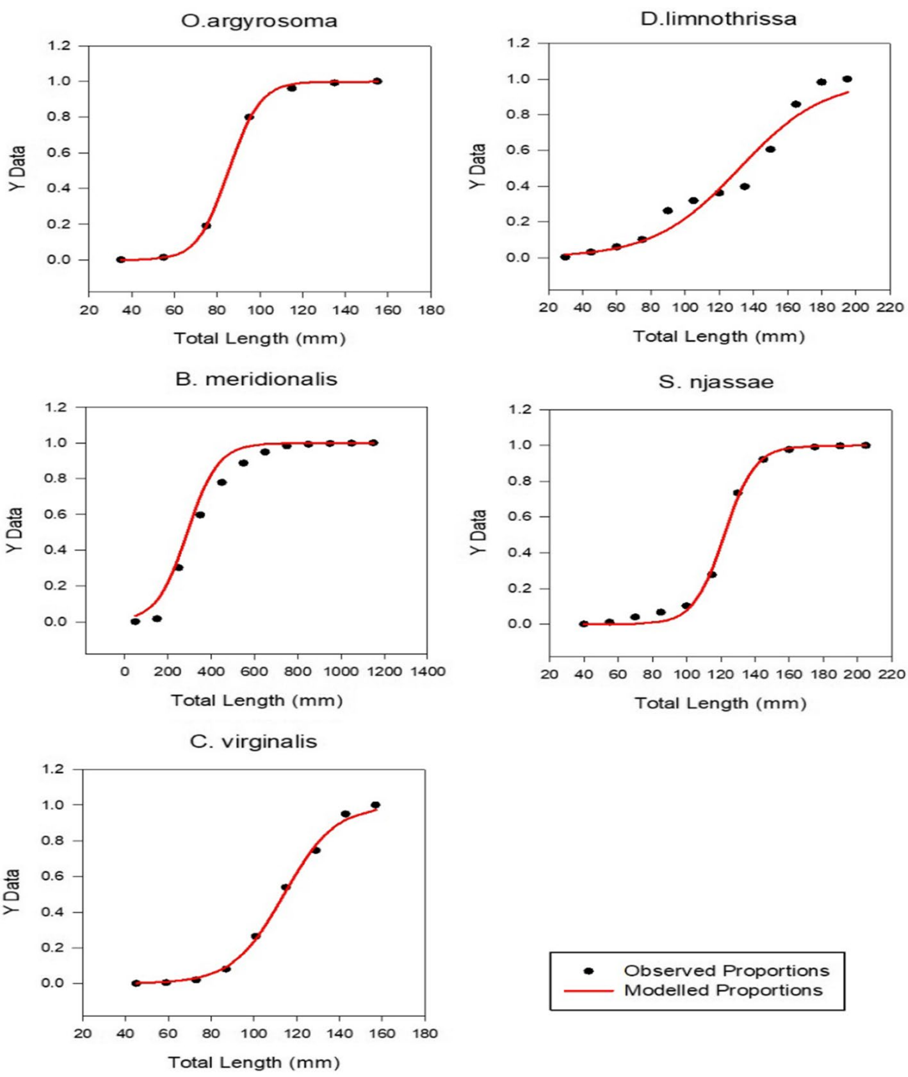

Fig. 8 Selection ogive for top 5 fish species sampled during the 1998 survey

3.4 Fish species diversity

An assessment of the fish diversity between the two surveys was conducted and the results indicated diversity indices of 3.84 and 4.06 for 2020 and 1998 surveys, respectively. Building on the estimated indices in both surveys, the effective number of species (ENS) was estimated as 47 for the 2020 survey and 58 for the 1998 survey. Besides reporting differences in the total number of fish species, the two surveys further differed on a number of fish species in that some species were appearing either in the 1998 or the 2020 survey.

The 2020 biomass assessment survey reported fish species amounting to 36 that were not there in the former survey whereas the 1998 survey registered a total of 43 fish species that were not recorded in the recent survey. Within the fish species that were only available in the recent survey, a total of 16 genera originating from Cichlidae and Mormyridae families were recorded. Out of the 43 fish species that were exclusively available in the 1998 survey, a total of 20 fish genera formed from 3 families namely Cichlidae, Clariidae and Cyprinidae were recorded. The study recorded unusually significant quantities of Mormyrids during the 2022 biomass assessment survey. A total of 18 specimens of the rare *Mormyrops anguilloides* measuring 1,110 mm to 1,215 mm with an average weight of 12.4 kg were caught around Luweya River mouth in Nkhata Bay.

4 Discussion

The Cichlidae family continues to dominate the demersal zones of the Lake Malawi fishery as witnessed by the significant occurrence in both surveys. Similar results have also been reported in Lake Victoria (Masai et al., 2004; Okaronon et al., 2022) and Lake Tanganyika (Kimirei et al., 2008). The uniqueness with Lake Malawi cichlids is that more than 90% of them are endemic (Sayer et al., 2019) and rapid radiation has produced the greatest number of these species (Albertson & Pauers, 2019). The small contribution of the larger Cyprinids in the recent survey points out to its overexploitation as it is highly targeted both in the open water seines and hooks (Department of Fisheries, Unpublished data). However, *usipa*, *Engraulicypris sardella* which falls under the Cyprinids family currently contributes significantly to the total fish landings of the country (Government, 2021; Kolding et al., 2019). Similar dominance of smaller cyprinids has been widely reported in many tropical lakes such as Lakes Kariba, Mweru, Kivu, Victoria and Tanganyika (Kolding et al., 2019) with several social-economic and ecosystem benefits being highlighted.

Significant presence of bigger genera like *Otopharynx, Rhamphochromis* and *Bagrus* was reported in the former survey but very little in the recent survey. Instead, these were replaced by smaller haplochromine species namely *Otopharynx* and *Placidochromis*. Similar results were reported by (Banda & Tomasson, 1997), later on concurred with Turner et al. (2005). The study findings revealed that the replacement of larger fishes with smaller ones has not improved over the years. Unlike in the previous studies, this continued species shift could recently be acerbated by the environmental degradation and climate change events. Kolding et al., (2019) reported of a complete takeover of smaller fishes in all inland water bodies in Africa. The scenario which primarily was created through overexploitation of larger fish fits well with the concept of fishing down the food web (Pauly et al., 2000), clearly demonstrating how fishers adjust their preferences in response to overfishing of particular large sized fish stock. Similar incidences of species shift have widely been reported in Lake Victoria where a deliberate introduction of *Lates niloticus* brought about substantial changes in the fish species particularly the haplochromines (Njiru et al., 2005; Ogutu-Ohwayo, 1990; Ouma et al., 2005).

This study further reported a dominant contribution of *Otopharynx. argyrosoma* which was one of the major haplochromine species to have taken over the fisheries. The fish species, widely distributed in the southern part of Lake Malawi (Konings, 2016; Turner, 1996). The substantial presence of the fish in Lake Malombe as reported by Kanyerere & M'balaka (2017) signifies the importance of the connection between the two water-bodies through the Shire River. The dominance of *Otopharynx species* can be explained by their increased presence in deep waters (Turner, 1996) currently under-exploited by both artisanal and commercial trawl fishers. The commercial trawl fishery is dominated by the semi-pelagic trawling (Government, 2021) hence most of the *Otopharynx* species are spared as they are predominantly bottom dwellers. Even with the few available bottom trawlers, harvesting of the bottom-dwelling fish is impinged by the nature of the lake bottom which in most cases act as 'silent policemen.' The nature of bottom of Lake Victoria (muddy bottom) has been reported to restrict full use of bottom trawling (Okaronon et al., 2022) while water depth in Lake Tanganyika is reported to serve the same purpose (Kimirei et al., 2008). The fish was reported by Turner (1996) to have a maximum length of 150 mm which agrees to the length range reported by this study. However, based on the maturity information which states that the fish matures at 92 mm, it was noted that the two surveys were catching most of the fish in an immature state which becomes a conservation challenge.

The zooplanktivorous *Copadichromis virginalis and Diplotaxodon limnothrissa* were the two pelagic fish species common in the study. Besides commonly recorded in trawlers, these two fish species are also in abundance in the small-scale gillnet fishers (Department of Fisheries, Unpublished Data) indicating that the two fisheries are exploiting the same resources. The study has revealed that the sampled *C. virginalis* were caught while sexually mature as most of them mature around 80 mm to 140 mm Turner (1996). Catch and effort statistics from the Department of Fisheries indicates that *Diplotaxodon* and *Copadichromis* species contribute to more than 80% of the commercial trawl landings (Department of Fisheries, Unpublished Data). The resilience of the two fish species has been noted indicating how buoyant the fish have been to fishing pressure coupled with environmental degradation in the lake and the catchment. The absence of trawlers in some parts of central and the northern region may also likely aid in the increased production of the offshore fish stocks. The study further recognised the contribution of rare fish species and a total of 13 species that contributed an individual specimen was recorded. The notable rare fish species that were recorded were *Labeo cylindricus* and *Placidochromis milomo*. The small contribution by these fish species may not necessary mean that they are less abundant in the lake but might point out to the sampling equipment not being appropriate for the job. The unusual significant appearance of fully grown *Mormyrops anguilloides* in the recent survey in Nkhata Bay was also observed. The adult fish are reported to prefer deep and quiet waters between boulders and overhangs that are away from strong water currents (Skelton, 2001). This habitat preference concurs with where the fish were sampled as the site was characterized by the presence of artificial reefs (*Zilundu*) submerged by the communities to act as fish aggregating devices.

The lake has undergone noticeable changes in the fish species diversity and this could be attributed to the overexploitation of the fish stocks through increased fishing pressure. Of great concern is the overexploitation of shallow water fish species like *Oreochromis species* whose preference for shallow waters for breeding and nursery is further threatened by their slow growth and low fecundity (Bulirani et al., 2005). The observation of overexploitation in the shallow water zones was previously reported by Banda and Tommason (1997), M'balaka and Kanyerere (2019). Elsewhere, illegal and destruction of spawning and nursery grounds have been blamed for the fisheries resource destruction in Lake Victoria (Masai et al., 2004), Lake Tanganyika (Kimirei et al., 2008) and in many inland waterbodies (Kolding et al., 2019). The lake just like elsewhere has recently been cleared in the shores for easy operations of beach seining while poor farming practices upstream have equally brought about siltation and chemical overload in the systems (Bootsma & Hecky, 2003; Kolding et al., 2019; M'balaka & Kanyerere, 2019; Ogutu-Ohwayo, 1990). Of late, the overfishing is not only occurring in the shallow waters, as the study results have indicated that the deeper water species are similarly threatened. The threat being caused to the deeper water demersal fish species is enormous since these fishes are naturally confined to particular environments with minimum mobility (Weyl et al., 2010). The restricted movements pose threat to their existence as some gears like trawl nets and lift nets have the potential to eliminate them in their designated habitats in a short period of time (Weyl et al., 2010). The demersal fish stocks are therefore more fragile in the sustainable fisheries management in comparison with the free swimming pelagic fish stocks.

Fish biodiversity is associated with a number of biophysical characteristics of the habitats (Danley & Kocher, 2001; Sayer et al., 2019). The area sampled in Karonga which reported the lowest fish diversity is characterized by shallow sandy habitats stretching from Kaporo to Chilumba (Turner, 1996). The central region (Salima and Nkhotakota) reporting high fish diversity is characterized by outcrops extending from the Chia River mouth to around Benga. The Nkhotakota District has artificial reefs installed by communities around the Nkhotakota Boma which deter active fishing operations. Mbenji Island in Salima, still managed by local leaders (Njaya, 2007) could be another site of higher fish diversity in the region. The central region is moreover well connected to three major tributary rivers namely Dwangwa, Bua and Linthipe (Sayer et al., 2019) and lagoons (Chia and Kambindingu) having potential of enhancing fish diversity in the lake. Rivers in Lake Tanganyika are reported to provide escape routes for overfished stocks of the lake (Kimirei et al., 2008) and it is therefore believed that similar cases occur in Central Lake Malawi. The high diversity in both SWA and SEA is accredited to the increased productivity of the regions, partly because of the shallowness of the regions (Weyl et al., 2010). The two regions are equally known for having many outcrops, islands and aquatic vegetation (Turner, 1996). Community initiated fish protected areas (fish sanctuaries) established around 2017 are similarly reported to increase fish diversity through spillover and recruitment effects (FISH, 2018).

Despite several challenges being faced in the management of the fisheries resources, positive strides have recently been registered in Lake Malawi fisheries. An adoption of vessel monitoring system (VMS) to monitor compliance of vessels regarding fishing areas and fishing times is one of such interventions. The system aims to monitor activities of all trawl vessels in the waters of Lake Malawi including fishing duration which directly provide accurate estimates of fishing effort; adherence to their designated fishing areas and depth zones. Another optimistic development is the introduction of 3-month closed season for the commercial trawl fishery from December to February which commenced in the 2020/2021 fishing season (Department of Fisheries, 2020). The local fisheries management authorities (LFMAs) such as the beach village committees (BVCs), fisheries association (FAs) and commercial fisheries associations (CFAs) have been resuscitated. In line with the Chambo Restoration Strategic Plan (2005), the fisheries have also seen a rise in the establishment of community-owned fish protected areas. In most cases, these areas are installed with fish aggregating devices (FADs) and other barriers to deter any active fishing within those zones (FISH, 2018). Recently, the Government of Malawi has also banned the importation and use of the ecologically damaging monofilament gillnets.

All in all, Lake Malawi demersal fishery has not significantly changed in terms of fish species richness and abundance. As previously reported, the fishery continues to experience fish species shift; larger and commercially important fish species have been replaced by smaller haplochromines species. The fishery is also going through a growth overfishing as the dominant fish species were being harvested prematurely. To avert this trend, previous studies (Duponchelle et al., 2003; Kanyerere, 1999) recommended an upward adjustment of the cod-end mesh-sizes from the current 38 mm. The small-scale and commercial trawl fisheries are harvesting the same fisheries resources and this was previously reported by Weyl et al., (Weyl et al., 2010), hence the need to revise the fisheries regulations that govern them particularly on the fishing areas and time of fishing.

5 Limitations

This study recognizes the following limitations likely to impact on the research results, conclusions and recommendations.

1. Bottom trawl surveys are always challenged by the nature of the lake bottom hence its sampling design and estimation of the fish diversity are to some extent negatively affected
2. Trawl net by design is selective based on the mesh-sizes of the cod-end hence the results on the fish stocks and species diversity may not be a full picture of the fishes in the study area
3. The *research vessel Ndunduma* used in both surveys has water depth limits as it cannot sample in waters of less than 5 m because of its bigger size. This means that it leaves out fish species that are found in those habitats thereby affecting the results on biodiversity and abundance

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Author contributions All authors contributed to the study's conception and design. Material preparation, data collection and analysis were performed by MSM. The study proposal was extensively edited by EK, GK, DJ and AM. The first draft of the manuscript was written by MSM and all authors commented from the first draft to the final versions of the manuscript. All authors read and approved the final manuscript.

Data availability The datasets generated during and/or analysed during the current study are not publicly available as this work is part of the thesis which is not yet defended but are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The main author who is also the corresponding author received financial support from the REFRESH Project for the study. Emmanuel Kaunda and Geoffrey Kanyerere, by being supervisors, have financial interest from the funders. Daniel Jamu is employed by the project as a Deputy Chief of Party, hence has a financial interest. Amulike Msukwa has no financial interest in the study.

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