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Gonadal development and fecundity of the smooth weakfish *Cynoscion leiarchus* (Teleostei: Perciformes: Sciaenidae) in a tropical Brazilian bay

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ABSTRACT. *Cynoscion leiarchus* (Cuvier, 1830) is a coastal fish species that is widely distributed along the Western Atlantic coast, from Belize to Southern Brazil. In Brazil, *C. leiarchus* It is an important resource for commercial and artisanal fisheries. Our objective was to describe the oogenesis and spermatogenesis stages of the species and to estimate batch size and relative fecundity of a population at a tropical bay in southeastern Brazil. The examined specimens were obtained from artisanal catches that took place from July 2013 to June 2014. A total of 18 individuals (11 females and 7 males) were examined for histological analysis and 20 spawning-capable females were used to estimate fecundity. Five stages of oocyte development (primary growth, pre-vitellogenic, vitellogenic, oocyte maturation and atresia) and four stages of spermatocytes (spermatogonia, spermatocytes, spermatids, spermatozoa) were described in different phases of gonad development (immature, developing, spawning capable and regenerating), suggesting that spawning happens in batches, oocyte development is asynchronic and fecundity is indeterminate. Batch fecundity ranged from 100 × 10^3 to 866 × 10^3 oocytes undergoing final oocyte maturation, and relative fecundity ranged from 232 to 1,225 oocytes, averaging 467 oocytes per gram of ovary-free body weight. Fecundity tended to increase linearly with gonadal weight, total weight, total length, and age, but the highest linear correlation obtained was between fecundity and gonadal weight. This study provides the first information on the gonadal development of *C. leiarchus* from the Brazilian coast and is a baseline to compare with other populations and/or congeneric species.

KEY WORDS. Histology, oocyte, reproductive tactics, Sepetiba Bay.

The assessment of the stages of gonadal development of fish species is an important issue in many studies of fish reproductive biology. Fish exhibit different strategies and tactics that maximize reproductively active offspring in relation to the available energy (Wootton 1984, Roof 1992, Brown-Peterson et al. 2011). These strategies have been assessed based mainly on the knowledge of germ cell lineage development and fecundity, which are essential to understand the maturation process and oocyte recruitment patterns (Murua & Saborido-Rey 2003, Costa et al. 2015). Bioimaging the dynamic processes of germ cell development of fish species is uniquely easy. Oogenesis is a very dynamic process in the ovaries. During it, the oocyte passes through various phases of development that are very similar among different fish species (Selman & Wallace 1989). For instance, staging based on the external appearance of the ovary is the simplest and most rapid method to assess the ovarian development phases. Moreover, oocyte size may be used to predict the developmental stage of the embryo when the size ranges of the various stages are known and do not overlap. When they overlap, however, histological techniques are a more accurate method of estimating the developmental stages and phases of the germinative cells.

Fecundity is another important aspect of fish reproductive biology (Lowerre-Barbieri 2009). Knowledge of the fecundity of a species is important to fish stock management. It is used to calculate the reproductive potential of a stock, and enhances our ability to estimate recruitment. For this reason, information on fecundity is very important for estimating individual reproductive potential, evaluating the productivity of the population, and characterizing specific populations (Lambert et al. 2003, Armstrong & Witthames 2012, Costa et al. 2016). Therefore, to understand the reproductive strategies in fishes, it is important to understand oocyte development, ovarian organization, and fecundity (Murua & Saborido-Rey 2003, Costa et al. 2015).

The smooth weakfish *Cynoscion leiarchus* (Cuvier, 1830) is a coastal fish species distributed along the Western Atlantic coast, from Belize to Southern Brazil. This species is usually found on mud and sand bottoms in estuarine areas, and along the coastline down to about 60 m depth (Menezes & Figueiredo 1980). It is an important resource for commercial and artisanal fisheries in Brazil. Records of catches of this fish are available between 2008 to 2010, of 910, 1003 and 948 t year^{-1}, respectively (MPA 2012). In the Southeast region, for example, the total landings of this species in 2006 were 325.5 t, of which approximately 38% were in the state of Rio de Janeiro (IBAMA 2008). In the Sepetiba Bay (22°54'-23°04'S, 43°34', 44°10'W), a 450 km^2 embayment in the Southeastern coast of Rio de Janeiro, this species ranks among the most abundant fish species, occurring mainly in the outer bay zone (Araújo et al. 2006) that has predominantly polyhaline waters (salinity average = 30), and mean temperature ranging between 21.5°C (winter) and 27°C (summer) (Araújo et al. 2002). Despite the wide geographical distribution and commercial value of *C. leiarchus*, information on the reproductive biology of the species is still lacking.

The reproductive strategies and tactics of other species of *Cynoscion* along the Atlantic coast of the United States, Gulf of Mexico, Mexico and South America have been studied. Such studies reported an extended reproductive season, multiple spawning, asynchronous oocyte development and indeterminate fecundity for *Cynoscion nebulosus* (Cuvier, 1830) in southern Texas and coast of Mississippi (Brown-Peterson et al. 1988, Brown-Peterson & Warren 2001) and for *Cynoscion othonopterus* (Jordan & Gilbert, 1882) in the Colorado River Delta, Mexico (Gherard et al. 2013). Brown-Peterson et al. (2002), studying *C. nebulosus* in five estuaries from Charlotte Harbor to Redfish Bay, USA, observed subtle but consistent differences in batch fecundity among the estuaries. Taylor & Villoso (1994) described aspects of the daily ovarian cycle and spawning of *Cynoscion regalis* (Bloch & Schneider, 1801) in the Delaware Bay (USA) and found that this species has batch fecundity, with spawning at irregular intervals during the early hours of the evening. In South America, Marcano & Alió (2001) reported a wide range of diameters of mature oocytes, indicating multiple spawning for *Cynoscion jamaicensis* (Vaillant & Bocourt, 1883) in the northern coast of Paria Peninsula, Venezuela. In Brazil, Vieira & Haimovici (1997) studying the oocyte development and batch fecundity of *C. guatucupa* (Cuvier, 1830) (synonymous of *C. striatus*), reported consistent similar reproductive patterns for this species from Southern Brazil to Argentina. Militelli & Macchi (2006) also estimated batch fecundity for *C. guatucupa* in the coastal waters of Argentina-Uruguay.

The objective of this study was to describe for the first time aspects of the reproductive strategy of *C. leiarchus* in the Sepetiba Bay: (i) to describe the stages of development of germinative cells, (ii) to determine oocyte size frequency distribution and (iii) to assess batch fecundity. We expected to find oocytes overlapping in different stages at individual level, suggesting multiple spawning and batch fecundity for this species, a general characteristic within *Cynoscion*. We also compare our results with another species within the family Sciaenidae, to test whether closely related species exhibit similar reproductive strategies to avoid interspecific competition among offspring.

MATERIAL AND METHODS

We collected specimens from artisanal catches from July 2013 to June 2014. The nets were 1,500 m long, 3 m in depth, and had three panels of different mesh sizes (35, 45, and 35 mm adjacent mesh). All fish specimens were stored in ice and transported to the laboratory, where they were measured (total length) (TL, nearest 1 mm) and weighted (TW, nearest 0.01 g). A ventral incision was made to expose gonads for sex determination and the development stage of the macroscopic gonad. Gonads were removed and weighed while wet (W_G, nearest 0.01 g). Voucher specimens were deposited in the ichthyological collection of the Laboratório de Ecologia de Peixes of the Universidade Federal Rural do Rio de Janeiro under number: LEP-UFRRJ#1600.

A subsample of 18 specimens (11 females and 7 males) was examined for histological analysis. The female subsample ranged from TL 215 to 484 mm, TW 316 to 958 g and W_G 13.20 g to 64.80g. Males ranged from 290 to 493 mm TL, TW 194 to 1269 g and W_G 0.10 to 4.00 g. A portion (<0.05 g) of each ovary and testis were taken from the middle part of the gonad, being weighed to the nearest 0.01 mg and fixed in Bouin's solution for histological study during 12 hours, being then transferred to 70% ethanol for preservation. Afterwards, the gonads were dehydrated and embedded in paraffin wax. Cross-sections, 4-6 µm thick, were made in a rotary microtome (Leica RM 2135, Wetzlar, Germany), stained with haematoxylin eosin (HE) and mounted on glass slides for light microscopy scrutiny (Spector & Goldman 2006). Microphotographs were taken with a MOTICAM 2300 3.0 megapixels camera coupled to an Olympus BX41 microscope.

Identification of the gonadal maturation phases and oocyte development stages were made following the criteria in Brown-Peterson et al. (2011) for histological analyses. Primary growth oocytes were determined based on the occurrence of oogonia, chromatin nucleolar and perinucleolar stages. Accordingly, all vitellogenic oocytes and cortical alveolar oocytes are secondary growth oocytes. Vitellogenesis is normally a long process during which important and visible changes occur within the oocyte: oocyte size increases noticeably, yolk progressively accumulates in the cytoplasm and several cytoplasmatic inclusions appear (vacuoles, yolk globules, etc.). In this study, vitellogenic oocytes are separated into three stages (primary (Vtg1), secondary (Vtg2) and tertiary (Vtg3) based on the diameter of the oocyte, the amount of cytoplasm filled with yolk globules, and appearance of the zona radiata. The Vtg3 oocyte has the necessary receptors for the maturation-inducing hormone and thus is able to progress to oocyte maturation (OM) (Brown-Peterson et al. 2011). Oocyte maturation is divided into four stages based on cytoplasmic and nuclear events, beginning with germinal vesicle migration (GVM) and ending with hydration (Jalaber 2005); ovulation is not considered a part of OM.

For each fish, the diameter of the oocytes and their nucleus were measured to the nearest 0.1µ using the Image J software and the mean diameter of each type of oocyte was then calculated. Measurements were taken on oocytes sectioned through the nucleus. The spermatogenic stages follow those outlined by Grier & Uribe-Aranzábal (2009) and include the stages spermatogonia (Sg), spermatocytes (Sc), spermatids (St), and spermatozoa (Sz), which can be differentiated by a decrease in size and an increase in basophilic staining as development progresses from Sg to Sz.

Batch fecundity was estimated by direct counts of oocytes undergoing OM (> 400 µm) in subsamples of 20 ovaries with intense yellow color in final maturation of the spawning capable phase, and calculated as: $F = N \times W_G \times W_{GS}^{-1}$, where F = fecundity, N = number, W_G = total gonad weight and W_{GS} = gonadal subsample weight. This criteria is in agreement with the statement of Hunter & Macewicz's (1985) that oocytes undergoing final oocyte maturation may be included as hydrated oocytes when hydration occurs very rapidly. Relative fecundity (number of eggs per gram of ovary-free body weight) was calculated to remove the effect of body size. A linear regression analysis was performed to assess relationships between fecundity with total length, total body weight, gonad weight and age. The age data were obtained from Silva (2015), who used otoliths for determining age in this species.

RESULTS

Stages of oocyte development

Primary Growth – PG (Figs. 1-2): Oogonia, chromatin nucleolar and perinucleolar stages are present in the ovary throughout the entire annual cycle, and are referred to as primary growth oocytes (diameter <30 µm). Oocyte diameter averaged 28.14 ± 0.50 µm (n = 60) and nucleus 12.64 ± 0.30 µm (n = 60). We observed this stage in in all phases of ovarian development.

Pre-vitellogenic (Figs. 3-4): Cortical alveoli formation: oocytes in different stages of development. Small vesicles and alveoli appear in the periphery of the cytoplasm. Mean diameter of oocyte 55.38 ± 2.85µm (n = 60) and nucleus 15.92 ± 1.43 µm (n = 60). Zona radiata visible, although not yet stained by eosin. Accumulation of lipid inclusions in cytoplasm has begun. Cortical alveoli were observed in in developing and spawning capable phases.

Vitellogenic (Fig. 3-4): Primary vitellogenic (Vtg1). In early stage, yolk granules small and numerous, also called yolk spheres or yolk globules, containing cortical alveoli, occupying the entire cytoplasm. Mean oocyte diameter 76.07 ± 5.52 µm (n = 60) and nucleus 24.79 ± 1.99 µm (n = 60); secondary vitellogenic (Vtg2). Cortical alveoli increase in size and gravitate towards the periphery as the yolk granules grow. Follicular layer and zona radiata are visible, with the latter being dyed with eosin. Mean oocyte diameter 164.60 ± 6.09 µm (n = 60) and nucleus 54.07 ± 3.40 µm (n = 60); Tertiary vitellogenic (Vtg3). Lipid inclusions dispersed in the cytoplasm. Mean oocyte diameter 293.03 ± 10.23 µm (n = 60) and nucleus 69.40 ± 3.36 µm (n = 60). Primary and secondary vitellogenic oocytes were present in the developing ovarian phase and all stages of vitellogenic are present in spawning capable ovarian phase.

Oocyte maturation (Fig. 4): Oocytes in early and late stages were observed. The following characteristics of oocyte maturation (OM) were noted: germinal vesicle migration (GMV), germinal vesicle breakdown (GVDB), yolk coalescence or clarification (Jalabert 2005). Early OM included GVM, but little yolk coalescence. Late OM was characterized by completed GVM or GVBD, yolk coalescence. Mean oocyte diameter 397.61 ± 7.13. Oocytes in final maturation stage represent the actively spawning subphase of the spawning capable ovarian phase.

Atresia (Fig. 2-3): Atretic oocytes were detected and characterized by disintegration of the nucleus and evident irregular shape as into alpha stage. The cells of the granular layer migrate to the interior of the ooplasm, absorbing the yolk; at the end of this stage the zona radiata disappears. Although thus stage could occur in any phase, except immature and actively spawning sub-phase, we only observed atresia stage in regenerating and spawning capable phases.

Stages of spermatocytes development

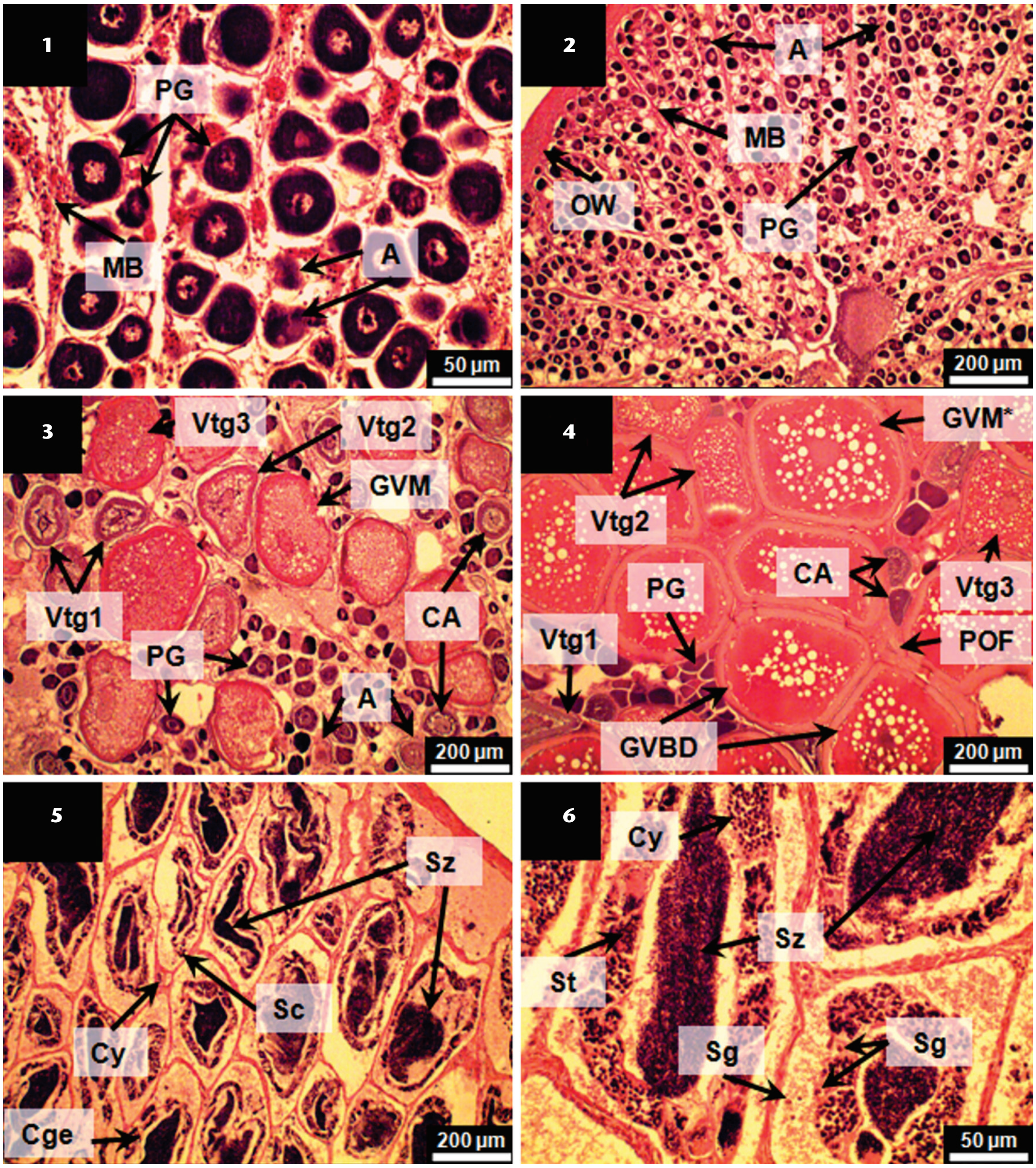
The spermatogenic cells appear in the interior of lobules at different stages during spermatogenesis (spermatogonia (Sg), spermatocytes (Sc), spermatids (St) and spermatozoa (Sz)), forming cysts (Cy). Each cyst is bound by a layer of connective tissue and contains cells at the same stage of development. In spawning capable testes, the lobules are filled with spermatozoa, continuo germinal epithelium at testis periphery (Figs. 5-6).

Oocyte size distribution

The size-frequency distribution of oocytes differed for each phase of gonadal maturation (Fig. 7). Oocytes in the reserve stock had diameter <25 µm and were present in large numbers in all maturation phases; the immature phase showed in second class oocytes ranging from 26 to 36µm in diameter. In the developing phase, a continuum oocyte distribution with diameter of oocytes ranging from 20 to 299 µm was observed. The spawning capable showed the same pattern with diameter of oocytes ranging from 250 to 407 µm. The regenerating phase oocyte distribution was similar to the immature phase, with diameter ranging from 20-42 µm.

Fecundity

Batch fecundity ranged from 100×10^3 to 866×10^3 oocytes undergoing OM. The relative fecundity ranged from 232 to 1,225 oocytes, averaging 467 ± 48 oocytes per gram of somatic body weight (ovary-free). We counted approximately



Figures 1-6. Photomicrographs of ovarian (1-4) and testicular (5-6) histology illustrating oocytes and spermatocytes at different development stages of *C. leiarchus*: (1-2) regenerating ovarian phase; (3) spawning capable ovarian phase; (4) actively spawning subphase; (5-6) spawning capable testis phase. (PG) Primary growth, (MB) muscle bundle, (CA) cortical alveolar, (OW) ovarian wall, (Vtg1) primary vitellogenic, (Vtg2) secondary vitellogenic, (Vtg3) tertiary vitellogenic, (A) atresia POF: postovulatory follicle complex, (GVM) germinal vesicula migration, (GVBD) germinal vesicular breackdown, (Sg1) primary spermatogonia, (Sz) spermatozoa, (Cy) spermatocyst.

220 oocytes for each of the 20 examined females, with a total of 4,500 measured oocytes. Fecundity tended to increase linearly with gonad mass, total mass, total length, and age ($p < 0.05$) with the highest linear correlation ($r = 0.82$) obtained between the gonad weight and fecundity (Fig. 8-11).

DISCUSSION

Histological analyses allowed the detection and description of changes in five oogenesis and four spermatogenesis stages of *Cynoscion leiarchus* from Sepetiba Bay. This species seems to

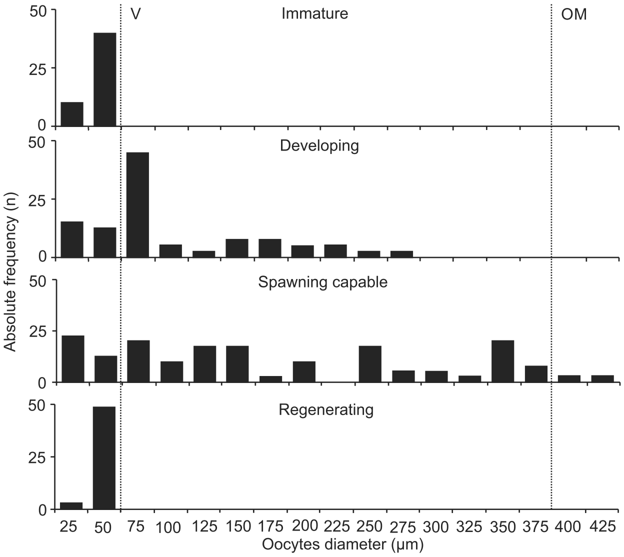


Figure 7. Oocyte size-frequency distribution through subsequent phases of gonad development of *Cynoscion leiarchus*. Dashed line (V) indicate early vitellogenesis and (OM) indicate early oocyte maturation.

spawn in batches, with asynchronic oocyte development and indeterminate fecundity, suggesting a long spawning season. According to Winemiller & Layman (2005), this type of behavior may be considered an adaptive response to environmental variations. This involves allocation of energy for different stages of life in order to ensure the survival of recruits and juveniles, as a result of a large investment of the parents to produce a high number of offspring at each reproductive cycle (Pianka 1970), even if each individual has little chance of surviving to adult age.

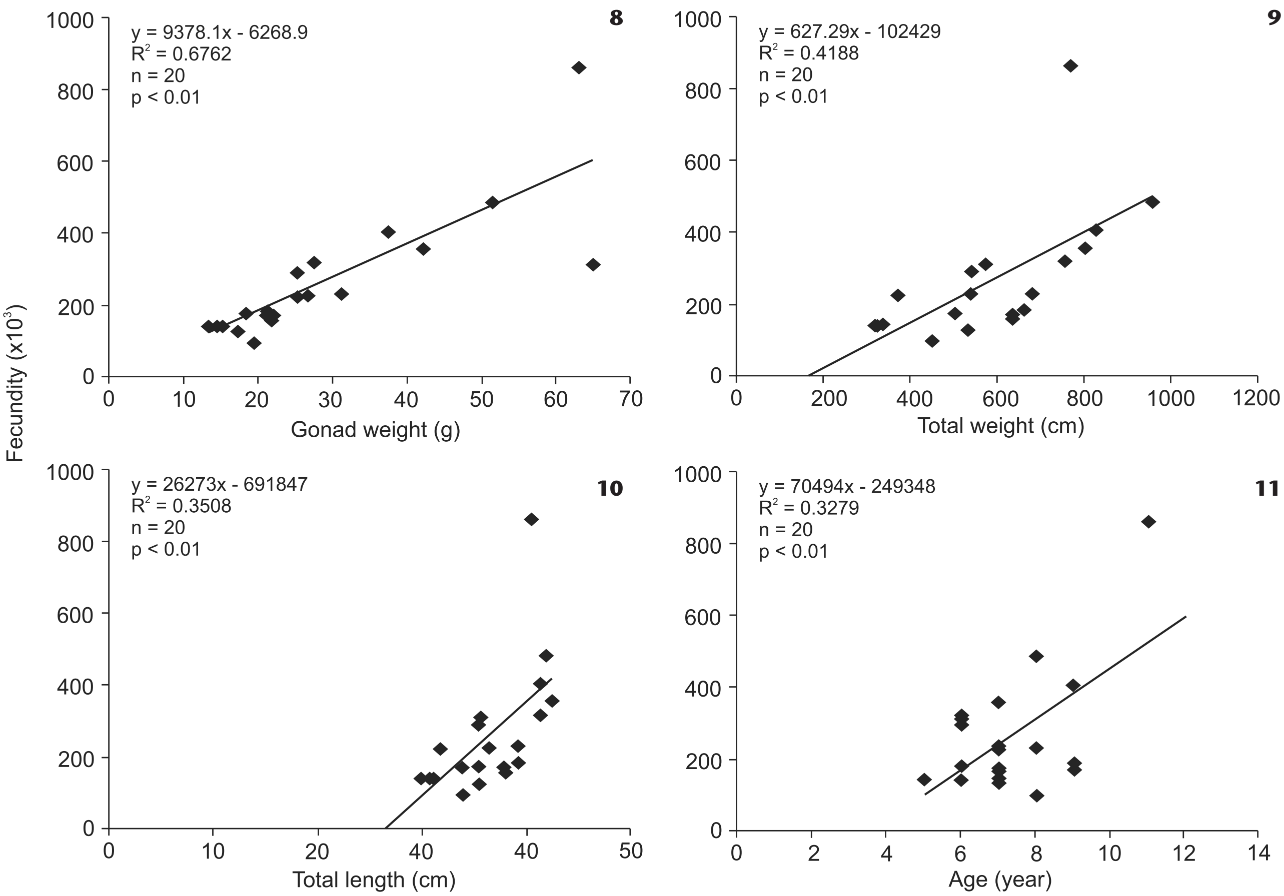
According to Fonteles-Filho (2011), batch spawning is common in tropical areas, and reflects adaptation to environmental constraints to optimize release of gametes in a synchronized process related with food availability for larvae and post larvae. This ensures a greater survival of the offspring. This reproductive pattern was also observed in other species of *Cynoscion*, for instance *C. nebulosus* from the Golf coast of Mississipi (Brown-Peterson & Warren 2001) and from the South Carolina (Roumillat & Brouwer 2004), *C. othonopterus* from the California Gulf (Gherard et al. 2013), *C. jamaicensis* from Venezuela coast (Marcano & Alió 2001), *C. guatucupa* from Southern Brazil (Vieira & Haimovici 1997) and Argentinian-Uruguaian coast (Militelli & Macchi 2006), thus confirming that batch spawning and indeterminate fecundity are common strategies in *Cynoscion*. These reproductive traits were also observed in other Sciaenidae species, for instance *Macrodon ancylodon* (Bloch & Schneider, 1801) (Juras & Yamaguti 1989), *Menticirrhus americanus* (Linnaeus, 1758) (Chaves 1989), *Isopisthus parvipinnis* (Cuvier, 1830) (Chaves 1989), *Stellifer rastrifer* (Jordan, 1889) (Chaves & Vendel 1997), *Paralonchurus brasiliensis* (Steindachner, 1875) (Costa et al. 2015). Thus, these patterns confirm that closely related species develop strategies to avoid interespecific competition for limited resources and to overcome environmental constrains (Wootton 1992, Amarasekare 2003). For instance, timing segregation in reproduction will enable offspring to maximize the use of the available resources, facilitating survival and reproductive success. We therefore consider that this trait is common to the entire family.

The analysis of oocyte size-frequency distributions in the developing and spawning capable phases reveals continuous oocyte recruitment into vitellogenesis. Batch spawners with these features exhibit asynchronous oocyte development and indeterminate fecundity, characterized by the presence of oocytes in several developmental stages in the ovary during the developing phase Brown-Peterson et al. (2011) and by the permanence of this oocyte recruitment during the spawning season, making it impossible to estimate fecundity with precision (Wallace & Selman 1981, Hunter et al. 1992, Gordo et al. 2008). Therefore, this pattern corroborates *C. leiarchus* as a batch spawner with asynchonic oocyte development and indeterminate fecundity. Furthermore, batch-spawning species with indeterminate fecundity will have different oocyte developmental patterns depending on how quickly the oocytes are recruited to various stages of vitellogenesis, which drives how asynchronous the oocyte pattern appears (Lowerre-Barbieri et al. 2011).

Despite the absence of hydrated oocytes, the presence of POFs represents a subsequent phase. According to Brown-Peterson et al. (2011), in warm-water batch spawners with indeterminate fecundity, oocytes in a batch normally undergo rapid OM and are released in a single spawning event. This author also reported that the late OM of *C. nebulosus* occurred within 10 hours in the natural environment in South Texas (Brown-Petersen et al. 1988). Taylor & Villoso (1994) also described that *C. regalis* oocytes undergo late OM during the day with ovulation probably occurring between late afternoon and early evening. Therefore, the absence of hydrated oocytes could be circumstantial, and allows us to suppose that the oocytes of *C. leiarchus* undergo rapid OM and hydration, as other species of *Cynoscion*.

The presence of postovulatory follicles has been reported as evidence of recent spawning (Vazzoler 1996, Dias et al. 1998, Maddock & Burton 1999) since they remain in the ovary for less than 24 hours (Wilson & Neiland 1994, Lowerre-Barbieri et al. 2011). Our records on postovulatory follicles in this study suggest that the Sepetiba Bay might be used as reproductive grounds by at least part of the population of *C. leiarchus*. Furthermore, the occurrence of young-of-the-year of this species in great numbers at the nearshore waters of the bay was reported by Pessanha & Araújo (2003) and Pereira et al. (2015). However, more studies are necessary to confirm this hypothesis.

Our findings indicate that *C. leiarchus* has higher relative fecundity than reported for *C. guatucupa* (292-649 oocytes × gram^{-1}) from the coast off the estuary of Rio da Prata (Cassia 1986), but lower than populations off the coast of the state of Rio Grande do Sul (1,220-1,251 oocytes × gram^{-1}, Vieira & Haimovici



Figures 8-11. Relationship between batch fecundity and gonad weight (8), total weight (9), total length (10), and age (11) of *Cynoscion leiarchus* in Sepetiba Bay.

1997), results which are based on late oocyte maturation. This suggests that changes in fecundity are associated with different areas of the Argentinian-Uruguaian and Southern-Southeastern Brazilian coast and that this pattern in not consistent, as reported by Vieira & Haimovici (1997). According to Brown-Peterson & Warren (2001), such changes are expected and are likely associated with differential environmental conditions or/and food availability.

In this study, gonadal weight was the best predictor of fecundity, compared with total length, body weight and age. This relationship is dependent of condition, in terms of absolute and relative body mass (Murua et al. 2003). Moreover, the direct relationship between length/age and fecundity suggests that older individuals are more fertile. Nevertheless, fecundity in teleosts could be affected by food availability, female condition, size and environmental conditions (Murua & Motos 2006, Dominguez-Petit & Saborido-Rey 2010). Thus, for a given size, females in better condition exhibit higher fecundity (Kjesbu et al. 1991), indicating that size and condition are the key parameters to properly assess fecundity at the population level.

This study provides the first information on the gonadal development of *C. leiarchus* form the southeastern Brazilian bay. Similarly to other species from the Sciaenidae family, we confirm that the reproductive strategy is characterized by batch spawning, wide reproductive season and indeterminate fecundity. We believe that our findings contribute to clear and update the knowledge of gonadal development patterns and to provide a baseline for comparisons with other South American species of *Cynoscion*. As no information on these biological aspects currently exists in FishBase, the present results may also contribute to this database.

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