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Population structure and reproduction of the African bonytongue *Heterotis niloticus* in the Sô River-floodplain system (West Africa): implications for management

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Abstract – Population structure of the African bonytongue, *Heterotis niloticus*, was examined in southern Benin within Lake Hlan and a region of the Sô River floodplain located approximately 60 km downstream from the lake. Both locations support important fisheries in which *Heterotis* is the principal target species during the flood period. Ripe adults comprised over 40% of the population in Lake Hlan, whereas only 3.5% of individuals captured from river sites were adults. Monthly averages for the gonadosomatic index and percentages of individuals with mature gonads peaked as water levels increased during the wet season then declined during the peak flood period. Oocyte size frequency distributions from ovaries suggested a potential to produce an additional cohort in the event of nesting disruption. During the peak spawning period (May to August), between 37 and 51 active nests per hectare per month were observed in Lake Hlan. The number of larvae per nest ranged from 3953 to 6125. Lake Hlan bonytongues appear to constitute an important source subpopulation that exports new recruits to river/floodplain areas downstream where intense fisheries harvest mostly juveniles and subadults. Consequently, restriction of harvest of adult bonytongues in Lake Hlan may be essential for sustenance of commercial fishing in downstream reaches of the So River.

A. Adite[1], K. O. Winemiller[2], E. D. Fiogbé[1]
[1]Unité de Recherches sur les Zones Humides, Département de Zoology et Génétique, Faculté des Sciences et Techniques, Université d'Abomey-Calavi, 01 BP 526 Cotonou, Bénin, [2]Section of Ecology and Evolutionary Biology, Department of Wildlife and Fisheries Sciences, Texas A & M University, College Station, TX, USA

Key words: Benin; fecundity; fishery; nest guarding; river floodplain; spawning season

A. Adite, Unité de Recherches sur les Zones Humides, Département de Zoology et Génétique, Faculté des Sciences et Techniques, Université d'Abomey-Calavi, 01 BP 526 Cotonou, Bénin; e-mail: aditealphonse@yahoo.fr

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Tropical rivers support extensive and intensive fisheries that provide the most important source of animal protein for people in many developing tropical countries (FAO Inland Water Resources and Aquaculture Service, Fishery Resources Division 2003). In Africa, rural people are particularly dependent on fish protein, and a great variety of species are harvested from river-floodplain ecosystems. The largest fish are frequently targeted first and most intensively because they are generally more valuable. As larger fish become depleted, fisheries naturally shift effort towards successively smaller and less-valuable species (Welcomme 2001). Among the most highly valued species in West African inland fisheries is the African bonytongue, *Heterotis niloticus* (Cuvier 1829), a species widely distributed in tropical rivers and freshwater lakes of western and central Africa (Moreau 1982;Levêque et al. 1990). The African bonytongue is exploited by fisheries in southern Benin, the middle Niger River delta and other regions of West Africa. Annual harvest of bonytongues in Benin has been estimated at 742 tons valued at U.S. $1,485,000 (Gbaguidi & Pfeiffer 1996). The principal

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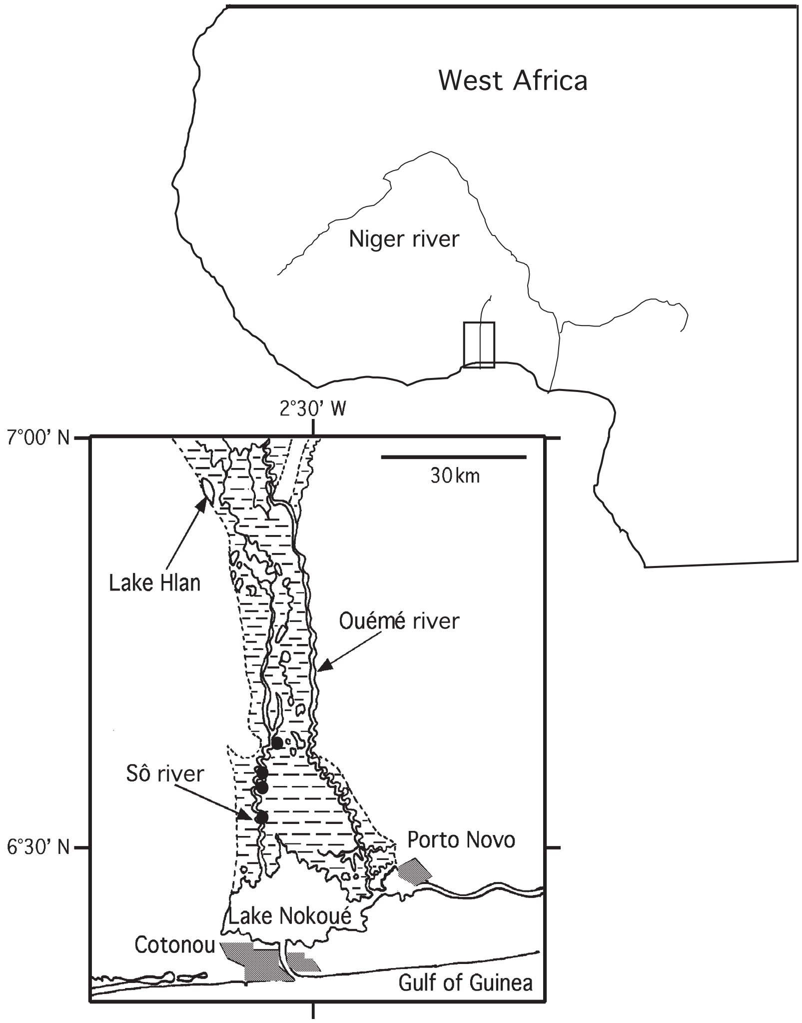

Fig. 1. Map showing locations of Lake Hlan and Sô River floodplain study regions in southern Benin, West Africa. Dots show locations of villages: Ahome-Blon, Ahome-Lokpo, Zoungome and Kinto (S to N, respectively) on the Sô River floodplain.

rivers supporting this fishery are the Ouémé, Mono, Couffo, Sô and Zou. Large bonytongue fisheries also are located at Lakes Nokoue, Hlan, Toho-Todougba and Toho (Van Thielen et al. 1987;Adite & Van Thielen 1995). In spite of the species' economic importance, relatively little research has been conducted on the African bonytongue (Moreau 1982). Micha (1973) described aspects of the reproductive biology of *Heterotis* from the Oubangui River (Congo Basin), and Moreau (1974) studied the reproductive biology and development of *H. niloticus* from a reservoir in Cote d'Ivoire, West Africa.

In southern Benin, fishery resources and aquatic habitats are negatively impacted by a rapidly increasing human population (Adite & Van Thielen 1995). Sustainable fisheries require sufficient annual recruitment to balance population losses to harvest. In floodplain river systems, recruitment can be strongly influenced by seasonal and interannual variation in the flood pulse (Welcomme 1979;Agostinho & Zalewski 1994). Moreover, the connectivity of lotic and lentic habitats in the river-floodplain landscape influences the growth and survival of many species (Lowe-McConnell 1987;Junk et al. 1989;Winemiller & Jepsen 1998;Ward et al. 1999). As the principal bonytongue fisheries of Benin are in rivers and associated floodplain lakes, it is imperative to understand the basic features of demography and distribution. At present, almost nothing is known about the species' spawning dynamics in these complex aquatic ecosystems. Reported here are findings from an 18-month study of the reproductive ecology of *Heterotis* in the Sô River and Lake Hlan, a natural lake in the river floodplain. The main objective was to describe seasonal variation in population structure, gonadal development, and nesting to indicate reproductive periodicity at each location. Population structure and patterns of recruitment are interpreted in relation to the potential sustainability of current fishing practices.

Materials and methods

Study area

Field surveys were conducted at two locations in southern Benin (Fig. 1): a reach of the lower Sô River

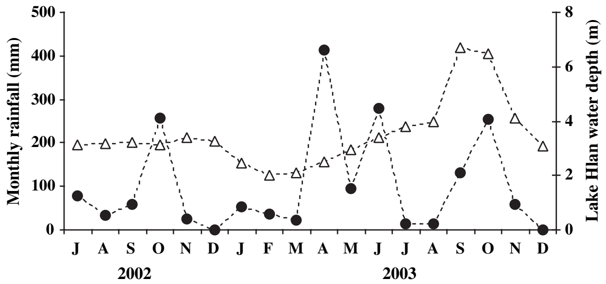

Fig. 2. Monthly rainfall (filled circles) in the study region (source: ASECNA Cotonou) and maximum water depth at Lake Hlan (open triangles) from July 2002 to December 2003.

(6°34.97′N, 2°23.75′E) and Lake Hlan (6°56.88′N, 2°19.48′E). This region has a sub-equatorial climate with long and short wet seasons (mid-March to mid-July; mid-September to October) and long and short dry seasons (November to mid-March; August to mid-September) (Fig. 2). Annual rainfall recorded for 2002 was 1167 mm (Service de la Metéorologie Nationale, Agence pour la Securite de Navigation Aerienne 2003), and the highest monthly rainfall during the investigation was 439 mm for June 2002. The Sô River is a tributary of the lower Ouémé River. The Sô flows southward, parallel to the Ouémé, approximately 100 km through a floodplain covering approximately 1000 km^2 (Van Thielen et al. 1987). Hydrology of rivers in southern Benin is strongly influenced by seasonal rainfall in the northern region. During the peak flood season (October to November), water from the Ouémé and Sô rivers covers extensive floodplains (Fig. 1). Several habitat features were characterised at each sampling site (water quality, aquatic vegetation, substrate, riparian vegetation and land use). Water depth was measured using a calibrated rope. Temperature and the dissolved oxygen were measured to the nearest 0.1 °C and 0.1 mg·l^{-1}, respectively, with a digital oxythermometer. Turbidity was measured to the nearest millimetre with a Secchi disk (HYDRO-BIOS, Kiel, Germany). pH was measured to the nearest 0.1 with a portable pH meter. Salinity, total dissolved solids (TDS) and conductivity were measured to the nearest 1, 0.1 and 0.1 mg·l^{-1}, respectively, with a conductivity meter. Nitrates, nitrites and total iron were measured to the nearest 0.01 mg·l^{-1} via titration with Merck reagents (AQUAMERCK, Darmstadt, Germany).

During the study period, water depth in the main river channel in the study area averaged 421 (±210 SD) cm and turbidity averaged 40 cm (±28 cm). Dissolved oxygen ranged between 0.4 and 4.5 mg·l^{-1} (9–77% saturation). Most other physical and chemical features reveal less variation; mean water temperature during the study was 28.6 (±2.2) °C, pH averaged 5.4 (±0.6), electrical conductivity averaged 99.45 (±3.1) μs·cm^{-1} and average TDS was 46.7 (±5.4) mg·l^{-1}. Nitrite and total iron concentrations averaged 0.002 (±0.0015) and 1.04 (±0.66) mg·l^{-1}, respectively. The dominant floating macrophyte on the Sô River is the water hyacinth (*Eicchornia crassipes*), a species that invaded the system about 20 years ago. Other common aquatic plants are *Pistia stratiotes* (Aracea) and *Ipomea aquatica* (Convolvulaceae). Palms (*Elaies guinensis*) are the dominant riparian tree.

Lake Hlan is located near Kpomey village (Sehoue County) about 80 km from the Atlantic coast. Locally known as 'the bonytongue lake', Lake Hlan receives comparatively low exploitation owing to local enforcement of traditional fishing regulations. Lake Hlan has a lower average depth (250 ± 128 cm SD) than the study reach on the Sô River. The annual flood was very low in Lake Hlan during August to November 2002, but occurred normally during this period in 2003 (Fig. 2). Dissolved oxygen (measured between 1000 and 1400 h) ranged from 0.1 mg·l^{-1} (1.5% of saturation) to 4.8 mg·l^{-1} (79%). Water transparency averaged 88.1 (±25.2) cm, mean water temperature was 27.60 (±1.80) °C, mean pH 5.3 (±0.20), average conductivity 97.0 (±5.5) μs·cm^{-1} and mean TDS 47.0 (±2.8) mg·l^{-1}. Nitrites and total iron concentration were low and averaged 0.002 (±0.001) and 0.67 (±0.26) mg·l^{-1}, respectively. Floating grasses, such as *Cyperus difformis* (Cyperaceae), cover large areas of the lake and hinder fishing activities. Wind-driven movement of grass mats sometimes damages fishing gear. These grasses also provide habitat for many aquatic organisms, including small fishes. Water hyacinth is present in Lake Hlan, but at low biomass compared with most areas of the river channel. Other common floating macrophytes in Lake Hlan were *P. stratiotes, Azolla africana*, *Nymphaea lotus* and *Nymphaea maculatus* (Nymphaeacea), *E. crassipes* and *Echinochloa pyramides* (Poacee). Submerged plants included *Ceratophyllum demersum* (Ceratophyllaceae) and *Utricularia inflexa* (Lantibulariaceae).

Taxonomy

Heterotis niloticus is one of the two living representatives of the family Osteoglossidae, a lineage within the ancient fish order Osteoglossiformes, on the African continent (the other species is the freshwater butterflyfish, *Pantodon buchholtzi*). According to Guo-Qing & Wilson (1996), the Osteoglossidae also contains two genera and three species in South America and one genus and three species in Southeast Asia-East Indies-Australian region. According to Ferraris (2003), *H. niloticus* and *Arapaima gigas* (South America) are considered by many ichthyologists as the sole members of a separate family, the Arapaimatidae. Other living Osteoglossiformes include the Mormyridae (Africa), Gymnarchidae

(Africa), and Notopteridae (Africa and Asia). Except for *Pantondon* (an egg scatterer), osteoglossids perform parental care – mouth brooding in *Osteoglossum* and *Scleropages* spp., and nest guarding in *Arapaima* and *Heterotis*.

Fish samples

Fish were surveyed each month from July 2002 to December 2003. In the Sô River, *Heterotis* were collected from both aquatic vegetation and open water at four sites located near the villages of 'Ahome-Blon', 'Ahome-Lokpo', 'Zoungome' and 'Kinto'. Patches of vegetation were encircled with a net (2 m high, 10-mm mesh), and vegetation and fish were removed. Open water areas of the river were sampled with a cast net (50–80 mm mesh). In Lake Hlan, fish were collected with traps (80 mm long, 50 mm opening), gill nets (20 m × 2 m, 60-mm bar mesh) and hooks. Local fishermen were enlisted to set traps in vegetation close to the openings of active nests. All captured size classes were retained for analysis. At Lake Hlan, monthly survey effort was determined by requirements to obtain at least 15 individuals pertaining to adult size classes. Adult size classes were rare at Sô River survey sites. Each month, sampling effort was continued until the total sample had a fairly consistent population size structure (i.e., additional castnet samples did not appreciably change the size structure of the sample). Sampling effort was greater during the high-water period (August to November) when fish were dispersed in the floodplain.

Heterotis nests are circular clearings within dense stands of rooted and submerged or emergent aquatic macrophytes in shallow (<2 m) water. Nests are highly conspicuous, even under moderately turbid water conditions (Secchi depth 0.5–1), due to the fact that rooted aquatic vegetation extends near or beyond the water surface. Each nest has a cleared channel through the vegetation that allows adult fish to pass between the confines of the nest and open water. Twenty active nests were randomly selected and 12 physical and chemical features (water depth, water transparency, nest diameter, nest opening, height of surrounding vegetation, temperature, pH, dissolved oxygen, oxygen saturation, conductivity, total iron and nitrite) were measured at the centre of the nest. Estimated each month at Lake Hlan were the number of active *Heterotis* nests per hectare, monthly fishing effort (number of traps placed in nest openings), number of nests trapped per hectare, and water depth in the middle of the lake. Abandoned nests with openings blocked by vegetation and lacking evidence of active use by brooding fish were not counted. The entire school of larvae was collected from seven nests to estimate brood size.

Specimens were measured [total length (TL) and standard length (SL)] *in situ* to the nearest millimetre then weighed to the nearest gram with an electronic balance. Pressure was applied to the ventral abdominal wall to determine if gonads were fully mature (indicated by expulsion of oocytes). Specimens were dissected, and gonads were removed for length, width and weight measurements. Gender was determined by macroscopical examination of gonads (Moreau 1982). Gonad maturation stages were estimated using a modified version of stages described by Amon-Kothias (1980). Female stages were: (1) immature (juvenile) – very small gonad, ovary pink with oocytes invisible to naked eye; (2) early maturation – intermediate size ovary with very small pale-yellow oocytes visible to naked eye; (3) advanced maturation – very developed ovary with yellow-orange (postvitellogenic) oocytes; (4) ripe ovary – fully developed ovary fills ventral region of the abdominal cavity, eggs are postvitellogenic (diameter 2.5–3.0 mm) and expulsed when external pressure is applied to the ventrum; and (5) postspawning – ovary is flaccid without significant presence of mature oocytes. Male maturation stages were: (1) immature (juvenile) – undeveloped testis consisting of a translucent filament; (2) early maturation – intermediate size testis having a very light yellow or tan colour; (3) advanced maturation – large testis, opaque white or light tan colour with numerous small, black spots; (4) ripe testis – fully developed testis, pressure applied to ventrum expulses white milt; and (5) postspawning–flaccid testis without milt.

After staging, gonads were fixed in 5% formalin and transported to the laboratory (Department of Zoology & Genetics, University of Abomey-Calavi). After 1–7 days, preserved gonads were removed from formalin and stored in 75% ethanol. Batch fecundity was estimated as the total number of mature oocytes extrapolated from three 1-g samples taken from each ovary (samples from anterior, middle and posterior portions of the ovary). Each sample was weighed to the nearest 0.1 g, and mature oocytes in each sample were separated with the aid of dissecting needles. Mature (fully yolked) oocytes have a yellow-orange colour. Diameters of 10 mature oocytes from each of nine gonads were measured using an ocular micrometer attached to a dissecting stereomicroscope.

Data analysis

Frequency histograms of fish size intervals were constructed for samples from both sampling areas. Length–weight relationships were examined for populations associated with different habitats, genders, size intervals and hydrological seasons according to the linear relationship. Log $W = \log a + b \log L$, where L is the total length, W the weight, a a constant and b the allometry coefficient (Tesch 1971). Univariate analysis of variance was used to test for between-group differences in slope.

Sex ratio was estimated for the collective samples from each region. The gonadosomatic index (GSI) was computed using the following formula:

GSI = (gonad weight/body weight) × 100

To evaluate reproductive periodicity, mean GSI was plotted for each month and region. Size at sexual maturation (L50) was estimated as the size at which 50% of individuals were classified as 'mature' or 'advanced maturation' stages (Albaret 1977). L50 was estimated from a sigmoid curve constructed with the percentage of mature individuals and associated size class categories. A frequency distribution was plotted for oocyte diameter based on ovaries in the top 10th percentile of GSI values. Fecundity was estimated for mature ovaries, and the allometric relationship between fecundity and body length was examined as $F = aL^b$, where F is the fecundity, L the total length, a a constant and b the allometry exponent. The linear relationship of fecundity with body weight was examined as $F = bW + a$, where F is the fecundity, W the body weight, a the intercept and b the slope.

Results

Population structure

Heterotis population size structure was markedly different in Lake Hlan (bimodal distribution) and the Sô River (unimodal distribution, Fig. 3). Even with many small fish forming the first mode in the size distribution, the average body size was larger in Lake Hlan than the river. The mean SL for Lake Hlan was 370 mm (range 74–762 mm) and mean weight was 1.13 kg (range 0.005–4.75 kg); Sô River fish averaged 305 mm (range 148–765 mm) and 0.46 kg (range 0.05–5.84 kg). Of 908 specimens collected from Lake Hlan, 36.4% were juveniles (<300 mm), most of which were collected during the high-water season. Subadults (300–500 mm) comprised 17.8% and adults (>500 mm) comprised 45.7% of the lake population. Of the 553 specimens collected from the river, 35.1% were juveniles (<300 mm), 60.2% were subadults

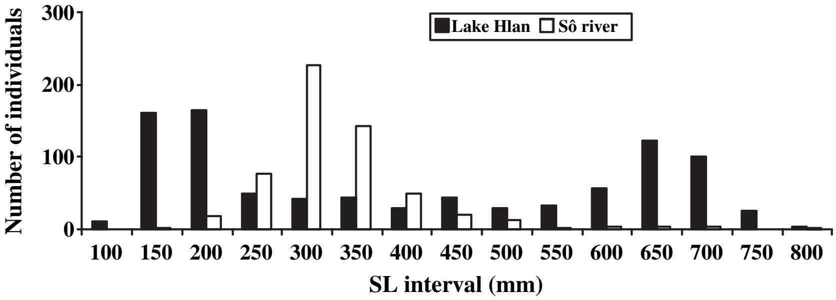

Fig. 3. Size structure of *Heterotis niloticus* samples from the Sô River and Lake Hlan during July 2002 to December 2003.

Table 1. Log (TL) – log (*W*) regressions for *Heterotis* by habitat, gender, size class and season from the Sô River and Lake Hlan.

	N	Slope	95% CI	r^2	Intercept	95% CI
Habitat						
Lake Hlan	908	2.81	2.79–2.83	0.99	−4.47	−4.51–(−4.42)
Sô River	553	2.94	2.87–3.01	0.92	−4.73	−4.90–(−4.55)
Gender						
Male – Lake Hlan	465	2.81	2.79–2.84	0.99	−4.47	−4.53–(−4.41)
Female – Lake Hlan	443	2.80	2.78–2.83	0.99	−4.44	−4.50–(−3.80)
Male – Sô River	320	3.03	2.95–3.11	0.94	−4.94	−5.14–(4.74)
Female – Sô River	233	2.81	2.67–2.94	0.88	−4.39	−4.73–(−4.05)
Size						
Juvenile – Lake Hlan	573	2.89	2.85–2.92	0.98	−4.63	−4.71–(−4.56)
Adult – Lake Hlan	335	2.75	2.57–2.92	0.74	−4.30	−4.79–(−3.81)
Juvenile – Sô River	543	3.00	2.92–3.08	0.91	−4.87	−5.07–(−4.67)
Adult – Sô River	10	4.05	2.83–5.27	0.90	−7.91	−11.34–(−4.48)
Season						
Wet – Hlan	139	2.77	2.62–2.92	0.91	−4.38	−4.80–(−3.96)
Flood – Hlan	561	2.82	2.80–2.84	0.99	−4.49	−4.54–(−4.43)
Dry – Hlan	208	2.74	2.65–2.83	0.95	−4.27	−4.50–(−4.04)
Wet – Sô River	29	2.79	2.53–3.05	0.95	−4.40	−5.08–(−3.71)
Flood – Sô River	309	2.94	2.87–3.00	0.96	−4.70	−4.78–(−4.54)
Dry – Sô River	215	3.26	3.09–3.43	0.87	−5.53	−5.95–(−5.11)

$P < 0.001$ for all regression slopes.

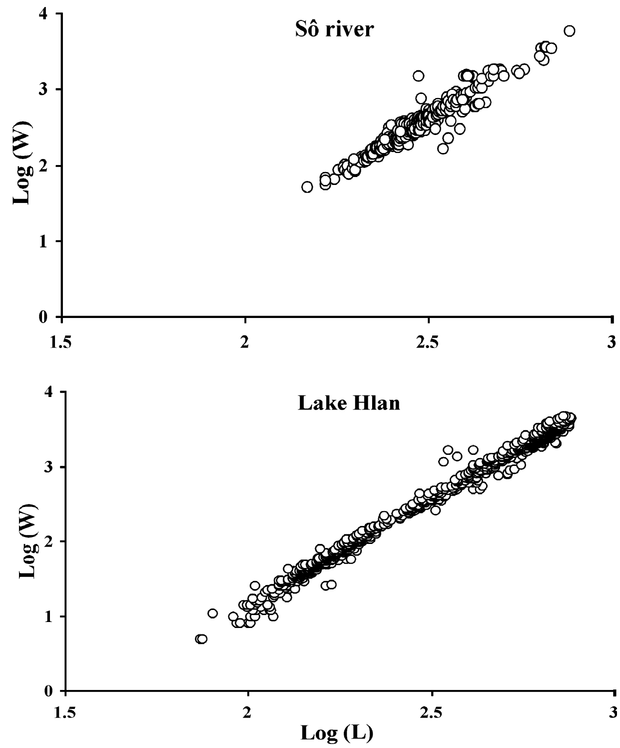

Fig. 4. Total length–weight relationships of *Heterotis* from the Sô River and Lake Hlan. Regression for Sô River is log $W = 2.94$ (log L)−4.73; $R^2 = 0.92$; $N = 553$. Regression for Lake Hlan is log $W = 2.81$ (log L)−4.47; $R^2 = 0.99$; $N = 908$.

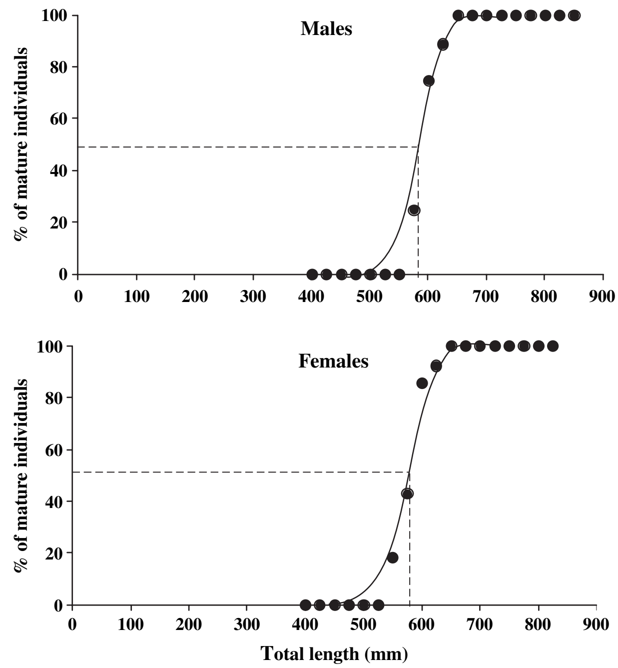

Fig. 5. Percentages of male and female *Heterotis* from the Sô River–Lake Hlan system with mature gonads (stages 2–5) by body length. Length at maturation is estimated as the length at which 50% of individuals are mature as predicted by a sigmoid curve fit to the data.

(300–500 mm) and 3.4% were adults (>500 mm). Of the 1461 specimens collected, 53.7% were males and 46.3% were females.

Body condition

Length–weight regressions by habitat, sex, size and season were significant ($P < 0.0001$) with correlation coefficients ranging from 0.74 to 0.99 and slopes from 2.74 to 4.05 (Table 1). Univariate analysis of variance showed significant ($P < 0.0001$) difference between slopes for genders, size classes (juvenile, subadult and adult) and seasons (wet [April to July], flood [August to November] and dry [December to March]). For fishes spanning the size interval 150–600 mm SL, fish from the Sô River had slightly but statistically higher slopes, an indication that their condition increased more with size (Fig. 4). Body condition of Sô River fish was greatest during the falling-water season (dry season), but condition of Lake Hlan fish was greater during the wet and flood seasons.

Maturation

Fish with gonads at stages 2–5 were considered sexually mature. The proportion of mature individuals increased rapidly between 550 and 800 mm SL for both males and females (Fig. 5). The size at which 50% of individuals were mature was about 575 mm TL for both genders. The smallest mature male (stage 2 gonad) was 560 mm TL (515 mm SL, 1.49 kg), and the smallest mature female (stage 2) was 545 mm TL (499 mm SL; 1.77 kg).

Spawning periodicity

Variation in the GSI was significantly affected by season for both males ($F = 10.67$; d.f. = 2, 156; $P < 0.01$) and females ($F = 20.98$; d.f. = 2, 175; $P < 0.01$). Monthly averages for GSI peaked during the wet season (May to August), then declined progressively throughout the flood period until the beginning of the dry season in November to December (Fig. 6). The percentage of individuals with mature gonads (stages 3 and 4) and mean monthly GSI were correlated for both males ($r^2 = 0.31$; $P < 0.05$) and females ($r^2 = 0.73$; $P < 0.01$), providing confirmation that spawning occurs during the wet season as floodwaters gradually rise. Proportions of ripe males and females each month were correlated ($r^2 = 0.60$; $P < 0.01$). The percentage of mature adults reached 100% during September 2002 and June 2003. No mature females were found in samples from November to January 2003, and a single mature female was recorded from samples taken from February to March 2003.

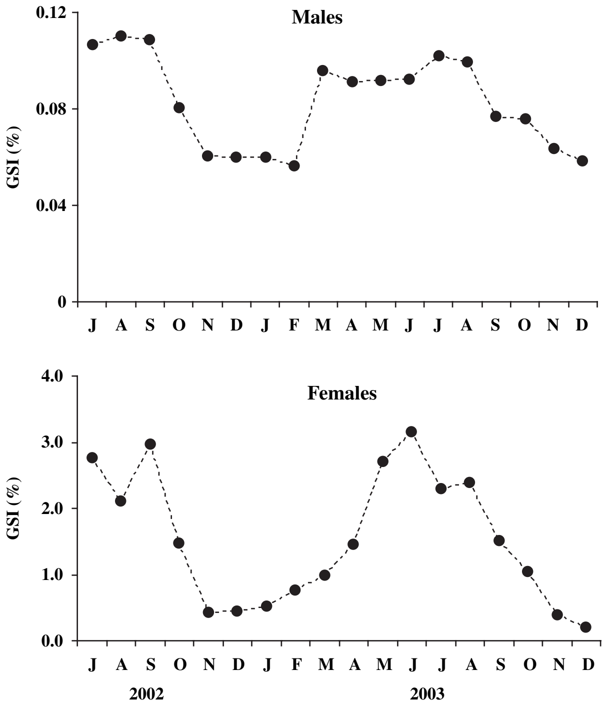

Fig. 6. Monthly trends of the gonadosomatic index (GSI) and proportion of ripe male and female *Heterotis* from the Sô River–Lake Hlan system during July 2002 to December 2003.

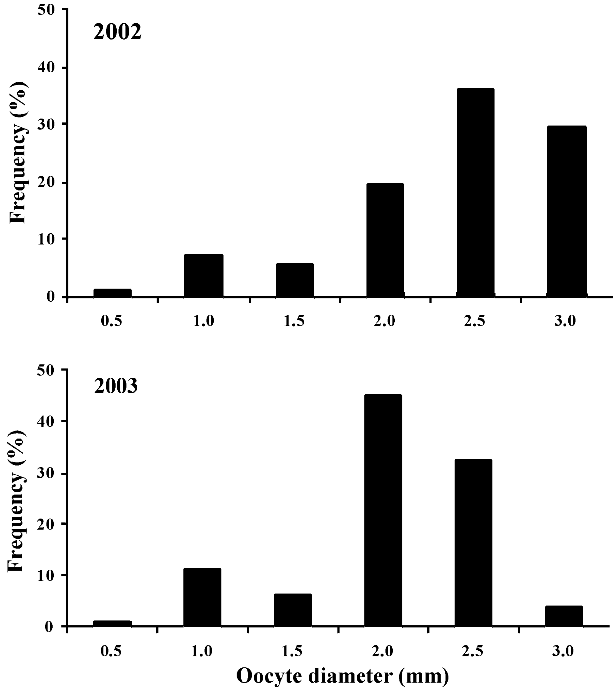

Fig. 7. Frequency distribution for oocyte size classes within fully mature ovaries of Lake Hlan *Heterotis* from the 2002 and 2003 spawning seasons (top graph: 14 July 2002, 525 mm TL, GSI = 4.1 and fecundity = 13,623; bottom graph: 30 May 2003, 650 mm TL, GSI = 4.7 and fecundity = 24,835).

Ovarian structure, egg size and fecundity

Heterotis possesses a single ovary (63 ovaries examined from 2002 sample, 115 ovaries examined from 2003 sample) with coloration that ranges from pink in completely immature fish (juveniles) to yellow–orange for ripe individuals. The ovary is elongate, laterally compressed with 54–76 (mean = 64) dorsally arranged lamellar folds. The diameter of oocytes in ripe gonads (i.e., ovaries associated with gonadosomatic indices ≥90th percentile) ranged from 0.5 to 3.0 mm (mean = 2.0 mm). Frequency distributions of oocyte size classes within females having highest GSI values during the 2002 and 2003 spawning seasons revealed cohorts of immature (latent) oocytes within mature ovaries (Fig. 7). The 2002 distribution was more strongly skewed toward the largest oocyte size classes, possibly indicating a greater degree of spawning synchrony.

Overall, fecundity (measured as the number of mature oocytes in the ovary) increased with body length ($r^2 = 0.47$; $P < 0.01$) and body weight ($r^2 = 0.43$; $P < 0.01$) (Fig. 8). Lowest and highest fecundities recorded for individual fish were 2697 (545 mm TL, 500 mm SL, 1.33 kg) and 27,508 oocytes (815 mm TL, 735 mm SL, 4.65 kg), respectively. Ovarian weight increased with body size, but the number of oocytes per gram of ovary was not influenced by body size (Table 2). Relative fecundity (number of oocytes per gram of body mass) revealed no general association with body size.

Nesting and brooding

The mean monthly density of active *Heterotis* nests encountered in Lake Hlan was 25.4 per hectare, with an average of 37–51 nests per hectare/month observed during the peak spawning period (May to August). No active nests were observed from December to February, with ≤10 observed during November and March. The percentage of identifiable nests that were active was >85% from July to September 2002 (January to June not surveyed) and from April to October 2003. Nests averaged 116 cm in diameter (range 77–165 cm) and occurred at an average water depth of 60 cm (range 40–86 cm). Height of submerged and emergent vegetation surrounding nests ranged from 30 to 135 cm (mean = 89 cm), and the diameter of nest entrances ranged from 20 to 47 cm (mean = 33 cm). Tending of nests and broods occurs from the time of hatching until juveniles disperse from the nest. When nests containing newly hatched larvae were disturbed, both parents took larvae into their mouths for transportation to another location (A. Adite, personal observations). *Heterotis* larvae were collected from seven active nests using a dipnet, and transported to the laboratory for enumeration and use in rearing experiments. The number of larvae per nest ranged from 3953 to 6125 (mean = 5028).

Fishing pressure on nesting bonytongues was assessed on a monthly basis by estimating the total number of active nests with fishing traps positioned at nest openings. Monthly trapping effort was positively correlated with the density of active nests ($r^2 = 0.92$; $P < 0.01$; $N = 18$), with 87.8% of active nests having traps.

Discussion

Bonytongues were captured from Lake Hlan during every month of the field study, and the numerous nests and brooding adults encountered during the rising water (wet) and peak flood seasons indicate that Lake Hlan is an important spawning site for bonytongues. In contrast, more than 90% of the bonytongues collected from the lower Sô River and associated floodplain were captured during the flood and early falling water periods (October to November), and almost all these individuals were juveniles and subadults. Thus, it appears that juvenile bonytongues migrate from lakes into the flooded plains, with many individuals making their way south to the vast, productive plains of the lower Sô and Ouémé Rivers. This hypothesis is supported by the size distributions in the two regions. The Lake Hlan population contained many large breeding adults and small juveniles but few intermediate size classes. These intermediate size classes strongly dominated the river floodplain region to the south. The densely vegetated river floodplains probably provide abundant food resources that support rapid growth of these omnivores (Adite et al. 2005). In the Sô River, fish condition increased gradually from the start of the wet season through the peak flood then falling water (dry) period. As floodwaters recede, invertebrate prey, a particularly important food resource for juvenile bonytongues (Adite et al. 2005), probably become concentrated within shrinking aquatic habitats. Adult bonytongues in Lake Hlan consume a mixture of aquatic invertebrates, seeds and detritus (Adite et al. 2005). Lake Hlan bonytongues, nearly half of which were adults, were in best condition during the wet and flood seasons when access to seeds from submerged and emergent terrestrial vegetation should have been greatest.

The spawning period of bonytongues was restricted to the wet and flood periods, a pattern commonly documented for large fish species inhabiting large rivers and wetlands in Africa (e.g., Winemiller 1991;Laleye et al. 1995). Flooding at Lake Hlan was more extensive during 2003 than 2002. As the lake level gradually rises during the wet season (March to July), bonytongues select sites and construct their nests in shallow marginal areas of the lake. During the high flood of 2003, most bonytongues abandoned their original nests when water depth became too great at these locations. From August to October, new nests appeared along newly flooded lake margins.

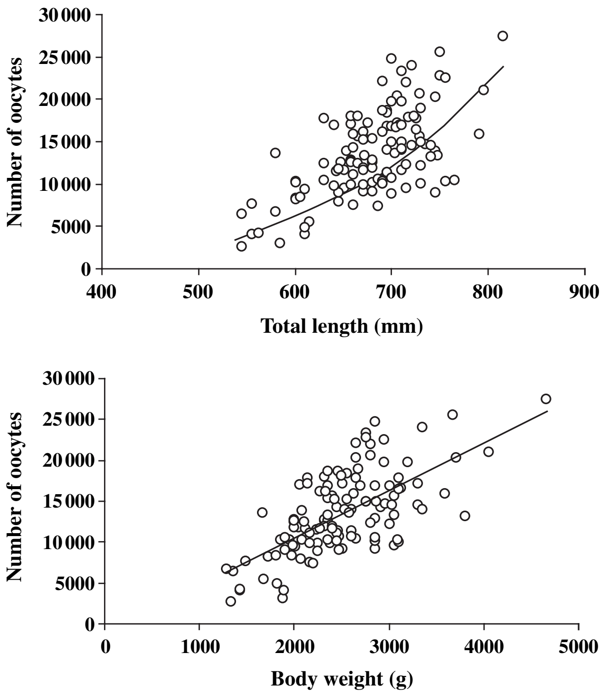

Fig. 8. Best fit relationships between fecundity (F) and total length ($F = 0.0000006(\mathrm{TL})^{3.65}$; $R^2 = 0.47$; $N = 123$) and weight ($F = 5.74W{-}748$; $R^2 = 0.43$; $N = 123$) of *Heterotis* from Lake Hlan.

Table 2. Fecundity of Sô River–Lake Hlan *Heterotis* size classes ($N = 123$).

TL class (mm)	Mean body weight (g)	Mean ovary weight (g)	Mean fecundity	Fecundity range	No. of eggs per gram ovary	Relative fecundity	Mean GSI	*N*
500	1343.0	14.0	4578	2697–6459	327	3.40	1.0	2
600	1881.6	39.2	9554	3108–17,850	271	5.00	2.1	28
700	2661.7	58.6	14,854	9048–25,584	359	5.60	2.2	89
800	3783.7	81.5	18,769	10,548–27,508	297	4.82	2.1	4

GSI, gonadosomatic index.

Re-nesting in response to excessive flooding could partially explain why the egg-size distribution in the most mature ovary was less skewed toward the largest diameters during 2003 relative to that from 2002. The 2003 ovary was from a second-time spawner (re-nester) that was responding to a sudden disruption of the reproductive cycle, whereas the 2002 ovary was from a female preparing to nest for the first time in response to seasonal environmental cues.

Fishing activity is intense in the Sô River system, and bonytongues dominate the catch during the flood season (Gbaguidi & Pfeiffer 1996). During this period, more than two-thirds of resident and migrant fishermen exploit this seasonally available resource. Large cast nets are the most efficient and popular means for catching bonytongues in this river fishery. As almost no adults were captured from the survey region in the lower Sô River, this subpopulation appears to be a metapopulation sink (Pulliam 1988) maintained by periodic immigration from a source subpopulation. Because spawning and brooding bonytongues are common in shallow waters along the margins of floodplain lakes, these habitats probably support source populations that sustain the large fishery in the river and floodplain downstream. Lake Hlan is one of the largest lakes in the Sô River floodplain, and is well known locally as the 'bonytongue lake'. In Lake Hlan, castnetting is prohibited by local regulations, but bonytongues are caught with fish traps placed at nest entrances. This practice increases mortality not only on adult stocks, but also on larval cohorts vulnerable to predators when parental brooders are removed from their nests. Between 1 and 7 days posthatch, larvae have large yolk sacs and are incapable of significant movement, and thus are particularly vulnerable.

The African bonytongue matures at 2 years (Moreau 1982) and has relatively large eggs (2.5–3.0 mm) and moderate batch fecundity (2700–27,500) for a fish of its size. Consequently, the species displays a life history strategy that is closer to the equilibrium endpoint than the periodic endpoint (Winemiller & Rose 1992), which implies that parental care is essential for early life stage survivorship and levels of recruitment needed for long-term population viability (Van Winkle et al. 1993;Rose et al. 2001). In theory, equilibrium life history strategies should be associated with significant density-dependent recruitment, such that minimum or optimal densities of spawners could be estimated. Maintenance of a healthy population of spawners in Lake Hlan (source subpopulation) is probably essential for sustainable fisheries (sink subpopulations comprised of immature fish) in the Sô River floodplain.

Nearly 90% of active nests in Lake Hlan had fishing traps positioned at their entrances. This suggests that high fishing effort that targets brooding adults could jeopardise this critical source subpopulation of bonytongues. In fact, adult bonytongues are exploited as they construct their nests, prepare to spawn and tend their broods. As local regulations prohibit use of cast nets in Lake Hlan, fish stocks in this system are less impacted than those in most other aquatic ecosystems in Benin. Nonetheless, the high economic value of bonytongues has induced many fishermen to adopt unsustainable fishing practices, such as trapping nests. Interviews with fishermen revealed that they are aware of potential negative impacts of trapping, yet they need this source of income to meet the most basic needs of their families. The chances for a sustainable bonytongue fishery in the Sô River system would be increased by better enforcement of fishing regulations governing the open-access river fishery coupled with community-based management of the Lake Hlan fishery that reduces harvest during the peak period of nesting from April to August. The other major lakes in the lower Sô River floodplain should be investigated to determine their potential for supporting source subpopulations of bonytongues and possibly other nesting fish species, such as tilapiine cichlids.

Resumen

1. La estructura poblacional del osteoglósido africano, *Heterotis niloticus,* fue estudiada en el Lago Hlan (sudeste de Benin), y en un área de la zona de inundación del Río Sô, localizada a unos 60 Km. del lago, aguas abajo. Ambas localidades mantienen importantes pesquerías, en las cuales *H. niloticus* es una de las especies más importantes durante el periodo de inundación.

2. Los adultos maduros constituyen >40% de la población del Lago Hlan, pero solo el 3.5% de los individuos capturados en el río fueron adultos. Los promedios mensuales del índice gonado-somático y los porcentajes de individuos con gónadas maduras aumentaron al incrementar el nivel de las aguas durante el periodo de lluvias, y disminuyeron posteriormente durante el pico del periodo de inundación. La distribución de frecuencias de tamaños de los oocitos en los ovarios, sugirió la posibilidad de producir una cohorte adicional en el caso en que halla perturbaciones durante la puesta. Entre 37 a 51 nidos activos por hectárea fueron observados en el Lago Hlan durante el pico de desove (Mayo-Agosto). El número de larvas por nido varió en el rango 3.953–6.125.

3. Los osteoglósidos del Lago Hlan parecen constituir una importante sub-población 'fuente' que exporta nuevos reclutas a las áreas bajas del río y zonas de inundación donde la intensa actividad pesquera explota principalmente juveniles y sub-adultos. Consecuentemente, restricciones a la cosecha de osteoglósidos adultos en el Lago Hlan puede ser esencial para una pesca comercial sostenible en la parte baja del Río Sô.

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