IMPACT OF OVERFISHING ON THE TEMPORAL DYNAMICS AND RESILIENCE OF THE *COPTODON GUINEENSIS* (GÜNTHER, 1862) POPULATION IN LAKE TOHO (BENIN, WEST AFRICA)

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ABSTRACT

This study analyzes the impact of fishing pressure on the dynamics and resilience of *Coptodon guineensis* in Lake Toho (southwestern Benin), using size-frequency data (2002-2003 and 2022-2024) processed with FiSAT II. Results show a decline in maximum length and weight (31.3 cm/908 g to 18 cm/119 g), earlier sexual maturity, and a reduction in mature individuals and large breeders. Growth and exploitation parameters indicate reduced longevity, lower yield per recruit, and persistent overexploitation. Overall, the biological and ecological status of the species has deteriorated, undermining its long-term resilience and threatening the food security of local communities dependent on this fishery resource.

RÉSUMÉ: Impact de la surpêche sur la dynamique temporelle et la résilience de la population de *Coptodon guineensis* (Günther, 1862) dans le lac Toho (Bénin, Afrique de l'Ouest).

Cette étude analyse l'impact de la pression de pêche sur la dynamique et la résilience de *Coptodon guineensis* dans le lac Toho (sud-ouest du Bénin), à partir de données de fréquence de tailles (2002-2003 et 2022-2024) traitées avec FiSAT II. Les résultats révèlent une diminution de la taille et du poids maximaux (31,3 cm/908 g à 18 cm/119 g), une maturité sexuelle plus précoce et une baisse des individus matures et reproducteurs. Les paramètres de croissance et d'exploitation indiquent une réduction de la longévité, une baisse du rendement par recrue et une surexploitation persistante. L'état biologique et écologique de l'espèce s'est détérioré, compromettant sa résilience et la sécurité alimentaire des communautés locales.

REZUMAT: Impactul pescuitului excesiv asupra dinamicii temporale și rezilienței populației de *Coptodon guineensis* (Günther, 1862) din lacul Toho (Benin, Africa de Vest).

Acest studiu analizează impactul presiunii pescuitului asupra dinamicii și rezilienței speciei *Coptodon guineensis* în Lacul Toho (sud-vestul Beninului), utilizând date privind frecvența mărimii (2002-2003 și 2022-2024) procesate cu FiSAT II. Rezultatele relevă o scădere a dimensiunii și greutății maxime (de la 31,3 cm/908 g la 18 cm/119 g), o maturitate sexuală mai timpurie și un declin al indivizilor maturi și reproductivi. Parametrii de creștere și exploatare indică o longevitate redusă, un randament scăzut și o supraexploatare persistentă. Starea biologică și ecologică a speciei s-a deteriorat, scăzând reziliența acesteia pe termen lung și securitatea alimentară a comunităților locale dependente de această resursă piscicolă.

INTRODUCTION

A high number of anthropogenical stressors impact the fish aquatic ecosystems all over the world including fishing and overfishing (Bănăduc et al., 2024, 2023, 2022). Africa is not at all an exception regarding fishing and overfishing, by contrary (Oluwakayode-Oluyi et al., 2025; Xitong Zhang et al., 2023; Adom et al., 2019), overfishing in Africa is a main issue induced by not sustainable fishing habits, pouchery, missing of appropriate management, accentuated diminishing of fish stocks due to overfishing, economic challenges for some local human populations, etc. Excessive exploitation of freshwater fishery resources in tropical ecosystems of West Africa poses a critical threat to the sustainability of artisanal fisheries (Koigny et al., 2024; Béné et al., 2015; Ayoubi and Failler, 2013; OCDE, 2008). In these heavily exploited aquatic ecosystems, sustainable fisheries management remains hindered by the lack of recent reliable biological and ecological information and data on targeted economic and ecologic valuable fish species. This is particularly true for Lake Toho, a continental waterbody located in southwestern Benin within Ramsar site 1017, which has been intensively fished for several years without rigorous monitoring of stock status for key species (Ahouansou Montcho, 2003; Tossavi and Adite, 2018; Lederoun et al., 2015). *Coptodon guineensis* (Günther, 1862) is a euryhaline fish species widely distributed along the West African coast, occupying various estuarine habitats. In Lake Toho, it accounts for 33.4% of individuals captured and 27.61% of total biomass, making it a major component of artisanal fishing and a species of significant economic importance (Ahouansou Montcho, 2003). Despite its prominence, no study has yet assessed the temporal dynamics of overfishing affecting this species.

Recent research on exploited fish populations has shown that overfishing induces significant changes in population structure, influencing size at first sexual maturity (Lm50), length at first capture (Lc50), growth parameters, and the proportion of large reproductive individuals in catches (Osman et al., 2024; Amponsah et al., 2020; Froese, 2004; Amponsah et al., 2016). Moreover, excessive exploitation of this natural resource contributes to reduced yield per recruit and exploitable biomass (Zhang et al., 2023; Froese and Pauly, 2021, Beverton and Holt, 1957).

In light of these sustainability challenges, this research aims to characterize the population dynamics of *C. guineensis* in Lake Toho between 2002-2003 and 2022-2024. It focuses on estimating critical size thresholds, the proportion of mature and mega-spawner fish individuals, and analyzing growth, exploitation, and maximum sustainable yield parameters.

This contribution seeks to provide essential uptodate reference data to support the sustainable management of *C. guineensis* stocks in Lake Toho within the broader West African context.

MATERIAL AND METHODS

Study areas

This research was carried out on Lake Toho, situated in the southwestern region of Benin. During low-water periods, the lake spans UTM coordinates from 302000 m E to 311000 m E in longitude and from 728000 m N to 737000 m N in latitude, within UTM zone 31N (Fig. 1). The lake sits at an average altitude of 64 m above sea level.

Lake Toho exhibits a crescent-shaped configuration stretching from south to north, with an approximate length of seven km. Its southern section reaches a width of about 2.5 km, narrowing to roughly 500 m in the north (Ahouansou Montcho, 2003). The lake is bordered by the districts of Kpinnou (Athieme municipality), Zoungbonou (Houeyogbe municipality), and Houin (Lokossa municipality).

It forms part of the Western Complex within the Mono River Basin and is recognized as Ramsar Site no. 1017. Hydrologically, the lake is fed by two principal tributaries the Diko and Atakpatohoun rivers while the Kpacohadji channel functions both as an inflow and outflow, playing a key role in regulating the lake's water dynamics.

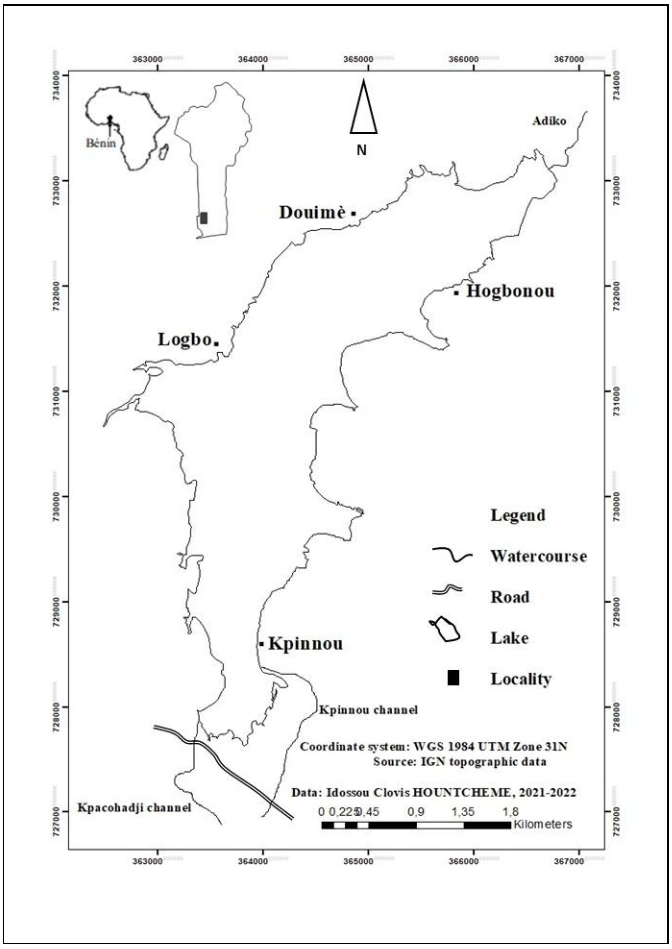


Figure 1: Lake Toho.

Lake Toho lies within a subequatorial climatic zone. According to precipitation and temperature records from the National Meteorological Agency (ANM) spanning 1993 to 2023, the region experiences a distinct seasonal pattern: a prolonged rainy season from March to July, briefly interrupted by a dry spell in August. This is followed by a shorter rainy phase from September to October, and then a sustained dry season extending from November through February.

Fish sampling and data analysis

Specimens of *C. guineensis* (Fig. 2) were collected through artisanal fishing activities at four landing sites Kpinnou, Logbo, Douimè, and Hogbonou during two distinct sampling campaigns: April 2002 to March 2003, and April 2022 to March 2024.

Throughout both periods, fishers utilized consistent gear types and techniques as documented by Ahouansou Montcho et al. (2023). These included hand nets (small “Sèguè”; large “Congo,” “Kounkouin,” or “Adjakpo”), gillnets (“Sito” or “Adoun,” and “Awlè” or “Dokpoè”), Malian traps (“Goura”), traditional fish traps (“Montocloué”), and single-hook lines (“Mlinvi”). These methods, in use for over twenty years, remain the principal means of harvesting *C. guineensis* in Lake Toho.

Species identification was performed using the taxonomic key provided by Paugy et al. (2003). For each fish, total length (TL, in cm) and total weight (TW, in g) were measured using an ichthyometer and electronic scales Kern model for the 2002-2003 period and Kitchen Scale for 2022-2024 both with a precision of 0.1 g.

To assess reproductive status, fish were dissected and their gonads examined macroscopically. Maturity stages were classified using the system developed by Micha (1973), as modified by Laleye (1995) for the earlier period, and the Brown-Peterson et al. (2011) framework for the later period. Gonads were extracted and weighed to the nearest 0.01 g using a Kern electronic scale during both sampling phases.

Figure 2: Sampled specimen of *Coptodon guineensis* (Günther, 1862).

According to Brown-Peterson et al. (2011), gonadal development in fish progresses through five stages beginning with immature gonads that are very small, translucent, and thread-like in appearance followed by developing gonads where ovaries begin to expand and testes become distinguishable then spawning-capable gonads characterized by large ovaries with visible oocytes and firm testes that release milt under slight abdominal pressure next regressing gonads with flaccid ovaries and soft testes that no longer release milt and finally regenerating gonads which are reduced in size and appear thin and filamentous.

Data structuring and statistical analysis

Total length (TL) measurements were grouped into size classes. The number of classes was determined using Sturges’ formula (1926): Number of classes = 1 + (3.3 × log N)**,** where *N* is the sample size, *Xmax* is the maximum total length, and *Xmin* is the minimum total length. The amplitude (a) of each class was calculated using the formula: $a = \frac{\text{Xmax}-\text{Xmin}}{\text{Number of class}}$.

Following this calculation, TL values were grouped into classes with a fixed interval of 2 cm**.**

A comparison of total lengths and mean weights between male and female *C. guineensis* specimens from the two sampling periods (2002-2003 and 2022-2024) was performed using analysis of variance (ANOVA) in R software (version 4.0.5). This aimed to detect potential sex-related growth dimorphism, a common biological phenomenon in fish species (Ahouansou Montcho et al., 2015; Ahouansou Montcho 2008).

Size at first sexual maturity (Lm50) and sexually mature individuals

The fish size at first sexual maturity (Lm50) is defined as the average length at which 50% of males and females reach sexual maturity (Stages III-V). It was estimated using a sigmoid logistic curve representing the proportion (*p*) of mature individuals as a function of total length (TL), following the model described by Amenzoui et al. (2005) and N'Guessan et al. (2018).

The logistic equation used was: $p = \frac{e^{(a+bLt)}}{1+e^{(a+bLt)}}$, where p represents the percentage of mature individuals relative to all fish of a given total length (TL), while a and b are model-specific coefficients. The values of a and b were obtained through logarithmic transformation of the equation, following the method described by Dagnelie (1973): p = $\frac{X}{1+X}$ where x = $e^{(a+bLt)}$). Thus, $\ln\left(\frac{p}{1-p}\right)$ = a + bLt where the value of Lm50 was calculated using the formula: Lm50 = – a/b, by substituting *p = 50%* into the equation. A reference point of 100% mature individuals in the catch was used for model calibration (Ndour et al., 2013).

The percentage of sexually mature individuals ($\%P_m$) in each size class was determined by setting the maturity threshold at Stage III, corresponding to vitellogenesis and gonadal maturation (Albaret and Legendre, 1985). The monthly percentage of mature fish was calculated using the formula: $\%P_M = \frac{n}{N} * 100$; n is the number of mature individuals in the sample, N is the total number of individuals.

The software StatView (Version 1992-98, SAS Institute Inc.) and Microsoft Excel were used to calculate observed proportions of mature fish, estimated proportions, and the logistic model coefficients *a* and *b.*

Growth parameters

Growth parameters including L∞, K, and Φ′ were estimated using the FiSAT II software (version 1.2.2), which incorporates the ELEFAN I routine based on length-frequency distribution analysis (Lederoun et al., 2015; Ahouansou and Montcho et al., 2015, Gaynilo et al., 2005). Growth was modeled using the Von Bertalanffy Growth Function (Von Bertalanffy, 1948), expressed by the equation: $Lt = L\infty\ (1\text{-}e^{-k(1-t_0)})$, where: Lt is total length of the fish at age t (cm), L∞ is asymptotic length (cm), K is growth coefficient or rate ($year^{-1}$), t_0 is theoretical age at which length is zero.

The growth performance index (Φ′) was calculated using L∞ and K, following the formula proposed by Pauly and Munro (1984): $\Phi' = \log_{10}K + 2\log_{10}L\infty$.

The theoretical age at zero length (t_0) was estimated using Pauly (1979) equation: $\log(-t_0) = -0.392 - 0.275 \log L\infty - 1.038 \log_{10}K$.

Potential longevity (t_{max}) was calculated using Pauly's (1980) formula: $t_{max} = 3/K$.

Mortality and exploitation rate

Total mortality (Z) was estimated using the length-converted catch curve method in ELEFAN I/FiSAT II, based on the formula by Gayanilo et al. (2005): $\ln (N/\Delta t_i) = a + bt$, where N is number of fully recruited fish in size class i, Δti is time required for fish to grow through size class i, it is mean age of fish in that size class, b is slope representing total mortality (Z), with sign reversal.

Natural mortality (M) was estimated using Pauly's (1982) empirical formula:

$$\log_{10}(M) = a - b\log_{10}(L\infty) + c\log_{10}(K) + d\log_{10}(T)$$

$$\text{were } a = -0.0066; b = 0.279; c = 0.6543; d = 0.4634;$$

$$M = \text{Natural Mortality}(an^{-1});$$

$$T \text{is mean annual water temperature } (°C) \text{of the study area.}$$

Fishing mortality (F) was calculated as: F = Z – M (Pauly, 1982).

The exploitation rate (E) was determined using Gulland's (1971) formula: E = F/Z.

According to Gulland (1971), the exploitation rate is a key indicator of stock status: if E = 0.5, exploitation is considered optimal, if E < 0.5, the stock is underexploited, if E > 0.5, the stock is overexploited.

Length at first capture (Lc50) and optimal length (Lopt)

The length at which 50% of fish from both sexes enter the exploitable stock (Lc50) was estimated based on capture probabilities.

The FiSAT II software facilitates the estimation of Lc_{50}, which is a key selectivity parameter. Using a logistic curve, data points were selected for regression based on:

$$\ln\left(\left(\frac{1}{P_L}\right) - 1\right) = S1 - S2 \times L$$

where P_L is the probability of capture at length *L*, and *S1* and *S2* are regression coefficients used to estimate capture probability in the logistic model. Lc50 value was calculated as:

$$Lc50 = \frac{S1}{S2}.$$

The optimal length (Lopt) for a given age class was estimated following Froese (2004), using the formula: $L_{opt} = L\infty \frac{3}{3+\frac{M}{K}}$, where *L∞* and *K* are parameters from the von Bertalanffy growth function, and *M* is the instantaneous natural mortality rate.

Relative yield per recruit (Y'/R) and relative biomass per recruit (B'/R)

FiSAT II version 1.2.2 was used to estimate yield per recruit (Y'/R) based on the Beverton and Holt (1966) model. The calculation follows the formula: $Y'/R = EU^{M/K} [1 - \frac{(3U)}{(1+m)} + \frac{3U^2}{(1+2m)} - \frac{(U^3)}{(1+3m)}]$ with $m = \frac{(1-E)}{M/K}$ et $U = 1 - \frac{Lc50}{L\infty}$, $E = F/Z$; where: E is exploitation rate (F/Z), $U = 1 - (Lc_{50}/L\infty)$, representing the proportion of potential growth achieved before capture, M is natural mortality rate, K is growth coefficient, m is mesh size parameter, calculated as (1 − E)/(M/K), Lc50 is length at first capture, L∞ is asymptotic length.

This model provides insight into the exploitation status of fishery resources.

The relative biomass per recruit (B′/R) was calculated using the formula:

$$(B'/R) = \frac{(Y'/R)}{F}$$

Yield per recruit (Y'/R) and maximum sustainable yield (MSY)

The yield per recruit model (Y/R)**,** based on the Beverton and Holt (1966) framework and simplified by Gilbert et al. (2017), was used to estimate the cohort-based production of *Oreochromis niloticus* in Lake Toho. The fundamental equation expresses the instantaneous production rate of a cohort as: $\frac{dYt}{dt} = Ft.Nt.Wt$, where: *Yt* is total production of a cohort from recruitment to time *t*, *Ft* is instantaneous fishing mortality at time *t*, *Nt* is number of surviving individuals at time *t*, *Wt* is average weight of survivors at time *t*. Population size evolves exponentially within each time interval between *ti* and *ti + 1*, such that: $Ni + 1 = Nie^{-(Fi+Mi)(ti+1-ti)}$. The catch within the interval is then given by: $Yi \int_{ti}^{ti+1} Fi.Ni.e^{-(Fi+Mi)(ti+1-ti)}.Wi$ Whether $Yi = \frac{Fi}{Zi}.NiWi.(1-e^{-Zi})$. The total catch, representing the yield per recruit**,** is calculated as: recrue$Yt = \sum_{i=1}^{n} Yi$.

To estimate the Maximum Sustainable Yield (MSY), **the** Thompson and Bell (1934) predictive model integrated within FiSAT II was applied. This model combines the Beverton and Holt yield-per-recruit approach with Virtual Population Analysis (VPA) data. The total yield (Y = ΣYi) is calculated using: Yi = Ci × wi, where body weight (*wi*) is computed as: $w_i = (\frac{1}{L_{i+1}+1-L_i})(\frac{a}{b+1})(L_{i+1}{}^{b+1}.L_i{}^{b+1})$ Here, *a* and *b* are the coefficients of the length-weight relationship, and *Li* and *Li + 1* are the lower and upper bounds of the length class, respectively.

Catch (*Ci*) is calculated as: $C_i = (N_i - N_{i+1})\left(\frac{F_i}{M+F_i}\right)$. Predicted population size (*Ni*) is given by: $N_{i+1} = N_i e^{(-(M+F_i).\nabla t_i)}$; et . $\nabla t_i = \frac{\frac{1}{K}\ln(L-L_i)}{L-L_{i-1}}$

Biomass (*Bi*) is calculated as: e $B_i = \frac{N_i - N_{i+1}}{M+F_i}.\Delta t_i w_i$ A series of *X* values (multipliers of *F*) were used to simulate fishing effort scenarios. FiSAT II was used to generate biomass and yield estimates under varying fishing pressures, while corresponding MSY graphs were produced using StatView software (version 5.0.1.0).

Toho Lake water temperature

In Benin, specifically in the Mono department where lake Toho is located, ambient air temperature has shown minimal variation over the past two decades, according to data from the Benin National Meteorological Agency. Within this context, the average water temperature of the lake was 29.30°C during 2002-2003 and 28.82°C during 2022-2023. These temperature values were incorporated into the data analysis using FiSAT II software (version 1.2.2).

RESULTS

Structural dynamics of the population

In the present study, a total of 2,263 *Coptodon guineensis* specimens were measured between April 2002 and March 2003, followed by 913 individuals from April 2022 to March 2023. These results prompted a third sampling campaign from April 2023 to March 2024, during which 1,642 additional specimens were collected. An analysis of variance (ANOVA) revealed no statistically significant differences ($p > 0.05$) in total length or mean weight between the 2022-2023 and 2023-2024 datasets. Consequently, the data from these two years were pooled into a single dataset referred to as "2022-2024" for comparative analysis.

Between the 2002-2003 and 2023-2024 periods (Tab. 1), the structure of *C. guineensis* catches showed a clear decline, marked by a substantial reduction in both total length and individual weight. In 2002-2003, total lengths ranged from 5.00 cm to 31.30 cm, and weights from three g to 908 g. By 2023-2024, these ranges had narrowed to 3.40 cm to 18.00 cm in length and 0.50 g to 119.30 g in weight. Previously, females and males were captured at maximum lengths of 23.8 cm and 31.30 cm, respectively. Currently, the largest individuals are predominantly 18.00 cm for females and 17.80 cm for males, with a sharp decline in maximum weights 119.30 g for females compared to 285 g previously, and 110.70 g for males compared to 633.20 g.

Additionally, the total number of immature fish in the catch has increased significantly, rising from 274 to 1,049 individuals. These juveniles now fall within a length range of 3.40 cm to 14.20 cm, whereas in the earlier period they ranged from 7.20 cm to 18.30 cm.

Table 1: Structural characteristics of *Coptodon guineensis* specimens sampled from Lake Toho between 2002-2003 and 2022-2024.

Sex/Maturity Status	Periods	Number (N)	Total length (cm) (mini-maxi)	Total weight (g) (mini-maxi)
	April 2002 – March 2003	2263	5.00-31.30	3.00-908.00
Females		503	8.60-23.80	11.50-285.00
Males		543	6.70-31.30	5.80-633.20
Immatures		274	7.20-18.30	6.50-120.00
Undermined		1217	5.00-29.60	3.00-908.00
	April 2023 – March 2024	2555	3.40-18.00	0.50-119.30
Females		887	4.50-18.00	1.40-119.30
Males		1552	3.40-17.80	1.50-110.70
Immatures		1049	3.40-4.20	0.50-48.50
Undermined		116	4.20-12.00	2.20-22.80

The observation of Total length structure (Fig. 3) across all subgroups populations (mature, immature, male, female, and undetermined) reveals a noticeable decline in the body size of captured individuals over time. Specifically, the Total length distributions of specimens collected during the 2022-2024 period show a significant reduction ($p = 0.023$) in class intervals compared to those recorded in 2002-2003. This trend is consistent across all biological categories.

Moreover, the 2022-2024 sampling campaign included a targeted effort to improve sex identification of *C. guineensis* individuals, resulting in a more detailed classification of male and female specimens than in previous years.

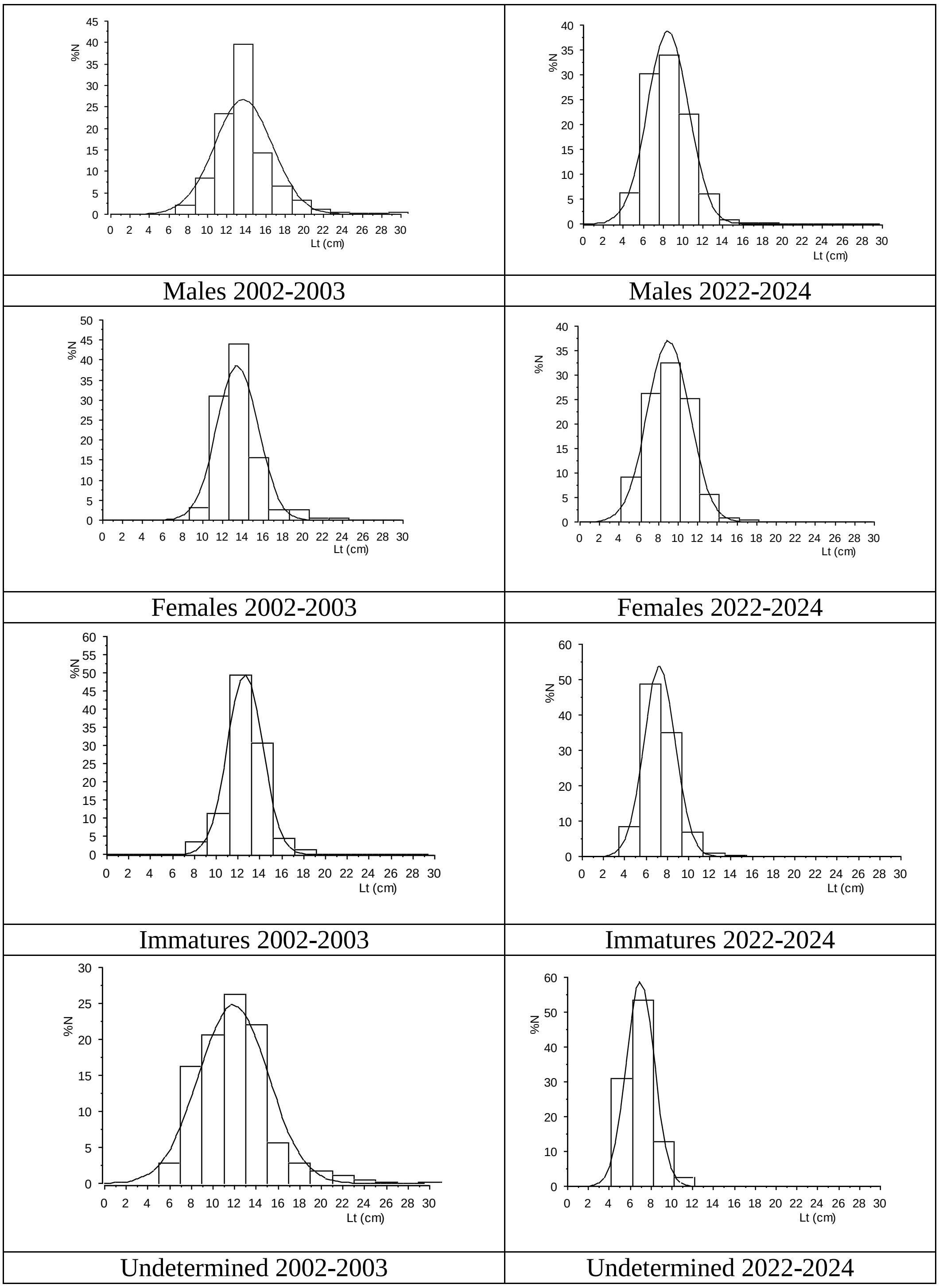


Figure 3: Total length distribution of males, females, immatures and undetermined individuals of *C. guineensis* caught in 2002-2003 and 2022-2024 in lake Toho.

Indeed, the undetermined sampled fish individuals are, on the one hand, those whose sex could not be identified during the study period, and on the other hand, those that were simply measured in large numbers during the first phase of data collection. The total lengths of the latter were used to assess the stock of the species using the FiSAT II software (version 1.2.2**)**. However, during the second sampling period, considerable efforts were made to minimize this bias.

A comparison of the mean total length and mean total weight of male and female fish individuals between the 2002-2003 and 2022-2024 sampling periods reveals that, in 2002-2003 period, there were no statistically significant differences ($p > 0.05$) in mean total length or mean total weight between female and male *C. guineensis*. During that research period, females exhibited an average length of 13.43 ± 2.06 cm and a mean weight of 48.99 ± 31.66 g, while males measured 13.68 ± 2.98 cm on average, with a mean weight of 53.36 ± 50.91 g. In contrast, the 2022-2024 period dataset showed significant sex-based differences ($p < 0.05$). Females fish had a lower mean length (9.00 ± 2.15 cm) and weight (16.30 ± 11.81 g) compared to males fish, who averaged 8.45 ± 2.05 cm in length and 13.58 ± 10.71 g in weight.

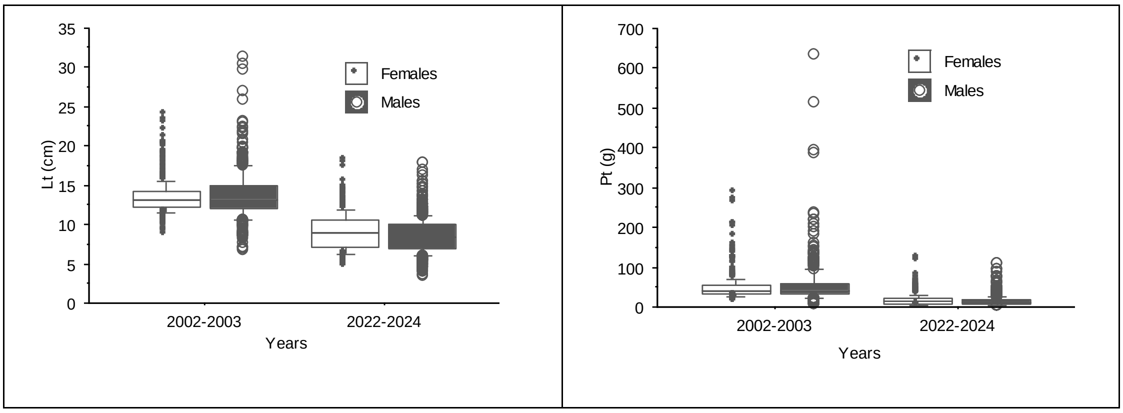
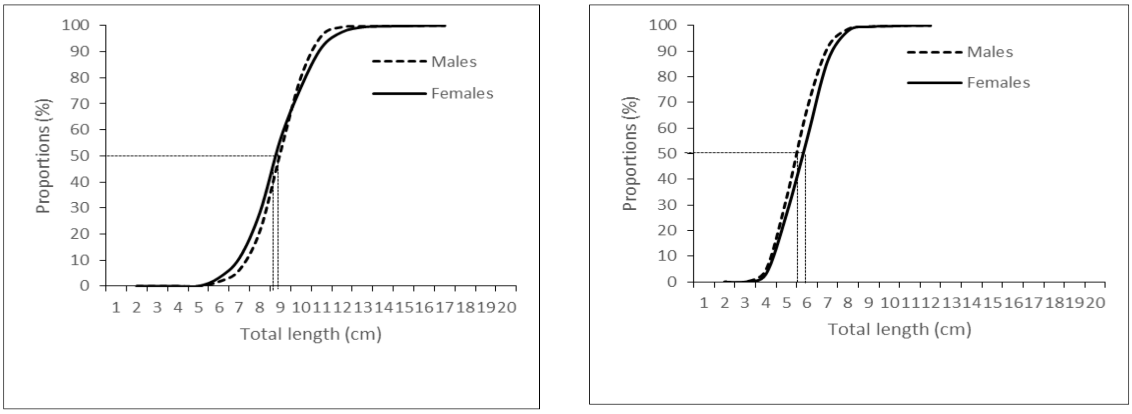


Figure 4: Changes in total length and body weight of *Coptodon guineensis* by sex between 2002-2003 and 2022-2024.

Size at first sexual maturity (Lm50)

Figure 5 illustrates the temporal changes in the size at first sexual maturity (Lm50) of *C. guineensis* individuals from Lake Toho across three sampling periods: 2002-2003, 2022-2023, and 2023-2024. The curves were generated based on the male and female counts obtained during population structure assessments. Over time, a notable decline in Lm50 was observed. For males, the size at first maturity decreased from 8.50 cm in 2002-2003 to 5.20 cm in 2022-2024. Among females, this threshold dropped from 8.10 cm to 5.80 cm during the same interval. These findings indicate a progressive reduction in the size at sexual maturity for both sexes of *C. guineensis* in lake Toho.



(a) (b)

Figure 5: Logistic curve estimating the size at first sexual maturity (Lm50) for male and female *Coptodon guineensis* specimens sampled from lake Toho in 2002-2003 (a) and 2022-2024 (b).

Percentage of sexually mature fish in the catch

The distribution of *C. guineensis* individuals across sexual maturity stages during the two study periods (Tab. 2) reveals an increase in the number of fish classified in stages I, II, and III between 2002-2003 and 2022-2024. Although the number of individuals in stages IV and V also rose, their increase was less pronounced compared to the surge in immature specimens. Notably, a substantial proportion of individuals in 2002-2003 were recorded as undetermined in terms of maturity stage. A chi-square test indicated a highly significant difference ($p < 0.0001$) between the two periods, reflecting a marked shift in the population's maturity structure over time.

Table 2: Frequency distribution of *Coptodon guineensis* specimens by sexual maturity stage during the 2002 - 2003 and 2022 - 2024 sampling periods.

Maturity stage	2002-2003	2022-2024	Chi-square test
I	71	552	P < 0,0001
II	203	505	
III	159	398	
IV	388	400	
V	216	583	

The assessment of relative abundance among *C. guineensis* individuals with identifiable maturity stages reveals a marked increase in immature specimens (Fig. 6). Specifically, the proportion of fish at Stage I rose from 6.84% in 2002-2003 to 22.64% in 2022-2024. Stage II showed a slight increase, from 19.57% to 20.71%, while Stage III rose modestly from 15.33% to 16.32%. In contrast, the proportion of individuals at Stage IV indicative of full sexual maturity declined sharply from 37.42% to 16.40%, suggesting a reduction in reproductively active fish. Stage V, representing post-spawning individuals, experienced a modest increase from 20.82% to 23.91%.

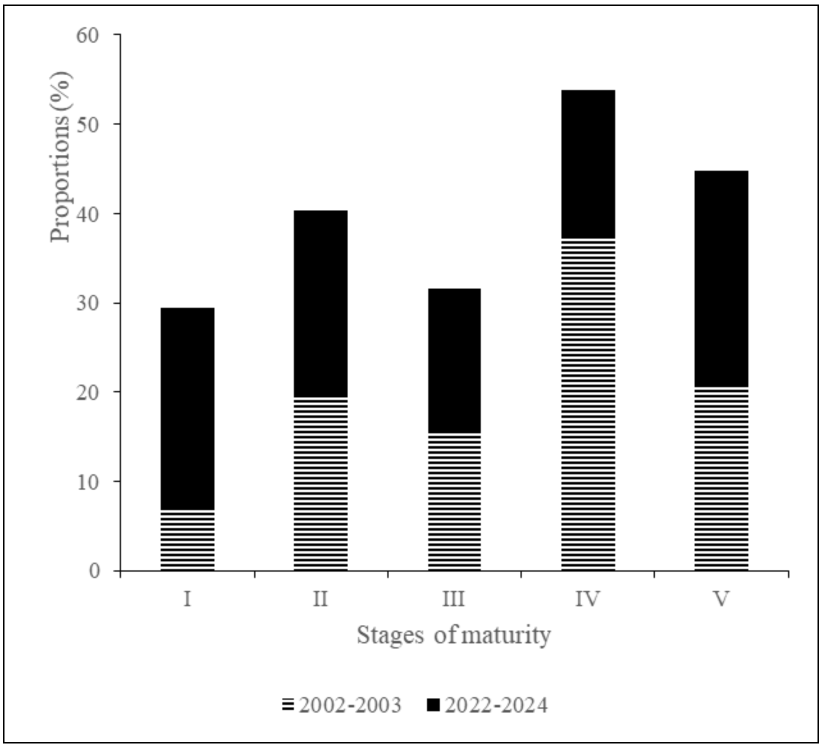


Figure 6: Relative frequency distribution of *Coptodon guineensis* individuals by sexual maturity stage during the 2002-2003 and 2022-2024 sampling periods.

Trends and growth parameters

Growth analyses conducted for the 2002-2003 and 2022-2024 periods revealed in the reseaech a gradual decline in biological performance among *C. guineensis* populations. The growth performance index (Φ') decreased from 2.72 to 2.43 (Tab. 3), indicating reduced individual growth potential. Asymptotic length ($L\infty$) also declined, dropping from 35.50 cm in 2002-2003 to 23.80 cm in 2022-2024. In contrast, the growth coefficient (K) remained relatively stable, estimated at 0.42 $year^{-1}$ and 0.48 $year^{-1}$, respectively. The theoretical age at zero length (t_0) showed minimal variation, with values of –0.38 and –0.36 years. As a result, the maximum life expectancy (t_{max}) decreased from 7.14 years to 6.25 years over the two decades.

Table 3: Temporal dynamics of growth parameters in *C. guineensis* from Lake Toho.

Periods	Φ'	L∞ (cm)	K ($year^{-1}$)	t_0 (year)	t_{max} (year)
2002-2003	2.72	35.50	0.42	–0.38	7.14
2022-2024	2.43	23.80	0.48	–0.36	6.25

Size at first capture (Lc50) and optimal capture size (Lopt)

Figure 7 illustrates the evolution of capture thresholds in *C. guineensis* between the 2002-2003 and 2023-2024 sampling periods. The estimated size at first capture (Lc50) declined from 9.35 cm in 2002-2003 to 5.64 cm in 2023-2024, indicating a temporal reduction in the length at which individuals are first harvested. This downward trend suggests increasing fishing pressure on younger, smaller fish, with potential implications for population renewal and long-term sustainability.

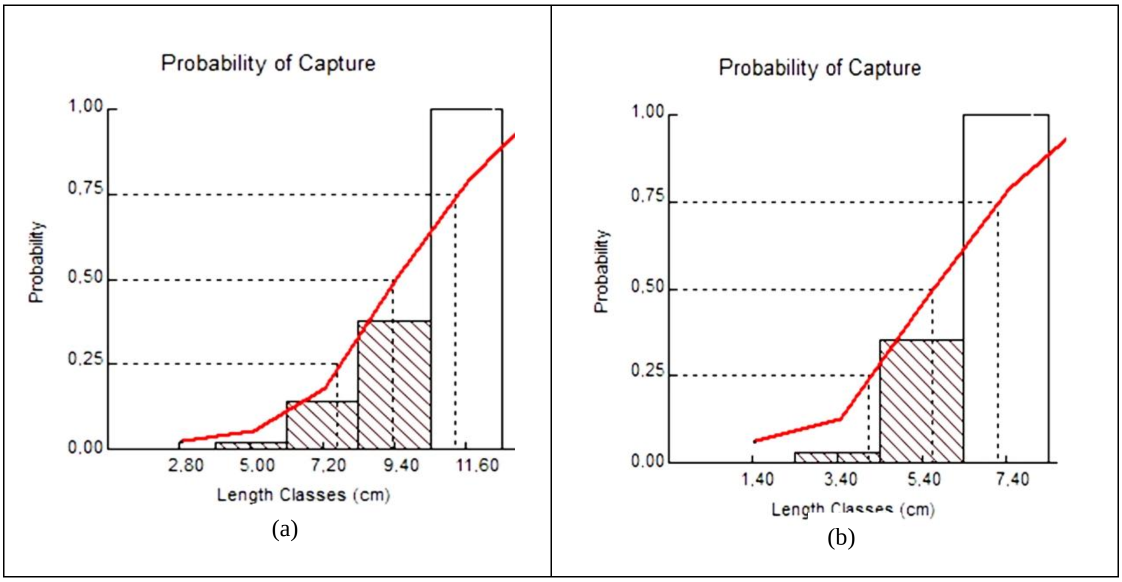


Figure 7: Probability of capture curves for *Coptodon guineensis* from lake Toho in 2002-2003 (a) and 2022 -2024 (b).

Between the 2002-2003 and 2022-2024 sampling periods, the optimal size for maximizing fishery yield in *C. guineensis* declined from 19.96 cm to 12.98 cm. This downward trend in Lopt reflects a progressive reduction in the size structure of the population over time, suggesting increased harvesting pressure on younger individuals and potential long-term implications for stock productivity in lake Toho.

Proportions of mega-spawners in the catch

Analysis of the present dataset (Tab. 4) indicates a relatively stable proportion of *C. guineensis* individuals captured at the optimal size across the two sampling periods, although a slight decline was observed. Of the 2,263 specimens collected in 2002-2003, 148 fish (6.54%) had reached the optimal capture size, compared to 160 individuals (6.26%) out of 2,555 specimens in 2022-2024. However, a notable decrease in the proportion of mega-spawners large, highly fecund individuals was recorded over time. Their representation dropped from 2.30% (52 individuals) in 2002-2003 to 1.37% (35 individuals) in 2022-2024.

Table 4: Changes in the proportion of *Coptodon guineensis* captured at optimal size and as mega-spawners in lake Toho between 2002-2003 and 2022-2024.

Periods	N	Lt (cm)	N fish at optimal size	% at optimal size	N mega-spawners	% Mega-spawners
2002-2003	2263	5-31.5	148	6.54	52	2.30
2022-2024	2555	3.4-29.6	160	6.26	35	1.37

Temporal evolution of exploitation parameters

Mortality parameters

Mortality estimates for *C. guineensis* were derived from length-converted catch curves (Fig. 8). During the 2002-2003 and 2022-2024 periods, total mortality (Z) was estimated at 3.14 year^{-1} and 3.56 year^{-1}, respectively. Natural mortality (M) increased from 0.98 year^{-1} to 1.20 year^{-1}, while fishing mortality (F) rose slightly from 2.16 year^{-1} to 2.37 year^{-1}. The corresponding exploitation rates (E) were 0.69 and 0.66, indicating sustained fishing pressure across both periods.

Additionally, the M/K ratios used to assess population resilience were 2.33 in 2002-2003 and 2.50 in 2022-2024. The Lc/L∞ ratio, reflecting the relationship between size at first capture and asymptotic length, declined slightly from 0.26 to 0.24, suggesting a shift toward harvesting smaller individuals relative to their maximum growth potential.

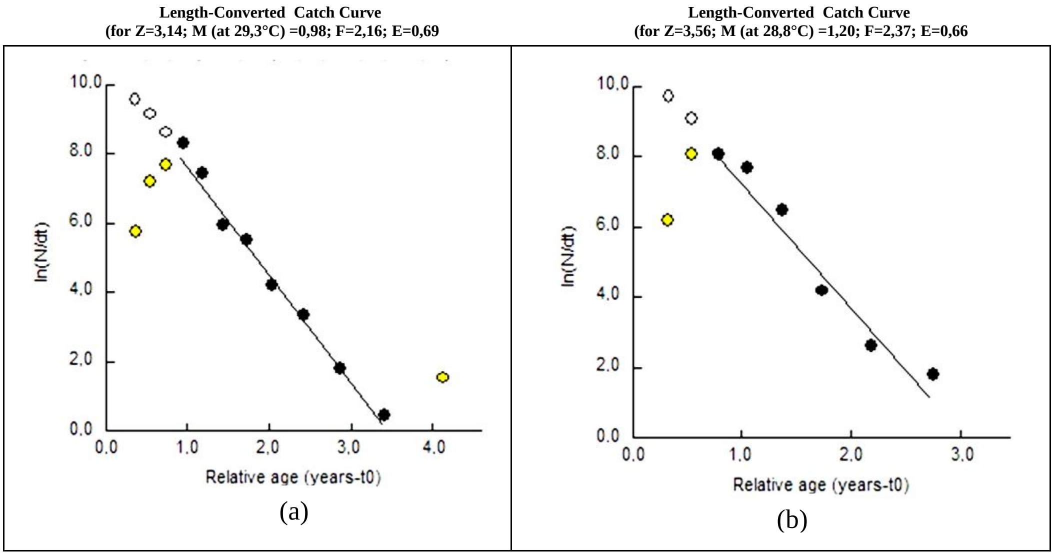


Figure 8: Length-converted catch curves of *Coptodon guineensis* from lake Toho in 2002-2003 (a) and 2022-2024 (b).

Relative yield and biomass per recruit

Figure 9 illustrates the relative yield per recruit (Y'/R) and relative biomass per recruit (B'/R) of *C. guineensis* from Lake Toho during the 2002 and 2022 sampling periods. The Y'/R values were estimated at 0.008 in 2002 and 0.007 in 2022, indicating a slight decline in fishery productivity per recruit over time. Similarly, B'/R values decreased marginally from 0.044 to 0.043, reflecting a subtle reduction in biomass contribution per recruit. These trends suggest a gradual erosion of individual yield potential, likely linked to shifts in population structure and exploitation intensity.

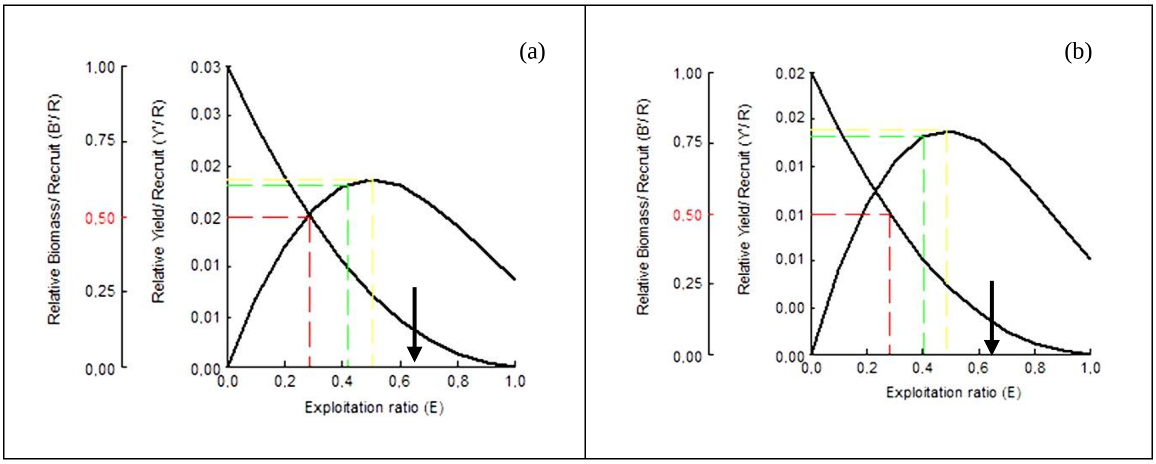


Figure 9: Yield and biomass per recruit curves (Selection Ogive) for *Coptodon guineensis* caught in Lake Toho during 2002-2003 (a) and 2022-2024 (b).

Maximum sustainable yield (MSY)

Figure 10 illustrates the temporal evolution of the average biomass quantities that can be sustainably harvested from *C. guineensis* stocks in lake Toho without compromising reproductive capacity. The estimated Maximum Sustainable Yield (MSY) declined from 389,799 kg in 2002-2003 to 177,506 kg in 2022-2024. The corresponding biomass levels at MSY (BMSY) were 452,770 kg and 170,748 kg, respectively.

The fishing mortality rates (F) associated with achieving MSY were 1.4 year^{-1} in 2002-2003 and 0.5 year^{-1} in 2022-2024. However, actual fishing mortality rates observed during these periods were substantially higher: 2.16 year^{-1} in 2002-2003 and 2.37 year^{-1} in 2022-2024. These discrepancies suggest that exploitation levels have exceeded sustainable thresholds, potentially threatening the long-term resilience and viability of this fish species stock.

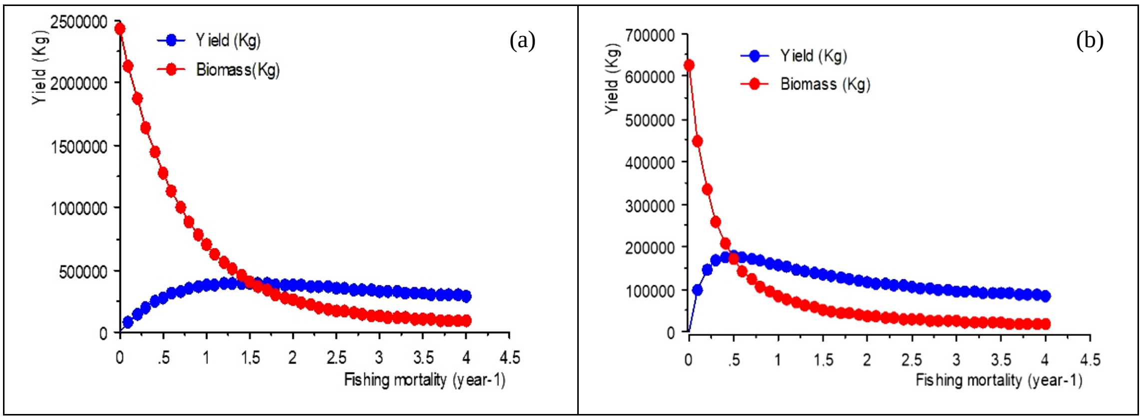


Figure 10: Trends in yield and biomass at varying fishing mortality levels (F) for *Coptodon guineensis* from lake Toho in 2002-2003 (a) and 2022-2024 (b).

DISCUSSION

The intensification of fishing activities with diverse gears and techniques, coupled with global population growth, has led to increased pressure on aquatic resources, resulting in reduced abundance and average size across numerous fish species (Christensen et al., 2003; Pauly et al., 2002). In this context, stock assessment becomes essential, particularly when significant shifts in population structure are observed.

The marked decline in the size of specimens captured between 2002-2003 and 2022-2024 across both sexes reflects intensified fishing pressure targeting unfortunately younger individuals too. According to Froese (2004), such unsustainable exploitation undermines stock renewal, as immature fish are harvested before contributing to local and regional populations reproduction. This leads to truncated size spectra, characterized by the scarcity of large individuals and dominance of smaller size classes (Bianchi et al., 2000). The reduction in size may also reflect ecophysiological responses to fishing pressure, affecting both growth and reproductive traits (Boni et al., 2019). This could explain the observed decrease in size at first sexual maturity during 2022-2024 and the increase in Stage V individuals, as fishing pressure tends to lower the age at first reproduction (Jørgensen et al., 2008; Hutchings, 2005).

Despite the reduction in size at first maturity, the size at first capture (Lc50) in 2022-2024 remains below the maturity threshold unlike in 2002-2003, when Lc50 slightly exceeded Lm50. In both cases, the proportion of sexually mature individuals in the catch remains below 100%. Froese (2004), identifies this scenario where Lc50 < Lm50 and < 100% of captured fish are mature as indicative of recruitment overfishing. The *C. guineensis* population in Lake Toho clearly exhibits this pattern from 2002 - 2003 through 2022-2024, with excessive pressure limiting the influx of new mature individuals (Froese, 2004; Pauly and Chua, 1988). The Lm50 values reported here differ from those of Fouseni et al. (2017) for the same lake, likely due to differences in sample size, sampling duration, and the number of landing sites surveyed.

Furthermore, for both periods, the size at first capture (Lc50) remains below the optimal capture size (Lopt) the length that maximizes fishery yield. The calculated yield per recruit (Y'/R) values are also below the maximum sustainable yield, suggesting that fish are being harvested before reaching their growth potential. These findings point to persistent growth overfishing, where individuals are caught prematurely, leading to biomass loss and undermining long-term harvest sustainability (Christensen et al., 2003; Pauly et al., 1998). This phenomenon also affects growth parameters, with reductions in $L\infty$, Φ', and t_{max} reflecting biological responses to overexploitation. According to Amponsah et al. (2016), low $L\infty$ and Φ' values in exploited fish populations signal intense fishing pressure that alters size structure.

When large spawners are excessively targeted, reproductive overfishing occurs a particularly critical form of overexploitation that impairs stock renewal capacity (Jennings et al., 2001; Pauly, 1995). In lake Toho, the proportion of mega-spawners in the catch remains below 20% in both 2002-2003 and 2022-2024, indicating a weakened reproductive segment of the population. Froese (2004) recommends a minimum threshold of 20% mega-spawners to ensure stock renewal. In this study, not only is that threshold unmet, but the exploitation rate ($E > 0.5$) and fishing mortality-to-growth coefficient ratio ($F/K > 1$) further support the diagnosis of reproductive overfishing. This sustained pressure on larger size classes justified the 24-month monitoring effort during 2022-2024 to ensure representative sampling.

The exploitation parameters observed in this study differ from those reported by Niyonkuru et al. (2007) for lake Nokoué, where the presence of acadja branch-based fish shelters helped mitigate fishing impacts and supported both growth and reproduction.

In light of these findings, the situation in lake Toho reflects more than a decline in catch volume or fish size; it signals a deeper ecological imbalance. The reduction in target stocks may disrupt ecosystem functioning by altering population structures and trophic relationships. According to Pauly et al. (2002), fishing pressure not only affects target species but also disturbs key ecological interactions and vital ecosystem functions a phenomenon known as ecosystem overfishing. In lake Toho, the continued decline in large spawners, yield per recruit, relative yield (Y'/R), and relative biomass (B'/R) points to a concerning shift toward ecosystem-level imbalance.

CONCLUSIONS

The results of this study reveal a troubling degradation in both biological and ecological status of *C. guineensis* population in lake Toho over the past two decades. Significant reductions in average length and weight, size at first sexual maturity, and growth performance (Φ', $L\infty$, t_{max}), along with declines in first capture and optimal capture sizes, reflect intensified fishing pressure targeting younger age classes. The high proportion of immature individuals in the catch reinforces this diagnosis.

The unfavorable trends in bioecological indicators, combined with exploitation rates exceeding biologically sustainable thresholds ($E > 0.5$) and fishing mortality surpassing MSY levels ($F > FMSY$), confirm a chronic state of overfishing that compromises both individual growth and reproductive potential.

Moreover, the persistently low proportion of mega-spawners and declining MSY values indicate a deep disruption in biological renewal processes. This imbalance may have cascading effects on ecosystem functions, jeopardizing the ecological roles fulfilled by the species. A rigorous revision of lake Toho's fisheries management is urgently needed.

Corrective measures such as increasing minimum capture size, implementing biological rest periods, protecting critical spawning habitats, and establishing effective co-management mechanisms involving local communities are essential to restore stock sustainability. Without decisive management action, the risk of irreversible functional collapse of *C. guineensis* populations in lake Toho cannot be ruled out.

Table 5a: Reference values for reproductive, growth, and exploitation parameters of *C. guineensis* across various African aquatic ecosystems. (Lm_{50}: size at first sexual maturity; M_1: male; F_1: female; $L\infty$: asymptotic length; K: growth coefficient; t_0: theoretical age at zero length; t_{max}: longevity; Φ': growth performance index; M: natural mortality; Z: total mortality; F: fishing mortality; E: exploitation rate; Lc50: length at first capture) (Ahoansou Moncho, 2015).

Ecosystems	Years	Reproduction parameters		References
		Lm50 M_1 (cm)	Lm50 F_1 (cm)	
Lake Toho (Benin)	2002-2003			Present study 2002-2003
Lake Toho (Benin)	2022-2023	8.90	8.60	Present Study 2022-2023
Lake Toho (Benin)	2012	7.50	7.90	Fousseni et al. (2017)
Sô River (Benin)	2016-2017	9.60	5.90	Cakpo Kiossa (2012)
Lake Nokoué (Benin)	2000-2001	–	–	Niyonkuru et al. (2007)
Lagoon Grand-Lahou (Côte d'Ivoire)	2013-2014	–	–	Coulibaly et al. (2022)
Southwest Lake (Nigeria)	2013	–	–	Adedolapo (2015)
Ebrié Lagoon (Côte d'Ivoire)	1991-1992	–	–	Villanueva (2004)
Gambia Estuary (Gambia)	1991-1992	–	–	Villanueva (2004)
Siné-Saloum Estuary (Senegal)	1991-1992	–	–	Villanueva (2004)

Table 5b: Reference values for reproductive, growth, and exploitation parameters of *C. guineensis* across various African aquatic ecosystems. (Lm_{50}: size at first sexual maturity; M_1: male; F_1: female; $L\infty$: asymptotic length; K: growth coefficient; t_0: theoretical age at zero length; t_{max}: longevity; Φ′: growth performance index; M: natural mortality; Z: total mortality; F: fishing mortality; E: exploitation rate; Lc50: length at first capture) (Ahoansou Moncho, 2015).

Ecosystems	Years	Growth and Exploitation Rates Parameters											References
		$L\infty$ (cm)	K ($year^{-1}$)	t_0 ($year^{-1}$)	t_{max} (year)	Φ’	M	M/K	Z ($year^{-1}$)	F (an^{-1})	E	L_C50 (cm)	
Lake Toho (Benin)	2002-2003	35.30	0.42	−0.37	7.14	2.71	0.98	2.33	2.36	1.38	0.58	8.03	Present study 2002-2003
Lake Toho (Benin)	2022-2023	19.30	0.35	−0.53	8.57	2.11	1.03	2.94	1.53	0.50	0.33	5.03	Present Study 2022-2023
Lake Toho (Benin)	2012	–	–	–	–	–	–	–	–	–	–	–	Fousseni et al. (2017)
Sô River (Benin)	2016-2017	19.43	0.12	−1.62	–	–	0.50	–	1.36	0.86	0.63	–	Cakpo Kiossa (2012)
Lake Nokoué (Benin)	2000-2001	21.00	0.90	−0.19	3.30	2.58	1.90	2.10	2.30	0.40	0.19	–	Niyonkuru et al. (2007)
Lagoon Grand-Lahou (Côte d’Ivoire)	2013-2014	44.10	0.19	−0.12	15.20	2.56	0.53	–	0.67	0.14	0.21	9.56	Coulibaly et al. (2022)
Southwest Lake (Nigeria)	2013	30.98	0.37	−0.44	8.11	2.55	0.92	2.49	1.19	0.27	0.23	–	Adedolapo (2015)
Ebrié Lagoon (Côte d’Ivoire)	1991-1992	33.00	0.51	–	–	–	1.12	–	–	0.32	–	–	Villanueva (2004)
Gambia Estuary (Gambia)	1991-1992	19.02	1.04	–	–	–	1.47	–	–	0.43	–	–	Villanueva (2004)
Siné-Saloum Estuary (Senegal)	1991-1992	32.50	0.46	–	–	–	1.01	–	–	1.39	–	10.13	Villanueva (2004)

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