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RESEARCH ARTICLE

Reproductive biology and recruitment of bluefish *Pomatomus saltatrix* (Perciformes: Pomatomidae) in the southwestern Atlantic

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ABSTRACT. The bluefish, *Pomatomus saltatrix* (Linneus 1766) is captured by industrial, artisanal, and recreational fisheries throughout its distribution range. The reproductive biology of *P. saltatrix* in the southwestern Atlantic was studied using 1,102 specimens captured by the Brazilian commercial fleet between March 2014 and December 2015. The recruitment period was identified from records of juveniles in experimental beach seine hauls carried out on sandy beaches in the external sector of Guanabara Bay for four years (2012–2015). Based on the reproductive indices and on the macro- and microscopic analyses of the gonads, spawning peaks were identified in autumn and spring. The size at first maturity was estimated at 35.5, 38.3, and 37.4 cm for females, males, and general, respectively. Ovary analyses and measurements of the oocyte diameters indicated that bluefish are multiple spawners with asynchronous oocyte development. The batch fecundity estimate was 202,752.5 eggs and ranged from 9,800.9 to 426,787.0 eggs. The species reproduces throughout the entire study area, but it is more active in the south of Arraial do Cabo. The young-of-the-year were recorded on shallow water in all seasons, with modal peaks in the summer months. The parameters estimated in this study expand and update information on this species, providing important data for the evaluation and fisheries management of the stock of *P. saltatrix* in the southwestern Atlantic.

KEY WORDS. Fecundity, histology, oocyte development, reproductive dynamics, spawning seasons, young-of-the-year.

INTRODUCTION

The bluefish, *Pomatomus saltatrix* (Linneus 1766), is a migratory pelagic species with a wide geographic distribution. It occurs preferentially in continental shelf waters in temperate and tropical regions (Briggs 1960, Champagnat 1983, Juanes et al. 1996, Haimovici and Krug 1996). It is an active piscivorous fish (Haimovici and Krug 1992), preyed upon by top predators, including sharks (Wood et al. 2009) and dolphins (Milmann et al. 2016), constituting an important link within coastal trophic networks. The bluefish is also an important fishery resource throughout its distribution range, being captured by industrial, artisanal, and recreational fisheries, especially in the south and southwestern Atlantic, off the Brazilian coast to Argentina (Krug and Haimovici 1989, Haimovici and Krug 1992, 1996, Begossi 1996, Lucena et al. 2002, Lucena and O'Brien 2005, Souza et al. 2019), in the North Atlantic along the coast of the United States (Buckel and Conover 1997, Buckel et al. 1999, Juanes et al. 2002, Wilson and Degnbol 2002), in the Mediterranean (Dhieb et al. 2005), and in Eastern Australia (Kailola et al. 1993, Zeller et al. 1996, Schilling et al. 2019).

The fishery production data series have indicated a decline in catches in the southwestern Atlantic, with a reduction of 14,000 tons per year between the 1960s and 1970s, to around 4,000 tons per year between the 1980s and 1990s, reaching an average production of 3,600 tons per year in the 2000s (CEPSUL/IBAMA 2009). In addition, *P. saltatrix* has been classified as an overexploited species (MMA 2004) in Brazil. Between 2000 and 2010, the state of Rio de Janeiro contributed 40% of national production and the rest originated in the southernmost states (IBAMA 2007, 2008, MPA 2007, 2010, 2012). As a consequence, most studies on this species in the southwestern Atlantic have been concentrated in the southern most distribution range (Haimovici and Krug 1992, 1996, Muelbert and Sinque 1996, Lucena et al. 2000, Silvano and Begossi 2010), with little information on the northern portion of the stock.

Despite its recognized importance as a fishery resource, management policies for the species have not been established throughout its distribution range. The current legislation governing bluefish fisheries in Brazil covers only part of its distribution along the southern coast (Rio Grande do Sul, Santa Catarina, and Paraná) (MPA/MMA 2009), which establishes criteria for vessel operations and catches and defines a closure period between December and March (reproductive season). In spite of this, the Ministério do Meio Ambiente (MMA) defines the minimum landing size (35 cm) for catches in Brazil (MMA 2005 – Instrução Normativa #53/2005), considering the entire Brazilian bluefish population as a single stock. The continuous survey of information about the life cycle, such as reproduction and recruitment, is essential for the conservation and management of fisheries and should, whenever possible, consider the entire range of species distribution.

The natural renewal of the population is a complex process, resulting from a series of events during the species' life cycle such as maturity, egg laying, metamorphosis, growth, survival in nursery areas, and migration to feeding areas (Pitcher and Hart 1982, Jørgensen et al. 2007). Reproduction and recruitment are two major events in the life history of a species (King 2007). To understand the reproductive strategy of any species, it is necessary to know the type of spawning, fecundity, sex ratio, and size at maturity, among other factors (Hunter et al. 1992, Murua and Motos 2006). Knowledge of these aspects is essential for understanding the population dynamics and spatio-temporal variations in abundance and size, as well as the use of the environment, energy allocation, and how they contribute in increasing the adult stock biomass (Wootton 1998, King 2007).

Studies on the reproductive biology of the species are important in fisheries science because these are used to determine the resilience of populations to fishing pressure (Morgan 2008). In addition, studies on fish reproductive strategies can improve our understanding of egg production methods, which will allow us to evaluate the reproductive stock biomass (Armstrong and Witthames 2012, Ganias 2013). These methods can also enable the evaluation of fish phenology in a scenario of constant climate change (Soria et al. 2008, Miranda et al. 2009, Pankhurst and King 2010, Strüssmann et al. 2010). Given that *P. saltatrix* has been experiencing high fishing pressure off the Brazilian coast, we have presented recent reproductive development patterns of bluefish along the southwestern coast of Brazil, including size at maturity, spawning, and recruitment periods, which would contribute to the reconciliation of stock exploitation with conservation, providing recent findings for the development of updated stock management strategies.

MATERIAL AND METHODS

Field sampling and laboratory processing

Between March 2014 and December 2015, 49 commercial landings of the fleet operating on the southeast coast of Brazil, between latitudes of 20°30' and 24°00'S (Fig. 1), were monitored as part of a biological monitoring program carried out in the main fishing ports in the state of Rio de Janeiro. Approximately two landings were monitored monthly. From each landing, a sample of 30 to 50 individuals of different sizes was collected.

The fishing area (Fig. 1) is located in an important transitional region of the Southwestern Atlantic, formed by the northern boundary of the southeastern Brazilian shelf (SBS), between São Sebastião (São Paulo state) and Arraial do Cabo (Rio de Janeiro state) and the southern portion of the Eastern Brazilian Continental Shelf, until Guarapari (Espírito Santo state) (Rossi-Wongtschowski and Madureira 2006). Arraial do Cabo is an important geomorphological feature, where the coastline exhibits a marked change of direction, from east (E)-west (W) to northeast (NE)-southwest (SW), accompanied by the narrowing of the continental shelf (Rossi-Wongtschowski and Madureira 2006). The morphological conditions and intense NE winds are the key factors responsible for the upwelling of cold and nutrient-rich waters from the South Atlantic Central Water (SACW), mostly during the summer (Artusi and Figueiredo 2007). This region also represents the boundary between the Brazilian southeastern and eastern marine ecosystems (Spalding et al. 2007).

We also collected data on the occurrence, abundance, and sizes of young-of-the-year (YOY) fishes on the shallow waters of the sandy beaches based on the monthly experimental beach seining conducted between January 2012 and December 2015 (SISBIO/IBAMA/ICMBio collection license #15787-1). Beach seining was conducted in the shallow surf zones of the three beaches located in the marine boundary and lower sector of Guanabara Bay. On each occasion, three hauls were carried out for a distance of 20 m in a direction parallel to the coastline at a maximum depth of 1.5 m. The beach seine used was 9.0 m long and 2.6 m wide, made of a 210/06 silk thread with a 13 mm bar mesh on the sides and a 5 mm bar mesh in the bag. Records of *P. saltatrix* juveniles were used to identify the recruitment periods in the beach shallow waters and to evaluate the size of the YOY. All individuals were measured for total length (TL, cm) and total weight (TW, g). Individuals from commercial fisheries had their

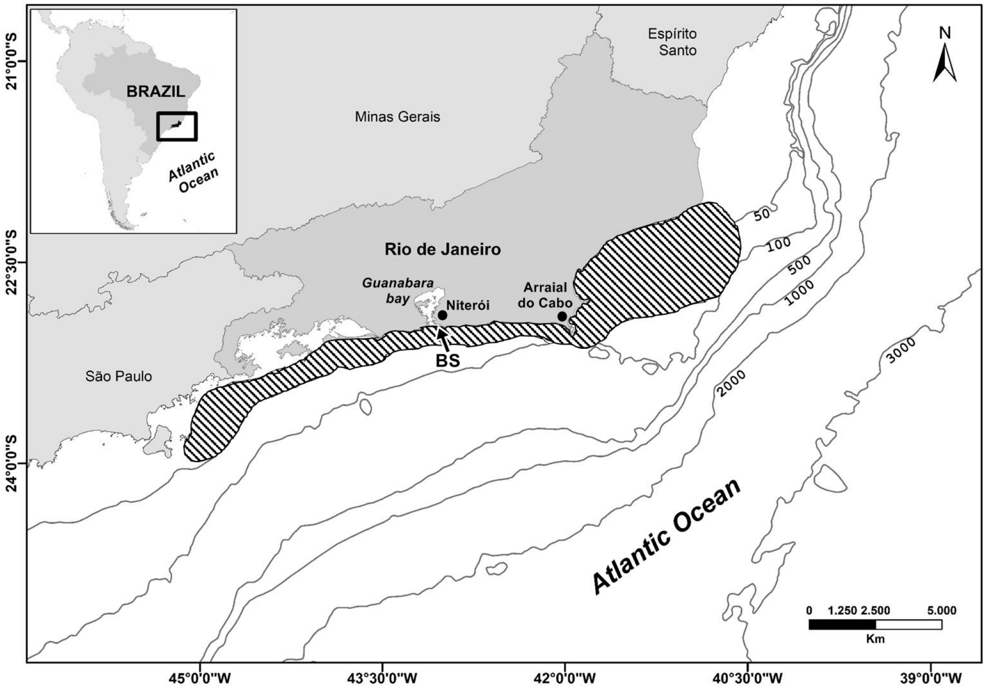


Figure 1. Fishing grounds for *Pomatomus saltatrix* for commercial boats based in Rio de Janeiro. BS stands for beach seining.

sex identified through a macroscopic examination of gonad characteristics (Vazzoler 1996, Brown-Peterson et al. 2011). The gonad weight (GW, nearest 1 g), liver weight (LW, g), and eviscerated weight (EW, g) were also recorded. The dissection of the fish was performed through a longitudinal incision made in the abdominal region. The ovaries were gently removed from the cavity and weighed to the nearest 0.1 g. Sub-samples of the ovaries were preserved in 10% neutral buffered formalin (Cuellar et al. 1996) for later histological examination.

Relative growth, sex ratio, and histological classification

The relative growth of the juveniles and adults (females and males) was evaluated using the length-weight relationship (LWR) according to the equation: $TW = aTL^b$ (Le Cren 1951), where a is the coefficient related to body shape, and b is an exponent related to changes in body shape (Froese 2006). To test the b value against the value of 3 (isometric), Student's t-test was employed to predict any significant deviation (Zar 1984). Analysis of covariance (ANCOVA) was performed to determine the difference between the b slopes of the LWRs of males and females.

The sex ratio was determined for the different length classes (intervals of 5 cm TL), and the austral seasons were defined as summer (January-March), autumn (April–June), winter (July–September), and spring (October-December). Deviations from the null hypothesis of a 1:1 ratio were statistically tested using the chi-squared test (χ^2) with a 5% significance level. Reproductive activity was assessed by observing the macroscopic characteristics of the gonads, microscopic examination of the ovarian histological slides, frequency distribution of the oocyte diameter, and the reproductive indices. All individuals had their gonads macroscopically classified according to the following stages: immature, developing, spawning capable, spent, and regenerating (Brown-Peterson et al. 2011). This classification was adjusted for females, considering the microscopic anatomy of 40 ovaries at different stages of development and during different seasons. For this purpose, each gonad was cross-sectioned, fixed in 10% formalin, and processed following the routine haematoxylin-eosin staining (Suvarna et al. 2012). The types and ovarian cell structures were identified based on the criteria proposed by Brown-Peterson et al. (2011), and macro- and microscopic characteristics of the examined gonads were used as reference for the construction of a descriptive table of maturity stages (Table 1). For this, photomicrographs were obtained from four observation fields of each examined ovary, with a camera coupled to a microscope. The diameter of all the oocytes within each field was measured to the nearest 0.1 µm, using a plugin for Image J version 1.46r (NIH, Bethesda, MD, EUA) (http://www.imagej.nih.gov/ij), considering the largest diameter of the oocytes with evident nuclei.

Reproductive indices and maturity

The gonadosomatic index (GSI), as a proxy of the degree of gonadal development, was calculated for each sex and grouped sexes based on the eviscerated weight to avoid possible variations from differences in the stomach content using the equation:

Table 1. Description of gonadal maturity stages of *Pomatomus saltatrix*, adapted from Brown-Peterson et al. (2011), where Vtg1 are oocytes in early vitellogenesis, Vtg2 are oocytes in intermediate vitellogenesis, and Vtg3 are oocytes in late vitellogenesis.

Maturity stage	Macroscopic and histological features in females
Immature	Ovaries are very small, occupy about 1/3 of the body length, and are thin and translucent. Only oogonia and primary growth oocytes (PG) are seen. There is little space between the oocytes. The ovarian wall (OW) is slightly thick.
Developing	Ovaries range from small to medium and occupy between 1/3 to 2/3 of the celomatic cavity. Ovaries are yellow in color, and blood vessels may be apparent. Only PG are seen, with cortical alveolar (CA) and are in vitellogenesis (Vtg1 and Vtg2).
Spawning capable	Ovaries are large, occupying more than 2/3 of the body length, are pale yellow in color, and have evident blood vessels. Hydrated oocytes are macroscopically visible. Primary growth oocytes are prevalent, with CA and vitellogenesis (Vtg1, Vtg2, and Vtg3). Oocytes are seen with germinal vesicle migration (GVM) and late germinal vesicle migration (LATE GVM). Hydrated oocytes (HYD) or post-ovulatory follicles (POF) are seen. There is the possibility of atresias (A).
Spent	Ovaries are small, occupying between 1/3 to 2/3 of the body length, are flaccid, and have prominent blood vessels. Atresic oocytes (A), post-ovulatory follicles (POF), and CA and vitellogenic oocytes (Vtg1 and Vtg2) may be present.
Regenerating	Ovaries are very small, occupying up to 1/3 of the body length, and with reduced blood vessels. Brown in color. Ovarian wall (OW) is thick. Only oogonia and PG are present. There are evident spaces between oocytes. Atresic oocytes and degenerating POF may be present.
Maturity stage	Macroscopic features in males
Immature	Testes are very small, filiform, and are clear or translucent, occupying 1/3 of the celomatic cavity.
Developing	Testes are small but easily identifiable, occupying up to 2/3 of the celomatic cavity. Light and homogeneous in color.
Spawning capable	Testes are large and firm with opaque white color, occupying more than 2/3 of the body length. They break easily when applied with pressure.
Spent	Testes are small and flaccid, may be brown in color, occupying about 1/3 of the celomatic cavity.

$GSI = (GW/EW) \times 100$, where GW is the gonad weight (g), and EW is the weight of the fish eviscerated. The condition factor under the influence of the gonad weight (K) and without the gonad weight (K') were calculated according to the methods of Le Cren (1951), allowing the estimation of the gonadal condition factor (KΔ), following the formula: $K\Delta = K - K'$, where $K = TW/TL^b$ (allometric condition factor) and $K' = SW/TL^b$ (somatic condition factor). The somatic weight (SW) is calculated as follows: $SW = TW - GW$. The hepatosomatic index (HI) was calculated using the formula: $HI = (LW/EW) \times 100$, where LW represents liver mass (Vazoller 1981, 1996). The calculated values for each of the indices were grouped by month and compared using the non-parametric Kruskal-Wallis test ($p < 0.05$). All statistical analyses were performed using the STATISTICA® software (version 8.0).

Finally, the size at 50% maturity (L_{50}) was estimated to define sexual maturity as a function of body length, according to the following equation (Moresco and Bemvenuti 2006): $Fr = 1 - (e^{-aTL^{b}})$, where Fr is the relative frequency of adult individuals in each size class, e is the base of the natural logarithm, a and b are coefficients estimated by the least squares method, and TL is the midpoint of the total length classes.

Batch fecundity

Batch fecundity (F) was estimated by direct counts of the hydrated oocytes (Hunter et al. 1985). Sub-samples of the median portion of the seven ovaries with intense yellow color in the spawning capable phase were weighed to the nearest 1.0 g, and the number of hydrated oocytes was counted. The estimate of individual F was back-calculated by the gravimetric method: $F = GWn\,(m)$, where n is the number of hydrated oocytes in the sub-sample, and m is the mass of the ovarian sub-sample. Power regression was used to determine the relationship between batch fecundity, TL, and TW.

RESULTS

Size distribution, relative growth, and sex ratios

Out of the 1,102 individuals sampled from the commercial landings, 671 were females ranging in size from 30.0 to 82.0 cm TL (mean ± SD; 48.9 ± 6.7 cm), and 431 were males, ranging from 29.2 to 61.6 cm TL (mean ± SD; 47.8 ± 5.6 cm) (Fig. 2). Most of the sampled fish were between 40.0 and 59.9 cm TL (greater than 90% of the fish). The YOY (N = 1,127) captured on beach seining ranged from 1.2 to 15.5 cm TL (mean ± SD; 4.5 ± 2.4 cm).

The length-weight relationship determined for the juveniles was $TW = 0.004\ TL^{3.281}$, which indicated a positive allometric growth ($b > 3$) ($p < 0.05$) ($t_{(1127)} = 18.45$, $p < 0.05$). The relationships for females and males were expressed by the following equations: $TW = 0.028\ TL^{2.693}$ and $TW = 0.036\ TL^{2.628}$, respectively, indicating a negative allometric growth ($b < 3$) ($p < 0.05$) (female $t_{(575)} = -14.97$, $p < 0.05$, and male $t_{(389)} = -15.19$, $p < 0.05$) for the commercial landings population stratum. There were no signif-

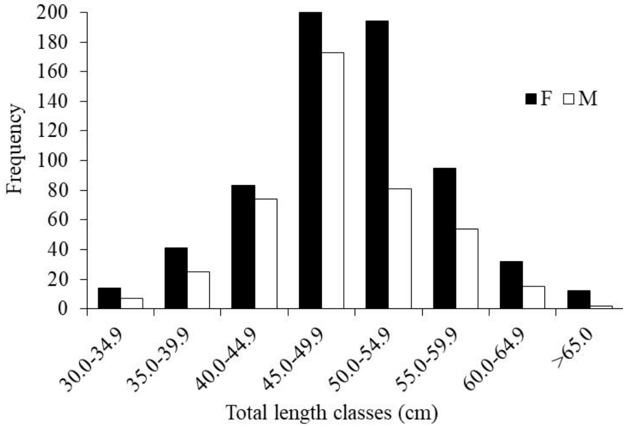


Figure 2. Frequency distribution of *Pomatomus saltatrix* caught along the southeastern coast of Brazil, across total length classes of females (F, n = 671) and males (M, n = 431).

icant differences between the sexes (ANCOVA: $F_{1,965} = 0.20$, $p > 0.05$). Thus, we assumed that the b value obtained for the grouped sexes would be representative of the study population (Table 2).

The total sex ratio (0.61; female:male = 1.6:1) was significantly different from the expected value of 0.5 (χ^2calc = 4.74, df = 1, $p > 0.05$). There were no significant differences (χ^2calc = 0.33 and 0.52, df = 1, $p > 0.05$) in the intermediate size classes (between 40.0 and 49.9 cm). In the other size classes, females predominated, especially above 65.0 cm (χ^2calc = 51.02, df = 1, $p < 0.05$). Females were more abundant during almost the entire study period. Males were more abundant only in the summer of 2014 (χ^2calc = 36.00, df = 1, $p > 0.05$).

General pattern of ovary development

Histological analyses of the ovaries revealed that the oocyte development showed a consistent pattern in batch spawning. In spawning capable ovaries, oocytes at all stages of development were recorded (Figs 3–6), indicating asynchronous oocyte development. Primary growth oocytes showed diameters between 18 and 135 µm, and those of secondary growth, that is, cortical alveolar, ranged between 89 and 226 µm. Vitellogenic oocytes (Vtg1) ranged from 127 to 277 µm, between 238 and 487 µm (Vtg2), and between 301 and 598 µm (Vtg3). Hydrated oocytes had diameters greater than 700 µm (Figs 3–9). There was an overlap in the diameter of the oocytes at different stages, except for the hydrated oocytes, which were clearly separated.

The presence of hydrated oocytes and oocytes at advanced stages of development (Vtg2 and Vtg3) in the same ovary indicates the possibility of more than one spawning event in the same season (Fig. 7). Gonads containing atretic oocytes (β-atresia) and secondary growth oocytes (Fig. 8) were recorded in individuals collected in April and October (reproductive peaks) and in both annual cycles. Gonads with primary growth oocytes and oocyte resorption were observed at the end of the reproductive season (December 2014 and May-November 2015). In addition, ovaries containing post-ovulatory follicles also presented vitellogenic oocytes, indicating batch spawning (Fig. 9).

The frequency distributions of the oocyte diameter by maturity stage revealed a similar unimodal pattern for immature oocytes and regeneration. Other stages showed multimodal distributions, especially the ovaries classified as spawning capable (Fig. 10), reinforcing an asynchronous pattern of oocyte development. Such patterns of oocyte size and ovarian development are consistent with a pattern of batch spawning and indeterminate fecundity.

Maturity

The size at 50% maturity (L_{50}) was estimated at 35.5 cm L_T for females, 38.3 cm for males, and 37.4 cm for both sexes (Fig. 11). The length at which all individuals were fully mature (L_{100}) was estimated to be 39.5 cm for females, 50.0 cm for males, and 47.0 cm for both sexes. Histological analysis confirmed that individuals larger than 36.0 cm had completely vitellogenic oocytes (stage 3) and advanced development.

Spawning patterns

To identify seasonal spawning patterns, we calculated the reproductive indices (GSI, KΔ, and HI) separately for females and males, considering only adult and spawning individuals. The mean values of GSI and KΔ varied similarly over time for both sexes. Despite the interannual variation in GSI values, the seasonal pattern was repeated in both cycles, revealing two annual reproductive peaks.

The highest GSI values for females were observed during autumn (May 2014 and April 2015) and spring (December

Table 2. Parameters of the length-weight relationship of juveniles (beach seine) and individual juveniles and adults (males, females, and grouped sexes in commercial fisheries) of *Pomatomus saltatrix*. n = number of individuals, a and b = coefficients of the exponential equation $TW = aTL^b$, SD = standard deviations of a and b respectively, R^2 = coefficient of determination.

Sex	n	Total Weight (TW, g)	Total length (TL, cm)	a	SD a	b	SD b	R^2
Juveniles	1,127	0.043–31.712	1.2–15.5	0.0042	0.0104	3.281	0.0153	0.973
Females	577	233.0–4036.0	30.0–82.0	0.0281	0.0345	2.693	0.0205	0.967
Males	391	234.0–2218.0	29.2–61.1	0.0367	0.0411	2.628	0.0245	0.967
Grouped	968*	233.0–4036.0	29.2–82.0	0.0310	0.0265	2.668	0.0158	0.967

*Some individuals were withdrawn to adjust the power equation.

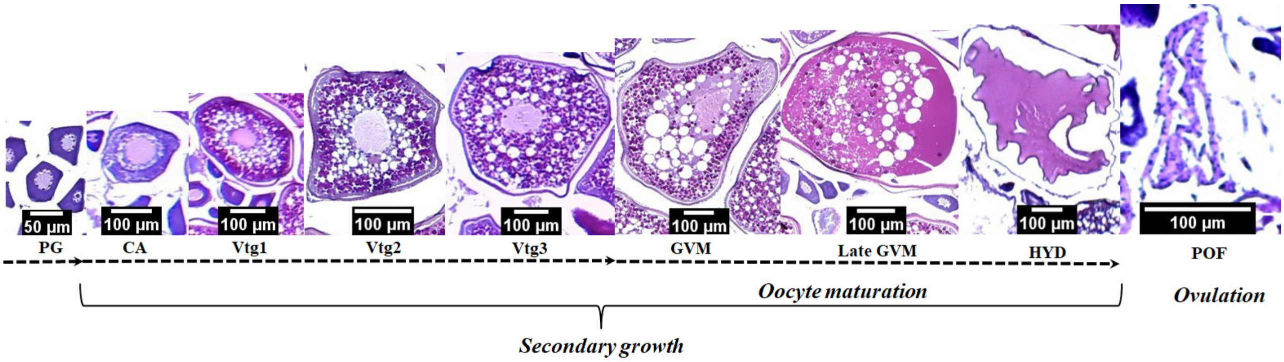
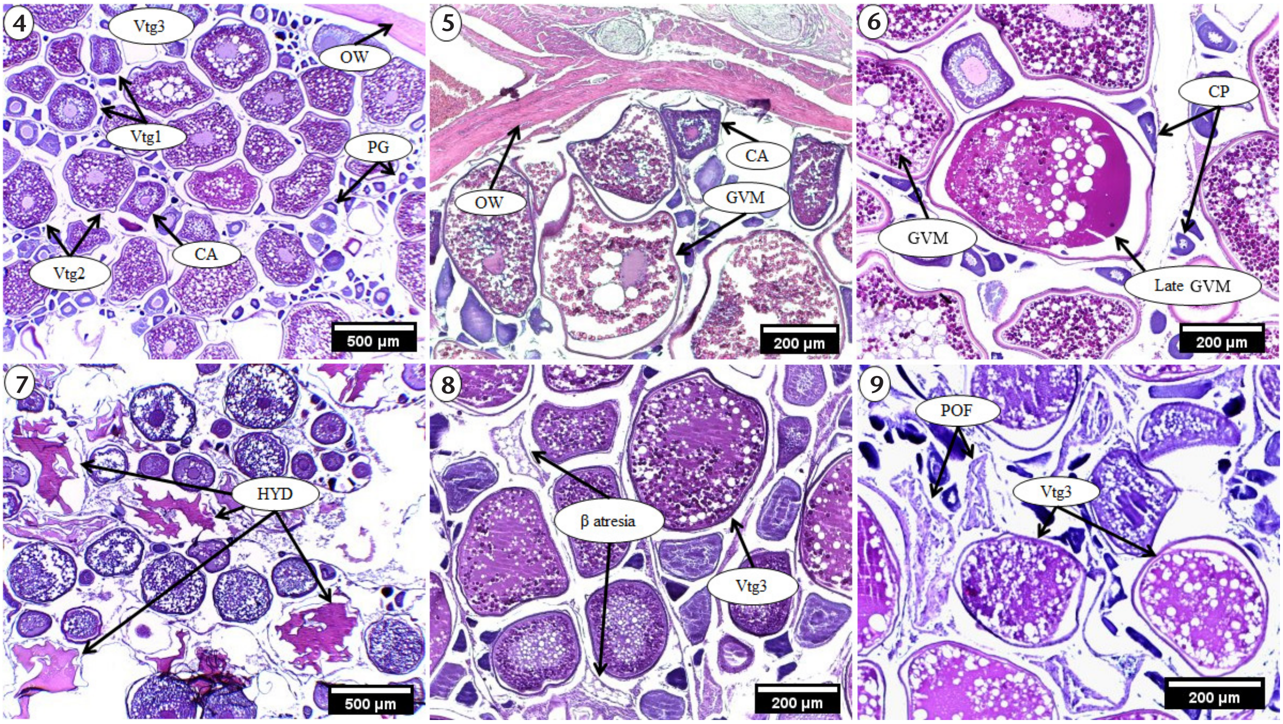


Figure 3. Steps and stages of oocyte development of *Pomatomus saltatrix*. Primary growth (PG), Secondary growth is cortical alveolar (CA), early vitellogenesis (Vtg1), intermediate vitellogenesis (Vtg2), late vitellogenesis (Vtg3). The interval between CA and germinal vesicle migration (GVM), late germinal vesicle migration (late GVM), and hydration (HYD) corresponds to oocyte maturation (OM), followed by post-ovulatory follicle (POF).



Figures 4–9. Histological sections of the ovaries of *Pomatomus saltatrix*. Spawning capable: (4) presence of oocytes at the different stages of development; (5, 6) oocytes in advanced secondary growth (GVM and late GVM); (7) Hydrated oocytes (HYD); Spent: (8) oocytes in β atresia; (9) oocytes in Vtg3 and POF. Oocyte primary growth (PG); cortical alveolar (CA); early vitellogenesis (Vtg1); intermediate vitellogenesis (Vtg2); late vitellogenesis (Vtg3); ovarian wall (OW); post-ovulatory follicle (POF); hydrated oocytes (HYD); germinal vesicle migration (GVM); late germinal vesicle migration (late GVM).

2014 and October 2015). The lowest GSI values were recorded during the summer months in both annual cycles (Fig. 12). The monthly variation in the gonadal condition factors (KΔ) followed the same pattern observed for the GSI (Fig. 13). The HI values presented a trend similar to that observed for the gonadal condition factor (KΔ). The lowest values were recorded in December 2015 for both sexes (Fig. 14). The Kruskal-Wallis test revealed significant differences ($p < 0.05$) between the months for all indices analyzed, which supported the monthly reproductive pattern.

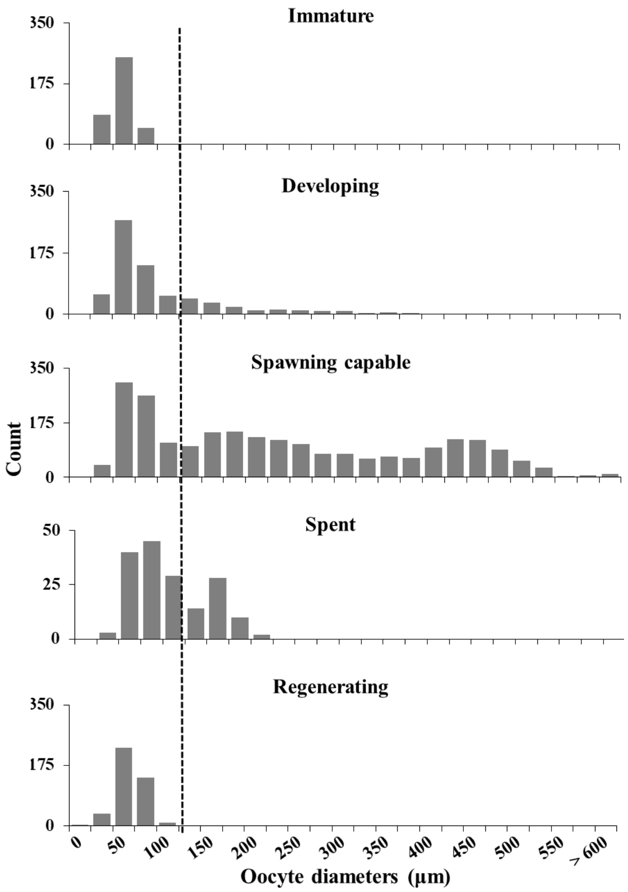


Figure 10. Frequency distribution of the oocyte diameters. Frequencies through the stages of gonadal development of *Pomatomus saltatrix* caught on the southeastern coast of Brazil. The vertical dashed line indicates the diameter at the beginning of vitellogenesis (Ø = 127 µm). Number of oocytes measured per maturity stage: immature (n fish = 4, n oocytes = 388), developing (n fish = 3, n oocytes = 673), spawning capable (n fish = 25, n = 2,330), spent (n fish = 3, n = 172), and regenerating (n fish = 4, n = 412).

Batch fecundity

Individual fecundity estimated from fresh ovarian samples of seven fishes (41.8–52.8 cm; 0.786–1.280 kg) was 9,800.9–426,787.0 eggs, with a mean ± SD of 202,752.5 ± 160,900.9. The estimates of individual relative fecundity ranged between and 81–548 oocytes g^{-1}, with a mean ± SD of 273.5 ± 152.3 oocytes g^{-1}.

The relationship between fecundity (F), total length (TL), and total weight body (TW) was fitted using the following equations: $F = 5E\text{-}08\ TL^{.476}$ ($R^2 = 0.734$) and $F = 5E\text{-}10\ TW^{3.866}$ ($R^2 = 0.985$).

Recruitment pattern

The sampling program carried out in the shallow surf zone of the sandy beaches recorded the occurrence of 1,136 individuals with TL varying between 1.0 and 15.5 cm (mean = 4.7 ± 2.6 SD), essentially during late winter and summer. No individual was caught in the autumn or early winter months.

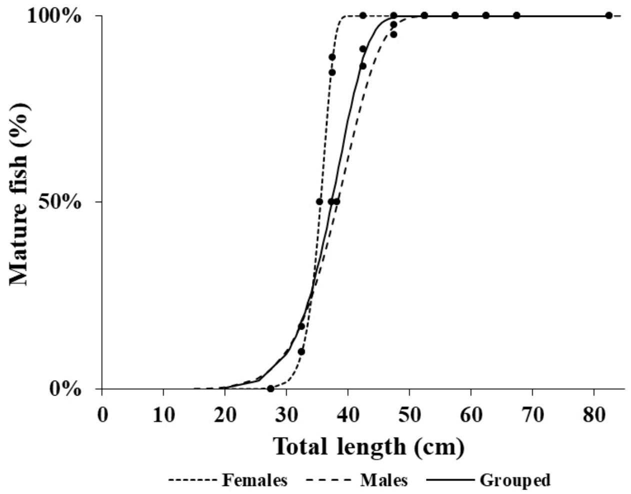


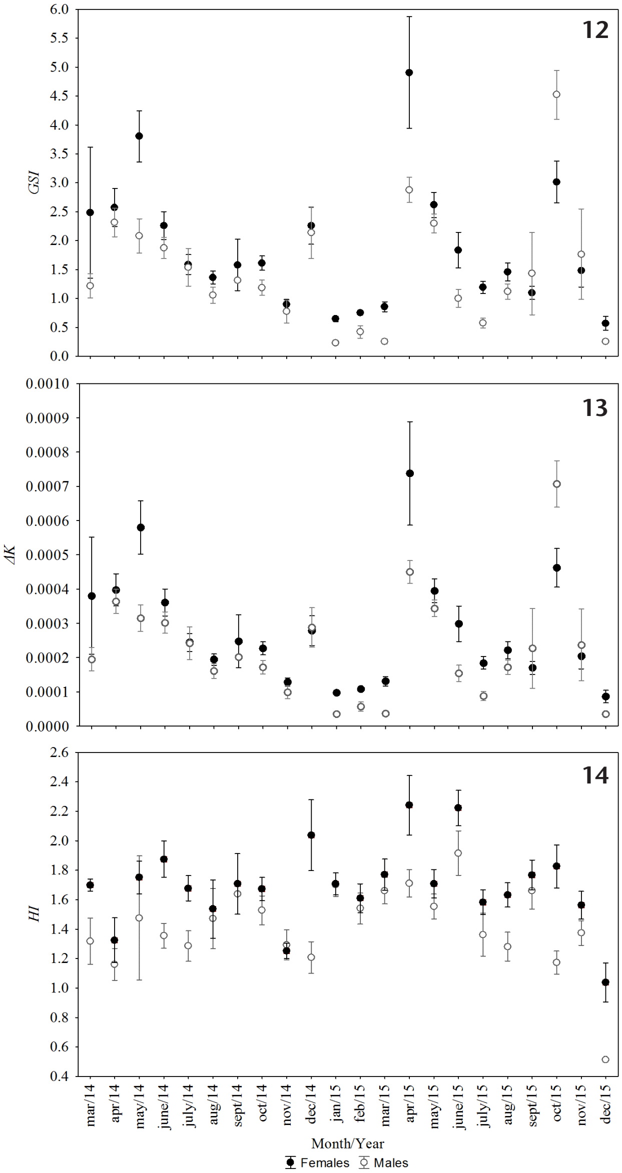
Figure 11. Logistic regression model for the estimated percent of sexually mature bluefish as a function of size for both sexes (L_{50} = 37.4 cm), for females (L_{50} = 35.5 cm), and for males (L_{50} = 38.3 cm) caught off the southeastern coast of Brazil.

The YOY was recorded between the end of winter and early spring, with an average size of 3.1 cm (± 1.9 SD) remaining in this environment for a period of three to five months, when they reached a TL of approximately 11.2 cm (± 1.9 SD) (Fig. 15). When analyzing the temporal variation patterns of GSI together with the data on the occurrence of juveniles on the beaches, there was a synchronous pattern of reproductive peaks and recruitment on the beaches of the external sector of Guanabara Bay (Fig. 15). Considering the two annual cycles and their reproductive pulses, we observed that the interval between the months of highest GSI and the arrival of the YOY on the beaches was approximately three months (Fig. 15).

DISCUSSION

Sex ratio and relative growth

The sex ratio of a population is an important population attribute because it varies throughout their life cycle, which depends on several ecological and evolutionary events that affect the individuals of each sex (Hutchings and Rowe 2008). In the present study, larger proportions of females were observed throughout most of the study period and length classes, with the exception of autumn (2014–2015), spring, and summer (2015), which coincided with spawning periods. According to Kraak and Pen (2002), teleosts exhibit a tendency for a balanced sex ratio, which is accentuated during the reproductive period (Vazoller 1996, Pavlov and Emel'yanova 2016). Krug and Haimovici (1989) reported similar results for the bluefish individuals caught in



Figures 12–14. (12) Gonadosomatic index (GSI); (13) gonadal condition factor (KΔ); (14) hepatosomatic index (HI). Mean monthly values ± SE for females and males of *Pomatomus saltatrix* caught off the southeastern coast of Brazil, between March 2014 and December 2015 (n = 646 and 404, females and males, respectively).

southern Brazil, agreeing that differences in sex ratios may be attributed to a variety of causes, such as mortality, migration, and influence of the selectivity of fishing gear (Vazoller 1996, Castro and Mejuto 1995, Montealegre-Quijano and Vooren 2009), with the last factor being a possible explanation for the pattern observed in the present study. Krug and Haimovici (1989) showed that *P. saltatrix* females had higher sizes, reaching significantly higher lengths than males at the same age. Recently, Cumplido et al. (2018) registered females in greater proportion than males and larger sizes in the coastal area of Arraial do Cabo. Schilling et al. (2019) recently observed that the sex ratio of the bluefish population in the southwest Pacific Ocean shifted significantly from an equal sex ratio to a female-dominated population. The authors suggested two potential causes: changing environment occasioned for global marine warming, influencing the sex determination in newly fertilized eggs, and the differences in growth or behavior between male and female *P. saltatrix*, resulting in differing mortalities.

The parameters derived from the length-mass relationship, i.e., condition factor and "b" observed, revealed different energy investments between the juveniles (b > 3) and adults (b < 3). This is in agreement with the classic pattern of fish development, in which juveniles allocate energy for somatic growth only, while adults allocate energy for growth and reproduction (Wooton 1998). These parameters are also useful for estimating biomass and weight growth (Froese 2006), allowing comparisons between fish species or populations from different habitats (Froese and Pauly 1998, Nahum et al. 2009). Previous studies have shown that the "b" values of *P. saltatrix* for juveniles (b = 3.051 to 3.336) and adults (b = 2.509 to 2.899) recorded in different habitats Barger 1990, Torres 1991, Haimovici and Velasco 2000, Frota et al. 2004, Kalayci et al. 2007, Ak et al. 2009, Vaz-dos-Santos and Rossi-Wongtschowski 2013, Cumplido et al. 2018) were in line with the values estimated in the present study. Therefore, the b coefficient becomes an essential parameter for the evaluation of stocks, which is used to determine the health status and well-being of the individuals of a population, influenced by environmental factors, food availability, and reproductive period (Rossi-Wongtschowski 1977).

Maturity

The estimated L_{50} for grouped sexes was 37.4 cm, greater than the estimates from previous studies on the south coast (Haimovici and Krug 1992). These differences may be associated with density-dependent factors such as environmental conditions, food availability, and local oceanographic characteristics, which may affect growth (Champagnat 1983, Krug and Haimovici 1989), or even with sampling biases during the capture because of a tendency to undersample the immature population. Nevertheless, our estimates for the separate sexes indicated that females reach sexual maturity at shorter lengths than males. In fact, such differences were previously observed for *P. saltatrix* in southern Brazil (Haimovici and Krug 1992), the northeast coast of the United States (Salerno et al. 2001), and Tunisia (Dhieb et al. 2006). Another potential factor associated with variations in size at maturity is the fishing pressure on these populations (Haimovici and Krug 1992, Wood 2013). Our findings suggest that the studied population reaches sexual maturity at comparatively larger sizes than those reported in the literature and in the minimum landing size (TL = 35.0 cm) defined in the Brazilian

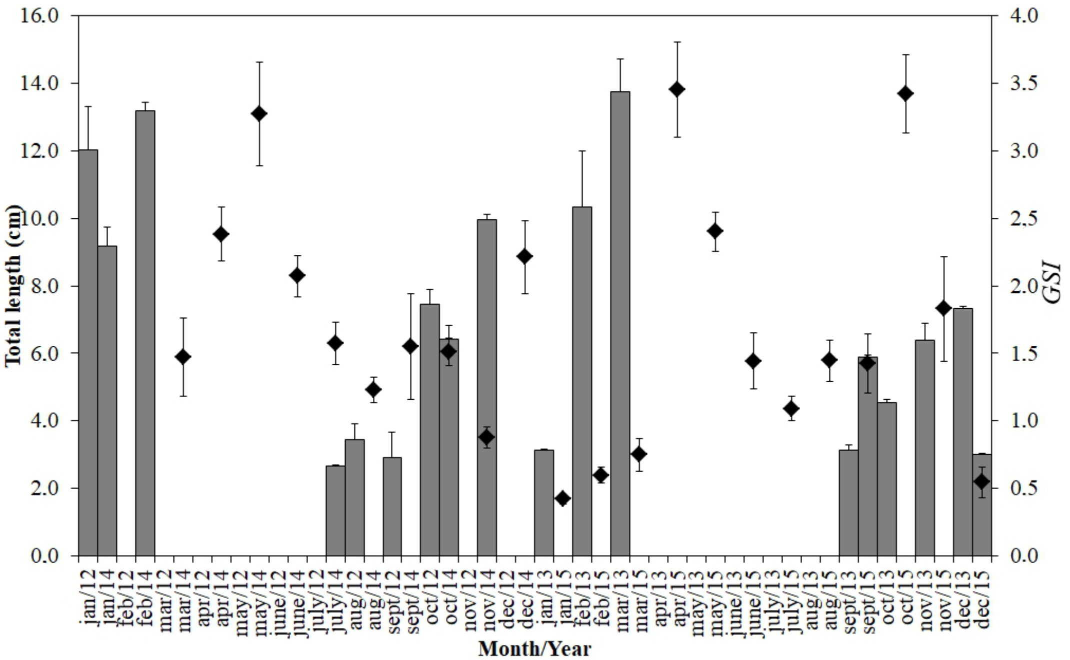


Figure 15. Monthly distribution of mean values (vertical bars ± SE) of the total length of juvenile fish caught by experimental trawls on the surf zone of three sandy beaches of Niterói (RJ), between January 2012 and December 2015 (n = 1,127). Variation of the mean monthly gonadosomatic index (GSI) (black triangle ± SE) of individuals of *Pomatomus saltatrix* caught on the southeastern coast of Brazil between March 2014 and December 2015 (n = 1,050). The annual cycles from 2012 to 2015 were organized by month.

legislation for management and protection of the species (MMA 2005 – Normative Instruction #53/2005). This indicates the need for a continuous and geographically comprehensive assessment of life history parameters used for management decisions.

Pattern of ovary development

Histological analyses of the ovaries confirmed the macroscopic stages observed and indicated that the bluefish have a batch spawning pattern, with asynchronous oocyte development and continuous reproduction. This is supported by the seasonal patterns of oocyte development widely documented in the literature (Hunter et al. 1992, Brown-Peterson et al. 2011), which includes the presence of hydrated oocytes. Oocytes in advanced stages of development in the same ovary suggest more than one spawning event in the same season. Similarly, ovaries containing POFs also had vitellogenic oocytes, which are indicative of batch spawning. In addition, the oocyte diameter distribution indicated that this is continuous and multimodal and has considerable overlap in size, reinforcing a pattern of asynchronous development with indeterminate fecundity. Other studies on the reproduction of bluefish bluefish (Haimovici and Krug 1992, 1996 Robillard et al. 2008) confirm that such tactics are common in the species, regardless of its location or population. However, the maximum oocyte diameter measured at all stages of development was comparatively lower than that observed in previous studies (Haimovici and Krug 1992, Robillard et al. 2008). According to Vazoller (1996) and Wootton (1998), this may indicate reproductive tactics adopted by the species due to local restrictions. Each oocyte represents a massive cytoplasmic investment; its diameter and quality can be largely influenced by temperature, food availability, and size of the breeding females. These factors may vary between years as well as between populations of the same species. Another explanation would be the evolutionary trend of oocyte minimization to maximize fecundity, which is commonly observed in overexploited populations (Wootton 1998).

The results of this study also showed the presence of individuals capable of spawning in almost all months, with clear seasonality in the reproductive period, having one spawning peak in spring and the other in autumn. The presence of HYT, which occurs a few hours before spawning (Hunter and Goldberg 1980), and GVM oocytes in the months of May and October in the ovaries of *P. saltatrix* are indicative of an imminent spawning event (Hunter et al. 1992). The presence of POFs, which tend to be resorbed between 24 and 48 hours, indicates recent spawning (Hunter et al. 1992, Brown-Peterson et al. 2011, Lowere-Barbieri et al. 2011). These histological observations corroborate the reproductive period indicated by the GSI and are in agreement with the values recorded for other *P. saltatrix* populations, illustrating a common characteristic of the species. The same pattern was observed on the southeast coast of Brazil (São Paulo to Rio de Janeiro) by Silvano and Begossi (2010) and Nunes et al. (2011); however, on the southern coast (Rio Grande do Sul to Santa Catarina), bluefish spawning occurred in the spring and summer months (Haimovici and Krug 1992, Muelbert and Sinque 1996, Silvano and Begossi 2005). This variability has already been observed along the distribution area of the species (Juanes et al. 1996).

Bluefish exhibit a characteristic migratory behavior, that is, migrating to higher latitudes in the spring and returning to lower latitudes in the fall and winter, which is linked to the displacement of warmer water bodies (14 to 30 °C) (Champagnat 1983, Juanes et al. 1996, Sabatés et al. 2011, Robillard et al. 2008). Our results suggest that *P. saltatrix* reproduces throughout the fishing area, however, the highest proportions of individuals in stage 3 (suitable for spawning), as well as the highest IGS values and evidence of imminent and recent spawning (presence of hydrate oocytes and POFs) were recorded in individuals captured in the south of Arraial do Cabo, suggesting an intense reproductive aggregation activity in this region. Haimovici and Krug (1996) have associated this pattern with the seasonal coastal upwelling that frequently occurs between Cabo de São Tomé and Cabo Frio (RJ) in southeastern Brazil (Castro et al. 2006). Therefore, the observed pattern may be associated with reproductive migratory behavior.

Batch fecundity

Fecundity is generally proportional to the size, weight, and condition of the fish, which are key parameters for assessing fecundity at the population level (Murua and Saborido-Rey 2003). The significant positive relationship between fish size and fecundity observed in the present study indicates a maximization of oocyte production. Oocyte production is influenced by factors not measured here, such as food availability. Some species are able to compensate for energy reserves with simultaneous food sources (Henderson et al. 1996). Our results were similar to the fecundity study conducted in southern Brazil for the species, wherein batches of 3,006 to 468,000 eggs were estimated for individuals with TL ranging from 40.0 to 57.0 cm (Haimovici and Krug 1992). The differences observed between our study (batches of 9,800 to 426,000 eggs, TL between 41.8 and 52.8 cm) and the previous study may be related to our strict decision to use only females at the final stage of maturity and totally hydrated oocytes for estimating fecundity. Both estimates, observed in South (S) and southeastern (SE) Brazil, showed great variability, proving that fecundity is affected by several factors, such as the year (interannual variation), the condition of the fish, the size of the fish, and the period during which the samples were collected (Hunter et al. 1985, Rijnsdorp 1991, Witthames et al. 1995).

Recruitment pattern

The recruitment pattern observed corroborates the reproductive period of the species in the southeastern Brazilian region. Inflows of YOY in the spring and summer months confirmed the occurrence of two recruitment pulses (winter and summer) linked with the two reproductive peaks observed. For instance, shallow coastal habitats such as nearshore waters of sandy beaches play an important role as a breeding site or nursery for the growth of *P. saltatrix*. Several studies have reported that the recruitment pattern of bluefish is similar between populations. Eggs and larvae are usually found along the coast in breeding habitats (Nyman and Conover 1988, McBride and Conover 1991, Muelbert and Sinque 1996, Juanes et al. 1996), with larger individuals (between 12 and 14 cm) moving into deeper waters (Juanes and Conover 1994, Scharf et al. 1998).

The integrated analysis of the reproductive dynamics and recruitment patterns in the present study suggests that reproduction occurs within the studied area. This result is further supported by the presence of POF and hydrated females concentrated in spring and summer months in the northernmost range of southeastern Brazil. Additionally, the size of the first maturity reported here is higher than the minimum landing size established in the legislation. In light of this evidence and the fact that the legislation was established based on information gathered three decades ago, fisheries regulations for *P. saltatrix* should be reviewed, including the updated results. Furthermore, future studies on the migratory movements and spawning dynamics of *P. saltatrix* in the southwestern Atlantic off the coast of Brazil must be elucidated to aid in the conservation and protection of spawning stock biomass from various fishery interactions.

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