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Full length Research Paper

Reproductive biology of the wahoo, *Acanthocybium solandri* (Teleostei: Scombridae) in the Saint Peter and Saint Paul Archipelago, Brazil

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The wahoo, *Acanthocybium solandri,* a cosmopolitan species distributed in tropical and subtropical waters of the Atlantic Ocean, is often caught by commercial fishing vessels in the vicinity of the Saint Peter and Saint Paul Archipelago (SPSPA) (Brazil). The aim of the present study was to investigate the reproductive biology of wahoo caught around the SPSPA, between July 1998 and June 2006. During this period, a total of 1,500 specimens were measured and 1,162 were sexed (610 males and 552 females), among which 774 had their gonads collected and fixed in a 10% formaldehyde solution. Fork length of the sampled specimens ranged from 63 cm to 197 cm. The results suggest that the peak of reproductive activity in the area occurs in April-May. Size at first maturity was estimated at 110 cm FL for females and 102 cm FL for males. The estimated batch fecundity was equal to 1,317.235 oocytes, ranging from 287,040 to 2,494.512. Spawning seems to be multiple and protracted throughout several months between February and September, with a clear seasonal reproduction cycle.

Key words: Perciformes, reproduction, GSI, fecundity, Oceanic Island.

INTRODUCTION

The wahoo, *Acanthocybium solandri* (Curvier, 1831), a member of the family Scombridae (Collette, 1999; Collette et al., 2001), is a pelagic and oceanic species, with a highly migratory behavior, distributed in tropical and subtropical waters of the Atlantic, Pacific and Indian Oceans, including the Caribbean and the Mediterranean Seas (Hogarth 1976; Collette and Nauen, 1983; Garber, 2005; McBride et al., 2008; Theisen et al., 2008). The species occurs only seasonally in temperate waters of the North Atlantic (Hogarth, 1976), but is present throughout the year in the Caribbean and in the Gulf of Mexico, although its abundant fishes exhibit seasonal patterns in different locations (Oxenford et al*.,* 2003). Fisheries targeting wahoo are increasingly common worldwide, enhancing the need for more accurate data on its biological aspects (Brown-Peterson et al., 2000; Oxenford et al., 2003; McBride et al., 2008).

The wahoo is one of the most important species caught in tropical oceans, being fished both directly as well as a by-catch in tuna longline and purse seine fisheries (Oxenford et al., 2003; Viana, et al., 2008). In Brazil, the species occur along the entire coast, being caught often by the artisanal fleet in the northeastern region, particularly around seamounts and oceanic islands, including Fernando de Noronha and the Saint Peter and

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Saint Paul Archipelago (SPSPA) (Campos et al., 2009) where, the species accounted for approximately 20% of the total number of fish caught during the last decade (Viana et al., 2008).

A considerable amount of information is already available on wahoo life history, reproduction, genetics, age and growth, fishery, depth distribution and population characteristics, from different regions of the world (Rathjen and Squire, 1960; Hogarth, 1976; Luckhurst et al., 1997; Murray and Joseph, 1997; Neilson et al., 1999; Brown-Peterson et al., 2000; Luckhurst and Trott, 2000; Franks et al., 2000; Franks et al., 2001; Nash et al., 2002; Oxenford et al., 2003; Garber et al., 2005; Theisen et al., 2008; McBride et al., 2008; Jenkins and McBride, 2009; Sepulveda et al., 2011; Zischke et al., 2012). However, no biological information on this species has been ever reported from the southwestern and equatorial portion of the Atlantic Ocean.

Wahoo is an indeterminate spawner species which exhibits seasonal and extended spawning season, generally associated with increases in water temperature (Jenkins and McBride, 2009; Zischke et al., 2012). Although in tropical regions environmental changes in water temperature is less considerable, and improvement in richness food web is more often related (Pereira et al., 2008). Given the paucity of published data on the life history of wahoo, in the southwestern and equatorial Atlantic, as well as the importance of this species to fishing activities off northeast Brazil, the reproductive biology of the wahoo caught in the vicinity of the Saint Peter and Saint Paul Archipelago was investigated, with a view to providing basic information required to ensure its conservation.

MATERIALS AND METHODS

The Saint Peter and Saint Paul Archipelago (SPSPA), located approximately 1.100 kilometers off the Brazilian coast, just north of the Equator (00º55'N; 29º21'W) and near the mid-Atlantic ridge, is comprised of six larger islands and four smaller ones, with a total emerged area of about 17,000 m^2 (Figure 1). The specimens examined in the present study were caught by commercial fishing vessels operating with multiple trolling gears in the vicinity of the SPSPA, between July 1998 and June 2006. The fork length (FL) of 1500 specimens caught was measured to the nearest centimeter, while the eviscerated weight, in kg, was obtained from a sub-sample of 297 individuals and for all specimens sampled, the weight was estimated by regression analyses ($W={}_aFL^b$). The identification of sex was possible in 1,162 specimens, and gonads were randomly collected from only 774 specimens for development evaluation. Immediately after capture, the fish were eviscerated and the gonads collected and fixed in a 10% formaldehyde solution. In the laboratory, after the weight, length and width of the gonads were measured; the formaldehyde solution was substituted by 70% ethanol for longer term storage of the tissues. The sex ratio was estimated from the total number of females and males caught throughout the sampling period. Statistically significant differences in the sex ratio were tested by the chi-square test ($p<0.05$) (Snedecor and Cochran, 1989).

The gonadosomatic index (GSI) was calculated by the following equation: GSI = (GW/ EW) x 100, where GW is the weight of both gonads (preserved tissues) and EW is the eviscerated weight. Mean monthly GSI were calculated from 159 females and 138 males. Immature specimens were excluded from the analysis, since they had not yet begun their reproductive cycle.

For histological evaluation, a small sample, taken from the mid section of the gonad, was dehydrated, cleaned and embedded in paraffin at 60°C (Behmer et al., 1976). The paraffin blocks were then sectioned to 6 µm, stained with hematoxylin and eosin, and examined under optical microscope. Histological analysis of the ovaries was performed and the maturity phases defined following the modified scale by Brown-Peterson et al. (2011), as follows: immature, developing, spawning capable, actively spawning, regressing and regenerating (Table 1). The classification of the maturity phases of the testes followed Grier and Taylor (1998) and Brown-Peterson et al. (2011), as follows: immature, developing, spawning capable, regressing and regenerating (Table 1).

The size at first sexual maturity (L_{50}) was determined by a logistic curve fitted to the relative frequency of individuals in each length class, according to the formula: Mf = 1 / [1 + exp (a + b * 100 * SL)], where Mf is the fraction of individuals who are able to reproduce (Beverton and Holt, 1956). The maximum likelihood method was employed for the adjustment of the logistic curve and a normal error distribution was assumed. To determine the spawning type, the maximum diameter of all oocytes in one field of view whose nucleus was in the central position was measured for 18 females, 3 for each maturity phase. The oocytes size-frequency distribution was then drawn for each stage in an attempt to determine the spawning behavior, following Marza (1938).

Batch fecundity was estimated following Hunter (1985) and Murua et al., (2003), by the gravimetric method. For this aim, three samples of 0.01 g from 10 females in spawning months were obtained and the hydrated oocytes were counted. Batch fecundity was then calculated as: F= [(Hi/Wi)/n)*GW], where: F= batch fecundity, Hi = number of oocytes from each sample, Wi = weight of each sample, n= number of repetitions (3), GW= weight of each ovary.

RESULTS

The fork length of the 1,500 specimens sampled, regard-

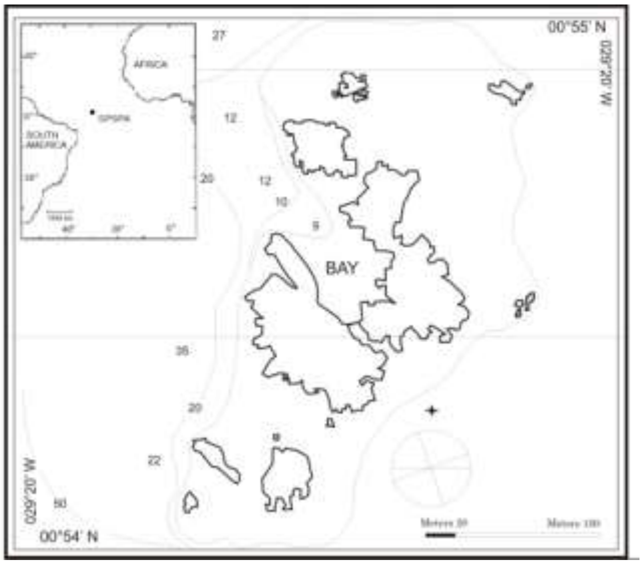

Figure 1. Saint Peter and Saint Paul Archipelago, Brazil, where wahoo samples were collected, from commercial fisheries, between July 1998 and June 2006 (Viana et al., 2012).

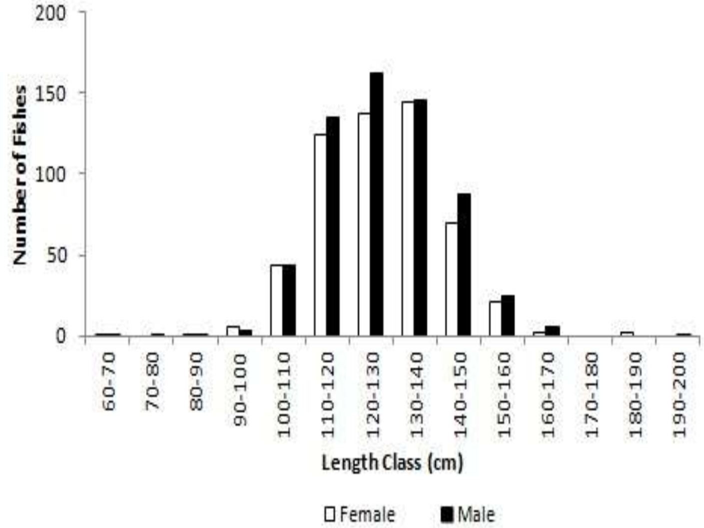

Figure 2. Size distribution of wahoo, *A. solandri*, caught in Saint Peter and Saint Paul Archipelago, Brazil.

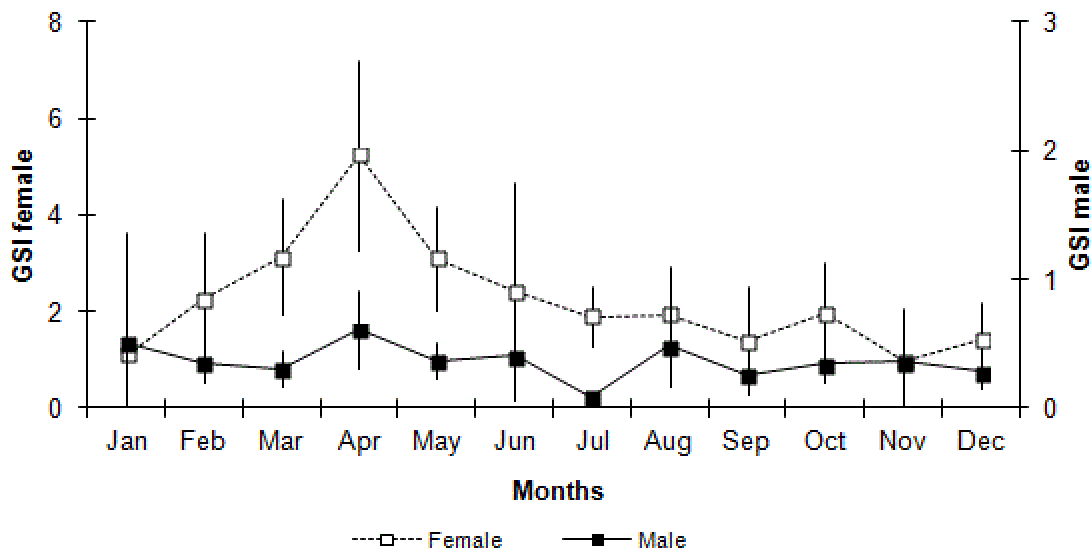

Figure 3. Monthly mean gonadosomatic index of male and female wahoo, *A. solandri*, caught in Saint Peter and Saint Paul Archipelago, Brazil (vertical bars represent the standard deviation).

less of sex, ranged from 63 cm to 197 cm. Fork length ranged from 63 to 183 cm for females and from 67 to 197 cm for males (Figure 2).

Males were significantly more frequent than females in the total sample (χ^2 = 25.15, df= 11, p<0.05), despite a sex ratio close to 1:1 (1.1:1.0/ 610 males= 52.5% and 552 females= 47.5%) (Table 2). Females were more frequent in the months of January, March, August, November and December, while males predominated in all other months. Only in May and June, however, when males were more numerous than females, the difference was statistically significant.

The monthly mean GSI of males was lowest in July (0.08), while for females the lowest value was observed in November (0.95). The highest mean values for females were recorded in April (5.26), and for males in January

Table 1. Microscopic characteristics of maturity phases of ovaries and testis of wahoo, *A. solandri*, caught in St. Peter and St. Paul Archipelago.

Maturity phases	Ovaries microscopic characteristics	Testis microscopic characteristics
Immature	Thin ovarian wall. Only oogonia and primary growth (PG) oocytes present. No atresia (any stage) and no vitellogenic oocytes stages.	Only spermatogonia (Sg1).
Developing	Oogonia, cortical alveolar (CA), primary and secondary vitellogenic oocytes (Vtg1 and Vtg2). No evidence of tertiary vitellogenic oocytes (Vtg3).	Spermatogonia in secondary stage (Sg2), spermatocytes, spermatids and rare spermatozoa.
Spawning capable	All oocyte stages present (from previtellogenic to vitellogenic oocytes), and abundance of tertiary vitellogenic oocytes (Vtg3).	Many spermatozoa in seminiferous tubules. All spermatogenesis stages. When actively spawning, continuous germinal epithelium (GE) in lobules, and discontinuous germinal epithelium (GE) near ducts
Actively spawning	*Imminent spawning* All oocyte stages present. Many oocytes in germinal vesicle migration (GVM), yolk coalescence (YC), and germinal vesicle breakdown (GVBD). Large amount of hydrated oocytes (HO) with few post-ovulatory follicles (POFs), when present. *Recent spawning* All oocyte stages. Generally tertiary vitellogenic oocytes (Vtg3) are abundant. New batch prior to start oocyte maturation. High number of POFs and rare hydrated oocytes. When in high spawning frequency, hydrated oocytes and old POF are simultaneously present.	
Regressing	Few POF, α-atresia and β-atresia in vitellogenic oocytes; some residual oogonia, PG, CA and Vtg1-Vtg2 oocytes.	Residual spermatozoa in sperm ducts. Little spermatocysts and spermatids.
Regenerating	Reorganization of unyolked oocytes to the beginning of a new reproductive cycle. Only oogonia and primary growth oocytes present.	

Table 2. Monthly sex ratio of wahoo specimens captured around the S. Pedro e S. Paulo Archipelago during the period from July 1998 to June 2006.

Months	Female (n)	Male (n)	Total	χ^2
Jan	137	135	272	0,01
Feb	42	47	89	0,14
Mar	44	27	71	2,04
Apr	16	25	41	0,99
May	19	49	68	6,62*
Jun	22	64	86	10,3*
Jul	4	4	8	0
Aug	45	37	82	0,39
Sep	76	80	156	0,05
Oct	43	65	108	2,24
Nov	26	24	50	0,04
Dec	78	53	131	2,39
Total	552	610	1162	25.15*

* Significant difference at a level of 5%; $p < 0.05$.

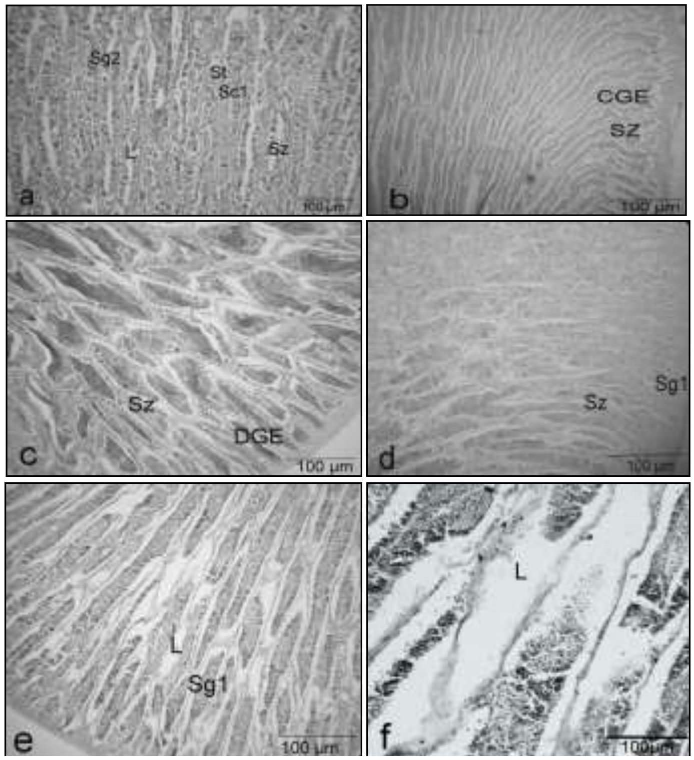

Figure 4. Microscopic photographs of *A. solandri* testis in different maturity phases. A: developing, B: spawning capable (with continuous Germinal Epithelium), C: spawning capable (with discontinuous Germinal Epithelium), D: regressing, E: regenerating, F: regenerating (detail in lumen of lobule fully empty). The spermatogenesis stages: secondary spermatogonia (Sg2), primary spermatocyte (SC1), spermatid (St), spermatozoa (Sz); lúmen of lobule (L). Staining by hematoxilin/eosin. Scale bar = 100 µm.

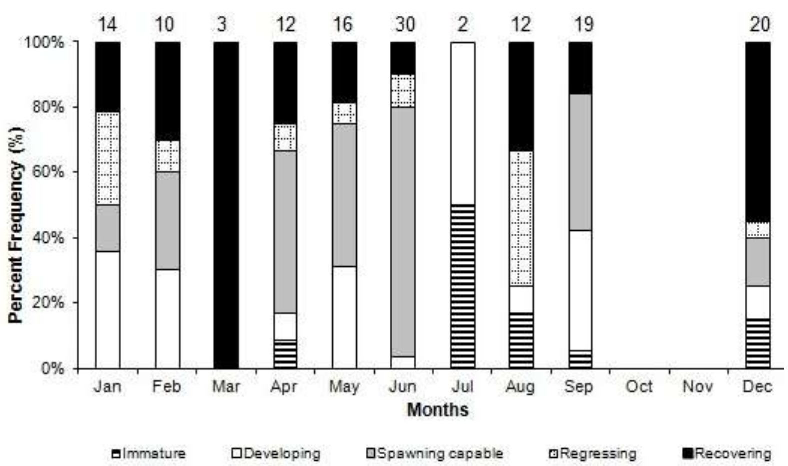

Figure 5. Monthly distribution of maturity phases of male wahoo, *A. solandri*, caught in Saint Peter and Saint Paul Archipelago, Brazil.

(0.59), April (0.61) and August (0.49) (Figure 3). The monthly mean GSI values throughout the year, as well as the results of the histological examination of ovaries, indicate that in the vicinity of SPSPA the spawning season for wahoo spans from February to September, with a peak in April-May.

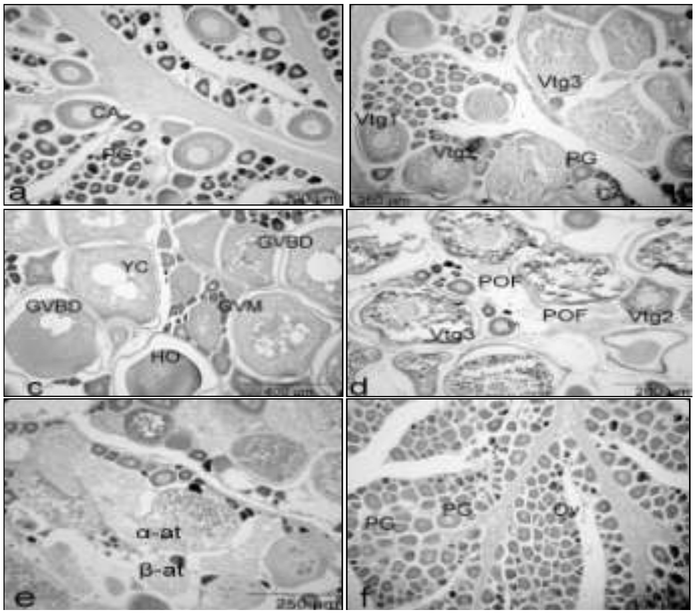

Figure 6. Microscopic photographs of ovaries of wahoo *A. solandri* in different maturity phases. A: developing (Scale bar = 100 µm), B: spawning capable (Scale bar = 250 µm), C: actively spawning (imminent spawning) (Scale bar = 400 µm), D: actively spawning (recent spawning) (Scale bar = 200 µm), E: regressing (Scale bar = 250 µm), F: regenerating (Scale bar = 100 µm). The oocyte stages: Ov (oogonia), PG (primary growth oocyte), primary vitellogenic oocyte (Vtg1), secondary vitellogenic oocyte (Vtg2), tertiary vitellogenic oocyte (Vtg3), germinal vesicle migration (GVM), yolk coalescence (YC), germinal vesicle breakdown (GVBD), hydrated oocyte (HO), post-ovulatory follicle, alpha atresia (α-at) and beta atresia (β-at). Staining by hematoxilin/eosin.

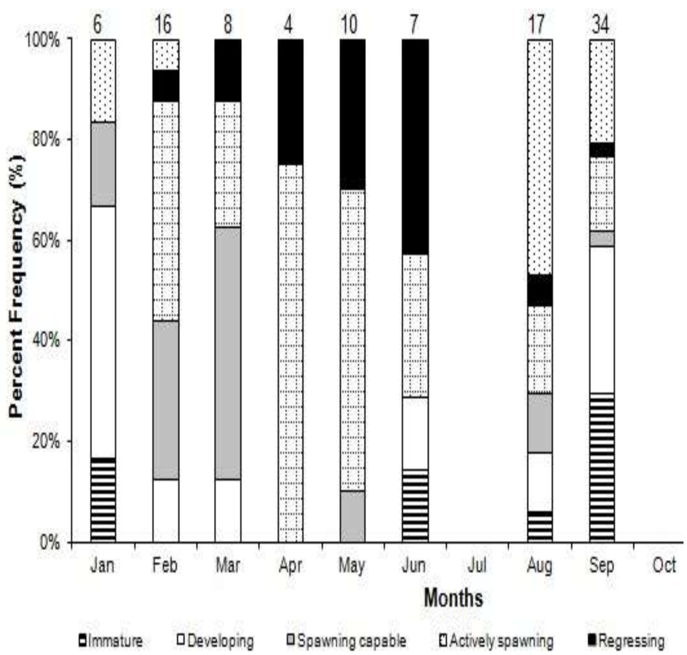

Figure 7. Monthly distribution of maturity phases of female wahoo, *A. solandri*, caught in Saint Peter and Saint Paul Archipelago, Brazil.

Of the 138 histological analyses of the testes, 5.8% of the males were immature (Figure 4a), 18.8% were in developing phase (Figure 4b), 37.7% were spawning capable (Figure 4c), 11.6% were either regressing (Figure 4d) and 26.1% or regenerating (Figure 4e-f). Males were in spawning condition during all year, with more prevalence between April and June. Regenerating males were present in all months, but mainly found between December and March. Immature males were present only in the second semester of the year (Figure 5).

From the 159 histological analyses of the ovaries, 16.4% were immature, 28.3% were in developing phase (Figure 6a), 15.7% were capable of spawning (Figure 6b), 17.6% were actively spawning (Figure 6c-d), 6.9% were regressing (Figure 6e) and 15.1% were recovering (Figure 6f). Spawning capable females were found from February to September, except in July and October, when there were no samples (Figure 7). The peak spawning was observed between April and May when high number of females in actively spawning phase occurred. Regressing females occurred from May to August, and regenerating females were mainly found between August and September. These data seem to confirm a reproductive season for the species in SPSPA between February and September (Figure 7).

For the females, the maximum likelihood adjustment provided the values of 6.839 for the parameter "a" and -0,068 for "b"; whereas, for males the parameters estimations were 28.67 and -0.279 for "a" and "b" respectively. Estimated size at first maturity for males (n= 138) and females (n= 159) was 102 and 110 cm FL, respectively (Figure 8). Among the 610 males examined for sex, just 6.2% (38) had a FL smaller than the size at first maturity, while this percentage was equal to 8.1% (45) for the 552 females. These figures indicate a strong predominance of adult individuals in the population sampled.

The size frequency distribution of oocytes stages showed a mode for all maturity phases at around 17.94 – 787.02 µm. As oocyte development progresses, new modes representing batches of ripening oocytes become visible (Figure 9). This pattern of ovarian development indicates that oocyte growth is asynchronous, with the oocytes ripening in a series of subsequent batches. The oocytes that compose each of these batches develop asynchronously and, as they reach full maturity, are released, characterizing a multiple spawning. The batch fecundity estimated from a sample of 10 ripe gonads ranged from 287,040 oocytes, in a female with a fork length of 121 cm and gonads weighing 130 g, to 2,494.512 oocytes, in a specimen with a fork length of 150 cm and gonads weighing 612 g. Mean relative fecundity was 1,317.235 oocytes and 1,246.591 oocytes/g

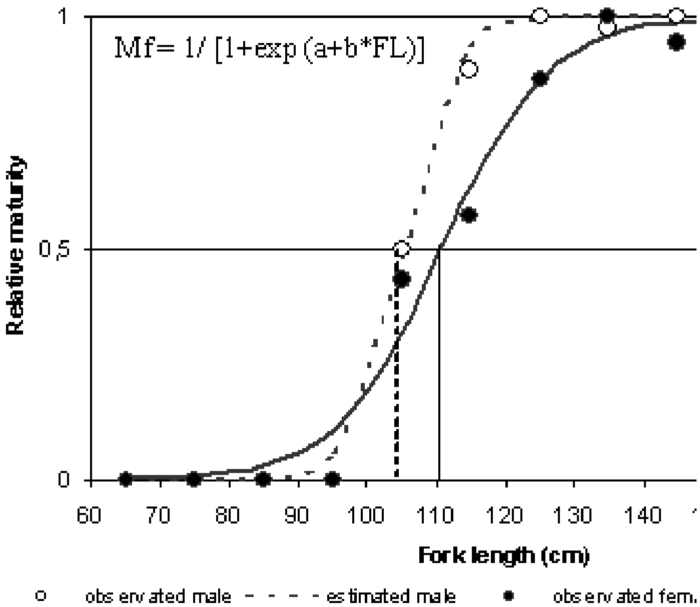

Figure 8. Maturation curve of male and female wahoo, *A. solandri*, caught in Saint Peter and Saint Paul Archipelago, Brazil.

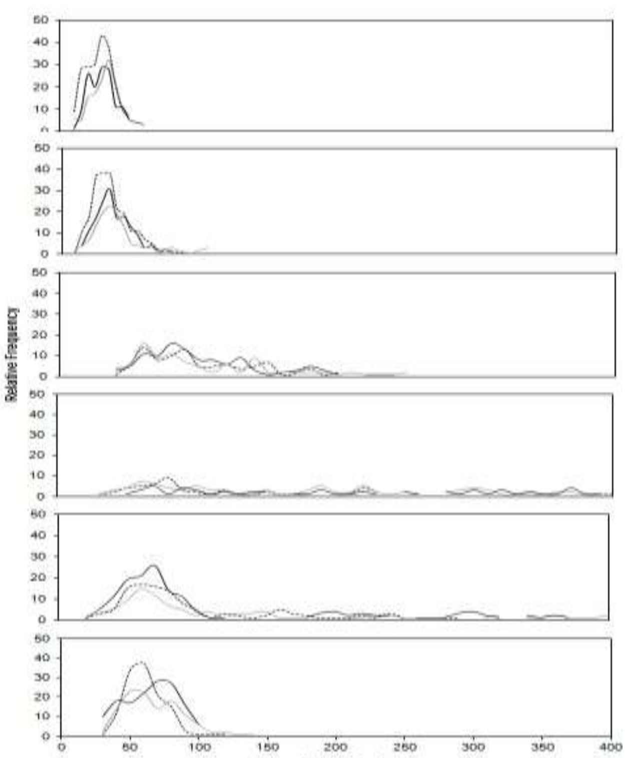

Figure 9. Frequency distribution of oocyte size by female maturity phase determined histologically, from wahoo, *A. solandri*, caught in Saint Peter and Saint Paul Archipelago, Brazil. Each line represents one female.

ovary (Figure 10).

DISCUSSION

Although the FL frequency distribution of the wahoo caught in the vicinity of the SPSPA (ranging from 63 to 197 cm, with a mode in 110-140 cm FL) may not express the actual size structure of the population, due to spatial segregation and selectivity of the fishing gear, the small number of juveniles sampled (about 14.3%) clearly indicates that the fishing effort is directed at adult specimens, which is a positive factor for the sustainability of the fishery. Many studies have reported a majority of adult individuals in wahoo samples due to fishing selectivity, especially from surface fishing gears as longline and purse-seine (Franks et al., 2007; McBride et al., 2008; Jenkins and McBried, 2009; Zischke et al., 2012).

Size and sex composition for wahoo in SPSPA differ slightly from other studies (Brown-Peterson et al., 2000; Oxenford et al*.,* 2003; Jenkins and McBride, 2009; Zischke et al., 2012), showing a reduced abundance of males in larger size classes (>170 cm FL). This should be, however, expected since female wahoo tend to grow larger and slower than males (McBride et al., 2008). The sex ratio observed in the present study, very close to 1:1, was also different from the predominance of females (1.4:1.0) encountered by Brown-Peterson et al*.* (2000), in the Gulf of Mexico and the Bahamas, or from Hogarth (1976) , who found an even stronger predominance of females (3:1) off North Carolina (USA). One possible reason for a sex ratio much closer to 1:1 found in the present study could be the fact that the concentration of wahoo around the SPSPA is probably the result of a reproductive aggregation (Batalyants, 1989; Koido and Suzuki, 1989 *apud* Boehlert and Mundy, 1994), and thus a sexual proportion close to parity might increase the chances of fertilizing the oocytes.

Wahoo showed a protracted spawning season in Saint Peter and Saint Paul Archipelago, spanning between February and September, with a peak between April and May, a spawning behavior that resembles most of those described in the literature, from other regions (Brown-Peterson et al., 2000; Oxenford et al*.,* 2003; Jenkins and McBride, 2009; Zischke et al., 2012).

The wahoo has a relatively low GSI, which is a common characteristic of large and medium-sized pelagic oceanic fish (Oxenford et al*.,* 2003). In the Gulf of Mexico, the maximum GSI found for wahoo was 9.5 for a female caught in June, whereas GSI values rarely surpassed 1.0 for males (Brown-Peterson et al*.*, 2000). In Bermuda, the maximum GSI recorded for a female was 5.8, from a specimen weighing 24.9 kg, caught in July (Oxenford et al*.*, 2003), which is close to the maximum GSI value recorded for a female in the present case (= 5.3).

Seasonal marked differences in GSI between males and females found in this study were not different from expected, considering multiple spawning behavior for ma-

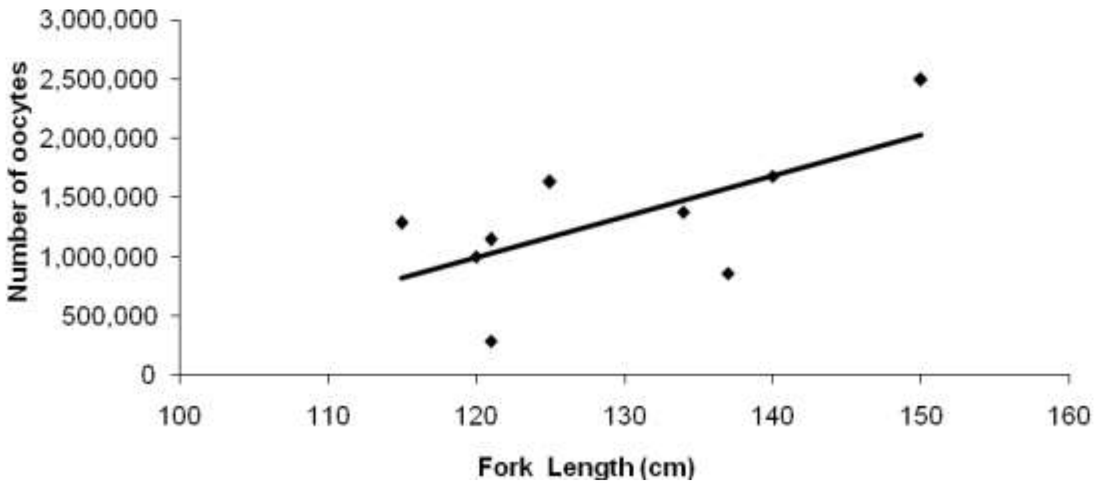

Figure 10. Relation between fork length and fecundity of wahoo, *A. solandri*, caught in Saint Peter and Saint Paul Archipelago, Brazil.

jority of tropical pelagic fishes (Brown-Peterson et al., 2011). Males still prepared for spawning during all year exhibiting testis full of sperm. Females generally show a more pronounced peak spawning where majority of ovaries are full of hydrated oocytes ready to be spawned, increasing GSI considerable in such period as the presence of some large females, following by a decrease in GSI due to reducing in fecundity with continuous spawning events. Although females in spawning condition were present during all year (Brown-Peterson et al., 2011). Peak spawning for wahoo in SPSPA (between April and May) is synchronized with the months after the flying fish (*Cheilopogon cyanopterus*) spawning and many species which spawns in same season as rainbow runner (*Elegatis bipinnulata*), increasing chances in food availability for larvae development (Pinheiro et al., 2011).

The size at first sexual maturity is a parameter of great importance for the adoption of conservation and management measures for any fish stock. Hogarth (1976) estimated as L_{50} for wahoo females of North Carolina to be 101 cm FL. For the same species in the northern Gulf of Mexico, Brown-Peterson et al*.* (2000) estimated as L_{50} of 102 cm FL for females, which would correspond to approximately two years of age (Franks et al., 2000). In Bermuda, preliminary studies suggested a size at first maturity of 95 cm FL for females (Oxenford et al., 2003). The size at first maturity found in the present study, therefore, equal to 110 cm FL for females, is higher than other values recorded in previous studies and might be a consequence of the higher proportion of adults in the sample.

Male wahoo in the SPSPA appear to mature at a lower size and possibly at a younger age than females. Hogarth (1976) reported a similar occurrence for the species of North Carolina, where males seem to reach sexual maturity at around 860 mm FL, while females mature only at 1,010 mm FL. Preliminary data from the Gulf of Mexico indicated that 50% of male wahoos are sexually mature at a length < 935 mm FL (Brown-Peterson et al., 2000), while in Bermuda, SAFMC (1998) suggested a slightly higher size at maturity for males, at around 102 cm FL (SAFMC, 1998 *apud* Oxenford et al., 2003), which is exactly the same value found in the present study (102 cm FL).

The few estimations of wahoo fecundity available in the literature vary considerably. Collette and Nauen (1983) estimated a number of 6,000.000 oocytes for a single mature specimen caught in the Central Atlantic. In a study carried out of North Carolina, Hogarth (1976) found the number of oocytes to range from 560,000 to 45,340.000. Offshore Florida and northern Bahamas, Jenkins and McBride (2009) reported a batch fecundity similar to the range found by Brown-Peterson et al*.,* (2000), who estimated a mean of 1,146.395 ± 291,210 eggs in female. The estimated fecundity for wahoo in the SPSPA, therefore, ranging from 284,040 (121 cm FL) to 2,494.512 (150 cm FL), with a mean fecundity of 1,317.235 oocytes, is close to the values found by these more recent authors.

Based on the oocyte size-frequency distribution, Brown-Peterson et al*.,* (2000) concluded that wahoo had a multiple spawning and an asynchronous oocyte development , similarly to the results found by other authors (Zischke et al., 2012), as well as in the present study. Some tropical pelagic fishes seem to develop a reproductive behavior of multiple spawning over an extended season as a strategy to compensate for the high rate of egg dispersal (Brown Peterson et al., 2011). The wahoo in vicinity of SPSPA may thus maximize its reproductive success by releasing several batches of oocytes during a protracted spawning season (Brown-Peterson et al., 2000). Jenkins and McBride (2009), studying wahoo reproduction in Florida and Bahamas found spawning intervals between 3 to 9 days, which would correspond to the time needed to a clutch of vitellogenic oocytes to increase and reach full hydration before spawning (Brown-Peterson et al., 2011).

The gradual increase in size of the specimens throughout the spawning period observed by Viana et al., (2008) appears to indicate the arrival of new recruits to the region at the beginning of the year (Jan-Feb), with spawning occurring in the following months, mainly between May and June, immediately after the period of highest surface water temperatures (Soares et al., 2009). Considering the geographically isolated nature of the SPSPA, the multiple spawning observed in the present study, with a marked seasonality and concentrated in a relatively narrow window (2 months), might be a reproductive strategy of the studied stock associated to long-distance migration. The fact that the vast majority of the fish caught were adults appears to reinforce the hypothesis of a reproductive aggregation around the SPSPA. Furthermore, the fact that the SPSPA is an archipelago of high biological productivity in a strongly oligotrophic region also suggests its probable use by the species as an area for feeding and energy gain, possibly necessary for the final process of gonad maturation prior to spawning. The high concentration of flyingfish, one of the preferred prey items of wahoo in the same area (Vaske-Jr. et al., 2003), from December on, appears to suggest a synchronism stemming from a predator-prey relationship, as observed for other species of large pelagic fish in the same region (e.g. the yellowfin tuna; Hazin 1993).

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