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RESEARCH PAPER

Reproductive Biology of the Hybrid *Coptodon guineensis* x *Coptodon zillii* within Two Marginal Lagoons Invaded by Macrophytes in South Eastern of Côte d'Ivoire

Koffi Bienvenu N'Goran[1], Kouadio Justin Konan[2,*], Kouassi Yves Narcisse Kouamé[3], Annigbé Justin Eyi[4], Koffi Kouakou[1]

[1]Université Félix Houphouët-Boigny, UFR Biosciences, Laboratoire d'Endocrinologie et Biologie de la Reproduction, Abidjan Côte d'Ivoire, 01 BP V 34 Abidjan 01 Côte d'Ivoire.
[2]Centre de Recherches Océanologiques, BPV 18, Abidjan, Côte d'Ivoire.
[3]Université Félix Houphouët-Boigny, UFR Biosciences, Laboratoire d'Hydrobiologie, 22 BP 582 Abidjan 22, Côte d'Ivoire.
[4]Université Nangui Abrogoua, Abidjan, UFR des Sciences de la Nature, Côte d'Ivoire, 02 BP 801 Abidjan 02, Côte d'Ivoire

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Corresponding Author
Tel.: +2250707625271
E-mail: konankouadjustin@yahoo.fr

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Abstract

Hybrids of *Coptodon guineensis* x *Coptodon zillii* are omnivorous species with a phytophagous tendency found in most of water bodies of Côte d'Ivoire. This study aims to better understand its reproductive biology and possible influence of macrophytes on the breeding season. A total of 608 fish were caught monthly from September 2017 to August 2019. The overall sex-ratio showed significant predominance of females in Ono (1:1.37; $\chi^2 = 7.10$; $P<0.05$) and Kodjoboue (1:1.84; $\chi^2 = 28.62$; $P<0.05$) lagoons. The sexual maturity recorded in Ono lagoon for males (148.2 mm, SL) and females (145.3 mm) was slightly higher than that of males (144.4 mm, SL) and females (141.8 mm) in Kodjoboue lagoon. March and August–October (Ono lagoon) and February and July–September (Kodjoboue lagoon) were the most intensive spawning months. The absolute fecundity was higher in Ono lagoon (1472–6116 oocytes) than in Kodjoboue lagoon (1676–4210 oocytes), indicating a better food supply due to the high abundance of macrophytes in Ono lagoon. Oocyte size frequency distributions show oocytes of different sizes, indicating more than one spawning within a reproduction season. These findings might facilitate future studies establishing its potential production and its exploitation and management.

Introduction

Hybridization between closely related species is ubiquitous in nature and occurs in at least 10% of animal and 25% of plant species (Mallet, 2005). Its effects can be positive (Anderson & Stebbins, 1954; Becker et al., 2013; Nolte & Tautz, 2010; Seehausen, 2004) or negative (Muhlfeld et al., 2009; Roberts et al., 2010) for native species or new species. Species of Cichlidae family are well known for their ability to hybridize naturally or in captivity. External fertilization, competition for limited spawning grounds, secondary contact of recently diverged sister taxa, spatial or dietary overlap in parental species, rarity of one or both parental species, sneak mating and absence of assortative mating are processes which can explain the abundance of hybrid fishes (Campton, 1987; Hubbs, 1955; van Herwerden et al., 2006; Marie et al., 2007; McMillan et al., 1999).

Coptodon hybrids are important to the commercial and subsistence fisheries in most of water bodies of Côte d'Ivoire (Gourène et al., 1999). These hybrids are from crosses between *C. zillii* and *C. guineensis* and comprise 24% of the Ayame man-made lake's Cichlid population, while parental *C. zillii* and *C. guineensis* make up 3.5 and 2.2 %, respectively (Thys Van Den Audenaerde et al.,

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1998). Although there is some research on their genetic and morphological characteristics (Gourène et al., 2006; Nobah et al., 2008), there is no information on the reproductive biology, particularly of small lagoons like Ono and Kodjoboue lagoons which are generally closed ecosystems. These lagoons contain in abnormal quantity, a diversity of native and non-native plants and surrounding industrial plantations which could strongly affect their ecological quality. Paugy et al. (2006) found that the reproductive cycle of a species presents a set of physiological and behavioural processes related to the abiotic and biotic parameters, such as salinity, water quality and food availability which are also known to affect gonadal maturity and fecundity and, hence, the timing of seasonal spawning (Van Der Kraak & Pankhurst, 1997). In addition, the accumulation of phosphorus and nitrogen from agricultural land and urban effluents, pesticides and faecal matter can deteriorate the water quality of Ono and Kodjoboue lagoons, leading to a proliferation of invasive plants (Eyi, 2019). According to Randall (1996), the macrophytes increase the structural complexity of the littoral habitats, which increases the influence of predator–prey interactions. Each species may react differently to environmental factors that affect its physiological rhythms. Thus, when aquatic macrophytes occupy large areas of a water body, a reduction in fish condition can occur, resulting in a stunted fish population (Colle & Shireman, 1980). The correlation between plant and fish seems to provide a crucial relationship in natural ecosystems since the vegetation could influence the fish diversity, feeding, growth, and reproduction. Observations collected from fishermen of several water bodies showed that *C. zillii* is increasingly rare whereas *Coptodon* hybrids are one of the main species of Cichlids encountered in catches. These hybrids therefore adapt perfectly to both freshwater and brackish waters and even those which are highly disturbed. In the light of their numerical prevalence, it is important to have a good understanding of the reproductive biology in order to show possible influence of macrophytes on the spawning season. These findings would be useful for the implementation of conservation measures and the development of aquaculture for *Coptodon* hybrids.

The present study aims to assess the reproductive cycles of the hybrid *C. zillii* x *C. guineensis* from Ono and Kodjoboue lagoons, with emphasis on identifying the timing of reproductive events and determining reproductive periodicity and fecundity. We hypothesize that the reproductive patterns are similar, and that its breeding strategies change depending on the abundance of macrophytes.

Materials and Methods

Study Area

Ono lagoon (5°22'22"N and 3°33'53"W) and Kodjoboue lagoon (5°14'11 "N and 3°35'9" W) are two small lagoons of the Southeast of Ivory Coast (Figure 1). Their surfaces are respectively 400 ha and 423 ha. The percentage of macrophyte abundance was determined using satellite images by the University Centre for Research and Application in Remote Sensing of the University Félix Houphouët Boigny, Côte d'Ivoire. Because Ono lagoon is invaded by several macrophytes

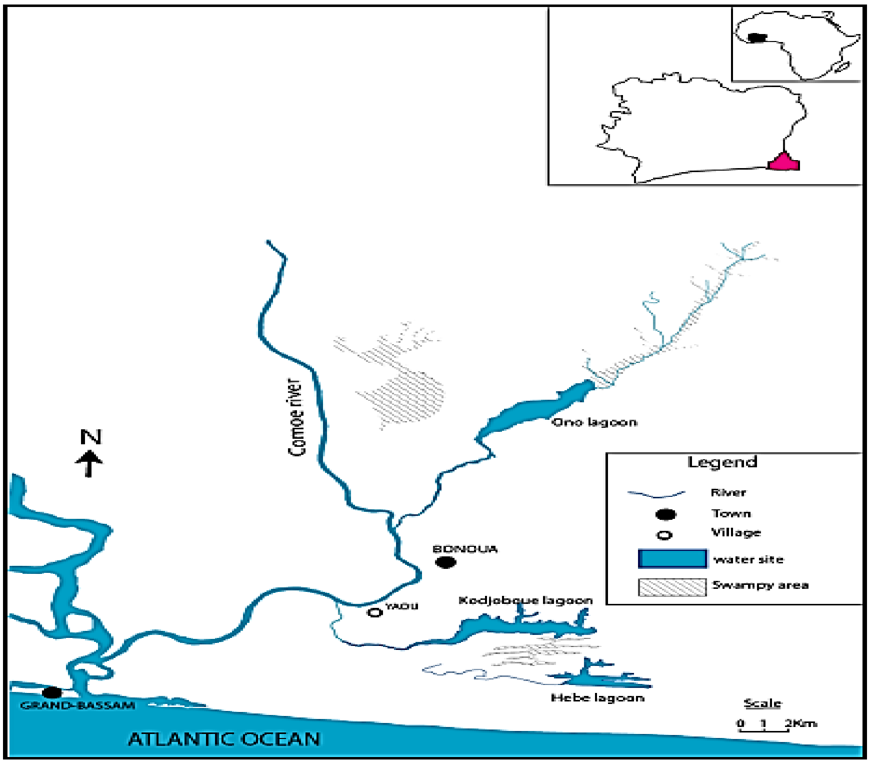


Figure 1. Geographic situation of the Ono and Kodjoboue lagoons.

(60-70 %), its exploitable surface is 162 ha. In Kodjoboue lagoon, only the banks are occupied by macrophytes with a coverage rate of 20%. The surface of these lagoons includes a wide variety of habitat types such as native (*Echinochloa Pyramidalis*, *Pistia stratiotes*, *Nymphaea lotus*) and non-native (*Eichhornia crassipes*, *Hydrilla verticillata*, *Salvinia molesta*) plants. These lagoons, permanently connected to the Comoe river have an equatorial climate, including two rainy seasons (April-July and October-November) and two dry seasons (December-March and August-September). The permanent linkage with the Comoe river produces typical freshwater characteristics of these lagoons. The abiotic parameters during the current study varied significantly among the sampling lagoons (ANOVA test, $P<0.05$), except for pH, Conductivity, TDS, nitrite and ammonium-nitrogen (Table 1). For the parameters such as temperature (29.73 ± 1.57°C) and dissolved oxygen (5.81 ± 0.97 mg/L), the values were significantly higher in Kodjoboue lagoon whereas the values of transparency (1.59 ± 0.29 m), nitrate (3.09 ± 0.93 m/L) and phosphate (0.48 ± 0.24 m/L) were higher in Ono lagoon (Table 1).

Sampling and Laboratory Procedure

Specimens were identified using the identification key of Nobah et al. (2006), based on the colour pattern of the caudal fin. The caudal fin of hybrids is bicoloured with upper half-clear yellowish and lower half-dark yellowish; with dots at least on upper part and may cover whole fin. Eighteen to 40 hybrid specimens were monthly sampled from September 2017 to August 2019 using traps, gill nets, harpoons and hawks. The harpoon fishermen were interviewed on the times and depths of fishing (at the bottom or in the water column, in galleries or nesting nests) to determine the mode of reproduction of the hybrids. The specimens were transported in iced boxes to the laboratory of the Department of Aquatic Living Resources of the Oceanological Research Centre, Abidjan. The individuals were measured to the nearest 1 mm (standard length [SL]), weighed in terms of total body weight to the nearest 0.01 g using a electronic balance. Each fish was then dissected, and the gonads were removed and weighed to the nearest 0.001 g. The weight of eviscerated fish was taken to the nearest. The sex and maturity stages of gonads were determined through visual inspection of the appearance, size and texture according to a scale inspired by that of Mahomoud et al. (2011) for *C. zillii*.

Stage I (immature): thin, translucent and pale in colour testicles. Small and thin ovaries occupying a small part of the body cavity; invisible oocytes. Both gonads are invisible to the naked eye.

Stage II (early maturing): testes enlarged, flat, increased in weight and volume, and creamy white in colour. Ovaries slightly larger and increased in weight. Whitish oocytes, occupying approximately half of the body cavity.

Stage III (developing): testes more vascularized, thicker in size. Ovaries distended occupying about 2/3 of abdominal cavity with large pale-yellow eggs.

Stage IV (pre-spawning): soft testicles, swollen, milky white, increased in weight and volume, occupying entire body cavity. More enlarged ovaries occupying the entire abdominal cavity with large number of big, turgid, spherical, translucent, swollen green ripe ova.

Stage V (spawning): white testicles. A simple compression brings out the sperm. Mature oocytes visible through the ovarian wall and some ripped eggs present in the oviduct.

Stage VI (spent): empty testes with evidence of haemorrhage. Flaccid, sac-like and reduced in volume ovaries.

The sex ratio was determined using the proportion of the number of males to that of females.

Average length at maturity was defined as the 10 mm length class at which 50% of individuals reached maturity. The percentage of sexual maturity was described by the logistic function described by Ghorbel et al. (1996) as follow:

$$P = \frac{1}{1+e^{-(\alpha+\beta SL)}}$$

where P = percentage of mature fish, SL = standard length, and α and β = coefficients.

Table 1. Average values (mean ± SD) of the physical and chemical parameters in Ono and Kodjoboue lagoons between September 2015 and August 2016.

Parameters	Ono lagoon	Kodjoboue lagoon
Temperature (°C)	$27.17\pm1,56^{a}$	29.73 ± 1.57^{b}
Dissolved oxygen (mg/L)	2.29 ± 0.84^{a}	5.81 ± 0.97^{b}
pH	6.32 ± 0.49^{a}	6.29 ± 0.58^{a}
Conductivity (µS/cm)	18.09 ± 5.92^{a}	13.97 ± 6.53^{a}
TDS (mg/L)	9.06 ± 1.58^{a}	6.96 ± 3.20^{a}
Transparency (m)	1.59 ± 0.29^{b}	1.21 ± 0.20^{a}
Nitrate (mg/L)	3.09 ± 0.93^{b}	2.31 ± 0.67^{a}
Nitrite (mg/L)	0.21 ± 0.40^{a}	0.24 ± 0.47^{a}
Ammonium-nitrogen (mg/L)	0.08 ± 0.04^{a}	0.06 ± 0.04^{a}
Phosphate (mg/L)	0.48 ± 0.24^{b}	0.27 ± 0.15^{a}

The value of L_{50} was estimated from the negative ratio $\frac{-\alpha}{\beta}$ by substituting P=0.5.

The gonadosomatic index (GSI) was calculated for each specimen as a percentage of gonad weight to that of eviscerated weight using the following equation:

$$\text{GSI} = \frac{\text{Gonad weight (g)}}{\text{Eviscerated weight (g)}} \times 100$$

The spawning season was determined following the monthly evolution of the gonadosomatic index and the percentages of sexual maturity stages.

The absolute fecundity was determined using the ovary of pre-spawning females by counting oocytes having the largest diameter. After weighing the ovaries, sub-samples were taken according to the size of the ovaries and the oocytes of each sample were counted. A mean fecundity from all samples was calculated using a "direct summation" procedure (Shoesmith, 1990). The oocyte diameters were determined for females at stages II, III, IV, V and VI. Oocytes of *Coptodon* hybrids showed an ovoid form with two dimensions (d_1 and d_2), measured to the nearest 0.01 mm under a binocular microscope. Therefore, the theoretical diameters (d) utilized to construct the frequency histograms of oocyte diameters were the geometric means (d) of d_1 and d_2, expressed as follow (Adité et al., 2017):

$$d = \sqrt{(d_1 \times d_2)}$$

Statistical Analyses

The Shapiro-Wilk normality test for homoscedasticity were applied to the data, to determine whether the assumptions of the parametric and nonparametric analyses for GSI were satisfied. The relationship between macrophyte abundance and the GSI was assessed by the linear regression. The difference between the observed and expected sex ratio was subjected to Chi-square test. A two tailed t test was used to compare the estimated fecundity between lagoons. ANOVA was used to determine the effects of months on the GSI in relation to sexes. Tukey's HSD multiple contrasts test was used to determine significant differences at the 0.05 level.

Results

Sex Ratio

A total of 285 specimens (120 males and 165 females) and 323 (113 males and 209 females) were collected respectively in Ono and Kodjoboue lagoons (Table 2). The overall sex ratio of 0.73: 1 and 0.54: 1 were in favour of females in Ono (χ^2 = 7.10; P<0.05) and Kodjoboue (χ^2 = 28.62; P<0.05) lagoons. Females dominated monthly for both lagoons, except months preceding the peaks of spawning (April and October) where males outnumbered females. The differences were highly significant between March–May, July–August and October in Kodjoboue lagoon. The sex ratio varied greatly following fish size, with predominance of females in size of 70–130 mm SL and males in size above 140 mm (Figure 2).

Size at Sexual Maturity

The average lengths at 50% maturity were 145.3 mm, SL for females and 148.2 mm for males in Ono lagoon and 141.8 mm for females and 144.4 mm for males in Kodjoboue lagoon (Figure 3). Individuals of each sex reached sexual maturity at a smaller size in Kodjoboue lagoon, but no significant difference was found (P>0.05). In Ono lagoon, the smallest female with ripe gonads measured 80 mm, whereas the smallest ripe male was 60 mm. In Kodjoboue lagoon, the smallest female and male with ripe gonads measured 80 mm and 70 mm, respectively.

Table 2. Proportion of sexes and sex-ratio of the hybrid (*Coptodon guineensis* x *Coptodon zillii)* caught in Ono and Kodjoboue lagoons from September 2017 to August 2019

	Ono lagoon				Kodjoboue lagoon			
Month	Males	Females	M: F	χ^2	Males	Females	M: F	χ^2
January	12	18	0,67: 1	1.20	5	11	0,45: 1	2.25
February	6	9	0,67: 1	0.60	11	21	0,52: 1	3.13
March	11	18	0,61: 1	1.69	8	26	0,31: 1	9.53*
April	6	5	1,20: 1	0.09	22	10	2,20: 1	4.50*
May	9	11	0,82: 1	0.20	6	21	0,29: 1	8.33*
June	11	19	0,58: 1	2.13	9	19	0,47: 1	3.57
July	9	14	0,64:1	1.09	5	16	0,31: 1	5.76*
August	10	12	0,83:1	0.18	9	24	0,38: 1	6.82*
September	6	11	0,55: 1	1.47	4	8	0,50: 1	0.47
October	13	10	1,30: 1	0.39	11	12	0,92: 1	4.00*
November	13	22	0,59: 1	2.31	12	19	0,63: 1	1.58
December	14	16	0,88: 1	0.13	11	22	0,50: 1	3.67
Total	120	165	0,73: 1	7.11*	113	209	0,54: 1	28.62*

*= significant difference.

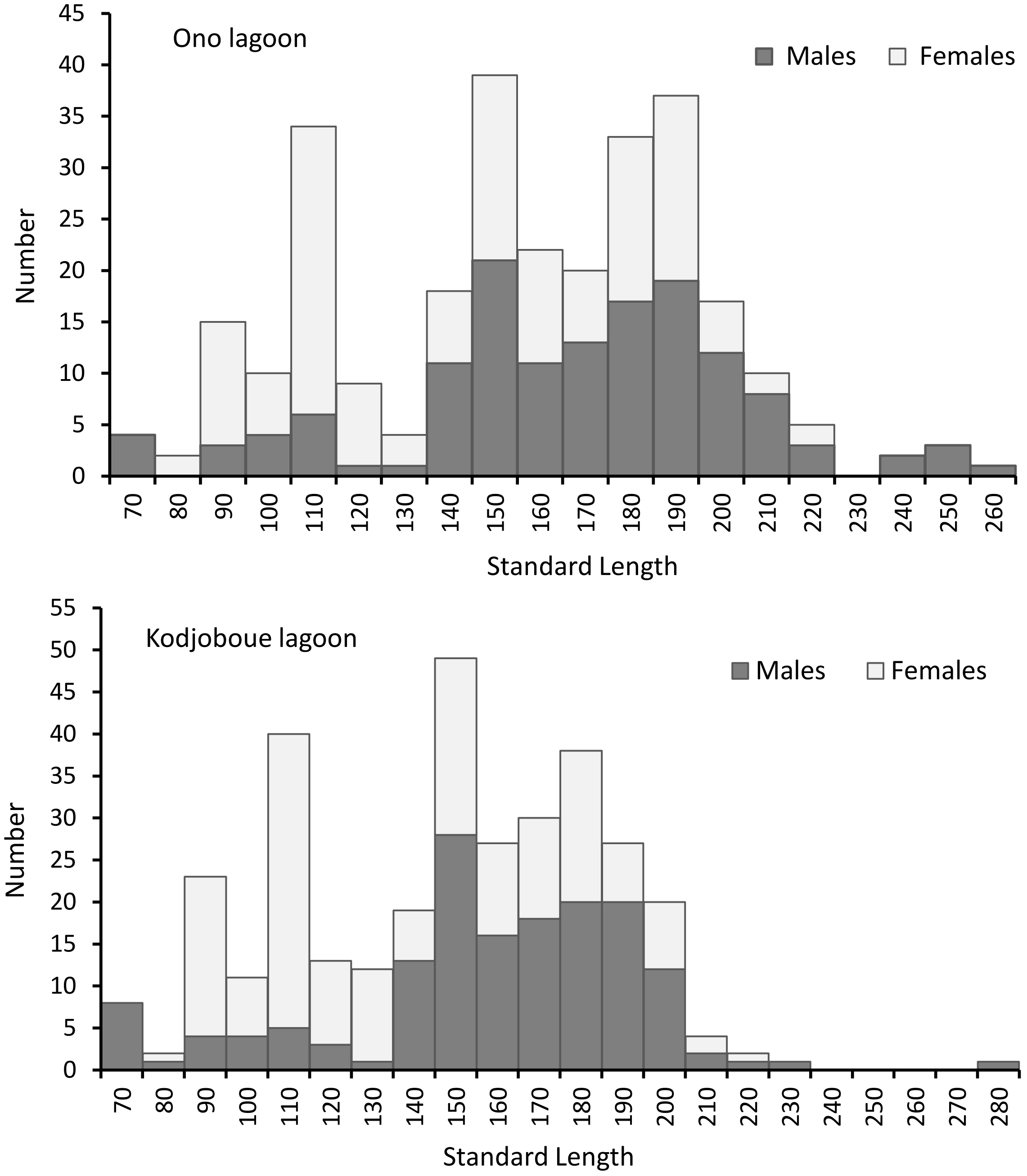


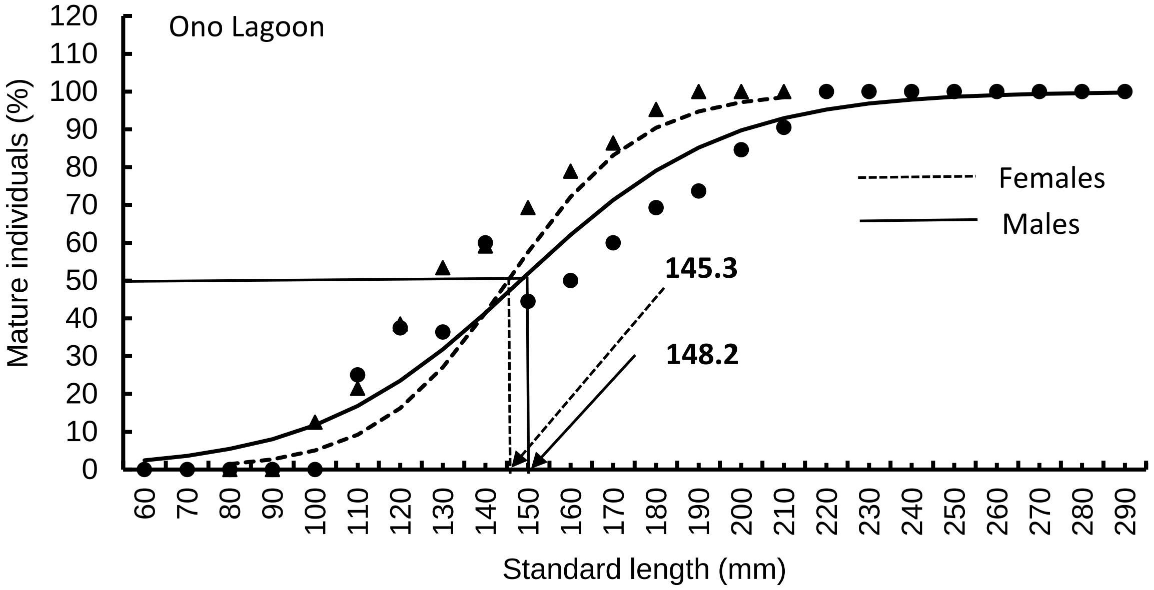
Figure 2. Length-frequency distribution for male and female of *Coptodon* hybrid (*C. guineensis* x *C. zillii*) caught in Ono and Kodjoboue lagoons from September 2017 to August 2019.

Distribution of Maturity Stages

All stages appeared throughout the sampling period in both lagoons (Figure 4). The immature stages (I and II) represented the dominant maturity stages in January and May–June for Ono lagoon and in December–January and May for Kodjoboue lagoon. The advanced stages of maturity (stages III, IV and V) were also recorded in all months but mostly from June to October and from February to March. The highest proportions of pre-spawning (stage IV) were obtained in July–August and February–March for both lagoons. The spent stage (stage VI) of Ono lagoon reached the maximum percentages in September–December and those of Kodjoboue lagoon in October–November.

Variations of Gonadosomatic Index

Monthly variations in Gonadosomatic index (GSI) revealed that both sexes followed nearly the same pattern in both lagoons. However, the GSI values were higher in Kodjoboue lagoon than in Ono lagoon (females, F = 6.352, p = 0.012; males, F = 1: 1.931, p = 0.166). The monthly GSI varied greatly, notably between individuals caught during similar and different months (ANOVA, $P<0.05$). However, sex by month interaction was insignificant (ANOVA, $P>0.05$), suggesting that the pattern of seasonal fluctuation in GSI was the same in both sexes (Figure 5). In Ono lagoon, the GSI of females and males increased after July and peaked in September (2.26 ± 1.65 and 1.56 ± 3.93, respectively), followed by a



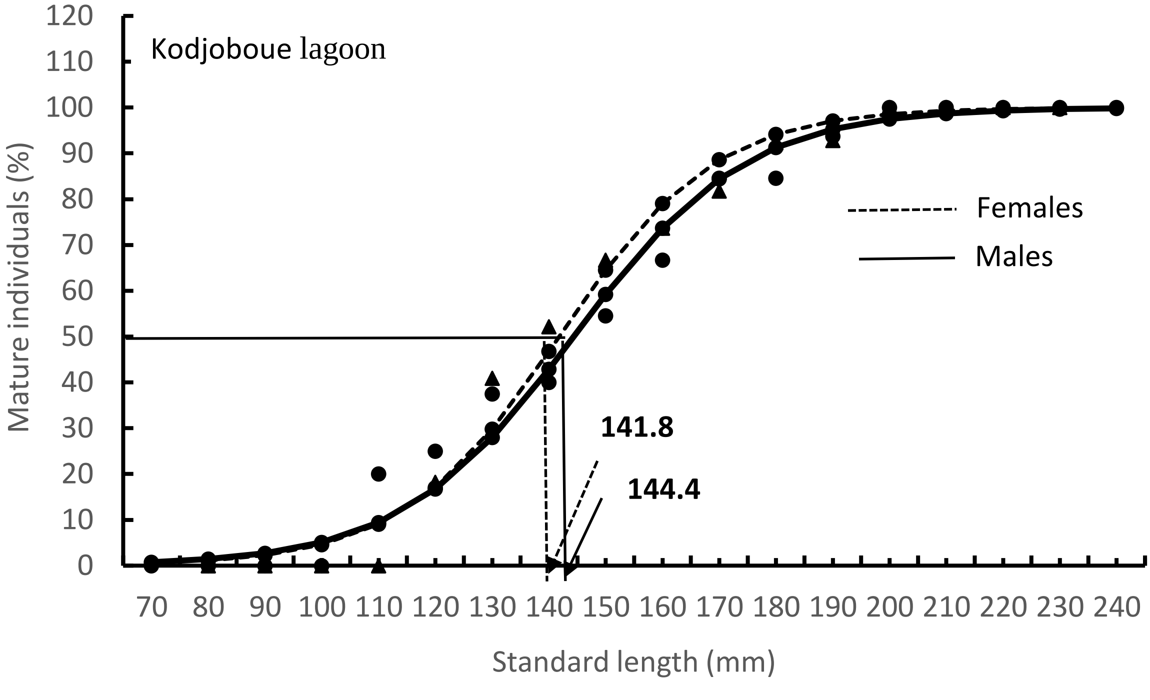


Figure 3. Length at first sexual maturity (L_{50}) of the male and female of *Coptodon* hybrids (*C. guineensis* x *C. zillii*) sampled from Ono and Kodjoboue lagoons.

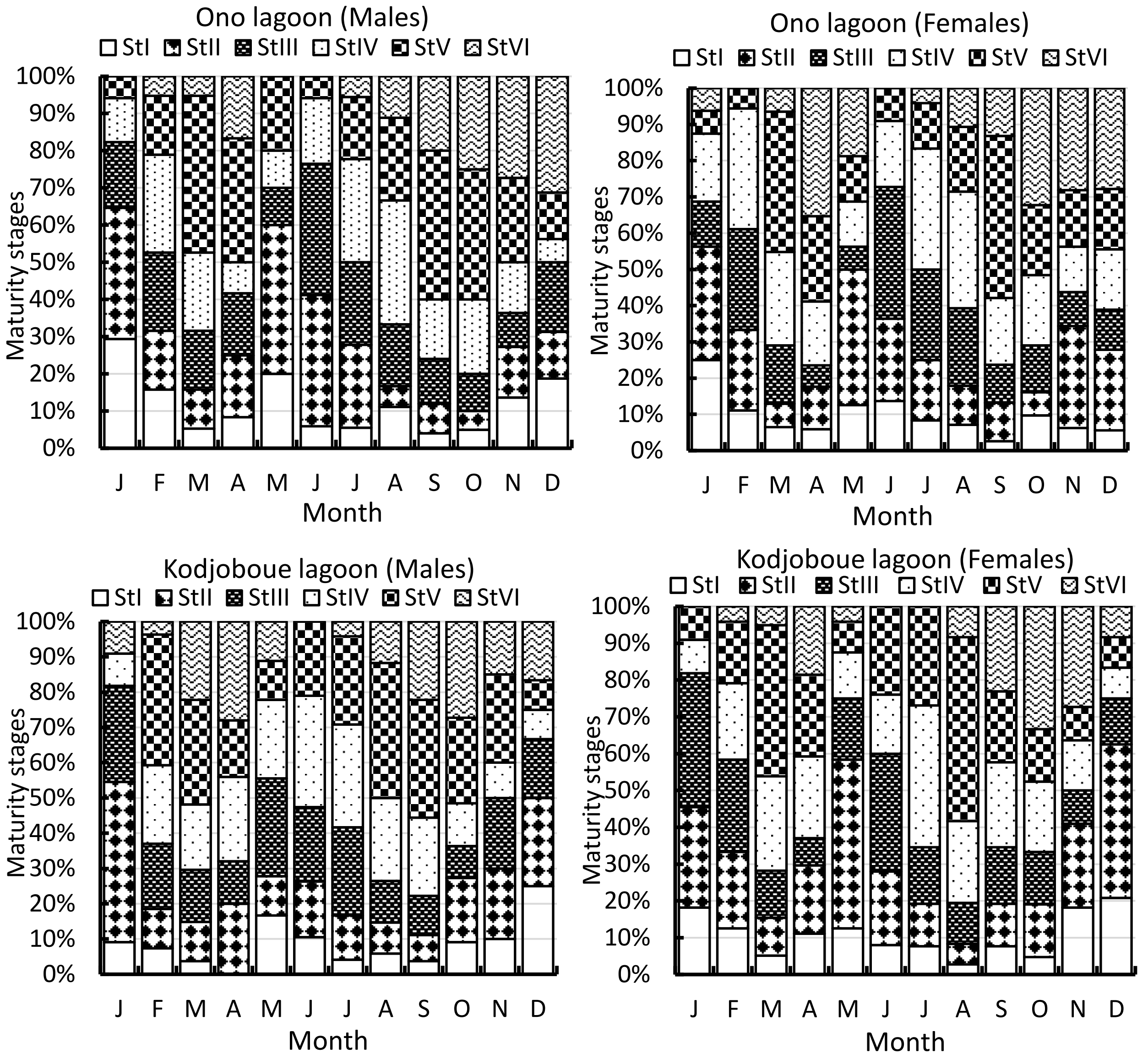


Figure 4. Percentage of maturity stages in *Coptodon* hybrids (*C. guineensis* x *C. zillii*) in Ono and Kodjoboue lagoons from September 2017 to August 2019. StI: immature; StII: early maturing; StIII: developing; StIV: pre-spawning; StV: spawning; StVI: spent

decrease from October to December. A second increase in GSI occurred from January to March, reaching a peak in February–March (2.11 ± 1.17 and 1.73 ± 0.97, respectively) and then declining from April to June. The same trend was observed in the GSI variation of Kodjoboue lagoon but the first peak occurred in August (2.87 ± 1.98 and 1.70 ± 1.23, respectively).

Mode of Reproduction and Spawning Periods

According to our own observations and surveys of harpoon fishermen, the hybrid *C. guineensis* x *C. zillii* is a substrate spawner cichlid. Also, based on the changes of GSI and percentages of maturity stages, this species spawned throughout the year. However, the peaks of spawning period were from July to November and from February to April in both lagoons. Most of spent females occurred in September for Ono lagoon and in August for Kodjoboue lagoon, corresponding to the peak of pre-spawning females in August and July, respectively.

Effects of Macrophyte Abundance on Reproductive Cycle

The variation of macrophyte abundance present the same trend in both lagoons, with values showed two peaks (February-March and July-September) followed by a relatively decrease from April to June and from October to November (Figure 5). The peak of reproduction occurred mainly in July-September and February-April when macrophyte abundance was higher. The Table 3 showed a significant positive correlation between GSI and macrophyte abundance regardless of sex in both lagoons.

Fecundity and Oocyte Diameters

The absolute fecundity ranged from 1472–6116 oocytes (3661 ± 1265 oocytes) corresponding to fish sizes of 100–195 mm, SL in Ono lagoon and from 1676–4210 oocytes (3515 ± 614 oocytes) for fish sizes ranging

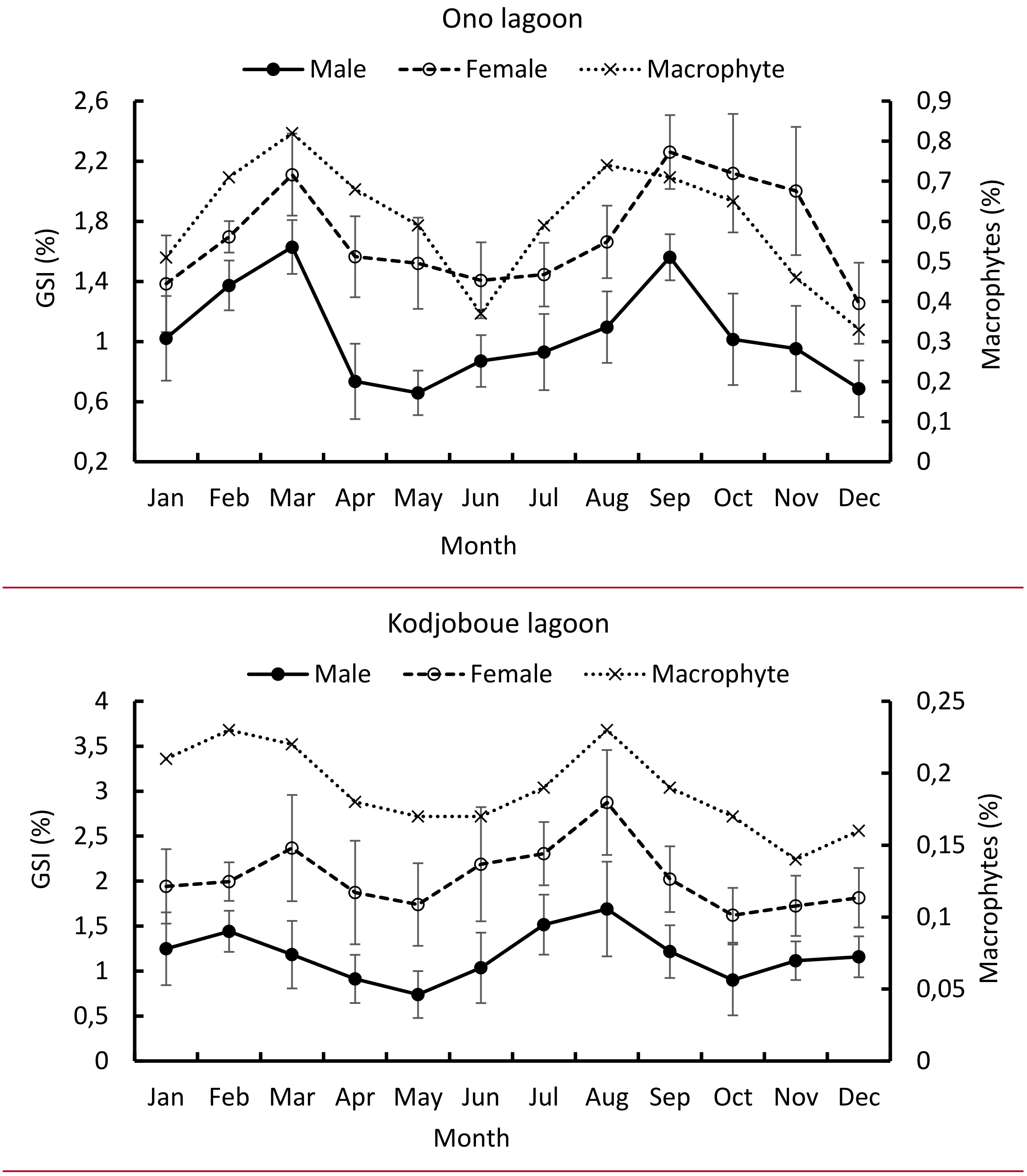


Figure 5. Monthly variations in macrophyte abundance and gonadosomatic index (GSI) in males and females of *Coptodon* hybrids from Ono and Kodjoboue lagoons between September 2017 and August 2019.

Table 3. Summary of correlation coefficients (*r*) between macrophyte abundance and GSI

		n	*R^2*	*r*	*p value*
Ono lagoon	Female	12	0.3575	0.5979	0.0400*
	Male	12	0.4309	0.6565	0.0204*
Kodjoboue lagoon	Female	12	0.4537	0.6736	0.0163*
	Male	12	0.4213	0.6491	0.0224*

* Significant at probability level 0.05

from 101 to 191 mm, SL in Kodjoboue lagoon. The absolute fecundity was significantly higher in Ono lagoon than in Kodjoboue lagoon (t = 33.94, df = 88, P<0.05). The relationship between absolute fecundity (F) and standard length (SL) was fitted using the following equations: F = 47.628 x SL – 4527 (r^2 = 0.72) for Ono lagoon and F = 22.926 x SL – 242.14 (r^2 = 0.80) for Kodjoboue lagoon.

The frequency distribution of oocyte diameters at stage II was unimodal with oocytes sizes of 0.1–1.5 mm and 0.1–1.2 mm in Ono and Kodjoboue lagoons, respectively (Figure 6). In contrast, the frequency distributions of oocyte sizes for mature females (stages III–V) were bimodal in both lagoons. The two modal groups consisted of oocytes with sizes of 0.1–0.7 mm and 0.9–1.9 mm in the developing stage (stage III), of 0.3–0.7 mm and 1.4–2.4 mm in the pre-spawning stage (stage 4) and of 0.5–0.9 mm and 1.3–2.7 mm in the spawning stage (stage V). In spent stage (stage VI), the frequency distribution of oocyte diameters was unimodal, with oocyte diameters varying from 0.1 to 1.3 mm. However, a few large oocytes (2.3–2.7 mm), which were not expelled during spawning were observed.

Discussion

The overall sex ratio of both lagoons was in favour of females, an observation which is consistent with those made for some Cichlid species in tropical water bodies (King, 1996; Sanogo, 1999; Koné & Teugels, 1999). Several assumptions including environmental parameters, displacement for foraging, reproduction, gregarious behaviour, differential growth and mortality strongly related to sex (Trewevas, 1983; Mellinger, 2002) could explain this result. In the current observation, since males and females take part in nest guarding during the breeding period, it would be expected that both sexes would be collected with equal ease. This hypothesis is not supported by our results, as females were more numerous throughout the year, except after each peak of spawning seasons. A possible explanation of the preponderance of males during peaks of spawning seasons period may be parental care as males exhibit aggressive territorial defence and protection of their offspring from any kind from invaders while females typically perform most of the intimate care, fanning and cleaning eggs, leave the males more vulnerable to capture. Schwanck (1987) specified that most of male’s attacks on intruders in tilapia species occur during the egg and wriggler phases, but once the fry is free-swimming, the female’s aggression increases and generally surpasses that of males. After spawning peaks, males possibly move from spawning areas toward submerged and emergent vegetation inaccessible to fishermen. We assume that the predominance of females results from the fact that they were more susceptible to exploitation because of their sedentary at the spawning grounds. The dominance of females in small sizes and males in large sizes may be either due to differences in the rate of activity between males and females. Indeed, the growth of male might be greater than female as the growth of female might be slowed at the start of maturity.

Females and males reached the length at first sexual maturity (L_{50}) at respective standard lengths of 145.3 mm and 148.2 mm (Ono lagoon) and of 141.8 mm and 144.4 mm (Kodjoboue lagoon). As we can see, females reached sexual maturity earlier than males in both lagoons and specimens from Ono lagoon became sexually active later than those from Kodjoboue lagoon. This sexual difference in L_{50}, mostly tardive in males was reported for several Cichlid species (Siddiqui, 1977; Moharram & El-Sayedat, 2007; Mireku et al., 2016). In addition, individuals of Ono lagoon matured at larger sizes than those of Kodjoboue lagoon. Some studies attributed these differences to genetical and environmental conditions such as food supply, population density and changes in temperature (Unlu & Balci, 1993; Chong et al., 2019). Other potential factors associated with variations in size at maturity were the fishing pressure on fish populations (Wood, 2013) and the presence of native and non-native plants on the waterbody which make them inaccessible to most of fishermen (Eyi, 2019).

The monthly changes in GSI index and percentages of maturity stages indicated that there is an extended reproductive period with spawning occurring throughout the year in both lagoons. However, the peak of reproduction takes place mainly one month earlier in Kodjoboue lagoon. These lagoons are ecosystems belonging to the same ecoregion and communicate permanently with the Comoe River, which could partly explain the similarity of the spawning season. According to Lowe-McConnell (1982), most species of tilapia breed continuously, but in some species, breeding activity increases during periods of intense sunshine and/or rainfall. A similar conclusion can be drawn for *Coptodon* hybrids because GSI and ripe fishes reaches peaks after just before or at the onset of the rainy season. In other words, the peak of reproduction occurred mainly when resource availability, assessed by the macrophyte abundance, was highest, just before the rainy seasons. For example, the rainfall at the onset of the rainy season might promote nutrient increase that stimulate macrophytes and surrounding terrestrial plants growth and their associated food (planktons, invertebrates and detritus) together with temperature and trigged the spawning of *Coptodon* hybrids. The high occurrence of stages V and VI in September-October (Ono lagoon) and July-August (Kodjoboue lagoon) probably indicate the onset of spawning activity which seemed to have continued until April. The peaks of spawning activity were observed: one in March and August–October (Ono lagoon) and February and July–September (Kodjoboue lagoon), indicating that this species displayed multiple reproduction with several offspring cohorts during the same spawning season. This starts when food abundance is higher, and autochthonous prey are

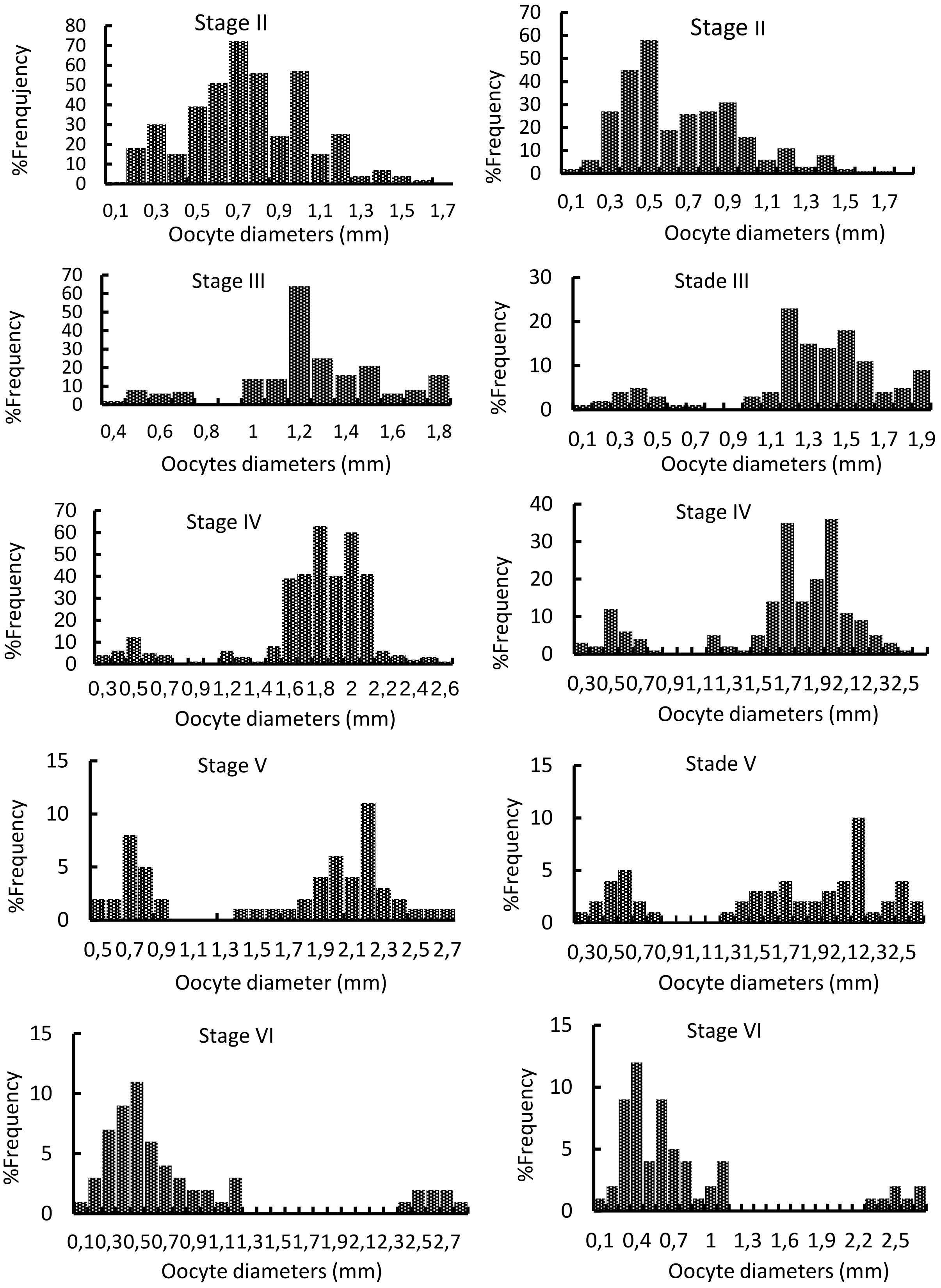


Figure 6. Oocyte diameter frequency distribution from stages II–VI of the *Coptodon* hybrids (*C. guineensis* x *C. zillii*) in Ono and Kodjoboue lagoons from September 2017 to August 2019.

concentrated in water bodies during the high-water phase (Lowe-McConnell, 1999). As is the case for many tropical fish species, the increase of water level during wet and flood seasons was the favourable condition that stimulated gonad maturation and led to spawning and recruitment (Lalèye et al., 1995; Vazzoler,1996; Adité et al., 2006; Atsé et al., 2009).

The absolute fecundity obtained in Ono lagoon was significantly higher when compared with that estimated in Kodjoboue lagoon. This higher fecundity in Ono lagoon appears to be related to a better food supply due to the high abundance of macrophytes as this species is omnivorous with a phytophagous tendency (Nobah et al., 2019). Rennie & Jackson (2005) pointed out that, macrophytes provide habitat complexity and breeding areas, as well as being substrata for periphyton and sites of abundant food production for many aquatic animals. So, this species is able to compensate for energy reserves with simultaneous food sources. This difference could also be associated with environmental factors such as the amount of rainfall, photoperiod, dissolved oxygen concentration and water temperature (Guèye et al., 2013). We found that fecundity varied linearly with fish body length in both lagoons. Fecundity is normally related to the length of the female's body, even though this relation can present some significant variations due to sampling periods and the variations in the biotic or abiotic environmental factors (Nikolsky, 1969; Zaret, 1980).

The oocyte diameters within any ovary of Ono lagoon presented a similar distribution pattern to that found in Kodjoboue lagoon. This range of oocyte variation was also similar to that reported in *C. guineensis* (Keremah & Ndah, 2013) and *C. zillii* (Jegede & Fawole, 2011). *Coptodon* hybrids have a synchronous oocyte development in two groups, which pointed to evidence of a total spawning pattern. This is confirmed by the distribution pattern of oocytes from ripe (V) and spent (VI) ovaries. Indeed, the oocytes disposition in ripe ovaries showed two modal groups: one mode of non-developed oocytes (diameters of 0.3–0.9 mm), which will not be released in the current reproductive season, and a mode of large oocytes (1.3–2.7 mm) that were developed and ready for spawning. As for spent ovaries, the frequency distribution of oocyte diameters was unimodal, with sizes varying from 0.1 to 1.3 mm and a few large oocytes (2.3–2.7 mm). This breeding pattern is typical to most Cichlid species (Paugy et al., 2006).

Conclusion

This study showed that *Coptodon* hybrids tolerate very low concentrations of dissolved oxygen and the sex ratio is not affected by the abundance of macrophytes. The spawning season for this species is year-round with peaks from July-November and February-April in both lagoons, coinciding with the abundance of macrophytes. However, the spawning peak of reproduction takes place mainly one month later in Ono lagoon. Individuals from Ono Lagoon reached length at first sexual maturity at large size and fecundity was higher compare to that of Kodjoboue Lagoon.

Ethical Statement

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Author Contribution

K.B. N'Goran and A.J. Eyi collected field data. K.J. Konan and K. Kouakou designed and coordinated the study. K.B. N'Goran, K.J. Konan and K.Y.N. Kouamé analysed the data and wrote the manuscript. All authors read and approved the final manuscript.

Conflict of Interest

The author(s) declare that they have no known competing financial or non-financial, professional, or personal conflicts that could have appeared to influence the work reported in this paper.

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