Regular paper

Life history traits and exploitation of Hampala barb (*Hampala macrolepidota* – Cyprinidae) in a subtropical reservoir (Lao PDR)

by

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Abstract. – The life history traits of *Hampala macrolepidota*, a common freshwater fish species in Southeast Asia that is of interest for fisheries and sport fishing, were estimated for a population from Nam Theun 2 Reservoir in Lao. The exploitation status of this species was also characterized using data from landing. Toluidine-stained transverse section of otoliths from 450 specimens, collected between November 2015 and January 2017 (by experimental gillnet fishing and landing surveys), were analysed to identify the periodicity of annulus formation and to age individuals. Length, weight, sex and sexual maturity stage were recorded. Life history traits were characterized by length-weight and length-age relationships. The periodicity of annulus formation was annual, with complete formation of the translucent zone at the end of the warm and dry season and the beginning of the warm and wet season (May-June). The length at first sexual maturity of females was estimated to occur at a standard length of 212 mm and at 3.3 years old (50% of matured females). The condition factor, which was between 1.04 and 1.09, was lower than for other studied populations. *H. macrolepidota* in the Nam Theun 2 Reservoir had a relatively slow growth (0.24 yr^{-1}) with a relatively short lifespan (maximum age of approximately 9 years old). The species exploitation in the reservoir mainly concerned individuals that had a standard length between 120 and 220 mm, meaning that 67% of landed individuals did not have time to reproduce before capture. The exploitation rate was 0.87, and according to the probability of capture, individuals had 50% chances of being caught after 182.5 mm, preventing them from taking part in the stock renewal. The present study suggests that the *H. macrolepidota* population in the reservoir is overexploited. These new findings should be considered for further improvements in fishery management and the sustainability of fisheries.

Résumé. – Traits d'histoire de vie et statut d'exploitation d'*Hampala macrolepidota* (Cyprinidae) dans un lac de retenue subtropical au Laos.

Les traits d'histoire de vie d'*Hampala macrolepidota*, poisson d'eau douce communément présent en Asie du Sud-Est et présentant un intérêt pour la pêche commerciale et sportive, ont été étudiés pour la population du réservoir de Nam Theun 2 au Laos. Le statut d'exploitation de cette espèce par la pêcherie locale a également été caractérisé *via* un suivi des débarquements de la pêche artisanale et de subsistance. Les sections transversales d'otolithes de 450 spécimens collectés entre novembre 2015 et janvier 2017 ont été analysées pour identifier la périodicité de formation de l'annulus et déterminer l'âge des individus. La taille standard, le poids, le sexe et le stade de maturité des gonades ont parallèlement été collectés. Les relations taille-poids et taille-âge ont été caractérisées. Les résultats ont indiqué qu'un annulus se formait par an avec une zone translucide totalement formée à la fin de la saison sèche-début de la saison des pluies (mai-juin). La première maturité sexuelle des femelles a été estimée atteinte pour une taille standard de 212 mm et un âge de 3,3 ans. Le facteur de condition compris entre 1,04 et 1,09 était inférieur à celui des autres populations asiatiques étudiées. La population d'*H. macrolepidota* du réservoir de Nam Theun 2 présentait une croissance relativement lente (0,24 an) avec une durée de vie assez courte pour cette espèce (âge maximal 9 ans). L'exploitation de cette espèce dans le réservoir concernait principalement les individus ayant une taille standard comprise entre 120 et 220 mm. Ainsi, 67% des individus issus de la pêcherie n'avaient pas eu le temps de se reproduire au moins une fois avant d'être capturés. Le taux d'exploitation était de 0,87 et selon la probabilité des captures, les individus avaient 50% de chance d'être capturés après avoir atteint la taille de 182 mm, les empêchant de prendre part au renouvellement du stock. Cette étude suggère que la population d'*H. macrolepidota* du réservoir de Nam Theun 2 est surexploitée. Ces conclusions devraient être prises en compte pour améliorer la gestion de la pêche actuellement en place et sa durabilité.

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Large man-made lakes, called reservoirs (water surface area equal or greater than 10 km²; ICOLD, 1992), are numerous worldwide (approximately 55,000), and more than 40% are located in tropical and subtropical regions (ICOLD, 2018). The construction of new tropical/subtropical reservoirs, primarily for flood control and crop irrigation and for electricity production, has significantly increased since the 1960s, especially in Asia, a region of the world which has approximately 25% of the world's reservoirs (Bhukaswan, 1980; Sugunan, 1995). In the Lao People's Democratic Republic (Lao PDR), water from tributaries contributes to 35% of the total flow of the Mekong River. Approximately 33 hydropower reservoirs are operational, 31 are under construction and approximately 56 are planned or are under feasibility study (Greater Mekong Dams Observatory, 2017). Phonvisay (2013) indicated that 40% of the fish production of the Lao PDR come from reservoirs and that this percentage should increase in the future (Mottet and Lasserre, 2014). In Lao PDR and other Asian countries, the reservoirs are important for both food security and income by contributing to valuable perennial fish resources (Fernando and Holčík, 1991; Thapanand *et al*., 2007; De Silva and Amarasinghe, 2009).

In Southeast Asia where natural lakes are rare, only a few native fish species are able to adapt to new environmental conditions induced by the impoundment (e.g., lentic system, restricted range of possible food organisms and substrates, little diversity of habitats) because of their riverine origin (Fernando and Holčík, 1982). Therefore, the catches realized by fisheries associated with these reservoirs are usually dominated by introduced species coming from Africa, such as tilapias, *Oreochromis niloticus* (Linnaeus, 1758) and/or *O. mossambicus* (Peters, 1852) (Amarasinghe, 1987; Fernando and Holčík, 1991; Moreau and De Silva, 1991; Pet *et al*., 1996; Cottet and Visser, 2017). However, a few native fish species can also dominate the catches, which can either be associated or not with the tilapias. The species most commonly found in these ecosystems in Southeast Asia is a Cyprinidae, *Hampala macrolepidota* Kuhl, Van & Hasselt, 1823 (Setadi *et al*., 1987; Costa-Perce and Soemarwoto, 1990; Muthmainah *et al*., 2015). This species is also dominant in Laotian reservoirs (Mattson *et al*., 2000; Cottet and Visser, 2017). With the significant contribution of this native species to the fisheries associated with reservoirs and the future rise of the number of reservoirs, it is necessary to strengthen the knowledge of its history traits for better catch management of this fish species. Gathering information on the limnologic features, characterization of the fisheries and the population and community dynamics could all provide valuable data for a more adequate management of introduced and native fish species.

However, although *H. macrolepidota* represents a major portion of the fisheries (Setadi *et al*., 1987; Costa-Perce and Soemarwoto, 1990; Mattson *et al*., 2000; Cottet and Visser, 2017) and is of major economic value for local human populations (Abidin, 1986; Ambak and Jalal, 1998; Rovie-Ryan *et al*., 2008; Makmur *et al*., 2014) and for several countries, sport fishing interest (Abidin, 1986; Zakaria *et al*., 2000; Christianus and Amin, 2013) and the characterization of its life history traits have received very little attention (Munro *et al*., 1990; Liu *et al*., 2012, 2015). The IUCN (2018) mentioned that research is required on *H. macrolepidota* to better understand the species distribution, population trends, threats, habitats and ecology. Furthermore, these rare studies had limited access because they were not published in English and/or the methods used and/or their results were not clear. Finally, there are not many biological parameters available in the literature or in international databases (fishbase.org) for this species.

To estimate the age and growth, which are among the most important life history traits for fish populations, otoliths (ear stones) and their seasonal growth marks are specific and relevant tools, even in tropical and subtropical areas (Panfili *et al*., 2002; Morales-Nin and Panfili, 2005). Otolith marks are the consequences of abiotic (e.g., seasons and temperature) and biotic factors (e.g., spawning period, food quantity and body condition) (Beamish and McFarlane, 1983; Yosef and Casselman, 1995; Panfili *et al*., 2002). Thus, it is also necessary to validate the periodicity of mark deposition in the different habitats of the species (Beamish and McFarlane, 1983; Panfili *et al*., 2002).

The aim of the present study was to estimate a few of the main life history traits (age, growth, size and age at first sexual maturity) of *H. macrolepidota*, which is one main fishery target in the Nam Theun 2 Reservoir (NT2 Reservoir), Lao PDR, to provide information for its management. The objectives were (i) to characterize otolith seasonal increments and validate their timing of deposition, (ii) to estimate the growth and demographic structure, (iii) to determine the mean length and age at first sexual maturity and ecological information from the *H. macrolepidota* population within the NT2 Reservoir, and (iv) to determine the sustainability of the species fishery within the NT2 Reservoir for further improvement of its management, which could be compared with or transferred to other reservoirs.

MATERIALS AND METHODS

Study site

The study was conducted for the Nam Theun 2 hydroelectric Reservoir (NT2 Reservoir), which is located at 538 m above sea level in the centre of Lao PDR at 17°50'N and 105°10'E (Fig. 1) (Descloux *et al*., 2011). This reservoir, which was impounded in 2008 (Descloux *et al*., 2011), experiences a monsoon regime (Descloux and Cottet, 2016). The

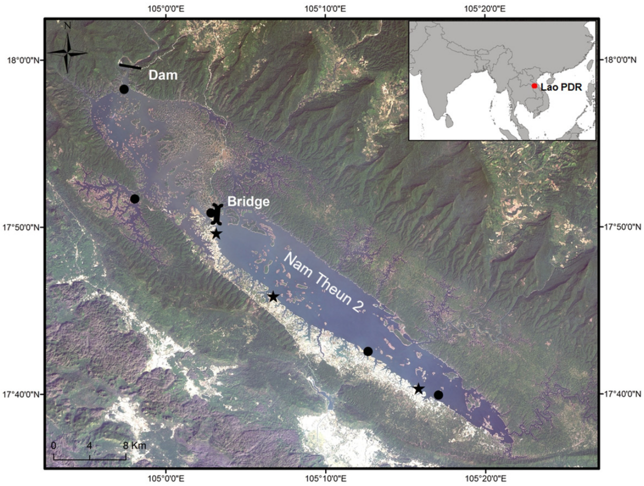

Figure 1. – Map of the Nam Theun 2 Reservoir in Lao PDR at its highest level (surface = 489 km²) and localization of sampling sites by experimental fishing gillnets (black dotes) and of villages (black stars) by landing/fishing effort monitoring. Source: Google Earth.

cold and dry (CD) season lasts from November to February, the warm and dry (WD) season is between March and May, and the warm and wet (WW) season is between June and October (Descloux *et al*., 2016). The surface of the NT2 Reservoir varies between 86 km² (theoretical minimum) at the end of the WD season in June and 489 km² at its full supply level at the beginning of the CD season in November (Descloux *et al*., 2016). It is a relatively shallow reservoir with an average depth of 8 m and a maximal depth of 38 m (Chanudet *et al*., 2012). It was classified as a meso-oligotrophic freshwater reservoir between 2008 and 2011 (trophic upsurge period) and as oligotrophic after 2011 (Descloux and Cottet, 2016; Martinet *et al*., 2016). The water transparency is on average at 1.8 m (range = 1.2-2.6 m, Martinet *et al*., 2014). The surface water temperature varies from approximately 18°C at the end of the CD season to 32°C at the end of the WD season (Chanudet *et al*., 2015). The NT2 Reservoir is monomictic, and a short mixing period occurs during the CD season (Chanudet *et al*., 2012).

Along the southwestern coastline of the NT2 Reservoir, 16 resettlement hamlets are present with approximately 2,200 households in 2014, and 84% of them practice fishing activities for income generation and subsidence (Cottet and Visser, 2017). Even though the fisheries of the NT2 Reservoir are composed of multiple species, the catches are dominated by one exotic introduced species, *Oreochromis niloticus*, and then by the native species *Hampala macrolepidota* (Cottet and Visser, 2017). The catches of *H. macrolepidota* have increased regularly to reach 21% of the total catch from the NT2 Reservoir in 2014 (Cottet and Visser, 2017).

Fish sampling

H. macrolepidota were collected monthly between November 2015 and January 2017 from various sites at the NT2 Reservoir by experimental fishing and during landing surveys (Fig. 1). Experimental fishing used two batteries of monofilament gillnets, which were each 25 m in length comprising ten panels of 10, 15, 20, 25, 30, 35, 40, 50, 60 and 70 mm mesh sizes between knots (Cottet *et al*., 2016). The experimental gillnets were set in the afternoon (for 15-16 hrs) at each site (Cottet *et al*., 2016). In addition, a landing survey was performed and allowed to collect individuals with a standard length of more than 250 mm to complete the size range for the sampling due to the larger range of mesh sizes used by fishermen (10 mm to 200 mm) (Unpubl. data, NTPC). The experimental fishing was performed at four sampling sites, and the landing surveys were conducted at three landing sites. This allowed a size sample of more than 1000 individuals to be obtained from the NT2 Reservoir.

All fish were measured (standard length in mm, SL) and weighed (total weight in g, W). Individuals were sexed by macroscopic examination of the gonads (juveniles, females and males). When there was doubt regarding the gonad examination, individuals were mentioned as undetermined. The "undetermined" individuals were not considered for the analysis to determine the mean length and age at first sexual maturity. The maturation stage was defined for male and female according to the scale described by Pilling *et al*. (2007). Otoliths (asteriscus) were extracted, cleaned, air-dried and stored dry in labelled plastic vials until processing for age estimation.

The experimental fishing were performed by the Nam Theun 2 Power Company who has the national authorization for fish population monitoring and research in rivers and reservoir by the Lao Government, namely the Ministry of Agriculture and Forestry representative on Province level and the Nakai Natural Protected area (Watershed Management Protection Secretariat). The sampling did not catch endangered or protected fish species, the targeted species are exploited species and the experimental fishing followed established guidelines for treatment of animals in research and teaching (Animal Behaviour Society, 2006). All the fish set in the nest were already dead when the nets were removed the next morning.

Otolith processing

Within the total fish sample, 30 individuals were selected each month by a length-stratified subsampling for otolithometry. The right otolith from each individual was embedded in polyester resin (SODY33 with catalyst, Escil®) and sectioned through the core along a transverse plan using a Buehler® IsoMet low speed saw. To improve readability, the transversal posterior side of the otolith (i.e., half section) was manually grinded to the core on using Escil® abrasive discs and water (1200 and 2400 µm) and then polished with an Escil® polishing cloth and a 1 µm alumina polishing suspension. The section was then etched for 5 minutes with a 5% ethylenediaminetetraacetic acid (EDTA) solution and rinsed well with tap water. This step partially demineralised the otolith, and the highly mineralized and more organic regions became clearly distinguishable. The section was then stained for 9 minutes with 1% toluidine blue and rinsed gently with tap water. The otolith translucent zones, induced by slow growth and containing rich proteins, are stainable by toluidine blue, whereas the opaque zones are not stainable (Panfili *et al*., 2002). After staining, all sections were examined under a binocular microscope (Olympus® SZ40) under reflected light, and images were acquired with a video camera (Olympus® SC50 and SZ CT V camera rack, CellSensEntry software).

Age estimation and validation

The type of otolith zone (stained translucent or opaque) was macroscopically identified, the aspect of the otolith edge (stained translucent or opaque) was evaluated, and the translucent stained zones were counted along the otolith sulcus on the ventral axis (Fig. 2). The counts of translucent stained zones for each section were performed twice by the same reader with a 1-month interval without knowledge of the fish length. To estimate ageing precision, the percentage of full agreement, the average percentage of error (APE, Beamish and Fournier, 1981) and the coefficient of variation (CV, Chang, 1982) between readings were calculated. Otoliths presenting vateritic calcification and indistinct zones were excluded from the analysis. They represented 19% of the subsampled otoliths. The individual age was estimated in years using the capture date, the mean birth date (assumed to be June 1st due to a peak of reproduction observed in May for the *H. macrolepidota* population in the NT2 Reservoir; unpubl. data NTPC), the number of translucent stained zones and the otolith edge aspect (stained or not) (Morales-Nin and Panfili, 2002). An age-length key was determined to examine whether ages could be reliably estimated from their lengths. Age-length data were grouped into 20-mm fish length classes. The choice of this interval referred to the interval used in the few studies available on *H. macrolepidota* (Watson and Balon, 1985; Abidin, 1986; Liu *et al*., 2015). The equations used to estimate the age in months came from Morales-Nin and Panfili (2002) and were adapted to the present study case. The equations are as follows, taking into account the validation of the zone deposition in the otolith:

– For an individual caught between January and June with a translucent edge: Age (month) = 12 × N + (13 + rank Cm – rank Bm);

– For an individual caught between January and June with an opaque edge: Age (month) = 12 × N + (rank Cm + rank Bm + 1);

– For an individual caught between July and December with a translucent edge: Age (month) = 12 × N + (rank Cm – rank Bm);

– For an individual caught between July and December with an opaque edge: Age (month) = 12 × N + (rank Cm + rank Bm – 1).

N is the number of translucent zones that totally formed and were counted, rank Cm is the rank of the month of capture (e.g., 11 for November), rank Bm is the rank of the month of birth (in the present study, it is 6 because June represents the time of maximum reproduction), and 1 month was added or subtracted because there was 1 month of shift between the average month of births and the formation of 1 new translucent stained zone. For the growth study, the age was calculated in months to achieve an accurate representation of the growth variability.

Life history traits

The sex ratio (males:females) was obtained using data collected between November 2015 and January 2017. The deviation from equilibrium (expected 1:1) was tested using the Chi-square test.

The regression equation, $W = a\ SL^b$, was used to describe the relationship between the standard length and weight, where a is a constant and b is the length-weight isometrical factor. The length-weight relationship was established after a log-transformation, $\mathrm{Log}_{10} W = \mathrm{Log}_{10} a + b\ \mathrm{Log}_{10} SL$ (Beckman, 1948). Differences in the above relationship between sexes were tested using an analysis of covariance (ANCOVA) on the transformed data. Growth was qualified as isometric if b was equal to 3 and as allometric if b was

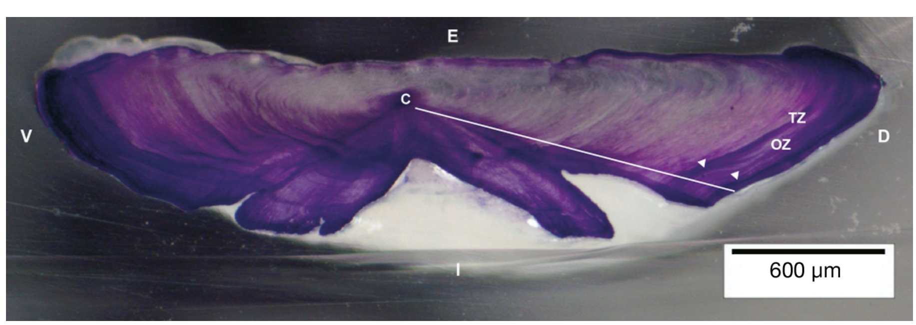

Figure 2. – Transverse section of an otolith (asteriscus) from a 2+-year-old *Hampala macrolepidota* from the Nam Theun 2 Reservoir. The section was acid etched, stained with toluidine blue and viewed using reflected light: 2 strained translucent zones (white triangle) were counted along the sulcus axis. Core (C), translucent stainable zone (TZ), opaque zone (OZ), ventral face (V), dorsal face (D), external face (E) and internal face (I).

different from 3 (Ricker, 1975). A Student's t-test was performed for each sex to identify whether *b* was significantly different from 3. The state of well-being of the *H. macrolepidota* in the NT2 Reservoir was estimated for each sex category using the Fulton's condition factor (Kf), which was calculated as $Kf = 100 \times (W/SL^3)$ (Tesch, 1971). This condition factor was used to compare sexes or periods (Wootton, 1999). After validation of the conditions of application, differences in the Fulton's condition factor between sex categories (juvenile, male and female) were tested using a Kruskal-Wallis test followed by a *post hoc* (Dunn's test) to identify the differences.

The ages in months and SL were fitted to the von Bertalanffy growth function (VBGF) using a nonlinear least squares method (Gauss-Newton) to estimate the growth parameters. The VBGF is defined by the following equation: $SL_{time} = SL_{\infty}(1 - e^{-K(time - t_0)})$, where SL_{time} is the standard length at age "time" (in months), SL_{∞} is the asymptotic length, K is the growth coefficient ($month^{-1}$), and t_0 is the theoretical age at a standard length equal to zero. The VGBF was calculated when pooling all sexes and for separated males and females.

The mean standard length at the first sexual maturity (SL_{50}) and the mean age at first sexual maturity (A_{50}) were considered to be the SL and age at which 50% of the females were sexually mature, respectively. The females at stage 3 or more on the maturity scale were estimated to be mature (scale from Pilling *et al*., 2007). They were grouped by size classes of 20 mm, and the relative frequency of females that were reproductively active was calculated for each size class. The SL_{50} was estimated by fitting the fraction of mature females (% $F_{mat.}$) to a logistic function using nonlinear regressions and a least squared reduction method (Lowerre-Barbieri *et al*., 1996; the Newton method, Duponchelle and Panfili, 1998). The SL_{50} calculation involved the following equation:

$$\% F_{mat.} = 100/(1 + \exp(-a (SL - SL_{50})))$$

where *a* as a constant.

The A_{50} was calculated from equation:

$$\% F_{mat.} = 100/(1 + \exp(-a (Age - A_{50})))$$

using the same least square reduction method by similarity with SL_{50}.

All statistical analyses were conducted using the R software (R Development Core Team, 2009).

Exploitation and fisheries

Monthly landing and fishing effort monitoring were achieved in three hamlets between January and December 2016 (Fig. 1). The villages were chosen to cover the different reservoir areas. No village was located north of the Thalang Bridge. For the landing monitoring, each village was sampled for 5 consecutive days per month. Each day, the first 10 fishermen reaching the landing site were individually interviewed regarding the fishing gear used, the mesh size or the hooks numbers and the length of net used. Their catches of *H. macrolepidota* were recorded. When the number of catches was equal to or below 30 individuals, each individual was measured (in mm, SL) and weighed (total weight in g, W) at the landing site. When the number of catches was higher than 30 individuals, only 30 individuals were randomly chosen, measured and weighted, and the total number of caught individuals was also recorded. In addition, fishing effort monitoring was conducted in these three same hamlets. During the 5 consecutive days of fish landing monitoring, 20 households in the same hamlet were interviewed on a daily basis to determine whether they were fishing or not, and if they were, which fishing gear and mesh sizes or hook numbers they used. With the data coming from landing and fishing effort monitoring, the effective number of individuals per size class (interval of 20 mm) was extrapolated by integrating the type of fishing gear and by weighting them to take into account their importance in the fisheries (Laë *et al*., 2004). The age-length key was transformed in proportion to provide the probability of a fish of age i given a length of j (Mesnil, 2002). Then, as mentioned by Mesnil (2002), the vector for the fish numbers caught for a particular size class was multiplied by the age-length key to obtain the vector for the numbers caught for a particular age group.

The total mortality coefficient (Z) was estimated from fish landings in 2016 (N = 4123) using the length-converted catch curve method (Pauly, 1983; the slope = Z) from the pooled length frequency data. The software used was the FAO-ICLARM (Fish Center) Stock Assessment Tool (FiSAT II) (Gayanilo *et al*., 2005). The natural mortality coefficient (M) was estimated following Pauly's empirical formula (Pauly, 1980): $Ln(m) = -0.052 - 0.279 \ln(SL_{\infty}) + 0.06543 \ln(k) + 0.463 \ln(T°C)$. Linking natural mortality with the von Bertalanffy parameters (K and SL_{∞}) and the mean annual temperature (T°C) of the surface water where the fish live (in this case, temperatures of the surface water were recorded at eight stations for the NT2 Reservoir every month). The average surface temperature for 2016 was 26.5°C. Fishing mortality (F) was computed from the relationship, whereas the exploitation rate (E) was calculated from (Sparre, 1998): $E = F/Z = F/(F+M)$ The probabilities of capture were inferred from the length-converted catch curves via backward extrapolation of the catch curve, and the numbers actually caught were compared with those that "ought" to have been caught (Sparre, 1998; Gayanilo *et al*., 2005). The standard lengths at which 25%, 50% and 75% of the fish were caught (SL_{25}, SL_{50}, SL_{75}) were estimated using logistic curves (Pauly, 1983) with FiSAT II. A virtual population analysis (VPA) estimated the stock (biomass, population size (N)) from fish landing data and the parameters determined above. For the biomass estimation, the standard length-weight relationship was used.

Based on the previous parameters and frequencies, FiSAT II was used to predict the relative yield and biomass per recruit (Y'/R and B'/R) of the fisheries. Plots of Y'/R vs. E (= F/Z) and of B'/R vs. E were made, from which E_{max} (exploitation rate that produces the maximum yield); $E_{0.1}$ (exploitation rate at which a marginal increase in relative yield-per-recruit was 10% of its unexploited biomass of E = 0) and $E_{0.5}$ (value of E under which the stock has been reduced to 50% of its unexploited biomass) were also computed using the first derivative of the Beverton and Holt function (Beverton *et al*., 1966). These were used as target reference points for the best fishing management.

Yield contours were plotted to assess the impact on yield of changes in exploitation rate (E) and critical length ratio, SL_c/SL_∞ (SL_c being the mean length of fish at first capture, $\approx SL_{50}$), and to determine the best E and SL_c/SL_∞ to reach the maximal Y'/R and B'/R for the current situation.

The Thompson and Bell yield and stock prediction routine in FiSAT II were used for prediction of the relative harvested fish and biomass changes with an example of management recommendation (Thompson and Bell, 1934). This model combines features of Beverton and Holt's Y'/R model with those of VPA, which it inverts. The current fishing rate and SL_c were compared with an increased value for SL_c without modification of F.

Table I. – Standard length (mm) and weight (g) per sex for *Hampala macrolepidota* sampled from the Nam Theun 2 Reservoir in Lao PDR. N: number of individuals; SE: standard error.

	Juveniles	Females	Males	Undetermined
***A** – For total collected individuals*				
N	137	304	289	466
Mean SL (± SE)	112 (± 3.0)	142 (± 3.1)	149 (± 2.2)	95 (± 1.4)
$SL_{min.}$	55	58	61	45
$SL_{max.}$	205	365	255	217
Mean TL (± SE)	144 (± 3.8)	182 (± 3.9)	190 (± 2.7)	122 (± 1.7)
$TL_{min.}$	73	74	77	52
$TL_{max.}$	265	463	316	279
Mean W (± SE)	37.9 (± 2.9)	93.5 (± 6.6)	85.9 (± 3.7)	22.8 (± 1.2)
$W_{min.}$	4.0	4.1	5.5	2.3
$W_{max.}$	195.1	980.0	352.6	209.3
***B** – For otolith analysis*				
N	31	161	129	36
Mean SL (± SE)	99 (± 6.5)	143 (± 4.8)	143 (± 3.3)	103 (± 5.3)
SLmin.	54	58	61	45
SLmax.	192	365	232	208
Mean TL (± SE)	127 (± 8.2)	182 (± 6.0)	183 (± 4.2)	130 (± 6.6)
TLmin.	73	74	77	52
TLmax.	252	463	299	258
Mean W (± SE)	28.8 (± 6.3)	101.6 (± 141.1)	77.9 (± 5.6)	27.5 (± 5.1)
Wmin.	4.0	4.1	5.5	2.3
Wmax.	161.0	980.0	325.7	176.4

RESULTS

From November 2015 to January 2017, a total of 1196 *H. macrolepidota* individuals were collected with 1187 (99.2%) from experimental fishing and 9 from fishermen (0.8%). The number of specimens from fishermen was lower because only the specimens with an SL higher than 250 mm were integrated to complete the size range. The individuals caught by experimental fishing ranged from 45 to 255 mm SL and from 2 to 356 g, whereas the individuals from landing ranged from 250 to 365 mm SL and from 379 to 980 g. In total, 61.5% of the fish samples were sexed and qualified as juveniles, females or males. The maximal SL and W were found for the females (SL = 365 mm and W = 980 g; Tab. I). Regarding the 38.5% that could not be sexed, individuals ranged from 45 to 217 mm and from 2 to 209 g.

Age estimation and validation

Of the 450 subsampled otoliths, 21.0% were excluded from the age and growth analyses due to vateritic growth, deformations or uninterpretable zones. For the interpretable otoliths, the individuals ranged from 45 to 356 mm SL and from 2 to 980 g (Tab. I). Interpretation of the zones was relatively easy because the translucent zone was rather well marked (well coloured) and had a fairly regular pattern. The mean percentage of error (APE) and the mean coefficient variation (CV) between readings were relatively low values (5.6% and 4.0%, respectively) indicating a good accordance between interpretations (94.7%). The edge analysis of *H. macrolepidota* otoliths indicated that the translucent zone began to be deposited for a majority of the specimens in March until August with a peak in May-June (86-82%, Fig. 3), which was opposite to opaque zone formation. Only one translucent zone was formed per year and appeared to start at the end of the WD season and continued during the first half of the WW season. Validation of the annual zone formation allowed the use of the translucent stained zones on the otoliths for estimating the ages of *H. macrolepidota*. The estimated ages from the NT2 Reservoir ranged from 0^+ to 9^+ years old. The 0^+ age group was the best represented in the samples (66.1%; Tab. II), followed by the 1^+ and 2^+ age groups (9.8% and 8.1%, respectively). The age-length key indicated a large variability of ages for a given size with important growth variability. For example, an individual with an SL of 165 mm could belong to the age from 0^+ to 4^+, although the majority of them (69.7%) belonged to the 2^+ and 3^+ age groups (Tab. II).

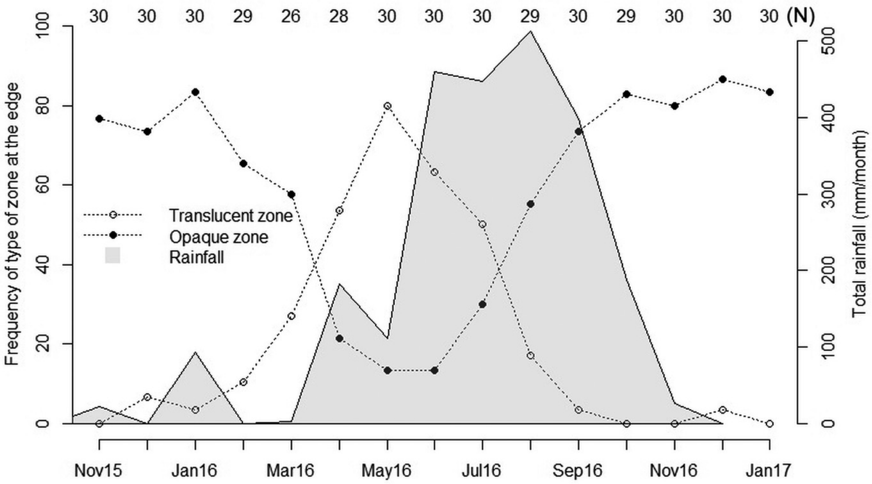

Figure 3. – Monthly frequency evolution of the translucent and opaque zones at the otolith edge from the *Hampala macrolepidota* from the Nam Theun 2 Reservoir in Lao PDR. The number of otolith samples is indicated at the top above each month (N).

Table II. – Age-length key for *Hampala macrolepidota* from the Nam Theun 2 Reservoir in Lao PDR based on transversal section reading of the asteriscus otoliths after coloration; sexes were combined, and unsexed specimen were included; standard length (SL) and standard error (SE).

SL intervals (mm)	N	Age group (years)									
		0^+	1^+	2^+	3^+	4^+	5^+	6^+	7^+	8^+	9^+
20-39	0										
40-59	5	5									
60-79	41	41									
80-99	54	54									
100-119	51	51									
120-139	52	51		1							
140-159	54	31	20	3							
160-179	33	2	13	10	6	2					
180-199	27	1	2	11	8	5					
200-219	13			4	4	2	1	2			
220-239	17				6	6	3		2		
240-259	3				2		1				
260-279	4						1	2		1	
280-299	0										
300-319	1							1			
320-339	1								1		
340-359	0										
360-379	1										1
Total	357	236	35	29	26	15	6	5	3	1	1
Percentage	100	66.1	9.8	8.1	7.3	4.2	1.7	1.4	0.8	0.3	0.3
Mean SL		106.7	159.0	179.9	202.3	204.7	233.2	254.6	260.0	262.0	265.0
SE		1.8	1.9	3.2	5.0	5.9	10.1	19.1	37.4	NA	NA

Life history traits

The sex ratio (M:F) was 0.95:1 and was considered to be balanced (x = 0.38, $p = 0.54$), as it was among months. The length-weight relationships (Fig. 4) differed slightly between sexes when juveniles were considered (ANCOVA: slopes, F = 52872, $p < 0.001$; intercepts, F = 2.16, $p = 0.115$; $R^2 = 0.98$) or not (ANCOVA: slopes, F = 36904, $p < 0.001$; intercepts, F = 0.01, $p = 0.906$; $R^2 = 0.98$). However, Student's t-tests showed that the value of b was not significantly different from 3 for all groups ($1.49 < t < 2.50$, p = 0.13 à 0.27). The relationships were considered isometric. The equations were:

– Juveniles: Log_{10} W = 2.99 Log_{10} SL – 4.66 or W = 0.00002 × $SL^{2.99}$ (n = 137; $R^2 = 0.99$; $p < 0.001$);
– Females: Log_{10} W = 3.02 Log_{10} SL – 4.70 or W = 0.00002 × $SL^{3.02}$ (n = 304; $R^2 = 0.99$; $p < 0.001$);
– Males: Log_{10} W = 3.00 Log_{10} SL – 4.67 or W = 0.00002 × $SL^{3.00}$ (n = 289; $R^2 = 0.98$; $p < 0.001$);
– Polled: Log_{10} W = 3.02 Log_{10} SL – 4.71 or W = 0.00002 × $SL^{3.02}$ (n = 730; $R^2 = 0.97$; $p < 0.001$).

The Fulton's condition factor (Kf) was 1.09 (± 0.01 SE) for juveniles, 1.04 (± 0.01 SE) for females and 1.06 (± 0.01 SE) for males. The Kruskal-Wallis test indicated a significant effect of the sex on the Fulton's condition factor (KW = 25.66, $p < 0.001$). The Fulton's condition factor of the juveniles was higher than those of males and females ($p < 0.001$).

The variability of the growth for this species is important during its lifetime and especially at early and late stages. An extreme variability for individuals less than 12 months was highlighted (Fig. 5). Upon polling all individuals (n = 357;

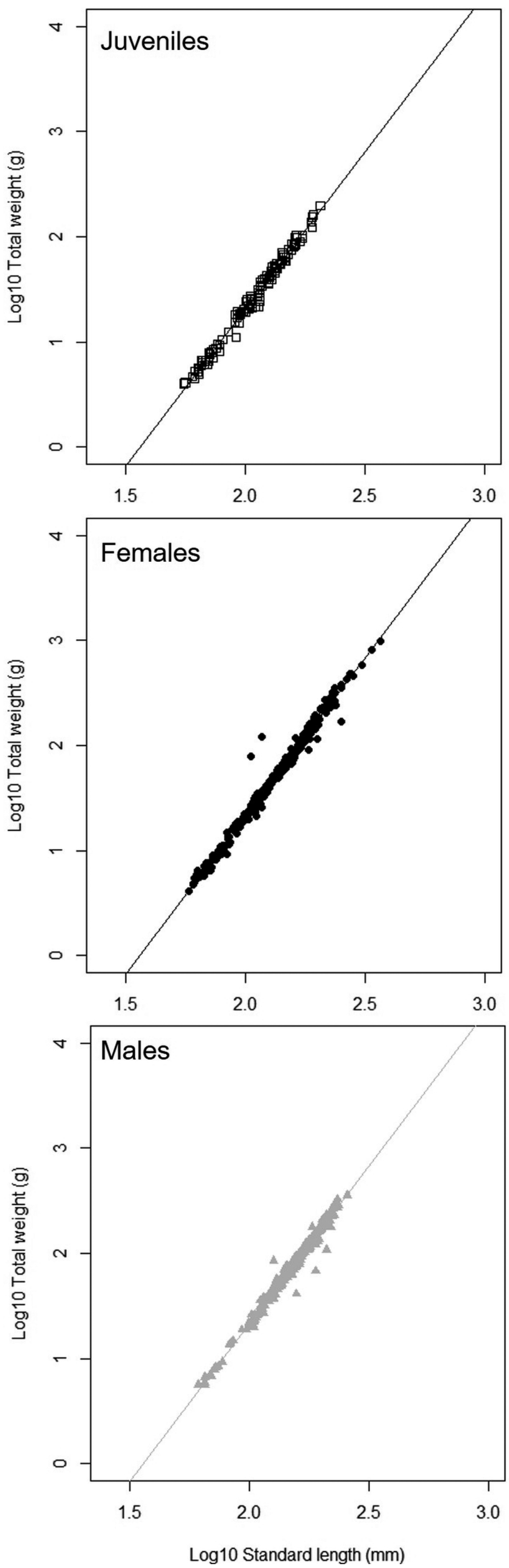

Figure 4. – Length-weight relationship of *Hampala macrolepidota* from the Nam Theun 2 Reservoir in Lao PDR between November 2015 and January 2017 according to sex.

$R^2 = 0.71$), the asymptotic length (L_∞) was 360 mm (95% IC: 294 to 500 mm), the hypothetical age at a standard length equal to zero (t_0) was –23 months (95% IC: –29 to –17 months), and the growth coefficient (K) was 0.01 month^{-1} (95% IC: 0.007 to 0.019 month^{-1}), indicating a relatively slow growth. For the males (n = 129; $R^2 = 0.79$) the asymptotic length (L_∞) was 259 mm (95% IC: 216 to 456 mm), the hypothetical age at a standard length equal to zero (t_0) was –26 months (95% IC: –45 to –15 months), and the growth coefficient (K) was 0.02 month^{-1} (95% IC: 0.006 to 0.03 month^{-1}). For the females, (n = 161; $R^2 = 0.81$) the asymptotic length (L_∞) was 411 mm (95% IC: 319 to 801 mm), the hypothetical age at a standard length equal to zero (t_0) was –21 months (95% IC: –30 to –15 months), and the growth coefficient (K) was 0.02 month^{-1} (95% IC: 0.004 to 0.02 month^{-1}). Globally, the lifespan is relatively short, and the growth is relatively slow.

The size at first sexual maturity for the females was 212 mm for the SL (n = 161; model adjustment parameters: $R^2 = 0.91$; $p < 0.001$; Fig. 6) and age at first sexual maturity was estimated to be 3.3 years old (n = 161; model adjustment parameters: $R^2 = 0.79$; $p = 0.001$; Fig. 7).

Fisheries

In 2016, landing monitoring data indicated that fishermen exploited *H. macrolepidota* with sizes ranging between 100 and 540 mm in SL; however, catches were dominated by individuals with an SL ranging from 160 to 240 mm (Fig. 8), which represented 78%. Because individuals with a standard length above 380 mm were not present in the otolith sampling, they were considered to be individuals belonging to age groups > 8^+. Fishermen exploited all age classes (Fig. 9) but mainly individuals between the 0^+ and 3^+ groups (67% of catches).

The estimated total mortality coefficient (Z) had a mean (± SD) of 1.13 ± 0.06 year^{-1} (95% IC_{95}: 1.00 to 1.25 year^{-1}; R = 0.97); natural mortality coefficient (M) = 0.15 year^{-1} (at 26.5°C); fishing mortality coefficient (F) = 0.98 year^{-1}; and exploitation rate (E) = 0.87.

The inferred probabilities of capture were $SL_{25} = 170.1$, $SL_{50} = 182.5$, and $SL_{75} = 182.9$ mm. Thus, individuals had a 50% of chance to be caught at 182.5 mm.

The exploitation rate was E = 0.87. This rate is higher than $E_{10} = 0.467$, $E_{50} = 0.312$ and $E_{max} = 0.559$ obtained by the relative yield and biomass per recruit. A population of 121,000 fish seemed to constitute the stock with a biomass of 185 tonnes. With the same gears, a decrease in the fishing mortality from 1 to 0.5 would increase the yield to 112% (177% for the biomass). However, for the current fishing mortality (0.98) with 1 more cm in the L_{50}, the yield would be 108% (117% for the biomass).

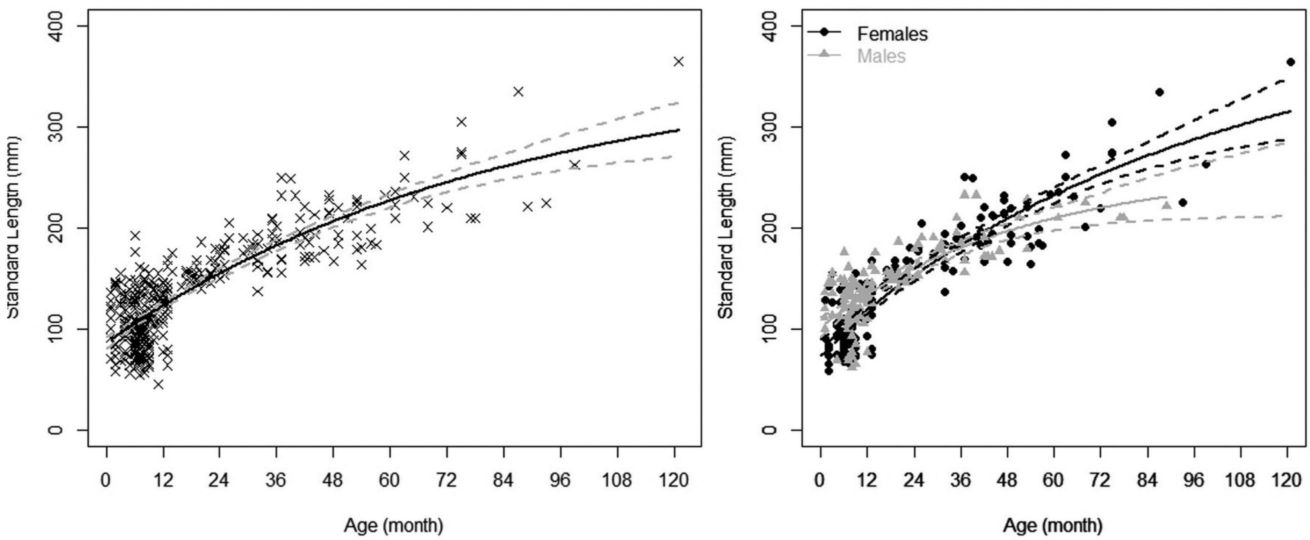

Figure 5. – Von Bertalanffy growth function adjusted to the age (month)-standard length of *Hampala macrolepidota* from the Nam Theun 2 Reservoir in Lao PDR between November 2015 and January 2017; at left, all polled and at right, by sex, grey dotted lines show the 95% confident interval.

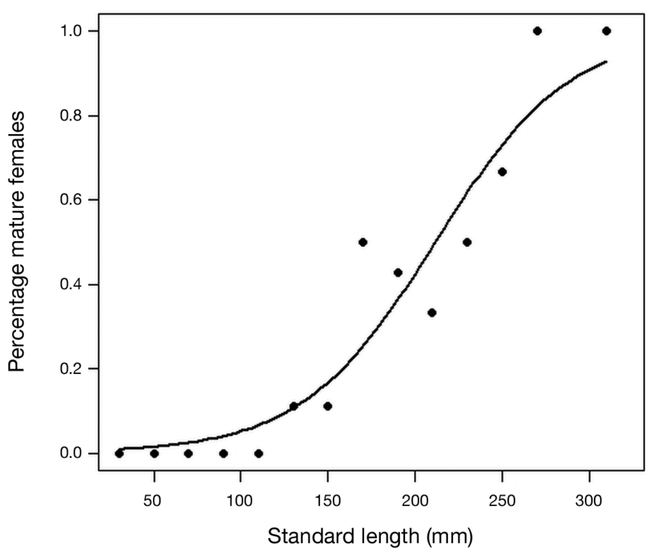

Figure 6. – Percentage of mature *Hampala macrolepidota* females in 20 mm standard length intervals from the Nam Theun 2 Reservoir in Lao PDR in 2016 fitted to a logistic function.

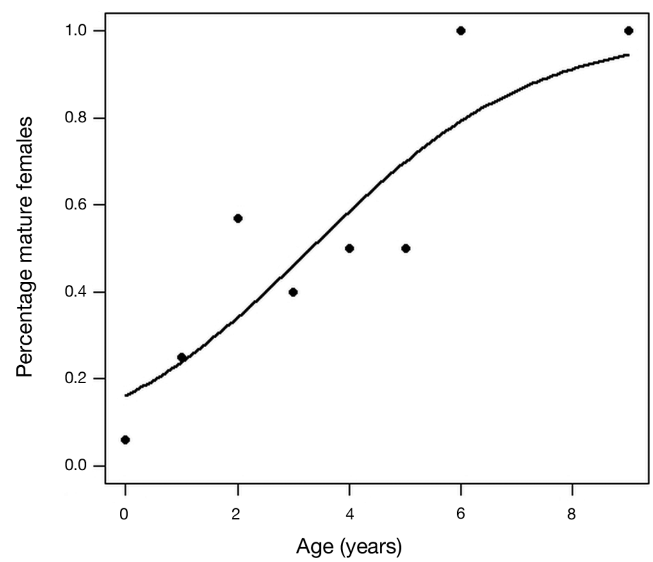

Figure 7. – Percentage of mature *Hampala macrolepidota* females by age (years) from the Nam Theun 2 Reservoir in Lao PDR in 2016 fitted to a logistic function.

DISCUSSION

For Cyprinidae, the lapillus otoliths are sometimes chosen for age estimation due to its relative size (Panfili *et al.*, 2002); however, asteriscus otoliths can also be used (Harvey *et al.*, 2000; Ellender *et al.*, 2016; Emre *et al.*, 2016). In the present study on *Hampala macrolepidota,* the asteriscus otolith was chosen because it is the largest and the least fragile. The use of transverse and stained sections of this asteriscus allowed interpretations of the chromophilic translucent zones to accurately estimate the age of *H. macrolepidota*. The annual periodicity of the translucent zone deposit was established at the end of the WD season and during the first months of the WW season (April to July). Studies on age and growth of this species or related ones are very scarce in the literature. The only one found was conducted in Northern Borneo, and it specified that annual zones were not discernible on the scales of *H. macrolepidota*; thus, they used length frequencies to estimate the growth (Watson and Balon, 1985). Munro *et al.* (1990) also used length frequencies under FiSat II to estimate the age of *H. macrolepidota*; Samuel and Suryati (2016) also probably used the same method (information not available). The validation of incre-

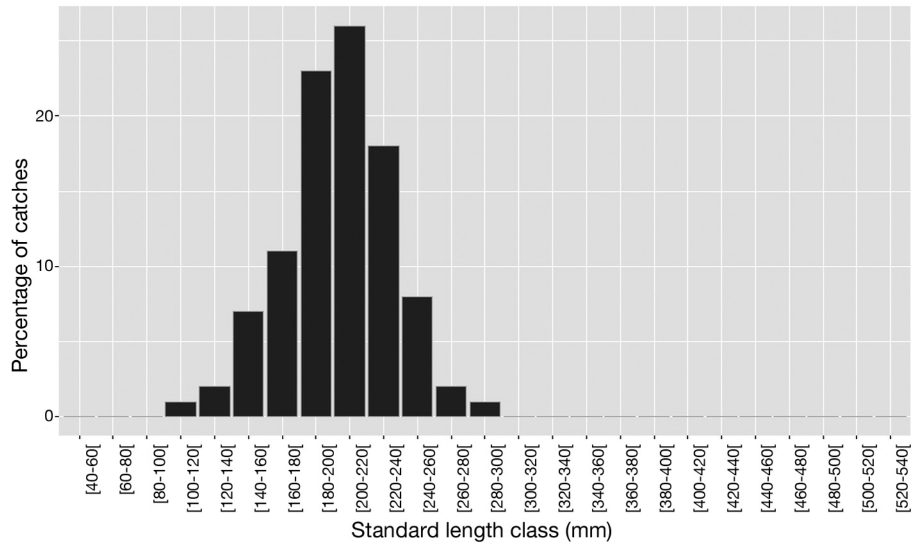

Figure 8. – Percentage of catches during 2016 according to size class of *Hampala macrolepidota* from the Nam Theun 2 Reservoir in Lao PDR.

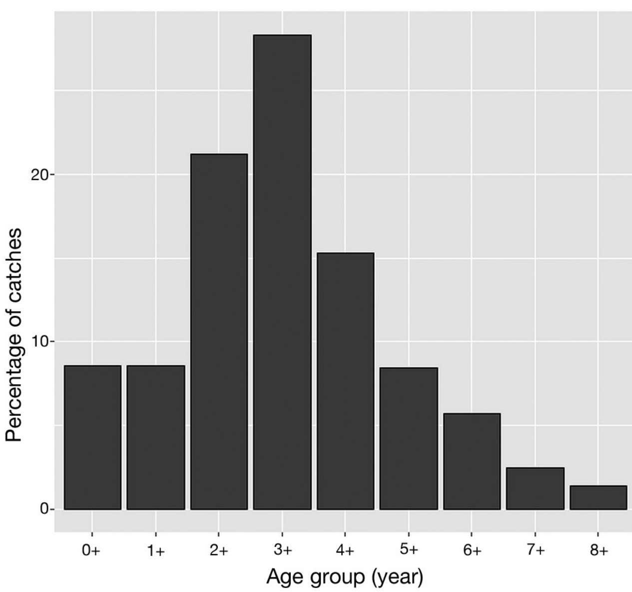

Figure 9. – Percentage of catches during 2016 according to age group (year) of *Hampala macrolepidota* from the Nam Theun 2 Reservoir in Lao PDR.

ment deposition in the otolith of *H. macrolepidota* for the present study was in line with several studies performed in sub-tropical countries on freshwater fishes (otolith or scale), e.g., *Oreochromis niloticus* in Zimbabwe (Grammer *et al.*, 2012; Chifamba *et al.*, 2014), *Cichla temensis* spp. in Venezuela (Jepsen *et al.*, 1999) or *Cyprinus carpio* in India (Dwivedi and Mayank, 2013). The annual periodicity found for *H. macrolepidota* matched the global knowledge on translucent zones (period of slow growth) in otolith. Translucent zone is characterized by less calcium carbonate rich and contain more concentrated proteins than opaque zone (Panfili *et al.*, 2002). The slower growth can be due to seasonal fluctuations in the water level, the photoperiod, the quality of the available food, a reduction in feeding activity, gonad maturation or spawning activity/behaviour (Yosef and Casselman, 1995; Jepsen *et al.*, 1999; Gümüş and Kurt, 2009). In southeastern China, Liu *et al.* (2015) indicated an increase in the gonadosomatic index between January and April for a population of *H. macrolepidota* with a peak in June and a decrease in July. Furthermore, even if this species is known to be able to reproduce over the year, a peak of spawning was recorded at the beginning of the rainy season in several different studies (Abidin, 1986; Setadi *et al.*, 1987; Costa-Perce and Soemarwoto, 1990; Zakaria *et al.*, 2000; Liu *et al.*, 2015). In Lao PDR, the rainy season starts in June and ends in October. The season change during the period of April to July can then induce a reduction in the growth of the *H. macrolepidota* Lao populations. A deposit of translucent zone in the otolith could also be associated with gonad maturation (Massou *et al.*, 2004). The individuals could allocate energy to reproductive activity instead of somatic growth between March and July, before the WW season. The fact that the formation of translucent zones may be linked to reproduction could be reinforced by the absence of these zones in otoliths of *H. macrolepidota* juveniles. Some studies on tropical fish have also indicated that the period of intense sunlight and high temperature of surface water during the dry season and preceding the rainy season could induce stress, which could initiate reproductive activity (Aronson, 1957; Pickford and Atz, 1957). In the case of NT2 Reservoir, no data are available regarding annual variations of sunlight. For water surface of NT2, some data indicate values higher in WD (around 27-28°C) than during CD, between November and February (around 22-23°C) (Descloux and Cottet, 2016; Martinet *et al.*, 2016).

This study shows that it is possible to estimate the age of *H. macrolepidota* with otolith interpretation when considering one annual deposit of increment per year related to the cycle of seasons in Lao PDR.

The validation of the age estimation in this study allowed elaboration of a length-age key, which could be a useful tool in fisheries management. The length-age key crossed with the data of landing (length, fishing effort, etc.) allows essential information to be obtained about exploited populations and identification of the potential risks of overexploitation. The established length-age key for *H. macrolepidota* included 10 age groups ranging from 0^+ to 9^+ years old. These age groups experienced a high variability in lengths, indicating a strong variability in growth. This observation could be explained by the fact that numerous populations of tropical fishes are able to reproduce all year (Gómez-Márquez, 1998; Bwanika *et al*., 2007; Gümüş and Kurt, 2009). A long reproduction period over the year can generate different growth rates due to seasonal changes of environmental conditions and due to a mixing of cohorts (Jiménez-Badillo, 2006). Even if a peak in reproduction exists in June (unpubl. data NTPC), *H. macrolepidota* is able to reproduce all year (Abidin, 1984, 1986) inducing a growth variability. The present length-age key could be useful for fishery management because standard lengths below 240 mm represented 88% of the landings.

The isometric relationship between length and weight was previously mentioned for populations of *H. macrolepidota* from Indonesia by Setadi *et al*. (1987) for the Jatiluhur Reservoir in Java and by Samuel and Suryati (2016) for the Kerinci Lake Sumatra Island. The values of Fulton's condition factor found in the present study were approximately 1, leading to isometric parameters. Wootton (1999) suggested that fish with high values of condition factor are heavy for their length, whereas those with low values are light for their length. These values were lower than the values mentioned by Kamaruddin *et al*. (2012), which ranged from 2.17 to 2.35 for a population from the Tasik Kenyira Reservoir in Malaysia in 2008-2009, or for those found by Zakaria *et al*. (2000), which ranged from 0.95 to 1.4 for the same population in 1997. Thus, *H. macrolepidota* in the NT2 Reservoir is in less robust condition than the population from this Malaysian reservoir. This difference could be due to a difference in available food organisms between the two reservoirs. The NT2 Reservoir is considered to be oligotrophic, whereas the Tasik Kenyira is hypereutrophic (Sharip *et al*., 2014).

The von Bertalanffy parameters calculated in this study for the growth indicated that *H. macrolepidota* has a relatively slow growth and is not a long-lived species with a maximum age of approximately 9 years old. This also indicated that the females presented an asymptotic length that was longer than that of the males. A comparison of the asymptotic length and the growth coefficient estimated considering age in year with values obtained from other studies indicated that the NT2 Reservoir population has a slower growth ($K = 0.24$ and $L_\infty = 295$ mm) than Indonesian populations (Munro *et al*., 1990; Samuel and Suryati, 2016). Munro *et al*. (1990) found a higher growth coefficient of 0.63 year^{-1} and an asymptotic length of 354 mm for the population in the Saguling Reservoir in Java, and Samuel and Suryati (2016) found respective values of 0.66 year^{-1} and 430 mm for a population from the Kerinci Lake Sumatra Island. First, these differences could be due to the different methods used for estimating the age; however, it is impossible to verify this hypothesis. Differences in growth between populations can be due to environmental factors (e.g., water temperature, nutrient), human pressures (e.g., fisheries, pollution), species plasticity or diseases. The lower growth rate of *H. macrolepidota* in the NT2 Reservoir could be due to environmental conditions, however recent physical and chemical data (e.g., pH, nutrients, dissolved oxygen) of NT2 reservoir were not available. Data were only available between 2008 and 2013 (Chanudet *et al*., 2016) which corresponded to unbalanced eutrophy and vulnerable stability preceding the current stabilization phase. The low growth rate could be also due to food limitation in this oligotrophic reservoir (Descloux and Cottet, 2016; Martinet *et al*., 2016). In comparison, Marselina and Burhanudin (2017) indicated that since 1999, the Saguling Reservoir has been classified as hypertrophic. Samuel *et al*. (2015) showed that the Kerinci Lake is also eutrophic. The diet of *H. macrolepidota* juveniles is composed mainly of zooplankton (*Daphnia* sp. and *Macrobrachium* sp. or larvae of insects). After the juvenile stage and until 200 mm, this species consumes shrimps and insects (Setadi *et al*., 1987). Then, at a size of 200 mm, it is piscivorous (Setadi *et al*., 1987; Makmur *et al*., 2014). *H. macrolepidota* is a tertiary consumer at the top of the trophic chain (Makmur *et al*., 2014)2014. It is known that the trophic status of an ecosystem influences the fish biology, and because the NT2 Reservoir is oligotrophic, this status could partially explain *H. macrolepidota* low growth. Other factors that could explain this growth have been discarded because there are no data available to reinforce those hypotheses. It is possible to conclude that this population grew more slowly than other populations in Indonesia.

The mean age at first sexual maturity is also a key parameter, as is the growth, to identify changes in the life history traits during the time period and for fishery management. This study indicated that females were able to reproduce at an SL of 212 mm, which corresponds to individuals that are 3.3 years old. These results were very similar to those of Liu *et al*. (2015) who mentioned that the females were mature at 4 years old and at an SL of 228 mm. Some females (11%) was able to reproduce beginning at an SL of 120 mm, which corresponds to other studies indicating reproductive ability at a TL of 160 and 180 mm (Abidin, 1986; Zakaria *et al*., 2000). The estimation of the mean age at first sexual maturity between 3 and 4 years old for the *H. macrolepidota* populations is relevant for the management of fisheries and indicates that most of the fish caught in the NT2 Reservoir were immature (88% shorter than 240 mm). This could have undeniable consequences for the maintenance of the population in the context of high fishing pressure.

The present study regarding fisheries of *H. macrolepidota* from the NT2 Reservoir indicated that the stock is overexploited. In 2016, fisheries exploited mainly individuals with a medium size (3/4 of landed individuals of *H. macrolepidota* had an SL between 120 and 220 mm), and only 25% of individuals were above the size at first sexual maturity. This is confirmed by the modelling yield, which shows overexploitation with too small fishes entering the fishery. The current exploitation rate of E = 0.87 is higher than E_{10} = 0.467, E_{50} = 0.312 and E_{max} = 0.559. According to the probability of capture fishes had 50% of chances to be caught after reaching 182mm without taking part of the stock renewal. This was confirmed from landing data, where 67% of landed individuals did unlikely have time to reproduce before capture. Consequently, the current population is overexploited, and the yield is under its maximal capability after only 5 years of ecological equilibrium. An optimal fishing strategy would be an increase in the mesh size to allow mature fishes to spawn and to decrease the fishing mortality. This would allow sustainability of the resource and a better yield with less effort.

CONCLUSIONS

This study of life-history traits of *Hampala macrolepidota* in Lao PDR was the first to use otolith for age estimation in this country. The results indicated that the asteriscus otolith can be used to estimate the age with accuracy, and then complete the list of tropical species for which otolithometry can be used (Morales-Nin and Panfili, 2005). This first estimation of growth parameters, size and age at first sexual maturity provides essential information regarding the fishery management for this native species. In the case of the Nam Theun 2 Reservoir, the population is overexploited by fisheries. These elements should be considered for further improvement of fisheries management. Finally, other studies should compare the population life history traits of this species in different Lao reservoirs to provide more details regarding fishing aspects and possible resilience of the species.

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