Population parameters and exploitation rate of *Sarotherodon galilaeus galilaeus* (Cichlidae) in Lakes Doukon and Togbadji, Benin

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**ABSTRACT**

Growth, mortality, recruitment and relative yield per recruit of *Sarotherodon galilaeus galilaeus* from Lakes Doukon and Togbadji were studied. Data on total length, total weight and sex were recorded on a monthly basis between January and December 2013 for *S. g. galilaeus* captured by local fishers. The estimated asymptotic lengths \(L\) were 26.2 and 23.6 cm for Lakes Doukon and Togbadji, respectively, while the growth rate \(K\) was 0.73 in Lake Doukon and 0.87 in Lake Togbadji. Estimates of fishing mortality, 0.27 and 0.47 \(y^{-1}\) for Doukon and Togbadji, respectively, were low relative to natural mortality, 1.51 and 1.74 \(y^{-1}\), respectively. Sizes at first sexual maturity were 12.8 and 13.2 cm for females and males, respectively, in Lake Doukon, and 11.5 and 12.4 cm for females and males, respectively, in Lake Togbadji. The size at first capture was estimated at 13.3 and 12.7 cm for Lakes Doukon and Togbadji, respectively, which, in the light of the size at maturity estimates, indicates that fish spawn at least once before capture. The current exploitation rates of 0.15 for Lake Doukon and 0.21 for Lake Togbadji suggest that their stocks of *S. g. galilaeus* are not overexploited in either lake.

**Introduction**

In Benin, water resources are free or open-access resources, in contrast to agricultural lands, and as such have been regarded as unlimited resources that people could tap at will. This has led to increased exploitation of fish stocks by local people and to the use of more sophisticated fishing gears and methods, in turn leading to unsustainable harvesting of some stocks (Hounkpè 1996). In many aquatic ecosystems in Benin, large-bodied fish have become very scarce in the fisheries (Lalèyè et al. 1997). However, few studies have quantified population traits of targeted fishery species. Previous studies focused on the cichlids *Sarotherodon melanotheron melanotheron*, *Tilapia guineensis* and *Hemichromis fasciatus* from Lake Ahémé in the Couffo basin and from Lake Nokoué in the Ouémé basin (Niyonkuru 2007) and on the cyprinids *Labeo parvus* and *L. senegalensis* in the Ouémé River (Montchowui et al. 2009, 2011). In a recent study, Lederoun et al. (2015) quantified population parameters and the exploitation rate of *S. m. melanotheron* in Lake Toho in the Mono Basin. In that study they noted the existence of numerous small lakes in the lower course of the Mono Basin that appeared to be heavily exploited, including Lakes Doukon and Togbadji.
Preliminary studies of Lakes Doukon and Togbadji (Brahim 2012) showed that the cichlid *Sarotherodon galilaeus galilaeus* (Linnaeus, 1758) was the most abundant species in fish catches, both in terms of numbers and weight. This species is usually harvested by local people using gillnets and represents a high-value food source. In addition to gillnets, scoopnets are used in Lake Togbadji. The mesh of these scoopnets ranges from 15 to 30 mm bar mesh. These nets are attached to oval wooden frames c. 1-2.5 m in diameter, forming a conical bag c. 1-1.5 m long, with a handle approximately 3 m in length. Scoopnets are forbidden in Lake Doukon under traditional regulations and, in this lake, only night fishing using a net of at least 25 mm mesh size is allowed. In addition, fishing is prohibited for at least two weeks a year in Lake Doukon, and sporadic fishing interdictions can be imposed, depending on circumstances.

Given the economic importance of *S. g. galilaeus*, numerous studies have been undertaken on the biology and demographics of this species in Africa (Bauchot and Bauchot 1978; Blay 1985; Moreau et al. 1986; Yamaguchi et al. 1990; Sadiku and Oladimeji 1991; Entsua-Mensah et al. 1995; Moreau et al. 1995; Baijot and Moreau 1997; du Feu and Abiodun 1998; Béarez 2003; du Feu 2003; Lalèyè 2006). These studies provide a good comparative framework on which to evaluate the population and exploitation parameters in the Benin Lakes Doukon and Togbadji. The objectives of the present study were (i) to quantify a series of population traits for *S. g. galilaeus* including: size at first maturity, growth, and mortality rates and exploitation, which are essential tools in the management of exploited fish stocks; and (ii) to compare key life-history traits (e.g. growth) to data available for this species in African inland waters.

**Materials and methods**

**STUDY AREA**

Lakes Doukon and Togbadji (Figure 1) are two small waterbodies located on the lower course of the Mono River (6°10’-9°00’ N to 0°30’-1°50’ E) in Benin. Lake Doukon covers an area of 0.7 km² and Lake Togbadji 5.5 km². The two lakes are fed by the Mono River during the annual flood period. Due to their geographical position, these lakes have a subequatorial climate characterised 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 which is dominated by continental winds and harmattan conditions. The annual rainfall varies from 544 to 1 376 mm, and temperatures range between 20.6 and 33.5 °C with an average of 28 °C (ASECNA 1981-2010, Cotonou station). Relative humidity is very high and varies from 65% in January to 80.6% in June (ASECNA 1981-2010, Cotonou station).

**SAMPLING METHOD**

*Sarotherodon galilaeus galilaeus* specimens (*n* = 1 478 from Lake Doukon and *n* = 1 401 from Lake Togbadji) were collected from artisanal catches between January and December 2013. The fish had been captured using monofilament gillnets of various dimensions and mesh sizes: 100-240 m long, 1-2 m deep, with 25-50 mm mesh. Fish recognised as *S. g. galilaeus* were randomly sampled from several fishers to ensure representation of all harvested size classes in the samples. All specimens (Table 1)
were brought to the laboratory where they were identified using the key by Teugels and Thys van den Audenaerde (2003). All fishes were measured for total length to the nearest 0.1 cm with a measuring-tape, individually weighed to the nearest 0.01 g using an electronic precision balance, and sexed (immature, male or female) following the criteria of Lalèyé et al. (1995a, 1995b).

**DATA PROCESSING**

**LENGTH-WEIGHT RELATIONSHIP**

The length-weight relationship was estimated using the equation:

\[ W = aTL^b \]  

where \( W \) represents the body weight in grams (g), \( TL \) is the total length in centimetres (cm), \( a \) is a constant or intercept, and \( b \) is the slope or the regression or allometric growth coefficient. This coefficient \( b \) varies between 2 and 4, but is often close to 3 (Froese 2006). The limit for \( b \) was assessed using Statview software (v. 5.0.1, SAS Institute). In order to check whether \( b \) was significantly different from 3, the \( t \)-test was performed following the equation of Sokal and Rohlf (1987):

\[ t_s = \frac{(b - 3)}{SE} \]  

where \( t_s \) is the \( t \)-test value, \( b \) the slope, and \( SE \) the standard error of \( b \). Differences were considered significant at 5% \((p < 0.05)\). ANCOVA was used to test for a difference in the bi-logarithmic weight-length relationships between lakes.

**SIZE AT FIRST MATURITY**

Size at first maturity \((L_{50})\), defined as the size at which 50% of the individuals were mature, was determined for males and females through the equation of the sigmoid curve of proportions \((P)\) of sexual mature fish based on size classes \((TL)\). The sigmoid curve was fitted using a standard logistic regression model of the form:

\[ P = \frac{e^{(\alpha+\beta TL)}}{(1 - e^{(\alpha+\beta TL)})} \]  

where \( \alpha \) and \( \beta \) are the model parameters. 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: \( L_{50} = -\alpha/\beta \). Individuals at maturity stages 2 to 5 were considered to have active gonads. Likelihood-ratio tests were performed to detect differences in \( L_{50} \) values between sexes and between lakes. Statview (v. 5.0.1, SAS Institute) was used to calculate the estimated proportion of mature fish and the coefficients \( \alpha \) and \( \beta \) of the model.

**Figure 1:** Map showing locations of Lake Doukon and Lake Togbadji in the Mono Basin, Benin
Table 1: Monthly length-frequency data for *Sarotherodon galilaeus galilaeus* from Lake Doukon and Lake Togbadji in 2013. ML = mid-length of class interval

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| Lake Togbadji (n=1 401) |
| 6.5     | 0    | 0    | 0    | 0    | 0   | 0    | 0    | 0    | 0    | 3    | 0    | 2    |       |
| 7.5     | 3    | 0    | 0    | 2    | 6   | 0    | 1    | 0    | 3    | 13   | 0    | 6    |       |
| 8.5     | 4    | 0    | 0    | 4    | 4   | 5    | 4    | 5    | 4    | 12   | 1    | 3    |       |
| 9.5     | 8    | 0    | 16   | 17   | 22  | 7    | 51   | 59   | 8    | 7    | 7    | 20   |       |
| 10.5    | 20   | 1    | 5    | 12   | 16  | 1    | 18   | 20   | 20   | 1    | 6    | 24   |       |
| 11.5    | 17   | 1    | 5    | 21   | 10  | 5    | 6    | 13   | 17   | 5    | 7    | 10   |       |
| 12.5    | 20   | 0    | 4    | 8    | 5   | 0    | 12   | 4    | 20   | 7    | 15   | 2    |       |
GROWTH PARAMETERS

Length measurements were grouped into 1 cm total length (TL) class intervals of which the mid-lengths (Table 1) were used for the growth analysis. The von Bertalanffy model was used, which expresses the length (TL) of a fish as a function of its age by:

\[ TL = L_\infty (1 - e^{-K(t - t_0)}) \]  

where TL is the total length of the fish at time \( t \), \( L_\infty \) the asymptotic length that the fish would reach at an infinite theoretical age, \( K \) the rate at which TL approaches \( L_\infty \), and \( t_0 \) 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) (Gayalino et al. 1996) was used to estimate the parameters \( L_\infty \) and \( K \) of the von Bertalanffy equation. Parameters \( a \) and \( b \) of Equation 1 were used; \( t_0 \) was estimated by the equation of Pauly (1979):

\[ \log_{10}(t_0) = -0.392 - 0.275 \log_{10} L_\infty - 1.038 \log_{10} K \]  

Estimates of \( L_\infty \) and \( K \) were further used to calculate the growth performance index using the equation of Pauly and Munro (1984):

\[ \phi' = \log_{10} K + 2 \log_{10} L_\infty \]  

Potential longevity, \( t_{\text{max}} \), was calculated using the following formula (Taylor 1962; Pauly 1980):

\[ t_{\text{max}} = \frac{3}{K} \]  

MORTALITY AND EXPLOITATION RATE

The total mortality coefficient \( Z (y^{-1}) \) was estimated following the linear length-converted catch curve method incorporated in the FiSAT II software using the formula:
\[
\ln\left( \frac{N_i}{dt_i} \right) = (8)
\]
where \(N_i\) is the number of individuals in length class \(i\) and \(dt_i\) the time needed by the fish to grow in that class \(i\) (Pauly 1990; Pauly et al. 1995). The natural mortality rate \(M\) (\(y^{-1}\)) was estimated according to Pauly's (1980) empirical equation:

\[
\text{Log}_{10} M = 0.654\text{Log}_{10} K - 0.28\text{Log}_{10} L_\infty + \text{Log}_{10} T \times 0.4634 - 0.0066
\]

where \(K\) and \(L_\infty\) are the parameters of Equation 4 and \(T\) the average annual temperature of the water which is 28 °C. Fishing mortality rate \((F)\) was estimated using the relationship:

\[
F = Z - M
\]

The exploitation rate \((E)\) was obtained from:

\[
E = F / Z
\]

**SIZE AT FIRST CAPTURE**

The size at first capture \((L_c)\), i.e. length at which 50% of the fishes are selected by the gear, was estimated using the ogive selection, assuming that the chance of capturing a fish is solely dependent on its length.

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

The model of Beverton and Holt (1966), as modified by Pauly and Soriano (1986), was used to predict the relative yield per recruit \((Y'/R)\) following:

\[
Y'/R = EU^{\text{exp}}\left[ 1 - \frac{(3U)}{(1 + m)} + \frac{(3U^2)}{(1 + 2m)} - \frac{(U^3)}{(1 + 3m)} \right]
\]

where \(E = F / Z\) corresponds to the current exploitation rate, i.e. the fraction of the total mortality caused by fishing activities. \(U = 1 - (L_c / L_\infty)\) is the fraction of growth to be completed by the fish after its entry into the exploitation phase \((L_c = \text{mean length at first capture}, L_\infty = \text{asymptotic length})\), \(m = (1 - E) / (M / K) = K / Z\). The relative biomass per recruit \((B'/R)\) was estimated as:

\[
B'/R = \left( \frac{Y'/R}{F} \right)
\]

The reference points used to determine the status of the \(S.\ g.\ galiellaeus\) stocks of Lakes Doukon and Togbadji were (i) the fishing mortality rate \((F)\), (ii) 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 \(E\) \((E_{0,1})\), (iii) the exploitation level that will result in a reduction of the unexploited biomass by 50% \((E_{0,5})\), and (iv) the exploitation level that produces the maximum yield per recruit \((E_{\text{max}})\).

**Recruitment patterns**

Fish recruitment patterns were obtained using the data on length-restructured frequencies. This implies the backward projection of all the data on length-restructured frequencies along the trajectory described by the von Bertalanffy growth curve on a one-year time-scale (Pauly 1987). Thus, using the method of maximum probability, the distribution is solved in its Gaussian components using the ‘NORMSEP’ procedure (normal separation) of Hasselblad (1966).
Results

LENGTH-WEIGHT RELATIONSHIP

In Lake Doukon the length of *S. g. galilaeus* in the fishers’ catches varied from 9.3 to 24.5 cm and the weight from 16.10 to 265.75 g; whereas in Lake Togbadji the length varied from 6.1 to 22.6 cm and the weight from 4.0 to 260.0 g. The length-weight relationship was described by the following equations for Lakes Doukon and Togbadji, respectively: $W = 0.021TL^{2.955}$ ($r^2 = 0.967$, SE = 0.015) and $W = 0.0172TL^{3.0545}$ ($r^2 = 0.984$, SE = 0.012). In Lake Doukon, the allometric coefficient was significantly lower than 3 ($t_s = -3$, confidence interval at 95% for $b$: 2.927–2.984). The allometric coefficient $b$ obtained from Lake Togbadji was significantly greater than 3 ($t_s = 4.583$, confidence interval at 95% for $b$: 3.031–3.078). The slopes of the regressions differed significantly between lakes ($F = 27.94$, df = 1, $p < 0.0001$); and we, therefore, did not test for a difference in the intercepts. For Lake Togbadji, the mass of the fish increased more quickly with increased length than in Lake Doukon.

SIZE AT FIRST MATURITY

The estimated size at 50% maturity for *S. g. galilaeus* in Lake Doukon was 12.8 and 13.2 cm for males and females, respectively (Figure 2a), and 12.4 and 11.5 cm for males and females, respectively, in Lake Togbadji (Figure 2b). There was no significant difference in the estimated size at maturity between males and females within the two lakes (Lake Doukon, $p = 0.754$; Lake Togbadji, $p = 0.885$). There was no significant interaction between lake and gender (df = 1, $p = 0.4762$).

GROWTH PARAMETERS

The asymptotic length $L_\infty$ and the growth coefficient $K$ were 26.2 cm and 0.73 y$^{-1}$, respectively, in Lake Doukon, and 23.6 cm and 0.87 y$^{-1}$ in Lake Togbadji. The growth performance index $\phi'$ was very similar between the two lakes, estimated at 2.70 in Lake Doukon and 2.68 in Lake Togbadji. The theoretical ages at which length is 0 was estimated at -0.22 year and -0.19 year for Lake Doukon and Lake Togbadji, respectively. The approximated longevity $t_{\text{max}}$ was 4.11 years in Lake Doukon and 3.44 in Lake Togbadji. During the study period, specimens of *S. g. galilaeus* captured in Lake Doukon belonged to 6 cohorts, and those of Lake Togbadji belong to 4 cohorts (Figure 3a, b).

MORTALITY AND EXPLOITATION RATE

Total mortality was estimated at about 1.76 y$^{-1}$ in Lake Doukon and 2.21 y$^{-1}$ in Lake Togbadji. Most mortality was due to natural mortality $M$, estimated as 1.51 and 1.74 y$^{-1}$, for Lakes Doukon and Togbadji, respectively. Fishing mortality $F$ was low for the two lakes, but higher in Lake Togbadji (0.47 y$^{-1}$) than in Lake Doukon (0.27 y$^{-1}$, Figure 4a, b). The exploitation rate $E$ was 0.15 in Lake Doukon and 0.21 in Lake Togbadji.

*Figure 2: Estimated size at first maturity for males and females of Sarotherodon galilaeus galilaeus from (a) Lake Doukon and (b) Lake Togbadji*
Figure 3: Length frequency data superimposed on the growth curve of Sarotherodon galilaeus galilaeus from (a) Lake Doukon ($L_{\text{m}} = 26.2$ cm total length, $K = 0.73$ yr$^{-1}$) and (b) Lake Togbadji ($L_{\text{m}} = 23.6$ cm total length, $K = 0.87$ yr$^{-1}$)

SIZE AT FIRST CAPTURE

For the current study, the logistic selection model showed that the estimated length $L_c$ of 50% of all the
fish caught by the gear in Lake Togbadji was 12.7 cm, while it was 13.3 cm in Lake Doukon (Figure 5a, b). Similarly, the model found that 25% and 75% of all the fish caught in Lake Togbadji had an estimated length of 10.5 and 15.0 cm, respectively, while 25% and 75% of the total caught in Lake Doukon had an estimated length of 11.4 and 15.2 cm, respectively. Overall, there was no significant difference detected in the selectivity of the catch gear between the two lakes (df = 1, p = 0.932).

**Figure 4:** Length-converted catch curve for *Sarotherodon galilaeus galilaeus* from (a) Lake Doukon and (b) Lake Togbadji. 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 grey dots are those not used in mortality estimation.

### RELATIVE YIELD PER RECRUIT $Y'/R$ AND REFERENCE POINTS

Overall, the exploitation rates were quite similar between the two lakes. In Lake Doukon, the curve of relative yield per recruit $Y'R$ relative to the exploitation ratio $E$, indicated an optimal exploitation rate ($E_{\text{max}}$) of 0.649, a rate relatively similar to the $E_{\text{max}}$ estimated for Lake Togbadji (0.60) (Figure 6a, b). The exploitation rate $E_{0.1}$ (exploitation rate at which the marginal increase of $Y'R$ is 10% of its entire stock) and $E_{0.5}$ (exploitation rate under which the entire stock is halved) were estimated at 0.515 and 0.290, respectively, for Lake Doukon, and 0.50 and 0.263 for Lake Togbadji.

**Figure 5:** Probability of capture of *Sarotherodon galilaeus galilaeus* from (a) Lake Doukon and (b) Lake Togbadji estimated from the ascending axis of the catch curve.
RECRUITMENT PATTERNS

Recruitment patterns of *S. g. galilaeus* in Lakes Doukon and Togbadji were similar (Figure 7a, b), with a notable bimodal distribution indicating two distinct spawning events (May-June and September-October).

*Figure 6:* Relative yield-per-recruit and biomass-per-recruit curves for *Sarotherodon galilaeus* from (a) Lake Doukon and (b) Lake Togbadji using the selection ogive option. The three dashed right-angled lines correspond to $E_{0.5}$, $E_{0.1}$ and $E_{\text{max}}$, respectively.
Discussion

The length-weight relationship of a fish is an important element of its productivity (Le Cren 1951; Lalèyè 2006; Tah et al. 2012). The slopes of the bilogarithmic masslength relationships differed between the Lakes Doukon and Togbadji; in Lake Togbadji, the increase in weight for a given increase in length was greater. Such variation in length-weight relationships is not unusual in *S. g. galilaeus* across inland waters in Africa. In Lake Kainji, Nigeria, du Feu and Abiodun (1998) reported positive allometric growth; negative allometric growth was reported for exploited *S. g. galilaeus* in the hydroelectrical dam of Buyo on the Sassandra River, Ivory Coast (Tah et al. 2012); while isometric growth was reported for exploited *S. g. galilaeus* of Zaria Dam, Nigeria (Sadiku and Oladimeji 1991). Such variation in length-weight relationships may reflect differences in the environmental characteristics of the sites, parasitism, harvest pressure, and/or other features that vary across sites. For example, high fishing pressure may reduce intraspecific competition for food and increase fish condition (greater mass for a given fish length); while high levels of parasitism may reduce fish condition. In the management of a fish stock the size at first sexual maturity (*L*_50) is of great importance in determining the optimal mesh size. In the current study, the *L*_50 values obtained for *S. g. galilaeus* in Lakes Doukon and Togbadji were smaller than those reported by other authors for the same species in other the areas of the subregion. Johnson (1974) recorded a size of 19.8 cm TL for *S. g. galilaeus* (pooled males and females) from Lake Volta, Ghana. Ita (1982) reported an *L*_50 of 15.5 and 16.8 cm TL, respectively, for females and males of Lake Kainji, Nigeria. Lengths measured by Baijot and Moreau (1997) in the small dams of Burkina-Faso were 12.6 and 13.8 cm TL for females and males. Differences in maturity size between habitats could be linked to the availability and quality of food and to fishing pressure (Pauly 1976; Panfili et al. 2004). Size at maturity may decrease, for example, in response to heavy fishing pressure (Chapman and Sharpe 2015).
**Table 2: Summary of growth parameters for *Sarotherodon galilaeus galilaeus* in various ecosystems in Africa**

<table>
<thead>
<tr>
<th>L∞ (cm)</th>
<th>Length</th>
<th>K</th>
<th>t₀</th>
<th>Sex</th>
<th>Country</th>
<th>Locality</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>14.7</td>
<td>TL</td>
<td>1.11</td>
<td>-0.42</td>
<td>—</td>
<td>Burkina Faso</td>
<td>Loumbila reservoir</td>
<td>Baijot and Moreau (1997)</td>
</tr>
<tr>
<td>17.4</td>
<td>TL</td>
<td>0.45</td>
<td>-0.5</td>
<td>—</td>
<td>Burkina Faso</td>
<td>Ramitenga reservoir</td>
<td>Baijot and Moreau (1997)</td>
</tr>
<tr>
<td>19.3</td>
<td>TL</td>
<td>0.64</td>
<td>—</td>
<td>—</td>
<td>Burkina Faso</td>
<td>Lake Ramitinga</td>
<td>Moreau et al. (1995)</td>
</tr>
<tr>
<td>20.1</td>
<td>SL</td>
<td>0.53</td>
<td>—</td>
<td>—</td>
<td>Egypt</td>
<td>Lake Manzala</td>
<td>Moreau et al. (1986)</td>
</tr>
<tr>
<td>24.0</td>
<td>TL</td>
<td>0.47</td>
<td>-0.61</td>
<td>—</td>
<td>Burkina Faso</td>
<td>Tapoa reservoir</td>
<td>Baijot and Moreau (1997)</td>
</tr>
<tr>
<td>24.2</td>
<td>SL</td>
<td>0.98</td>
<td>—</td>
<td>—</td>
<td>Egypt</td>
<td>Noussa Hydromé</td>
<td>Moreau et al. (1986)</td>
</tr>
<tr>
<td>26.6</td>
<td>SL</td>
<td>0.6</td>
<td>—</td>
<td>—</td>
<td>Chad</td>
<td>Lake Tchad</td>
<td>Moreau et al. (1986)</td>
</tr>
<tr>
<td>27.2</td>
<td>SL</td>
<td>0.66</td>
<td>—</td>
<td>—</td>
<td>Chad</td>
<td>Chari Lagone</td>
<td>Moreau et al. (1986)</td>
</tr>
<tr>
<td>27.3</td>
<td>SL</td>
<td>0.68</td>
<td>-0.05</td>
<td>M</td>
<td>Egypt</td>
<td>High Dam Lake</td>
<td>Yamaguchi et al. (1990)</td>
</tr>
<tr>
<td>28.8</td>
<td>SL</td>
<td>0.53</td>
<td>-0.2</td>
<td>F</td>
<td>Egypt</td>
<td>High Dam Lake</td>
<td>Yamaguchi et al. (1990)</td>
</tr>
<tr>
<td>29.9</td>
<td>SL</td>
<td>0.34</td>
<td>—</td>
<td>—</td>
<td>Chad</td>
<td>Lake Tchad</td>
<td>Moreau et al. (1986)</td>
</tr>
<tr>
<td>30.1</td>
<td>TL</td>
<td>0.51</td>
<td>—</td>
<td>—</td>
<td>Senegal</td>
<td>Sénégal River</td>
<td>Moreau et al. (1995)</td>
</tr>
<tr>
<td>35.5</td>
<td>TL</td>
<td>0.17</td>
<td>-0.15</td>
<td>—</td>
<td>Burkina Faso</td>
<td>Sourou reservoir</td>
<td>Baijot and Moreau (1997)</td>
</tr>
<tr>
<td>36.2</td>
<td>TL</td>
<td>0.22</td>
<td>-0.94</td>
<td>—</td>
<td>Burkina Faso</td>
<td>Petit Balé reservoir</td>
<td>Baijot and Moreau (1997)</td>
</tr>
<tr>
<td>41.0</td>
<td>SL</td>
<td>0.29</td>
<td>—</td>
<td>—</td>
<td>Egypt</td>
<td>Lake Nasser</td>
<td>Moreau et al. (1986)</td>
</tr>
<tr>
<td>45.7</td>
<td>FL</td>
<td>0.47</td>
<td>—</td>
<td>—</td>
<td>Nigeria</td>
<td>Lake Kainji</td>
<td>du Feu (2003)</td>
</tr>
<tr>
<td>48.4</td>
<td>SL</td>
<td>0.47</td>
<td>—</td>
<td>—</td>
<td>Nigeria</td>
<td>Lake Kainji</td>
<td>Moreau et al. (1986)</td>
</tr>
<tr>
<td>26.2</td>
<td>TL</td>
<td>0.73</td>
<td>-0.22</td>
<td>—</td>
<td>Benin</td>
<td>Lake Doukon</td>
<td>Present study</td>
</tr>
<tr>
<td>23.6</td>
<td>TL</td>
<td>0.87</td>
<td>-0.19</td>
<td>—</td>
<td>Benin</td>
<td>Lake Togbadji</td>
<td>Present study</td>
</tr>
</tbody>
</table>

The estimates for von Bertalanffy growth parameters (L∞, K and t₀) for *S. g. galilaeus* in Lakes Doukon and Togbadji seem realistic, as L∞ was reasonably close to the maximum length observed in the samples (Moreau et al. 1986), t₀ was smaller than zero, and K varied between 0 and 1 per year, as expected for fish species with a long life span (Pauly 1978). Growth parameters for *S. g. galilaeus* show a high degree of variation across African inland waters (Table 2). The growth performance
indexes $\phi'$ calculated in the present study, 2.68 and 2.70 for Lake Togbadji and Lake Doukon, respectively, fall within the range of those reported in the literature. It is also notable that the growth parameters were quite similar between the two focal lakes.

Total mortality, natural mortality and fishing mortality were higher in Lake Togbadji than in Lake Doukon. In both lakes, natural mortality due to predation, shortage of food, diseases, pollution, spawning stress and senility (King and Etim 2004) was much higher than fishing mortality. The use of scoopnets in Lake Togbadji is likely to account for the higher level of fishing mortality here. Generally, the $M/K$ ratio is used as an index for checking the reliability of $M$ and $K$, estimated through different methods. This ratio should vary between 1.12 and 2.5 (Beverton and Holt 1959), and the ratios obtained for Lake Togbadji (1.99) and Lake Doukon (2.06) fell within this range. Following Gulland (1971), the state of exploitation of a stock can be assessed on the basis that an optimal yield is obtained when $F = M$. Pauly (1987) put forward a more conservative $F$ equalling 0.4$M$. In the present study, $F$ for both lakes was smaller than the two values of more conservative $F$ given by these authors, indicating that the stocks of *S. g. galilaeus* in Lakes Doukon and Togbadji are not overexploited.

A second indication that the stocks are not overexploited was obtained by comparing the size at first capture, $L_{\infty}$, i.e. the length at which 50% of the fish measuring that size are vulnerable to capture, with $L_{50}$. Size at first capture was estimated at 12.7 cm in Lake Togbadji and 13.3 cm in Lake Doukon, which are both greater than the $L_{50}$, both for males and for females.

The curve of relative yield per recruit $Y'/R$ shows that the current exploitation rates in the two lakes (0.15 in Lake Doukon vs 0.21 in Lake Togbadji) are lower than the exploitation rate predicted to give the maximum $Y'/R$ (0.649 in Lake Doukon vs 0.60 in Lake Togbadji), and the estimate of the rate which maintains 50% of the stock biomass, $E_{0.5}$ (0.290 in Lake Doukon vs 0.263 in Lake Togbadji) for the two lakes, again indicating that the stocks are not yet overexploited. However, the apparent underexploitation of the populations of *S. g. galilaeus* could easily switch to overexploitation in the future if sensitisation sessions advocating sustainable fishing methods are not organised. This is especially the case for Lake Togbadji, where scoopnet fishing is becoming more common and correlates with higher fishing mortality in this system.

**Conclusion**

The current study of the state of the population of *S. g. galilaeus* based on the samples collected from artisanal catches in Lakes Doukon and Togbadji provides no evidence of overexploitation of the species under the current fishing regime. However, the higher fishing mortality in Lake Togbadji may reflect the increasing use of scoopnets. Therefore we recommend maintenance of the current exploitation level, in addition to the development of a monitoring programme to detect shifts in the exploitation rates, indices of overexploitation and changes in life-history traits that may reflect harvest-induced change.

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