



RESEARCH PAPER

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Population parameters and exploitation rate of *Sarotherodon melanotheron melanotheron* rüppell, 1852 (Cichlidae) in Lake Toho, Benin

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Abstract

Aspects of the population dynamics of *Sarotherodon melanotheron melanotheron*, which is a commercially important fish species in Lake Toho, were described based on 1558 specimens collected monthly between January and December 2012 from artisanal captures. The size at first maturity was estimated at 6.9 cm for males and 7.7 cm for females. The asymptotic length obtained by analyzing frequency data with FiSATII software (FAO-ICLARM) has been estimated at 21.5 cm. Further, the von Bertalanffy growth coefficient was 0.58 year⁻¹ and the overall growth performance index was 2.43. The estimates of the total, natural and fishing mortalities were 1.95, 1.37 and 0.58 year⁻¹ respectively. The current exploitation rate was 0.30 and as such, remains below the maximum exploitation rate which was 0.55 according to the selection ogive procedure. However, this value is superior to the exploitation rate at 50% of its unexploited biomass ($E_{0.5} = 0.27$). Therefore, a reduction of the current exploitation rate is needed by, at least, 10% to maintain a sufficient biomass. The size at first capture was estimated at 6.7 cm which is lower than the size at first maturity for both sexes, but especially for females. These parameters clearly reflect a current trend of overexploitation.

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Introduction

The Mono basin, shared between Benin and Togo, counts many lakes within its modest surface (0.2-15 km²) in its lower course in Benin (Amoussou, 2010). Amongst them is Lake Toho, in which Cichlidae fish constitute about 98% of the total captures. *Sarotherodon melanotheron melanotheron* Rüppell (1852) (A.A. Brahim, unpubl. data) is the most abundant species both in number (92%) and weight (95%). The species abundance coupled with its lucrative market value subjects it to intense fishing activity by varied fishing methods, mainly large scoops. Such an intense exploitation may cause a depletion of this resource and further the deterioration of social conditions of fishermen. The annual statistics of fish (unpublished) from Benin's Department of Fisheries show that the species abundance has declined between 1990 and 2012. Therefore, knowledge of the population dynamics of the species is necessary for its rational management in view of its importance as a socio-economic resource (Lowe McConnell, 1999; Al-Barwani *et al.*, 2007).

Prior to this study, no studies had been conducted to estimate growth parameters and exploitation rate on fish from Mono basin despite its importance as a fisheries resource. One study (Niyonkuru, 2007), was done on three species of Cichlidae i.e *S. m. melanotheron*, *Tilapia guineensis* (Bleeker in Günther, 1862) and *Hemichromis fasciatus* (Peters, 1852) in Lake Ahémé (Couffo basin) and Lake Nokoué (Ouémé basin). The present study was undertaken to assess the population parameters and the level of exploitation of *S. m. melanotheron* in Lake Toho. The study intends to contribute essential scientific information for rational management and exploitation of *S. m. melanotheron*.

Materials and methods

Study area

Lake Toho (6°35'-6°40'N, 1°45'-1°50'E), is located in the lower course of the Mono basin in Southern Benin. It covers an area of 9.6 km² at low water level

and 15 km² during the flood season (Fig. 1). Its average length and width are 7 km and 2.5 km respectively. The lake was once directly connected to the Sazué River, a tributary of the left bank of the Mono River that fed it with brackish water. This connection is now only re-established only during periods of extreme floods, a scenario that justifies the presence of an isolated population of *S. m. melanotheron* which forms the rationale of this study.

Due to its geographical location, Lake Toho is influenced by a sub-equatorial climate characterized by four distinct seasons: (1) a long rainy season from mid-March to mid-July, (2) one dry season from mid-July to mid-September, (3) a short rainy season from mid-September to mid-November and (4) a long dry season from mid-November to mid-March dominated by continental winds and harmattan. The annual rainfall varies between 544 mm and 1376 mm while the temperature is between 20.6 and 33.5°C with an annual average of 28°C. Relative humidity is very high and varies from 65% in January to 80.6% in June (ASECNA 1981-2010, Cotonou station).

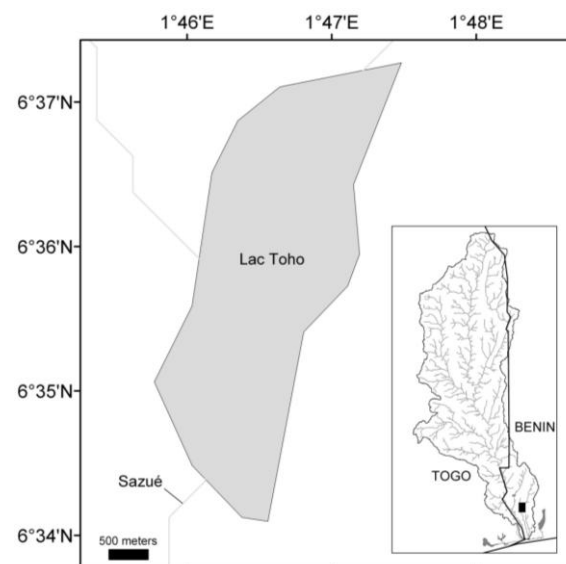


Fig. 1. Study area.

Sampling method

Samples of *S. m. melanotheron* were collected from commercial captures. The fish were caught between January and December 2012 using locally assembled

scoops (handle: 2.5-3.0 m, opening: 1.0-1.5 m in diameter, variable mesh). All specimens collected each month were brought to the Laboratory of Hydrobiology and Aquaculture (LHA) of the University of Abomey-Calavi (Benin), where they were identified using the Teugels and Thys van den Audenaerde (2003) key. Some specimens were deposited to the Royal Museum for Central Africa (RMCA), Tervuren, Belgium for establishment of a reference collection and verification of the species identification. At LHA, the total length of all fish was measured to the nearest centimeter using an ichthyometer. They were also individually weighed using an electronic precision balance (0.01 g) and sexed (immature, male or female) following Lalèyè *et al.* (1995a, b).

Length Weight Relationship (LWRs)

The LWRs was estimated through the equation of Le Cren (1951):

$$W = aTL^b \quad (1)$$

where W represents the body weight in grams (g), TL is the total length in centimeters (cm), a is a scaling constant and b is the slope or the allometric growth coefficient. The coefficient b varies between 2 and 4, but is often close to 3. The confidence limits for b was assessed using Statview software (Version 1992-1998). In order to check whether b was different from 3, the t-test was performed following equation of Sokal and Rohlf (1987):

$$ts = (b-3)/SE \quad (2)$$

where ts is the t-test value, b the slope and SE the standard error of b. The test was considered significant at 5% ($p < 0.05$).

Size at first maturity (L_{50})

The size at first maturity (L_{50}), defined as the size at which 50% of all individuals are mature, was determined for males and females, through the equation of the sigmoid curve of percentages (P) of sexual maturity based on size classes (TL). Sigmoid curve was computed according to the following formula:

$$P = e^{(\alpha + \beta TL)} / (1 - e^{(\alpha + \beta TL)}) \quad (3)$$

where α and β are parameters of the model. The logarithmic transformation of the previous formula corresponds to the following: $\ln [P/(1-P)] = \alpha + \beta TL$, and by substituting $P = 50\%$ in the equation, L_{50} is obtained by the formula: $L_{50} = -\alpha/\beta$. Statview (version 1992-98) was used to calculate the observed proportion of mature fish, the estimated proportion and the coefficients α and β of the model. Specimens at stages 2-5 of ovarian development were considered as mature.

Growth parameters

Length measurements were grouped into 1 cm mid-length size classes for growth analysis. The von Bertalanffy model was used for this purpose. It expresses the length (TL) of fish as a function of its age according to the following expression:

$$TL = L_{\infty} (1 - e^{-K(t-t_0)}) \quad (4)$$

where TL is the length of the fish at time t, L_{∞} the asymptotic length that would be reached by the fish to an infinite theoretical age, K the rate at which the TL approaches L_{∞} , and t_0 is the age of the fish when TL is equal to zero.

The ELEFAN I (Electronic Length Frequency Analysis) software tool included in FiSAT II (FAO ICLARM Stock Assessment Tools) (Gayanilo *et al.*, 1996) was used to estimate L_{∞} and K parameters of the von Bertalanffy equation. Parameters a and b of the equation (1) were used. L_{∞} and K estimates were used to assess the growth performance index using the equation of Pauly and Munro (1984):

$$\phi' = \log_{10} K + 2 \log_{10} L_{\infty} \quad (5)$$

The age of the fish at zero length was obtained by the equation of Pauly (1979):

$$\log_{10}(-t_0) = -0.392 - 0.275 \log_{10} L_{\infty} - 1.038 \log_{10} K \quad (6)$$

Potential longevity, t_{max} , was worked out of the following formula (Taylor, 1962; Pauly, 1980):

$$t_{max} \approx 3/K \quad (7)$$

Mortality and exploitation rate

The total mortality coefficient, Z (year^{-1}), was estimated following the linear length-converted catch curve method incorporated in FiSAT II software. The final estimates of L_{∞} and K and the length distribution data for the species were used in this calculation (Pauly, 1983, 1984, 1990; Pauly *et al.*, 1995). Natural mortality rate M (year^{-1}) was estimated according to Pauly's (1980) empirical equation:

$$\log_{10}M = 0.654\log_{10}K - 0.28\log_{10}L_{\infty} + \log_{10}T^{\circ}C^{*} \\ 0.4634 - 0.0066 \quad (8)$$

K and L_{∞} are the parameters of the equation (4) and T , the average annual temperature of the water which is 28°C . Fishing mortality rate (F) was evaluated using the equation:

$$F = Z - M \quad (9)$$

The exploitation rate (E), was obtained from the relation:

$$E = F/Z \quad (10)$$

E expressed the proportion of a given cohort/population that ultimately dies due to existing exploitation pressure (Beverton and Holt, 1966).

Size at first capture and optimal size

The size at first capture (L_c) was estimated from the Ogive selection method whereby it is assumed that the chance of capturing any fish is a function of its length. The optimal length L_{opt} was estimated using Froese's (2004) equation:

$$L_{opt} = L_{\infty}(3/(3+(M/K))) \quad (11)$$

where L_{∞} and K are function of the von Bertalanffy growth and M the natural mortality rate.

Relative yield per recruit (Y'/R) and reference points

Beverton and Holt's (1966) modified model (Pauly and Soriano, 1986), was used to predict the relative yield per recruit (Y/R) of the species to the fisheries following the formula below:

$$Y'/R = \frac{EU^{M/K}[1-(3U)/(1+m)+(3U^2)/(1+2m)-(U^3)/(1+3m)]}{(13)} \quad (12)$$

where E corresponds to the current exploitation rate i.e. the fraction of death caused by fishing activity, F the fishing mortality rate, M the natural mortality coefficient and Z the total mortality coefficient. $U = 1 - (L_c/L_{\infty})$ is the fraction of growth to be completed by the fish after its entry into the exploitation phase (L_c = mean length at first capture, L_{∞} = asymptotic length), $m = (1-E)/(M/K) = K/Z$ (with K being the von Bertalanffy growth parameter). Relative biomass per recruit (B'/R) was estimated as:

$$B'/R = (Y'/R)/F \quad (13)$$

The reference points used to determine the status of *S. m. melanotheron* stock of Lake Toho were the fishing mortality rate (F); the exploitation level at which the marginal increase in yield per recruit reaches 1/10 of the marginal increase computed at a very low value of E ($E_{0.1}$); the exploitation level that will result in a reduction of the unexploited biomass by 50% ($E_{0.5}$); and the exploitation level that produces the maximum yield per recruit (E_{max}).

Recruitment patterns

The recruitment patterns were obtained by projecting length frequencies backward onto a one-year time scale (Moreau and Cuende, 1991).

Results*Length weight relationship*

The measurements of length and weight of all specimens ($N = 1558$) were used to describe the length-weight relationship of *S. m. melanotheron* in Lake Toho (Fig. 2). The total length ranged between 3.5 cm and 20.5 cm, while the total weight ranged between 0.8 g and 167.1 g. The following equation was obtained: $W = 0.0205TL^{2.9593}$ ($r^2 = 0.9893$, $SE = 0.008$). The allometric coefficient b was significantly different from 3 (Student's t -test: $p < 0.05$) and growth was of a negative allometric type ($b < 3$, confidence interval 95% of b : 2.944-2.975).

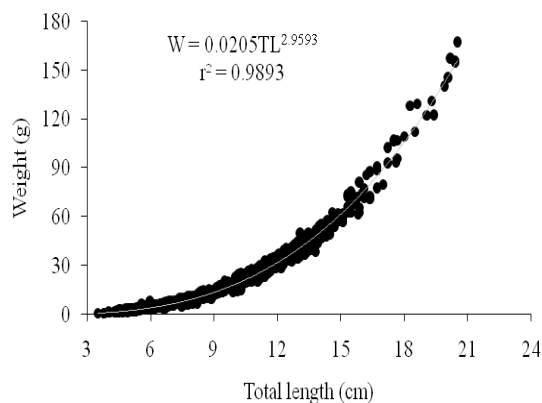


Fig. 2. Length-weight relationship of *Sarotherodon melanotheron melanotheron* from Lake Toho (N = 1558).

Size at first maturity

The maturity ogives for *S. m. melanotheron* (Fig. 3) showed that 50% of males and females were sexually mature at 6.9 and 7.7 cm respectively. The resultant equations were as follows:

$$P(\text{males}) = \frac{e^{(-6.365 + 0.935TL)}}{1 - e^{(-6.365 + 0.935TL)}} \quad (r^2 = 0.809)$$

$$P(\text{females}) = \frac{e^{(-6.631 + 0.86TL)}}{1 - e^{(-6.631 + 0.86TL)}} \quad (r^2 = 0.932)$$

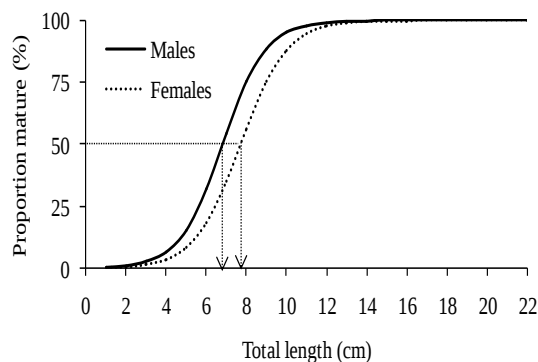


Fig. 3. Estimated size at first maturity for males and females of *Sarotherodon melanotheron melanotheron* from Lake Toho.

Growth parameters

Values for asymptomatic length L_{∞} and growth coefficient K were respectively 21.53 cm and 0.58

year⁻¹. This coefficient indicated that the species had a relatively low growth rate. The performance growth index Φ' was 2.43 and the theoretical age at which the size is zero was estimated at - 0.31 year. The potential longevity t_{max} was 5.17 years. Figure 4 (A & B) shows the presence of several growth curves superimposed on the histograms of size; the former being much more distant from the later. This demonstrates that captured fish belonged to six cohorts.

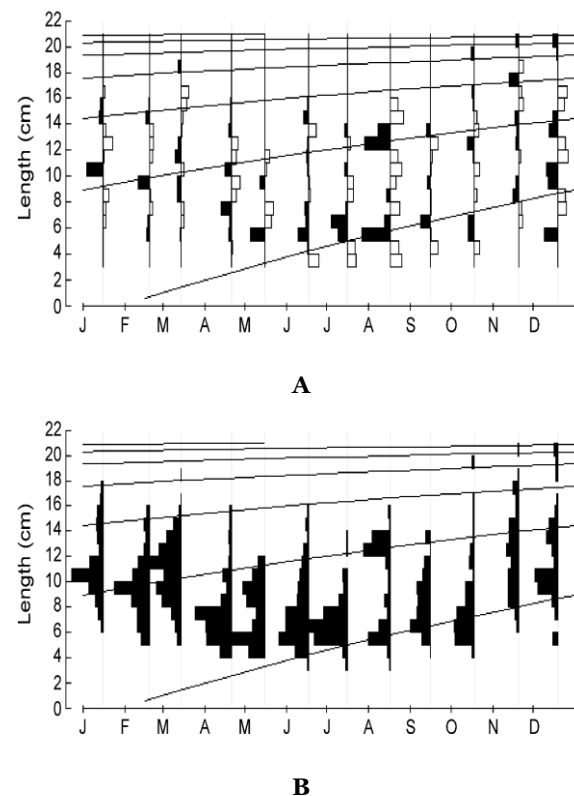


Fig. 4. Seasonalized von Bertalanffy growth curves (L_{∞} = 21.53 cm total length, K = 0.58 year⁻¹) of *Sarotherodon melanotheron melanotheron* from Lake Toho as superimposed on (A) the restructured length-frequency histogram (black and white bars are positive and negative deviations from the running average of three), and on (B) the normal length-frequency histograms.

Exploitation rate and mortality

Total mortality (Fig. 5) was estimated at 1.95 year⁻¹. Natural mortality was 1.37 year⁻¹. The average values of Z and M gave a value of fishing mortality (F) of 0.58 year⁻¹ and an exploitation rate E of 0.30.

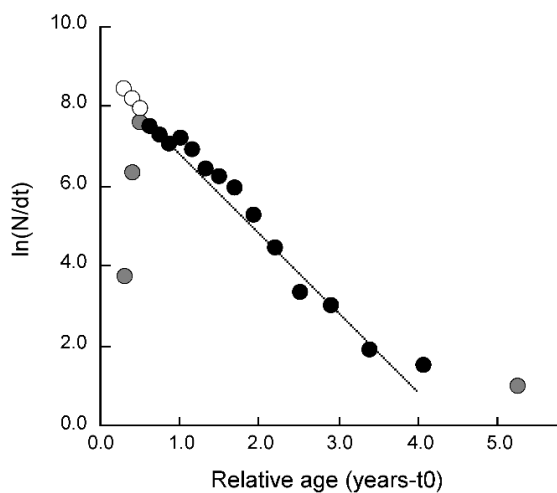


Fig. 5. Length-converted catch curve for *Sarotherodon melanotheron melanotheron* from the Lake Toho. Solid dots are those used in calculating the parameters of the straight line, the slope of which (with sign changed) is an estimate of Z . Open dots represent fish not fully selected by the gear used in the fishery and/or not used in mortality estimation.

Recruitment

The recruitment patterns of *S. m. melanotheron* from Lake Toho suggested that recruitment was continuous throughout the year with only one main peak (Fig. 6). The peak was obtained in May-July during the long rainy season.

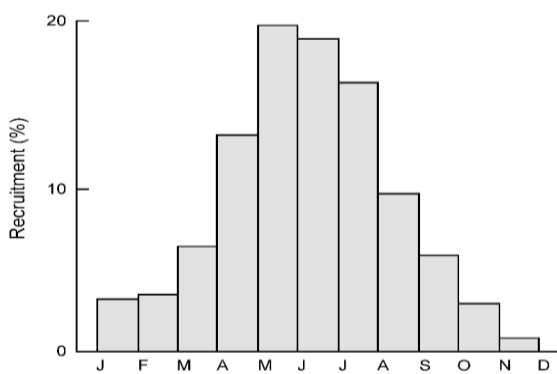


Fig. 6. Recruitment pattern of *Sarotherodon melanotheron melanotheron* from Lake Toho showing one recruitment peak a year.

Size at first capture/relative yield per recruit Y'/R

The length at first capture (L_c) i.e. the length at which 50% of the *S. m. melanotheron* species are vulnerable to capture was estimated at 6.7 cm (Fig. 7). The

logistics model selection also showed that 25% of fish at 4.2 cm and 75% of fish at 9.3 cm were caught. All fish over 18.5 cm were systematically caught. The estimated optimal length was 12 cm. The curve of the relative yield per recruit Y'/R as a function of exploitation rate E (Fig. 8) gave an optimal level of exploitation rate E_{max} of 0.55. Exploitation rates $E_{0.1}$ and $E_{0.5}$ were estimated at 0.42 and 0.27 respectively.

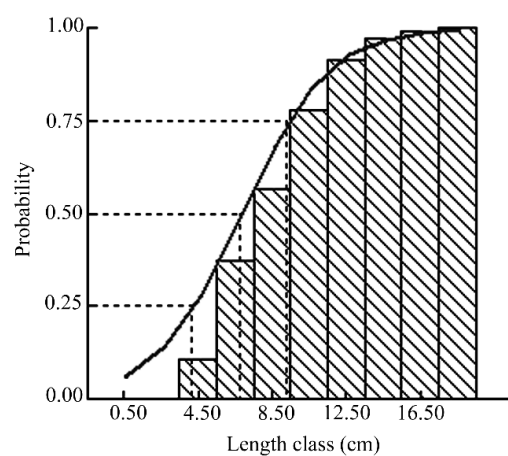


Fig. 7. Probability of capture of *Sarotherodon melanotheron melanotheron* from Lake Toho estimated from the ascending axis of the catch curve. Length at first capture, $L_c = 6.7$ cm.

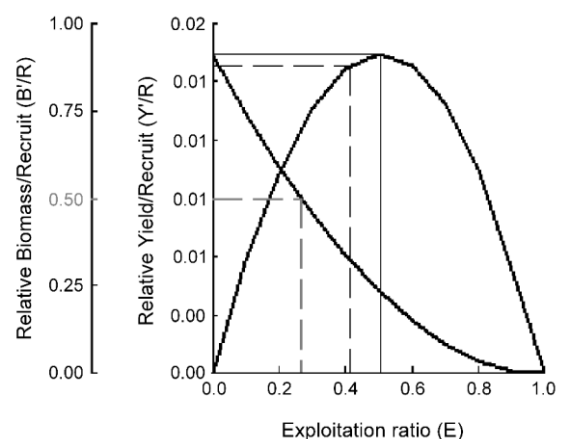


Fig. 8. Relative yield-per-recruit and biomass-per-recruit curves for *Sarotherodon melanotheron melanotheron* from Lake Toho using the selection ogive option ($E_{10} = 0.42$, $E_{50} = 0.27$, $E_{max} = 0.55$).

Discussion

Size frequency distribution of *S. m. melanotheron* in this study showed that sampling considered young as well as adults specimens, and therefore it was assumed that the samples were representative of the population. The L_{50} obtained for males (6.9 cm) and females (7.7 cm) were relatively small for a species that can reach 250 mm standard length (SL) (Teugels and Thys van den Audenaerde, 2003). Fish species in tropical river systems are particularly noted for their very rapid maturity, which is considered as an adaptive response to unstable conditions in these systems (Lowe-McConnell, 1987). The L_{50} obtained for males in Lake Toho is lower than that reported by Diouf (1996) for males (10.2 cm TL) in Sine-Saloum Estuary in Senegal. But the L_{50} obtained for females in Lake Toho is slightly higher than that of females (7.1 cm TL) in Sine-Saloum Estuary (see Diouf, 1996). Overall, the L_{50} obtained in this study are lower than those stated by Koné and Teugels (1999) who reported 12.9-12.6 cm and 13.5-13.6 cm SL respectively for males and females in Lake Ayamé I in Ivory Coast. Food, poor physiological conditions and fishing pressure are the most commonly cited factors accounting to the decline in the size at first maturity of cichlids (Leonardis and Sinis, 1998; Panfili *et al.*, 2004). However, it is also well known that in conditions of overcrowding, cichlids may present a phenomenon of dwarfism and reproduce at a smaller size (Plisnier, 1990). Early maturity observed in this study may be linked to the fishing activity.

The estimation of growth and mortality parameters are vital in fishing because stock assessment and management are often based on these population parameters (Alhassan and Armah, 2011). As for growth, Moreau *et al.* (1986) reported that the estimates of the von Bertalanffy growth parameters, L_{∞} should be reasonably close to the maximum fish length observed in the samples, while t_0 should be smaller than zero so that the fish at age zero could have a positive length. According to Pauly (1978), K might vary between zero and one per year for fish species with a long life span, and an excess of one for short

lived species. Relevant estimates for *S. m. melanotheron* from Lake Toho conform to these criteria. Comparison of the parameters that describe the growth in length of *S. m. melanotheron* in this study to those in the literature (Table 1), showed a little growth. Several factors may explain the reduction of the asymptotic length of a species from one ecosystem to another. In Lake Nokoué, for example, the presence of many acadjas that are exploited at least six months after installation and which are places of protection and a food source for some fishes in general and populations of *S. m. melanotheron* in particular. As a result of this protection, the local population of *S. m. melanotheron* is not directly affected by fishing and large-sized specimens are not all eliminated. This contributes to bigger sizes noticed as compared by those reported in this study. Such an hypothesis is supported by the weak asymptotic size obtained outside acadjas system (Table 1). Apart from the impacts of fishing, other factors may explain these differences. Indeed, Beverton and Holt (1957) reported that intraspecific differences in parameters of the life cycle of the fish can be explained by local environmental conditions and/or genetic differences. According to Pauly (1994), differences in growth could also result from differences in temperature, food availability or disease. In Lake Toho, the asymptotic size is reduced probably due to fishing pressure.

According to Pauly (1991), the growth performance index Φ' is the basis for the comparison of growth parameters, assuming that the species grows according to the von Bertalanffy model. Sparre and Venema (1997) indicated that this index is the best way to calculate the average growth parameters of a given species and should not differ significantly when comparing different groups of data for the same species. The result of this study ($\Phi' = 2.43$) seemed to be within the acceptable range. Comparable results have been obtained by other authors. For example, Fagade (1974) and Legendre (1983) obtained respectively 2.24 in the Lagos Lagoon (Nigeria) and 2.73 in the Ebrié Lagoon (Ivory Coast), while Niyonkuru (2007) recorded 2.75 and 2.42

respectively in Lake Nokoué and Lake Ahémé (Benin) for *S. m. melanotheron*. Moreover, Baijot and Moreau (1997) estimated that the range of Φ' mean values for some important fish in Africa ranged between 2.65 and 3.32, and considered these as low growth rates. In this study, the Φ' estimate fell within this range; thus, fish in Lake Toho might also be considered to show a slow growth.

The total mortality rate, Z , recorded in this study is the sum of natural and fishing mortalities. According to Beverton and Holt (1957), the reliability of the estimated natural mortality, M , is determined using the M/K ratio which is within the range of 1.12-2.50 for most fish. The ratio M/K of 2.36 obtained in this study was within this range and suggested that the estimated natural mortality for this species was reliable. The results showed that natural mortality remains higher than fishing mortality. For fish to be caught before they die of natural causes, it is normally expected that fishing mortality be higher than natural mortality. In Lake Toho, high natural mortalities are related to several factors. This include predation from species such as *Hepsetus odoe* (Bloch, 1794) and *Parachanna obscura* (Günther, 1861) which are part of the fish diversity of the lake (L. Lederoun, unpubl. data). After heavy rains, the lake shores become flooded, and fish often move in these floodplains. When the lake recedes, many fish are often stuck in the small residual ponds and die when these ponds dry up. Since preliminary results (A.A. Brahim, unpubl. data) have shown that *S. m. melanotheron* represents more than 90% of the total capture, it is reasonable to assume that many individuals of this species die in such conditions.

According to Barry and Tegner (1989), if the ratio $Z/K < 1$, there is a predominance of growth on the mortality of the population. If $Z/K > 1$, then mortality is predominant on growth. However, when $Z/K = 1$, the population is in a state of equilibrium where the mortality is in equilibrium with the growth. In a population where mortality predominates on growth, if $Z/K \approx 2$, this is a slightly exploited population. In

Lake Toho, the Z/K ratio obtained (3.4) is greater than 2, which means that there is a predominance of mortality on growth on one hand, while on the other hand, there seems to be an overexploitation of the species. This may be true because many fishermen are directly dependent on the fish resources of the lake and operate every day except Fridays. Excessive fishing effort may lead to a collapse of fish resources, which not only reduces the potential captures and capture rates, but also the size of the stock to a point where reproduction is jeopardized (Peixer *et al.*, 2007). Overfishing also leads to a small group of age classes which is effectively caught, and a decrease in the average size of the capture (Caddy and Mahon, 1995; Peixer *et al.*, 2007).

From the probability curve of capture, the size at first capture ($L_c = 6.7$ cm) indicates that fish are caught at smaller sizes before having the opportunity to grow large enough to contribute to substantial stock biomass. Evidence of overfishing is shown by the fact that L_c is less than the L_{50} for both sexes and the optimal length (Beverton, 1992). Therefore, the mesh size used for fishing nets should be increased to catch fish measuring 12 cm and above. Appropriate regulations should be formulated and implemented in Lake Toho to ensure that small fish can escape during fishing. Existing regulations in Benin are inadequate and contain severe gaps both in terms of depth of the guidelines and in terms of rimplementation (which is almost nonexistent). Indeed, no administrative regulations are currently observed at Lake Toho, and the problem may intensify due to an increasing number of fishermen as a result of human population expansion and a limited number of other value-added activities.

The curve of the relative yield per recruit Y'/R in function of exploitation rate E (Fig. 8) provides an optimal level of exploitation rate $E = 0.55$. The current exploitation level ($E = 0.30$) is lower than that which gives the maximum Y'/R . In addition, the current exploitation rate is higher than the exploitation rate ($E_{0.5}$) that maintains 50% of the biomass of the stock. For management purposes, the

exploitation rate of *S. m. melanotheron* should be reduced from 0.30 to 0.27 (10%) to maintain sufficient spawning biomass.

Based on L_c/L_∞ (indicator mesh) and the current exploitation rate E (reflecting the effort), Pauly and Sorriano (1986) showed that the relative yield contours derived from the equation (12) (see materials and methods) could be grouped into four quarter (A, B, C, D) circles, each with its distinct characteristics. With the data obtained ($L_c/L_\infty = 0.31$, $E = 0.30$), the current yield (Fig. 9) falls into quadrant B. In terms of fishing regime, this result indicates that small fish are captured with a low fishing effort. In terms of assessment, the eumetric fishing can be developed, efforts could be increased in this direction, but the reduction of mesh size should follow (Pauly and Moreau, 1997). Obviously, with such a result, the current situation does not allow management intervention, which did not correlate to the results of L_c compared to the size at first maturity and Z/K report which already reflected overexploitation.

The importance of environmental factors on recruitment is widely recognized (Eckmann *et al.*, 1988; Welcomme, 2001). Studies on different watersheds showed that the seasonality of reproduction of fish species is influenced by water temperature, precipitation and hydrological conditions (Baijot *et al.*, 1994; Dadebo *et al.*, 2003; Lalèyè *et al.*, 1995a, b). According to Lowe-McConnell (1999), the reproductive success depends on a favorable period for the production of young individuals who will determine the perpetuation of the species. In this study, the peak of reproduction occurred during the great rainy season where the banks are flooded. As a result of expansion of the habitat in flooded areas, and an increased availability of resources, juveniles of *S. m. melanotheron* certainly find shelter and could extend their feeding.

Conclusion

To maintain a sufficient reproductive stock of fish, restrictive measures should be taken mainly by (1)

increasing the size of fish at first capture by imposing the use of fishing gears that release small fish to allow each fish to spawn at least once, (2) reducing fishing mortality (which would allow a reduction of total mortality) by sensitizing the fishermen and fishmongers.

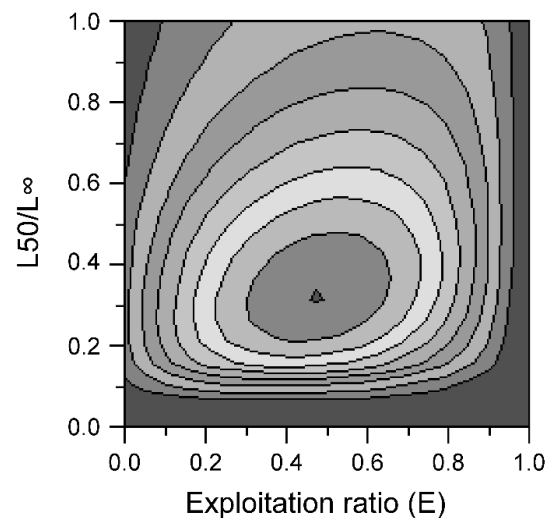


Fig. 9. Yield curve (selection Ogive option) for *Sarotherodon melanotheron melanotheron*. The curve predicts the response of relative yield per recruit of the fish to changes in L_c (size at first capture) and E (exploitation rate). L_c/L_∞ represents the different scenarios changing mesh size. The line is the actual computed critical ratio $L_c/L_\infty = 0.31$.

Table 1. Summary of growth parameters for *Sarotherodon melanotheron melanotheron* in some lagoon ecosystems in West Africa.

Study areas	L_∞ (cm)	K (an ⁻¹)	References
Sine-Saloum (Senegal)	22	0.60	Villanueva, 2004
Ebrié (Ivory Cosat)	34	0.42	Villanueva, 2004
Gambie (Gambie)	37	0.39	Villanueva, 2004
Lagos (Nigeria)	33.1	0.16	Fagade, 1974
Sakumo (Ghana)	25.5	0.74	Pauly, 1976
Togo (Togo)	25	1.78	Laë, 1992
Nokoué acadjas non-included (Benin)	24.1	0.55	Niyonkuru, 2007
Nokoué acadjas included (Benin)	26.7	0.79	Niyonkuru, 2007
Ahémé (Benin)	22.5	0.52	Niyonkuru, 2007

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