

Macroscopic gonad staging and reproductive seasonality in the Gorean snapper, *Lutjanus goreensis* a gonochoristic West African Lutjanid

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Abstract

In Nigeria, the Gorean snapper *Lutjanus goreensis* is an important component of artisanal fisheries and trawl landings although substantial gap exists on some aspects of the species' reproductive biology in the entire Gulf of Guinea. The main objective of the study was to characterize the sexual differentiation and ratio, spawning seasonality and pattern through observation of three somatic indices: gonadosomatic index (I_G), hepatosomatic index (I_H) and the Relative Condition Factor (K_{rel}), macroscopic staging and size at first sexual maturity of the species. Spawning seasonality and pattern were best determined from temporal trends of I_G and macroscopic gonad stage frequencies. The fish is monogamous with sex ratio of 1 male: 1 female. Five distinct gonad maturity stages and lack of population synchrony in gonadal development were distinguished. Mean sizes at first sexual maturity were 34.61 cm TL and 34.21 cm TL for females and males, respectively. Multiple spawning peaks reflected by high I_G occurred in December, May to June and August indicated protracted spawning while lowest I_G occurred in March-April, denoted a resting phase. The species is a multiple spawner as evinced from asynchronous development of the gonads. It showed continuous reproduction throughout the year, particularly at higher intensity during the heavy rains (May to September). While these findings imply continuous recruitment into fishery, it is recommended that for optimal exploitation, minimum capture size has to be increased above sizes at sexual maturity.

Introduction

Lutjanidae popularly known as snappers comprise a large family of the order Perciformes, important in both tropical and subtropical waters. The family is represented by 4 subfamilies: Lutjaninae, Apsilinae, Etelinae and Paradicichthyinae. The first is the largest subfamily grouped into 6 genera: *Lutjanus*, *Macolor*, *Pinjalo*, *Hoplopagrus*, *Ocyurus* and *Rhomboplites*. Within the family, *Lutjanus* represents, by far, the most widespread genus and abundant, with at least 70 species in the Atlantic, Pacific and Indian Oceans (Allen, 1985; Martinez-Andrade, 2003). Generally, the characteristic life-history traits of lutjanids implies low productivity which culminates in a slow rate of population increase and predisposes several species of shallow and deepwater stocks to overfishing with serious consequences for conservation and management (Grandcourt et al., 2006). Typically, most tropical snapper

species spawn year round with spawning peak during moderate warm water temperature (Thresher, 1984), and on the basis of spawning periodicity, two distinct spawning populations are distinguished: a restricted spawning period centered around summer for continental populations and species, and a year-round spawning period with pulses of activity in spring and autumn for insular populations and species (Grimes, 1987).

Gonadosomatic index (I_G) and macroscopic staging have been used with relative success in determining the time of spawning in many snapper species. A five - stage scheme modified from Nikolsky (1963) consisting of: immature, maturing including recovery, ripe, spawning and spent was used to classify gonad development and also determine time of spawning in the vermillion snapper, *Rhomboplites aurorubens* (Manickhand-Heilemann and Phillip, 1996). The Red snapper, *L. campechanus* spawns in June

with less peaks in July and August (Collins et al., 1996). Likely, *L. fulviflamma* in Kenyan inshore waters and South Arabian sea, *L. griseus* and *L. analis* from different locations in Florida waters, Fort Pierce South, Cuba and Puerto Rico also exhibited extended periods indicated by a main peak season and a shorter season, laying eggs in batches (Domeier et al., 1996; Kaunda-Arara and Ntiba, 1997; Grandcourt et al., 2006; Faunce et al., 2008). This spawning strategy was also observed in *L. peru* in Mexico with a main season in August, and a second period during February corresponding with the highest values of the gonadosomatic index (Gallardo-Cabello et al., 2010) and *L. argentiventris* from March to July with a peak in activity during April-June (Garcia-Contreras et al., 2009).

Liver size is related to its lipid content and is indicative of lipid accumulation during favorable environmental conditions and utilization to support gonad development or adverse conditions (Lloret and Planes, 2003). The hepatosomatic index (I_H) is used as an indicator of the reproductive period and is related to the relocation of energy resources from the liver to the vitellogenesis process (Veloso-Junior et al., 2009). In most fish species including *L. guttatus* (Sarabia-Mendez et al., 2010) and *O. chrysurus* (Trejo-Martínez et al., 2011), the I_H has an inverse relationship with the gonadosomatic index when a species has a definite spawning season. This is because the process of gonad development requires energy which is usually drawn from the body reserves or visceral tissues such as the liver (Wootton, 1998; Ekanem et al., 2004). A higher I_G value is an indication of increased reproductive activity; it shows that the gonads are developing and increase feeding activity (Tyler and Dunn,

1976; El Habouz et al., 2011), with lipid content of marine fish increasing during the feeding period and gonad development (Lloret and Planes, 2003). A lower value indicates decreased reproductive activity or the end of the spawning period, and suggests that the fish may decrease its feeding activity during reproduction (Simon et al., 2009).

Size rather than age may be more closely linked with respect to the onset of sexual maturity (Schaefer, 1987; Lowerre-Barbieri, 2009). Functional statistical relationships or fitting of a logistic curve between proportion mature and size and/or age is the traditional method of estimating sexual maturity (Lowerre-Barbieri et al., 2011). In *L. analis* from Florida waters, fifty percent of females achieved sexual maturity at 353 mm TL_{max} and 2.07 years of age (Faunce et al., 2008). The red snapper, *L. campechanus* reaches sexual maturity at approximately two years of age when they are about 26–27 cm in length (Morans, 1988; Phelps et al., 2009; Brule et al., 2010). Grandcourt et al. (2006) estimated the size at first maturity of *Lutjanus fulviflamma* (blackspot snapper) to be 16.7cm and 18.7 cm for males and females respectively, while Pinon et al. (2009) reported 32.60 cm total length at first maturity for the female yellowtail snapper, *L. argentiventris*, from the Southwest Gulf of California. Different studies identified a minimum length of 25.45 cm TL in female *L. peru* as first sexual maturity for female in the state of Michoacan, but in the State of Guerrero, higher values were calculated (Gallardo-Cabello et al., 2010). Sexual maturity of *L. jocu* in the Abrolhos Bank is attained at about 32 cm for females and 34 cm for males (Freitas et al., 2011), similar to conspecifics from the Caribbean. Also, similar values ranging between 29–31.50 cm

were calculated for *L. guttatus* from Mexico and Costa Rica (Sarabia-Mendez et al., 2010). Teixeira et al. (2010) reported minimum maturity length of 28 cm fork length (FL) in females and 35 cm FL in males of *L. analis*, respectively, while in *L. alexandrei*, the size of first sexual maturity was estimated at 17.1 cm standard length (SL) for females and 16.8 cm SL for males (Fernandes et al., 2012).

Along the West African coast in the Gulf of Guinea, four of six naturally occurring Lutjanid species widely distributed between Senegal and the Congo are morphologically distinguished as red snappers. The Gorean snapper, *Lutjanus goreensis* is a red, medium to large and deep-bodied species (over 350 mm TL) (Martinez-Andrade, 2003), common to 50 cm but capable of attaining maximum total length of 80 cm (Allen, 1985) and easily distinguished from co-existing species by a characteristic blue stripe or narrow blue band or row of broken spots below the eye (Fisher et al., 1981; Allen, 1985). The species is a demersal fish of the subthermocline Lutjanid community in the Gulf of Guinea (Longhurst, 1969; Ssentongo et al., 1986). Adults are marine forms inhabiting sandy, rocky or coral areas (Allen, 1985; Newman, 1995) while juveniles are classified as estuarine-dependent (Martinez-Andrade, 2003).

Snappers are among large-sized fish species over-exploited in Nigerian inshore waters (Amiengheme, 1999). Red species of *Lutjanus* are among the most appreciated fish species in regional and international markets due to their excellent flesh quality as food fish (Blaber et al., 2005; Zhang et al., 2006; Fry et al. 2009; Sustainable Fisheries Partnership, 2009). However, there is no major study for *L. goreensis* as substantial gaps exist for both systematic and biological information in

Nigeria and in the Gulf of Guinea. In addition, there is no published data on any aspects of the species' reproductive biology in the entire Gulf of Guinea and little is known of the recruitment and exploitation status. Therefore, based on the general life-history traits of snappers, it may be particularly vulnerable to fishing and in need of information for management. Hence, this study aims to contribute basic knowledge on its reproductive traits like gonadal development, spawning pattern and season, length at first maturity which will be used for fishery management and future artificial reproduction study in the study region.

Materials and Methods

Study Area

The fishing grounds of Lagos coastal waters extend approximately from 6° 24' 54" - 6° 25' 30" N and 3° 23' 06" - 3° 23' 06" E covering the Nigerian – Benin Republic Border in the West and to Lekki in the East. To the North, it is bounded by Five Cowrie Creek and to the South by the vast Atlantic Ocean (Ediang and Ediang, 2013). Prior to promulgation of the 1971 Sea Fisheries Regulations, this area supported almost all of the industrial fishing activities in Nigeria in the 1960's, which led to the collapse of the fishery. The Lagos coast is a narrow coastal shelf which lies between 14,816 km and 27,780 km with a total area of 41,000 km² (Adebisi, 2012). The continental shelf is relatively narrow about 15 km and predominantly soft and muddy (Tobor, 1991). There is a range of clean sand in the turbulent waters behind the Lagos Harbour through a narrow belt of fine sand and clay in the quiet waters offshore (Ugwumba, 1984). Off Lekki, there are rock outcrops and a sunken vessel at 15–20m. Bottom deposits consist primarily

of hard rock substrate (Wilson, 1983). Dead Holocene coral banks interrupt the middle to outer continental shelf East and West of Lagos (Awosika, 1990) and precisely around Longitude 3° 55' 00" E and Latitude 6° 10' 99"N, the largest of the three major submarine canyons (the Avon deep) also interrupts the shelf (Awosika, 2008). Most demersal fish stocks off the Lagos Coast are concentrated in an area of about 1,800 km² which is located between the highwater mark on the shore and lower limit of the thermocline (Ssentongo et al., 1986). Fishing season along the Nigerian coastline is affected by the eastward flowing warm Guinea current; oceanic fronts which alter the characteristics of surface water within a short period (a few days); southwest monsoon, the equatorial undercurrent or south equatorial (Lomonosov current), the Benguela and the Canary currents and possible extension of the coastal upwelling phenomenon to the coastal sector of the Bights of Benin and Biafra (Ssentongo et al., 1986).

Sample and data collection

Samples of *L. goreensis* were purchased fortnightly from commercial catches of licensed trawlers (cod-end with maximum stretch mesh size of 76 mm), and also from artisanal fishermen using hook and line operating in the marine coastal waters of Lagos from December 2008 to December 2010. The fish samples were transported in a cooler packed with ice to the laboratory where they were immediately analyzed fresh or preserved in a deep freezer for examination. Frozen specimens were sufficiently thawed and wiped to remove excess moisture. Samples were measured (total length, TL to the nearest 0.1 cm) using the traditional one-meter fish measuring board, and weighed

(whole body weight, to the nearest 0.1 g) with an electronic balance (Mettler 400 PM). Each fish specimen was cut open and sex noted by visual examination of the gonads. Both gonads and liver were removed from each specimen and their wet weights weighed to the nearest 0.01 g.

Sex Ratio

The proportion of the two sexes relative to one another was used to calculate the sex ratio and also to infer the mating system.

Macroscopic Gonadal Staging

Classification of ovaries and testes on a macroscopic scale of gonadal development was initially accomplished according to colour, texture, vascular irrigation and relative occupation in abdominal cavity. The classification was based on 5 maturity stages: immature, maturing (including recovery), ripening, ripe and spent modified after gonadal staging of the mangrove snapper, *L. argentimaculatus* (Russell et al., 2003); black spot or dory snapper, *L. fulviflamma* (Kaunda-Arara and Ntiba, 1997; Grandcourt et al., 2006). Newer and simplified terminologies for classifying gonad maturity phases adapted after macroscopic criteria (Brown-Peterson et al., 2011) corresponding to developmental stages I-V were incorporated into the study.

Estimation of size at first maturity

This is considered to be the length at onset of its sexual maturity. For this analysis, fish identified by macroscopic gonad stages II-V were used, because females can be considered to be "sexually mature" or reaching maturity from the ovarian stage II onwards or males reach spermatogenesis (stage II) onwards (Núñez and Duponchelle, 2009). The length

at which 50% of fish attain maturity or size at first reproduction (L_{50}) was estimated by plotting the total length against distribution of percentage cumulative frequency of DV/RT (Stage II) and more advanced stages fish in the various size of 2 cm group classes (Russell et al., 2003; Bhendarkar et al., 2013).

Spawning Seasonality and Pattern

The timing and frequency of spawning were established by counting and estimating percentage of the proportion of sexually mature fish in each reproductive phase and also the mean indices: gonadosomatic index (I_G), hepatosomatic index (I_H) and the relative condition factor (K_{rel}) by month against the sample period. Changes in monthly I_H was used as a proxy to study dynamics of lipid reserves accumulation and depletion. Complemented with I_G and K_{rel} , it was used to assess role in gonad maturation.

Gonadosomatic Index (I_G)

Temporal variation in the I_G in all sexually mature specimens was calculated using the formula by Trejo-Martínez et al. (2011):

$$I_G = 100 \cdot Mg \cdot MG^{-1}$$

Where: Mg is the gonad weight and MG is the body weight, both in grams.

Hepatosomatic Index (I_H)

Similarly, temporal variation in the I_H in all sexually mature specimens was calculated using the formula by Trejo-Martínez et al. (2011):

$$I_H = 100 \cdot M_L \cdot MG^{-1},$$

Where: M_L is the liver weight and MG is the body weight.

Relative Condition Factor, K_{rel} for each fish was calculated according to Le Cren's equation (1951):

$$K_{rel} = MG / a TL^b$$

Statistical analyses

Data were analyzed using the IBM SPSS statistical package (Version 20.0) and Microsoft Excel 2007 software. Data were expressed as mean \pm standard error of mean (SE). The sex ratio was tested for any deviation from the expected 1:1 ratio by using Chi Square analysis. A significance level of $p < 0.05$ was considered in the analysis.

Results

Sex Ratio

Sexes were best distinguished by dissection of the gonads. A total of 189 male and 188 female *L. goreensis* were identified and examined. Males ranged in total length and body weight from 21.90 to 56.10 cm TL with a mean of 32.30 cm TL (SE \pm 0.48) and 156.0 to 2975.0 g with a mean of 622.83 g (SE \pm 31.52), respectively. Females ranged in total length and body weight from 22.60 to 47.60 cm TL with a mean of 33.47 cm TL (SE \pm 0.41) and 200.0 to 2000.0 g with a mean of 669.93 g (SE \pm 26.15), respectively. Overall sex ratio of male : female was balanced at 1.01 : 1 (Chi-Square $X^2 = 0.003$, d.f. = 1, $n = 377$, $p > 0.05$) and did not differ significantly from the expected 1:1 ratio.

Macroscopic Gonad Maturity Staging in L. goreensis

In the present study, five stages of gonadal development were identified in male and female *L. goreensis*. The stages ranged from immature (IM); Developing (DV)/Regenerating (RT); Spawning Capable (SC); Actively Spawning (AS) and Regressing (RG). Major macroscopic characteristic features of each reproductive phase of ovaries and testes are shown in Table 1. Fish in all reproductive phases were found occurring throughout

the study period. In both sexes, there was lack of population synchrony in gonadal development, that is, not all the breeders showed the same gonadal stage maturity in a month. IM and DV/RT fish were most predominant. Distinguishing between RT and DV fish was difficult hence their synonymous classification under one phase. Individuals with ripe - running ovaries were not observed

Occurrence of adipose fats was most in IM fish and least in SC specimens. Adipose fats were also distributed among other parts such as the stomach.

Estimation of Size at First Maturity

Based on a 5-stage macroscopic scale, only IM fish were excluded from the estimations of the maturity ogives while other reproductive

TABLE 1
Macroscopic characteristics used to describe the gonadal maturity stages of *L. goreensis* modified after Kaunda-Arara and Ntiba (1997), Russell *et al.* (2003) and Grandcourt *et al.* (2006)

Maturity Stage	New Terminology	Old Terminology	Males	Females
Stage I	Immature (IM): corresponds to a never-spawned fish	Juvenile/immature	Testes appear as two long, thin grayish – white or semi-transparent strings with fats attached to gonads.	Cylindrical, translucent, slightly pink or glassy ovary with a rounded end in appearance. Fats attached to gonads
Stage II	Developing/Regenerating (DV/RG): corresponds to fish going to finalize their maturation by the forthcoming spawning season	Maturing virgin/resting/ recovering spent	Testes showing increase in size from Stage I. Grayish – white, opaque and strap-like with thin lateral edges. No milt is expressed when cut. Fats attached to gonads.	Increased size from Stage I. Ovaries are compact, creamy yellow to light orange, well vascularized with small cream coloured eggs. Fats may be attached to gonads. Ovaries of recovering spent individuals are soft, flattened and flabby to touch.
Stage III	Spawning capable (SC): SC fish are developmentally and physiologically able to spawn	Mature/ ripening	Creamy or white testes with wave-like lateral edges; milt is expressed when cut but not free flowing.. Little or no fats may be attached to gonads.	Large orange coloured ovaries with dense network of blood capillaries visible internally. Unovulated hyaline (clear) oocytes not free running. Little or no fats may be attached to gonads.
Stage IV	Actively spawning (AS): corresponds on spawning fish	Ripe	Testes are large, white with rounded lateral edges; milt freely flowing when cut.	Ovaries are distended and fill most of the body cavity; Hyaline oocytes free running, expressed when pressed.
Stage V	Regressing (RT): fish in which spawning has ceased	Spent	Testes are flaccid, smaller in size from Stage IV and have a dark brown bruised appearance. A very small amount of residual milt may be present when squeezed.	Ovaries are flaccid, elongated and appear bruised or dark in colour. Few residual eggs may be present.

and very few RG male and female individuals were observed. Paired lobes of the testes and ovaries were symmetrical with adipose fats usually attached in IM to SC fishes.

phases from the second to the fifth were considered. As a result, 119 males and 139 females were considered as sexually mature. The L50 for males and females were roughly

equal. L50 for males was 34.21 cm while that for females was 34.61 cm (Figure 1). Minimum sizes at maturity were 25.30 cm TL and 24.20 cm TL for males and females, respectively (Figure 2). Largest male and female with maturing gonads were 56.10 cm TL and 47.60 cm TL, respectively.

phase, 0.8% in AS phase and 5.9% in the RS phase. Males in SC phase did not occur in June but were most abundant in February (53.8%), April (36.4%), and July to October (33.3 – 66.7%). The only male in the AS phase was present in August (12.5%). With the exception of January, few males (7.1 – 14.3%) in RS

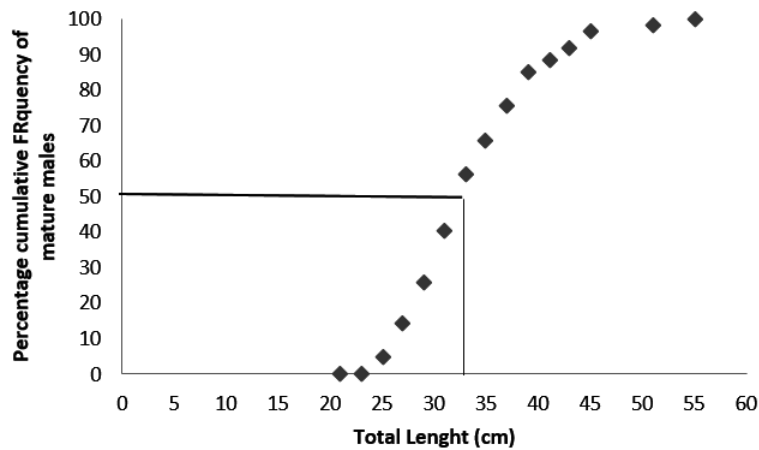


Figure 1 Size at first sexual maturity for 119 male *L. goreensis*

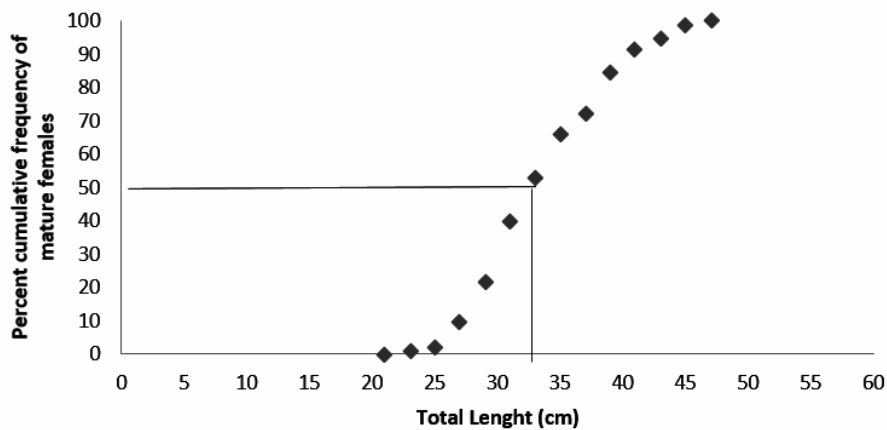


Figure 2 Size at first sexual maturity for 139 female *L. goreensis*

Spawning Seasonality and Pattern in male L. goreensis

During the study period, 119 males were identified as sexually mature. Males in DV/ RG phases were found all year round and consisted 64.7% of the gonads (Figure 3). Advanced gonadal stages in SC to RT phases accounted for the remaining proportion (35.3%) and consisted of 28.6% in the SC

phase were recorded from December to May and also occurred in September (8.3%).

The proportion of mean somatic weight devoted to gonads was low (< 0.5) in all months. The gonadosomatic index (I_G) ranged from 0.04% to 1.87% while mean I_G was 0.21%. There appeared to be a direct relationship between the occurrence of individuals in SC phase and high mean values I_G in February (0.37%), May

(0.25%), July (0.26%) and August (0.27%). Also, there was correlation between mean I_G and mean I_H from February to May, although mean I_H appeared to lag behind those of I_G . In contrast to mean I_G , mean I_H increased at a faster rate from May to August. Highest monthly values of I_H were observed in August (0.95%), January (0.92%) and July (0.91%). Lowest mean values of I_G and I_H were observed from March to April and in November. Though mean I_G values were also low in January and May their mean I_H values were contrastingly high (Figure 4). Mean K_{rel} was dome - shaped, indicating relative stability with marginal increments between January and June. K_{rel} appeared relatively stable between March (1.01%) and May (1.00%). However, it was

lowest in June (0.80%), rose to its peak in July (1.17%), declined in September (0.99%) and maintained a uniform trend till November (1.03%). From December to June, K_{rel} showed inverse relationships with I_H and with also I_G between March and May. However between June and November, it showed a parallel trend with I_G and I_H .

Spawning Seasonality and Pattern in female L. goreensis

A total of 139 females were sexually mature of which approximately 66.9% were in DV / RT phases during the study period (Figure 5). Sexually mature females in the DV or RT phases were most abundant (66.9%) all year round with the highest percentages observed

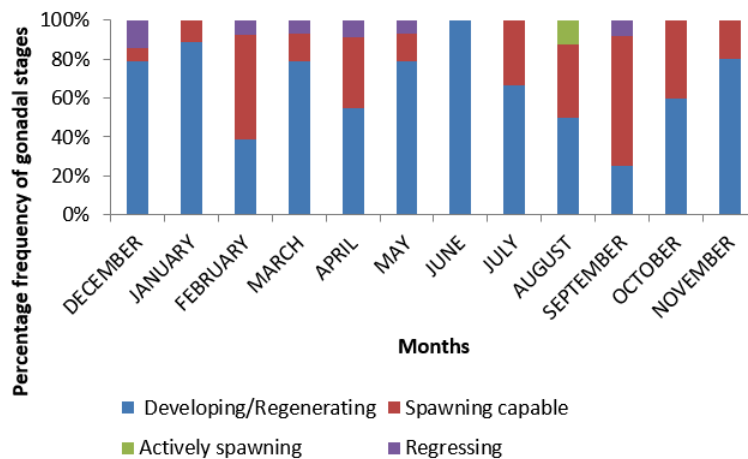


Figure 3 Monthly trend of reproductive phases (macroscopic stages II –V) in 119 male *L.goreensis*

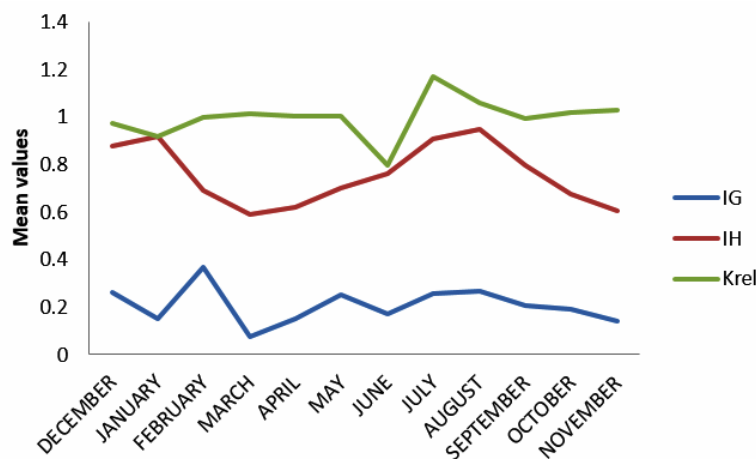


Figure 4 Mean monthly trends in I_G , I_H and K_{rel} in 119 male *L. goreensis*

between January and April. Females in SC to RG phases presented a lower proportion of 33.1% of gonadal stages. Females in SC phase were most abundant in May (33.3%), July (38.5%), August (41.7%), October (50.0%) and November (60.0%). The only four females in AS phase coincided with mean high GSI in December (1.37%), June (1.34%), July (1.00%) and a lower GSI in May (0.85%). Also, very few females in the RG phase were recorded in December (6.2%), January (7.1%), March (6.2%) and August (16.7%).

I_G ranged from 0.04% to 4.42% while mean I_G was 0.96%. Highest individual I_G values were 4.42% in November, 4.15% in June and 4.11% in December. Mean I_G and mean I_H followed similar parallel trend between December and

May. Initially, mean I_G exhibited a slower pace than the corresponding mean I_H (Figure 6). Thereafter, the relationship appeared inverse when mean I_H appeared to lag behind mean I_G till September. Mean I_G peaked in December (1.37%), June (1.34%), August (1.34%), October (1.88%) and November (2.41%). I_H peaked in December (0.95%), July (1.03%) and increased through October (0.97%) to November (0.99%). Lowest mean values of I_G and I_H occurred simultaneously between March (0.56%; 0.73%) and April (0.53%; 0.65%), respectively. Low mean values of I_G were also observed in January (0.59%), February (0.61%) and September (0.74%) while a low mean I_H was recorded in June (0.77%) in contrast to a high mean I_G (1.34%). K_{rel} appeared relatively stable throughout

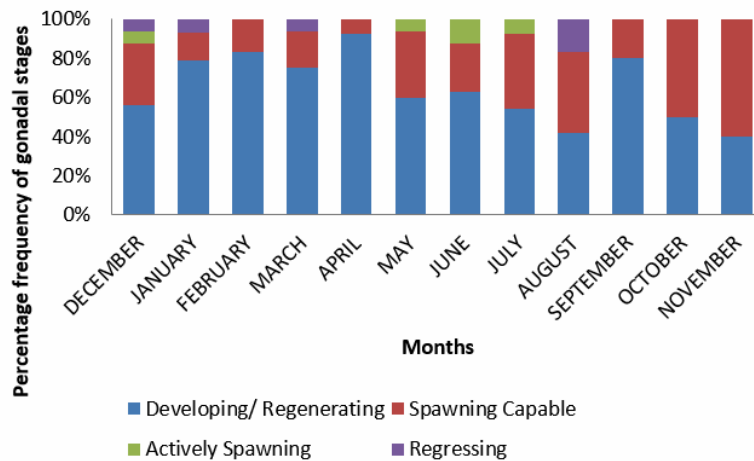


Figure 5 Monthly trend of reproductive phases (macroscopic stages II –V) in 139 female *L.gorensis*

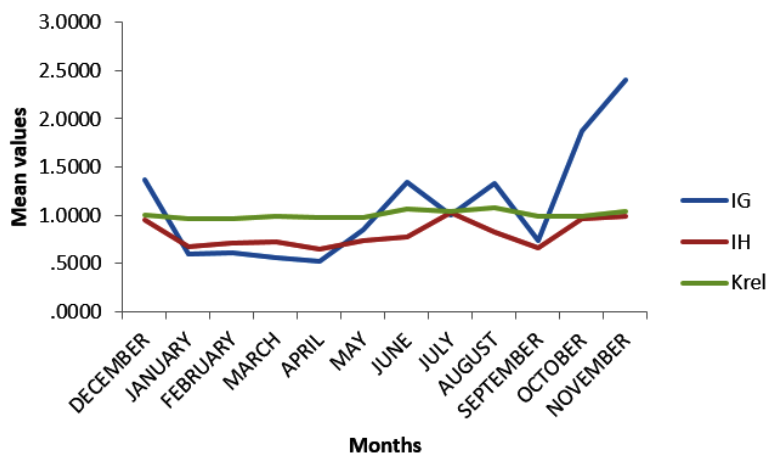


Figure 6: Mean monthly trends in I_G , I_H and K_{rel} in 139 female *L. gorensis*

the period of study showing slight increases which were barely discernible in June and August. With respect to both I_G and I_H , K_{rel} showed similar temporal trend from January to April with I_G and beyond June with I_H .

Discussion

Sexual differentiation, size distribution by sex and sex ratio

In this study, secondary sexual characters which suggest sexual dimorphism and enable identification of sexes were not observed. Hence, sexes were differentiated into males and females by primary sexual characters. Absence of sexual dimorphism is not uncommon in snappers except in 2 species of genus *Pristipomoides* from the Indo-West Pacific (Grimes, 1987). Examination of gonads showed that specimens of *L. goreensis* sampled are sexually dioecious and gonochorists. Gonochorism is a characteristic of snappers (Grimes, 1987) attributed to factors such as similar sizes of sexual maturation of the sexes and absence of individuals undergoing sexual transition (Domeier et al., 1996).

L. goreensis presented a sex ratio which did not differ from unity, meaning that there was no statistical difference in the number of males and females. There are several interpretation for the unity sex ratio observed in the species, which can suggest monogamous mating systems. Secondly, it is the ratio expected for species in the family Lutjanidae (Texeira et al., 2010). Thirdly, a unity sex ratio is associated with gonochorism and also being sexually dioecious (Allen, 1985; Sadovy and Shapiro, 1987; Grandcourt et al., 2006; Trejo-Martínez et al., 2012) and this was proven from examination of the gonads. Fourthly, size distributions coupled with sex ratios in

snappers convey different interpretations of mating systems and also could provide anecdotal evidence of spawning aggregations offshore. Thus, on the basis of maximum size compositions of many species in sub-family Lutjaninae, the Gorean snapper can be classified as a medium to large snapper with maximum total lengths (TL) of 35.0 cm. Size distribution data from the present study showed that approximately 31.6% of the specimens were above 35 cm TL. Furthermore, in the Gulf of Guinea, this species is common to 50 cm TL and is capable of attaining a size of 80 cm (Allen, 1985). Therefore, the sex ratio observed in the Gorean snapper is indicative of such monogamous pairing systems. Fernandes et al. (2012) reported paired sex ratios in large lutjanids as suggestive of such monogamy systems.

Although there has been no published report of spawning aggregation in *L. goreensis*, the paired sex ratio presented in this study is a strong indication of spawning aggregation. To buttress this hypothesis, Martínez-Andrade (2003) posited that large lutjanids migrate offshore during the spawning season. Domeier et al. (1996) opined spawning migration of snapper species from inshore to offshore to be a strategy to increase the survival of the offspring. They suggested that spawning migration of snappers to be borne out of the need for more spatial and nutritional resources to survive than smaller fish, in order to overcome the difficulty of finding mates during the spawning season as a result of increased space. Therefore in view of this, large sexually mature *L. goreensis* may aggregate to spawn. Carter and Perrine (1994); Domeier and Colin (1997) also stated paired sex ratio as common in snapper species which spawn in offshore aggregation. Caveriviere (1996)

reported spawning aggregations of 2500 large African red snappers (*L. agennes*), caught accidentally by tuna purse seiners in surface waters off the Guinea Gulf coast on western Africa. The African red snapper is a congeneric or sympatric species to the Gorean snapper, *L. goreensis* in the Gulf of Guinea with striking similarities in common and maximum sizes observed. Therefore, this portends that the two snapper species may also exhibit similar reproductive behaviours inclusive of migration, and also supports the postulation that the Gorean snapper forms spawning aggregations.

Macroscopic Gonadal Staging

Females with small, glassy ovaries and those with slightly bigger, pinkish ovaries were categorized as sexually immature. This is a classic instance of continuous gonadal development and the artificial nature of gonadal staging in fishes (King, 2007). A lack of population synchrony in gonadal development was observed in both sexes. This was also noted in *L. argentiventris* where possibly individuals breed at different times of the year with the consequence of gonads with different macroscopic stages and varied gonad weights which could result in significant differences in the values of gonadosomatic index (Bonilla-Gomez et al., 2013). Trejo-Martínez et al. (2011) also noted that the occurrence of RG/DV fish year - round suggested that females did not mature synchronously. The occurrence of very few female *L. goreensis* in the RS phase were probably because an individual fish would quickly release its eggs in several batches at the end of which the ovary quickly recovers to regenerating stage. According to Macer (1974), spawning process in fish is rapid which can obscure certain maturity stages.

To corroborate this view, Kaunda-Arara and Ntiba (1997) did not find any fish in the RS phase or spent condition in their samples of *L. fulviflamma*.

In this study, the occurrence of adipose fats attached to gonads in the Gorean snapper had been previously reported in *L. campechanus*, *L. argentimaculatus*, *Lutjanus carponotatus*, *L. griseus* and *L. fulviflamma* (Collins et al., 1996; Domeier et al., 1996; Russell et al., 2003; Kritzer, 2004; Kamukuru and Mgaya, 2004). They were also observed attached to the stomachs. Adipose fats in these fishes could imply that they are used for gametogenesis and spawning of sexually mature fish during the spawning season (Domeier et al., 1996; Kamukuru and Mgaya, 2004). Declining amounts of adipose fats noted in specimens of *L. goreensis* from IM to SC phases most probably indicate progressive mobilization of stored energy reserves primarily lipids to support a gradual increase in gonad development and maturation. Therefore, this also suggests that the species relies on stored energy reserves, one of which is the adipose fat to develop gonads.

Estimation of Size at First Maturity

In both sexes, fishes macroscopically classified as DV/RT (developing/ recovering spent), SC (ripening), AS (ripe) and RS (spent) according to schemes of Kaunda-Arara and Ntiba (1997); Russell et al., (2003) and Grandcourt et al., (2006) were treated as sexually mature adults. *L. goreensis* attains a maximum size of 80 cm TL in the Gulf of Guinea (Allen, 1985) while mean sizes at first sexual maturity in the study were estimated at 34.61 TL and 34.21 cm TL for females and males, respectively. Populations and species associated with continents mature at a relatively smaller

size (43% of maximum length) than those associated with islands (51%), while deep-water species and populations mature at a significantly higher percentage of maximum size (49%) than shallow-water species (43%) (Allen, 1985; Martinez-Andrade, 2003; Fernandes et al., 2012). Consequently, this sampled population of *L. goreensis* attained sexual maturity at ~approximately 43% of the reported maximum size. Hence, *L. goreensis* in this study conformed to the sexual maturity pattern observed for populations and species associated with a continental margin and shallow - water, *i.e.* they matured at a smaller size than island populations and deep - water species.

The minimum sizes of mature fish individuals in this study indicated that coastal samples could attain sexual maturity at sizes as low as 25 cm TL. Sexual maturity has been reported to occur from this length in some snapper species such as *L. argentiventris*, *L. griseus*, and *L. apodus* of marine habitats (Aburto-Oropeza et al., 2009; Jaxion-Harm et al., 2012) in contrast to individuals from estuarine environments which are sexually immature and remain as functional juveniles regardless of the size they attain in the estuarine environments (Sheaves, 1995).

Spawning Seasonality

Spawning season in *L. goreensis* was identified by mean I_G and maturity stage or reproductive phase frequencies rather than by mean I_H and mean K_{rel} . The season extended year round with multiple spawning peaks reflected by high mean I_G in December, February, May/June, August/September, October and November. Spawning pattern showed a peak in the early part of the year coinciding with the dry season; in the major rainy season and during the short

August break. Presence of high number of SC males and females for most part of the year indicated possibility of year-round spawning. Fish of both sexes in the AS phases observed in December, May to August/ September suggested that a period of peak spawning took place between May and August.

Tropical species spawn almost continuously because longevity of the reproductive period shortens with increasing latitude (Miller and Kendall 2009). Several previous studies have demonstrated that gonadal development and/or spawning for lutjanid species occurs over a period of several months (Nanami et al., 2010). Over time, reproductive cycles and time of spawning in marine fishes have been studied by macroscoping staging of gonads and the relative size or weight of gonads (King, 2007). In *Rhomboplites aurorubens*, fish with gonads in all reproductive phases or stages of development from mature to spent (*i.e.* SC to RS) throughout the year indicated year-round spawning while increase in frequency of spawning (AS) fish during some months suggested peak period of spawning (Manickhand- Heilemann and Phillip, 1999). This aligns with the view that spawning for some tropical snappers may take year round (Thresher, 1984).

Mean monthly I_G values of 0.5 or more throughout the year suggested that oocytes in ovaries of *L. goreensis* were being continuously recruited in preparation for maturation and spawning. In many asynchronous spawners, the gonadosomatic index of a mature or SC female is not very high because the ovary contains eggs in various states of maturity. Mean I_G values above 0.5 in the red snapper, *L. campechanus* from the Gulf of Mexico corresponded approximately to the onset of vitellogenesis (Fitzhugh et al., 2004). Hence,

the species investigated in this study is indicated to have a protracted spawning season provided the process of oocyte maturation is not interrupted and leads to skipped spawning. In *L. goreensis*, I_G values were low in females and even lower (less than 0.5%) in males. Low I_G of less than 0.5% have been reported in brown meagre male (Grau et al., 2009). Lower I_G values in males suggests that energy invested for gamete production or spermatogenesis is probably less than that invested by females which could be due to physiological and hormone effects on the gonadal development of fish (Abdallah et al., 2013). Similarly, in *L. fulviflamma*, ovaries were heavier than testes in gonad maturity stages II-V or DV to RS phases (Kaunda-Arara and Ntiba, 1997). Mature eggs were found in the ovaries of female red snapper, when I_G was 1 or more in the northern Gulf of Mexico from May to September (Phelps et al., 2009). Similarly in the present study, mean I_G values of 1 or more recorded in December, June, August, October and November indicated that there were mature eggs in the ovaries of the female *L. goreensis* and spawning imminent. Although I_G in December was high, occurrence of higher mean I_G and peaks in I_G in the second half of the year from May- August connotes that a peak breeding season occurs during the heavy rains and possibly better environmental conditions. Between 2008 and 2010, peak precipitation months (>200 mm) for the Lagos Marine Area were between May and October while the peak months for higher values of gonadosomatic index were December and from May to August. The latter months appear to be linked to maximum rainfall and minimum water temperatures during times of increased river flood in the rainy season leading to increased productivity in surface waters supporting

greater food production for early life stages. Monthly variations of gonadosomatic index in Serra Spanish mackerel also showed that peak breeding coincided with rainy season and possibly better environmental conditions (Chellappa et al., 2010). In tropical regions, rainfall plays an important role in determining the reproductive cycles of fishes and collective reproduction occurs during the time when environmental conditions are favorable for the survival of juveniles and when adequate food is available, besides protection from predators (Grimes, 1987). These periods are coincident for some lutjanids that inhabit continental and large islands (Andrade-Rodriguez, 2003). Collins et al. (1996) estimated the peak of gonadosomatic index in red snapper (*L. campechenus*) to be in June with less peaks in July and August. In *L. fulviflamma* from Kenyan inshore marine waters, a prolonged period of weight loss in gonads or decline in gonadosomatic index from a peak in November/December to April/ May, indicated an extended spawning period during which several batches of eggs and sperm were released (Kaunda-Arara and Ntiba, 1997). Grandcourt et al. (2005) estimated a spawning season from highest values of gonadosomatic index for *Lutjanus fulviflamma* in the southern Arabian Gulf to be in May to September while a shorter season from April to July was determined from maturity stage frequencies. In *L. peru*, the main spawning period occurred during August, and a second period during February corresponding with the highest values of the gonadosomatic index (Gallardo-Cabello et al., 2010). Based on gonadosomatic index and the presence of gonad macroscopic stages 3 and 4 females, the reproductive season for *L. argentiventris* spanned March to July with a peak in activity during April-June

(Garcia-Contreras et al., 2009). In *L. griseus*, spawning began in late May and continued into early September (Domeier et al., 1996).

Dynamics of lipid reserve storage and interplay of Hepatosomatic Index (I_H), Gonadosomatic Index (I_G) and Relative Condition Factor (K_{rel}) in gonad maturation.

Liver and muscles are main organs responsible for lipid reserve storage (Abdallah et al., 2013). However in *L. goreensis* lipid reserves were distributed among other parts such as the gonads and stomach besides the liver. Similarly, the occurrence of more than one lipid reservoir was also reported in demersal fishes such as brown meagre, *Sciaena umbra* and the red drum, *Sciaenops ocellatus* (Craig et al., 2000).

I_G and I_H displayed similar temporal trends which were not inversely related and such patterns have been observed in *L. peru* (Gallardo-Cabello et al., 2010) and in *L. argentiventris* (Pinon et al., 2009). The combined increase in K_{rel} , I_H , and I_G from June to August suggested that increased feeding activities could be a major source of energy primarily for testicular maturation during peak spawning period. A positive correlation between I_H and I_G suggest that the liver reserves may not be used in the final maturation stages (Sousa et al., 2003). Decline in K_{rel} , I_H , and I_G from September to November may be interpreted as increased mobilization of energy reserves to testes for maturation during low reproductive activity while feeding activities also supply some of the energy needed for gonad maturation. Concomitant increases in the three indices have been reported in the female sciaenid, *Menticirrhus littoralis* in southern Brazil (Braun and Fontoura, 2004). In female of *L. goreensis*, the interplay of I_H ,

I_G and K_{rel} between January and May can be interpreted as a period of depletion in energy reserves primarily proteins and lipids from the liver towards ovarian growth and maturation. Reproductive activity in females was low between January and April and high between May and August; November/December as indicated by the values of I_G . From June, there was a buildup of energy reserves in the liver which peaked in July followed by mobilization of the reserves to the ovaries for vitellogenesis till September. Vitellogenesis is linked to liver size as the precursors of the yolk are synthesized in the liver (Albieri et al., 2010) and the liver might enlarge during the female reproductive season in response to vitellogenin needs (Plaza et al., 2007). Increase in storage of energy reserve in liver was repeated during another period of high reproductive activity from October to November/December. Fish species differ in their ways of utilizing food reserves in reproduction and generally gonad development in many fish lead to a high drain of energy from other tissues such as the liver in the case of *L. goreensis* in the present study. Similar trends in I_H , and I_G were replaced by a divergence from May to September during which the indices exhibited opposite trends and also a smaller divergence in December. The divergence represents an inverse relationship between the gonadosomatic index and hepatosomatic index suggesting a definite spawning season (Ekanem et al., 2004). Prior to reproduction, increase in liver weight is associated with the synthesis of lipids and proteins necessary for gonad development (Palazón-Fernández, 2007). Inverse relationship between I_H , and I_G was also reported in *Ocyurus chrysurus* (Trejo-Martínez et al., 2011) and in *L. guttatus* (Sarabia-Méndez et al., 2010).

Maintenance of a constantly low K_{rel} during periods of decreased and increased reproductive activity may be explained by the fact that energy reserves are also drawn from fish muscles and there is some level of feeding activity to replenish the energy reserves. In many fish species, minimal values in condition factor during spawning season are interpreted as the result of mobilization of somatic energy reserves needed for reproductive development and energy in spawned fish, influenced by reduced feeding (Zin et al., 2011). Development of gonads limits the size of the digestive tract which in turn limits fish feeding (Valinassab et al., 2011). Therefore, condition of the sexually mature fish might be little influenced by reproductive effort even in the peak of spawning period; on the other hand, there may be little interpretation of K_{rel} on reproduction because sampled fish were at various phases of the reproductive cycle. In both sexes, coincidence of very low mean I_G and I_H from March to April and implied a resting period or period of very low reproduction. A resting period of March - May was also noted in the vermilion snapper, *Rhomboplites aurorubens* in Trinidad and Tobago (Manickchand-Heileman and Phillip, 1999).

Spawning Pattern

The population in this study consisted of a coastal/marine species associated with continental Nigeria. Snapper species exhibit protracted spawning seasons during summer while insular populations tend to reproduce throughout the year (Grandcourt et al., 2006; Fernandes et al., 2012). The spawning season of *L. goreensis* was however longer than the restricted season expected of a continental population of lutjanids and

conformed more to the extended spawning pattern characteristics of insular species and population. Continental populations of *L. campechanus* from Campeche Bank (Brule et al., 2010) and *Ocyurus chrysurus* from Mexico (Trejo-Martínez et al., 2011) also exhibited continuous year-round spawning, typical of insular species and populations. Observations on the protracted spawning pattern throughout the year may be as a consequence of: (i) individuals of both sexes had gonads at different macroscopic stages and varied gonad weights indicating lack of population synchrony in gonadal development during the study period which is suggestive of a multiple spawning species and (ii) longer warmer season in the equatorial region than at higher latitudes. Protracted seasons are typical of tropical regions because of duration of suitable temperatures and food availability for survival of juveniles (Schaefer, 1987). For coastal lutjanids in northeastern of Brazil, all year round warm water and increment in richness from estuaries on food web appeared to account for a long spawning season, like insular populations (Fernandes et al., 2012). The Nigerian coast is basically warm with temperature generally greater than 24°C. Therefore it is not impossible that being in the tropics, the rather long spawning period of *L. goreensis* may be caused by the prevalent warm temperatures of more than 20°C.

L. goreensis showed continuous reproduction throughout the year, particularly at higher intensity during the heavy rains (May to September). The species is a multiple spawner with a protracted spawning season as evinced from asynchronous gonadal development. Findings could imply continuous recruitment into fishery. However to ensure optimal exploitation, minimum capture size has to

be increased above sizes at sexual maturity calculated in this study.

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