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Recent Findings on Spawning Patterns and Recommendations for the Fishery Management of the Southern Red Snapper—*Lutjanus purpureus* (Poey, 1866)—On the Amazon Continental Shelf of Brazil †

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Abstract: The southern red snapper, *Lutjanus purpureus*, is one of the primary fishery resources of the Amazon continental shelf. Due to the demand for specimens of less than 900 g in weight, increased fishing effort focusing on this size class has led to a drastic decrease in catches. The present study was based on the analysis of cellular structures in the female gonads (formation of oocytes and other reproductive tissues) to identify reproductive processes and evaluate the effectiveness of current fishery management practices. The presence of postovulatory follicles (POFs) peaked in April, which was interpreted as a period of intense spawning. In addition to POFs, hydrated oocytes peaked in July, indicating either reproductive continuity or a second peak, based on the presence of atretic oocytes and atresia. Given that the local snapper fishery preferentially targets very young individuals, an extension of the closed season from March to July would be recommendable to guarantee the reproductive potential of the spawning stock.

Keywords: oocyte development; POF; Lutjanidae; Brazilian north coast; Amazon; sustainability development objective of the United Nations—SDO#14

Key Contribution: Reproductive biology and spawning period of the red snapper on the Amazon continental shelf.

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1. Introduction

Since the 1960s, stocks of the southern red snapper, *Lutjanus purpureus* (Lutjanidae), have been exploited intensively on Brazil's northern continental shelf, using the two principal fishing systems of vertical lines and "manzuá" traps [1,2]. Despite this long history of exploitation, the social, ecological, and economic aspects of this fishery are still poorly understood.

Three quarters (75%) of this *L. purpureus* catch is destined for export, with the remaining 25% of the fish being channeled to the domestic market [2]. In Brazil, these snappers are sold in fish markets and stores, sometimes in the form of fillets [2–4]. Because this species commands a high price as an export commodity, catches are often underreported, and monitoring is unreliable, resulting in a mismatch between the few available catch statistics and the volume reported by the Brazilian foreign trade control system SISCOMEX [2,3,5].

Export-size specimens, which typically weigh less than 900 g, are juveniles, and are usually caught over gravel beds or rhodolite reefs [3,6,7]. This preference for smaller individuals, together with the high price of the fish, drives local interest in participation in the local snapper fishery, and it has been estimated that the number of clandestine vessels operating in the region is even larger than that of the licensed ones [3]. This demand appears to be driving growth overfishing, which occurs when large quantities of individuals smaller than the size of first sexual maturity are harvested, as shown by data collected from the fishing ports at which the catches are landed [8–11].

The traditional practice of exporting smaller specimens has stimulated research into the reproductive strategies of the species, which provide some data for the calculation of estimates of recruitment rates. Given this, the classic management measures based on a minimum capture size determined by the size at first sexual maturity, the regulation of net mesh sizes, and the establishment of official fishing seasons or no-go areas have been replaced or complemented by more dynamic strategies, based on ultrastructures, such as cellular and DNA analyses [3,12–14].

The traditional hypotheses on the possible reproductive migratory patterns of *L. purpureus* were refuted by Freire [3], who proved that the species engages in reproductive aggregations typical of snappers (family Lutjanidae), in the region of the newly discovered Amazon reef system [7]. Since this system was identified, the assessment of the impacts generated by local fisheries has become an urgent priority [2].

The southern red snapper has external fertilization, with spawning occurring continuously throughout the year, but with two principal peaks as follows: one of greater intensity during the first quarter and a secondary peak in October [13,15,16]. Freire [3] recently confirmed that the spawning peak of *L. purpureus* occurs between January and March, which coincides with the period of maximum discharge of the Amazon River.

The first sexual maturation (L_{50}) of *L. purpureus* has been estimated at a female total length of between 39 cm and 46 cm [13,14]. However, the most recent study [3] has estimated a furcal length of 32.1 cm.

A number of methods have been developed in recent years for the analysis of reproductive patterns, although the assessment of the phases of oocyte development, and the association of these phases with specific periods and environmental parameters provide fundamental insights for the conservation and management of fish stocks [17,18]. One important stage of oocyte development is the follicular body or postovulatory follicle (POF) of the follicular cells that arise from the empty follicles following spawning. The identification of POFs is fundamental to confirm the effective periods of spawning, which is essential for the effective management of commercial fisheries, especially in the case of high-value species, such as *L. purpureus* [2].

The characteristics of the POF and the timing of its degeneration phases have been analyzed in a number of different aquatic organisms [19–29], reinforcing the importance of understanding this cell phase to ensure the accurate delimitation of the spawning period. Given the lack of studies that have focused on the reproductive patterns of *L. purpureus*, and the urgent need for effective management measures for the stocks of this species, especially considering the commercial focus on the smaller individuals, the present study provides new insights into its reproductive parameters. This study is based on recent biological data, which indicate certain shifts in these characteristics, in comparison with previous studies.

The present study identified the reproductive period of *L. purpureus* based on the microscopic analysis of the principal cell structures involved in the spawning process, which are as follows: hydrated oocytes (HOs), which indicate imminent spawning; postovulatory follicles (POFs), present following recent spawning; atretic oocytes (ATPs), which arise late in the spawning process, and at the onset of the regenerative process; and atresia (ATY), which denotes total regression following the spawning process.

The chronology of the involution of the gonads of *L. purpureus* was compiled to provide diagnostic tools that can be used as management parameters. The identification of POFs appears to be an effective strategy for the delimitation of the reproductive period, especially in the case of a vulnerable species under intense fishing pressure [23,24,30].

2. Materials and Methods

2.1. Study Area

The specimens analyzed here were collected by the commercial fishing fleet operating on the Amazon continental shelf (Figure 1), an area that stretches along the coast of northern Brazil, between Cabo Orange, in the state of Amapá (51° W), and São Marcos Bay, in the state of Maranhão (46° W). This area is dominated by sedimentary sand banks with gravel [31], which are deposited by the Amazon River, which forms a massive freshwater plume that extends far out into the tropical North Atlantic, with its size varying seasonally in accordance with regional rainfall patterns and the discharge of the Amazon [32].

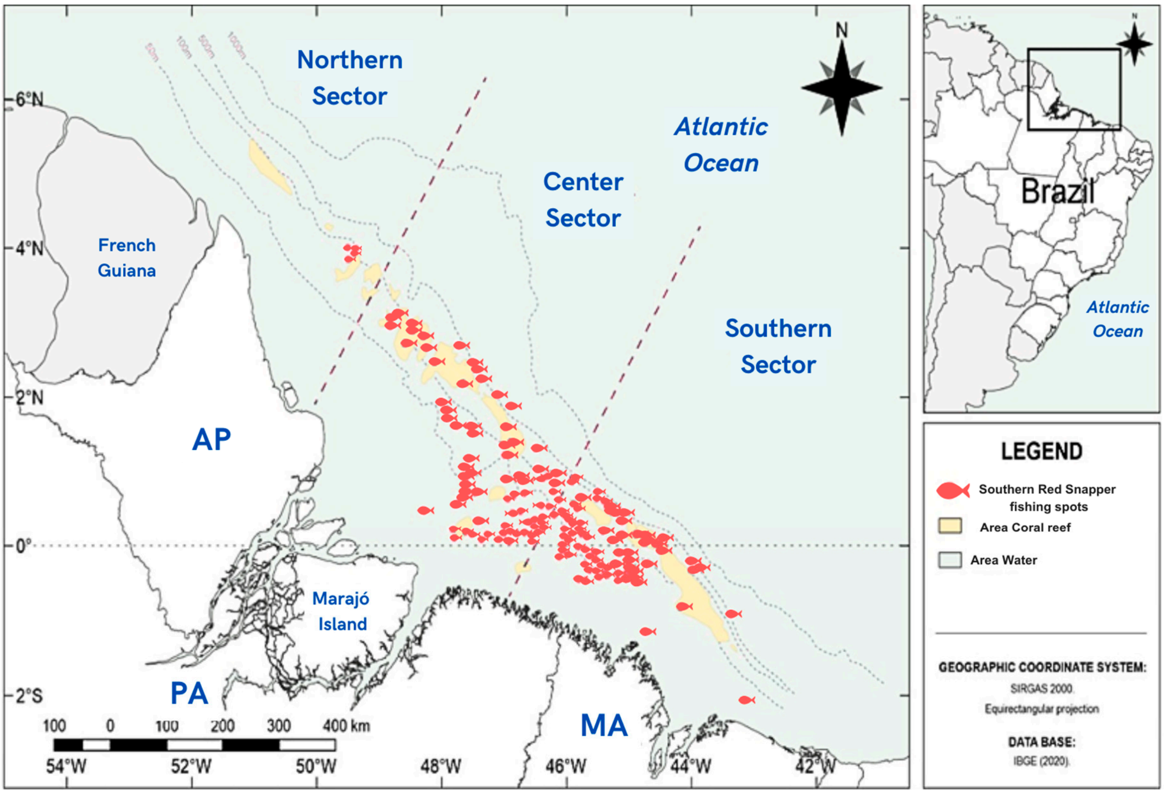

Figure 1. Fishing grounds of the southern red snapper (*Lutjanus purpureus*) on the Amazon continental shelf. The area is distributed off the coasts of the Brazilian states of Amapá (AP), Pará (PA), and Maranhão (MA). Adapted from [7].

A large coral reef area of approximately 56,000 km^2 has recently been identified on the Amazon continental shelf [7,33]. This reef system has unique characteristics that make it a hotspot for many endemic species [33]. A number of commercial fisheries focus on this area, including that of spiny lobsters and southern red snapper [7].

2.2. Collection and Laboratory Screening of the Biological Samples

Samples were collected between May 2016 and February 2018, through the Northern Fishing Improvement Project (FIP), with the snappers being obtained from the local *Lutjanus* fishery during the fishing season established by Brazilian Normative Instruction number 42 of 27 July 2018, which runs from 1 May to 15 December. In the laboratory, the specimens were identified using taxonomic keys [34–36] and their sex was determined. Their total length (TL) in centimeters was then measured from the anterior extremity of the snout to the end of the upper lobe of the caudal fin, and they were weighed to determine their wet weight (W) in grams.

After this initial processing, the gonads were extracted and examined macroscopically to determine their maturation stage, based on the scale proposed by Alves [37], with some modifications, and the nomenclature proposed by Brown-Peterson et al. [26]. Each specimen was thus assigned to one of three (in the males) or four (females) classes as follows: IMM (immature), DEV (developing, not applied to the males), SPW (spawning capable), or REG (regressing or regenerating).

2.3. Histology and Reproductive Indicators

The gonads were fixed in Bouin solution (15 parts of picric acid, 5 parts of formaldehyde, and 1 part of acetic acid) and once fixed, the organs were inserted into histological cassettes for the preparation of slides following the standard protocol for the extraction of histological sections developed by Vazzoler [38]. One histological slide with two sections was prepared for each gonad, which were first examined to identify, count, and measure the structures indicative of spawning, i.e., hydrated oocytes (HOs), postovulatory follicles (POFs), atretic oocytes (ATPs), and evidence of atresia in the muscle bundle (ATY) (Figure 2). Histological description and classification of the developmental stages followed the standard terminology (Table 1) [26,39,40]. In addition to the quantitative description of cell types, the area of the POFs identified in the slides was calculated in micrometers (μ) using the Zen 3.4 Blue edition software, linked to a Zeiss Axio Scope A1 microscope [23].

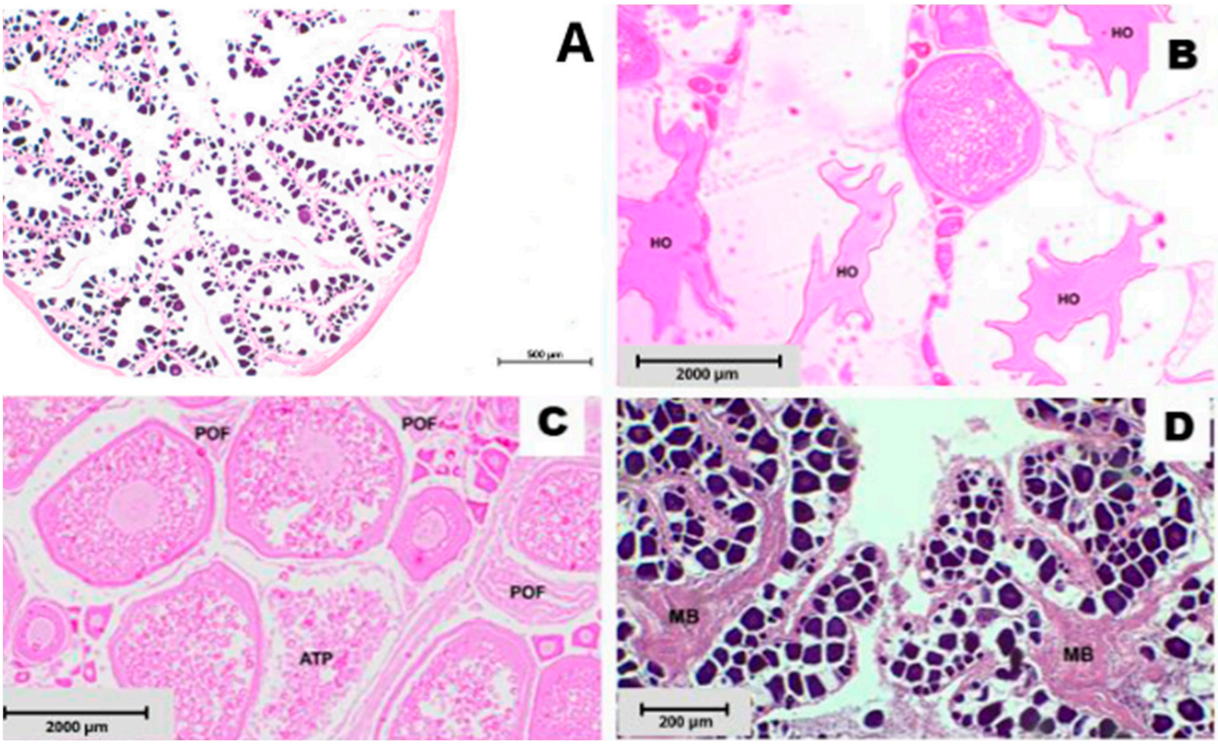

Figure 2. Histological sections showing the oocyte development stages of the *Lutjanus purpureus* specimens obtained from the Amazon continental shelf between 2016 and 2017. (**A**) immature ovary, (**B**) actively spawning ovary in the spawning capable substage (HO = hydrated oocyte); (**C**) recently spawned ovary (POF = postovulatory follicle, ATP = atretic oocyte, indicating cell death); (**D**) ovaries in the regression stage, with thickened muscle bundles (MB), thickened and irregular ovarian walls, and atresia (which differs from the immature stage).

Table 1. Terminology used for the histological stages of the gonads of *L. purpureus*, following Brown-Peterson et al. (2011) [26]. PG = primary growth; CA = cortical alveoli; Vtg1 = primary vitellogenic; Vtg2 = secondary vitellogenic; Vtg3 = tertiary vitellogenic; MO = maturing oocyte; GVM = germinal vesicle migration; GVBD = germinal vesicle breakdown.

Phase	Previous Terminology	Macroscopic and Histological Features
Immature (never spawned)	Immature, virgin	Small ovaries, often transparent, with indistinct blood vessels. Only oogonia and PG oocytes present. No atresia or muscle bundles. Thin ovarian wall and little space between the oocytes
Developing (ovaries beginning to develop, but not ready to spawn)	Maturing, early developing, early maturation, mid-maturation, ripening, previtellogenic	Enlarging ovaries, blood vessels becoming more distinct. PG, CA, Vtg1, and Vtg2 oocytes present. No evidence of POFs or Vtg3 oocytes. Some atresia may be present. Only PG and CA oocytes are present in the early developing subphase.
Spawning capable (fish are developmentally and physiologically able to spawn)	Mature, late developing, late maturation, late ripening, total maturation, gravid, vitellogenic, ripe, partially spent, fully developed, prespawning, running ripe, final MO, spawning, gravid, ovulated	Large ovaries, blood vessels prominent. Individual oocytes visible macroscopically. Vtg3 oocytes or POFs present in batchers. Atresia of vitellogenic and/or hydrated oocytes may be present. Early stages of MO may be present. Actively spawning subphase: oocytes undergoing late GVM, GVBD, hydration or ovulation.
Regressing (spawning ceased)	Spent, regression, postspawning, recovering	Flaccid ovaries, blood vessels prominent. Atresia (any stage) and POFs present. Some CA and/or vitellogenic (Vtg1, Vtg2) oocytes present.
Regenerating (sexually mature, reproductively inactive)	Resting, regressed, recovering, inactive	Small ovaries. Blood vessels reduced, but present. Only oogonia and PG oocytes present. Muscle bundles, enlarged blood vessels, thick ovarian wall and/or gamma/delta atresia or old, degenerating POFs may be present.

The POF is the remnant membrane of the oocyte that persists after spawning, which is an important indicator of the spawning period, and provides a measure of the age of the follicles, based on the degree of degeneration of this structure, which lasts 24 h, on average. During this period, it changes shape as it shifts from spawning to the total degeneration of the follicle [19–22]. The phases of this degeneration are classified as recent, intermediate, and old (Table 2; Figure 3).

Table 2. Stages in the degeneration of the postovulatory follicle and their duration. Adapted from [19–22].

Structure	Duration	Description
Recent POF	6 h	The remaining membranes (theca and granulosa) are easily distinguished from each other, with the basal membrane still intact. The follicular cells are shaped like a twisted cord. The lumen is clearly visible.
Intermediate POF	12 h	Advanced degenerative process in the follicular cap, sinusoidal alignment still present, but with a considerable reduction of the lumen. Granulosa minor.
Old POF	24 h	Lumen not visible, smaller follicles, absence of the sinusoidal alignment, follicular layers loosened.

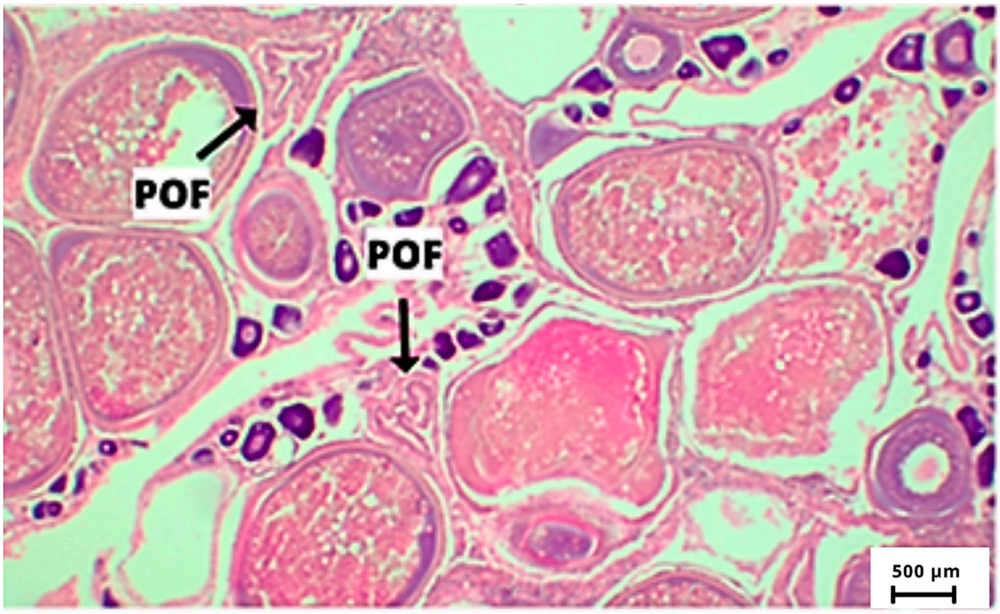

Figure 3. Postovulatory follicles (POFs) in the intermediate degeneration phase (2), indicating that spawning took place approximately 12 h ago.

2.4. Data Analysis

The variation in the number of cells of each type, as well as the area of the POF, was evaluated among months and specimen size classes using the median tests of Scheirer–Ray–Hare [41] and the Kruskal–Wallis test, considering $\alpha = 0.05$ in both cases. A redundancy analysis (RDA), a direct linear ordering method, was also applied. This method does not need to satisfy the assumptions of variance analyses, given that the permutations are run directly on the data. In this approach, the response variables are projected onto a system of axes, in which axis 1 explains a given percentage of the variability in the data set, axis 2 explains the next smallest percentage, and so on, to determine any potential relationships between the two sets of data.

Separate matrices were constructed for each dependent variable, in which each row was a sample with the number of each cell type per specimen. These matrices were then related to a second, "treatment" matrix, in which the independent variables (months, years, and length and weight classes) were added one by one. For this analysis, the length classes were TL1 = 27–35 cm, TL2 = 35.1–40 cm, TL3 = 40.1–45 cm, and TL4 = 45.1–50 cm, and the weight classes were W1 < 200 g, W2 = 201–500 g, W3 = 501–800 g, W4 = 801–1000 g, and W5 > 1000 g. Following the RDA, the Monte Carlo test was run with 9999 permutations to assess the robustness (significance) of the results.

The analyses were run in the Vegan package [42–44] of the R Studio® software version 4.0.3 (R Development Core Team, 2020) and CANOCO 7.0 (Software for Canonical Community Ordination; Copyright Petr Šmilauer © 2012–2021).

3. Results

A total of 120 female *L. purpureus* were analyzed in the present study. These individuals had a mean total length of 41.5 ± 4.74 cm (Table 2). All the reproductive cell types were identified in the female specimens analyzed, with peaks of HO in July and November, which were not significant (F = 0.84, $p > 0.05$), and POFs, in April (F = 2.57 $p > 0.05$). Atretic oocytes and atresia of the regressed individuals were found in larger quantities in August and September (F = 0.19, $p > 0.05$) (Figure 4 and Table 3).

The frequency of the different cell types did not vary significantly (F = 0.14; $p > 0.05$) among the body length classes (Table 4), although the frequency POFs did tend to decrease with increasing body length, as shown in particular in the 43.1–50 cm TL class (Figures 5–7).

All the independent variables together accounted for 97% of the variability in the data, and the RDA ordination plot indicated a high level of correlation between the POFs in April and the HO in July and September (Figure 5). The decomposition of the axes by the length and weight classes indicated a higher correlation of POF with the TL4 and W5 classes, and of HO with the TL2 and W2 and W3 classes, which denotes spawning from the TL2 class onward (Figure 5). A decreasing trend in the quantity and area of the POFs was observed from the 43.4–45.4 cm (TL3 and TL4) class onward, which correspond to snappers weighing more than 650 g (Figure 5).

The analysis of the histological sections revealed seven individuals with POFs, all of which were captured in April, which indicates that these individuals spawn during the closed season. All the POFs analyzed were in the intermediate phase (age 2).

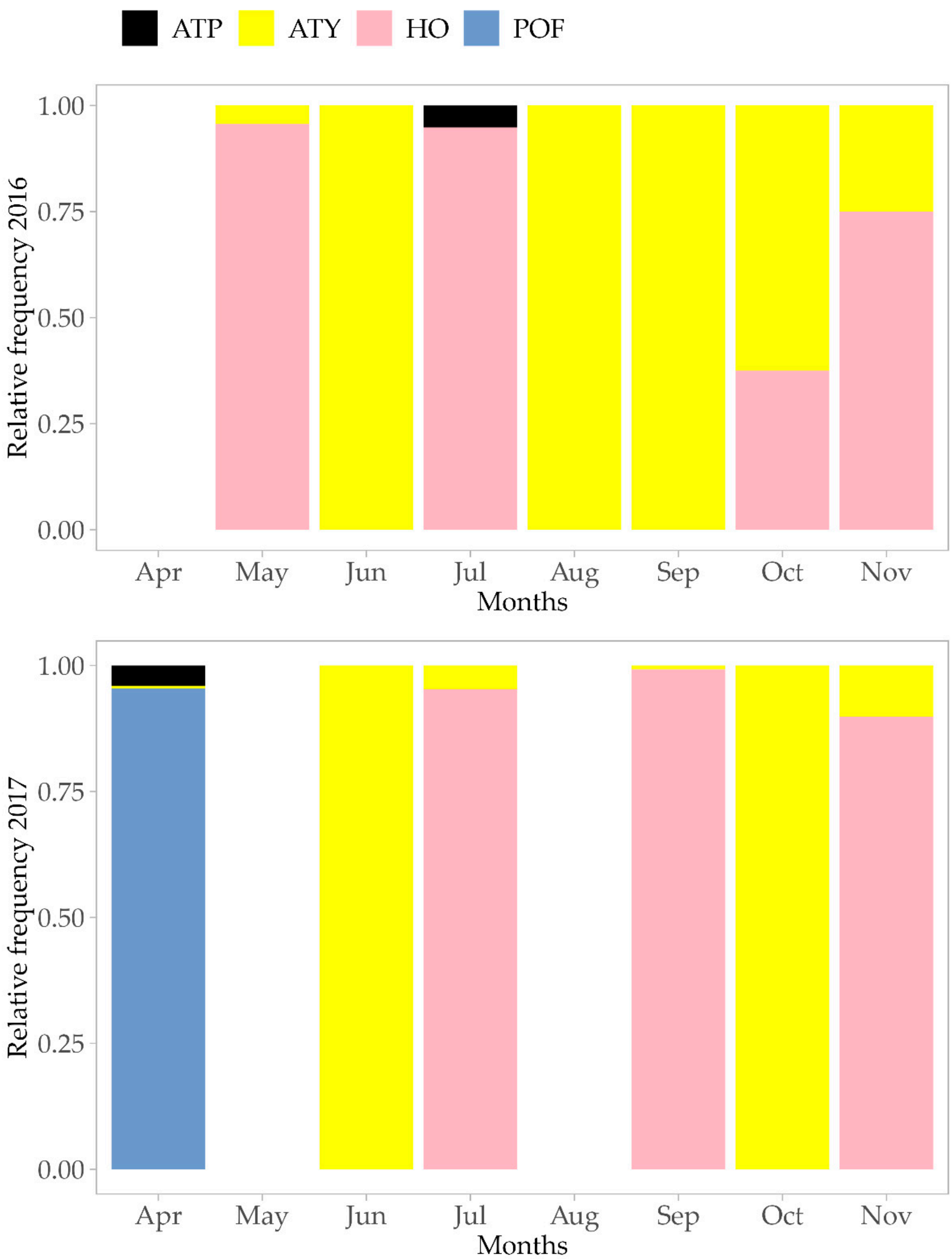

Figure 4. Monthly variation in the relative frequency of the different types of cell that are indicative of spawning in the *Lutjanus purpureus* specimens obtained from the Amazon continental shelf in 2016 and 2017. HO = hydrated oocyte (pink); POF = postovulatory follicle (blue); ATP = atretic oocyte (black), and ATY = tissue in atresia (yellow).

Table 3. Number of *Lutjanus purpureus* samples analyzed per month by length class between 2016 and 2017.

Year	TL Class (cm)	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Total
	27–28					2	1			3
	28–29		1			1				2
	31–32					1				1
	32–33					1				1
	34–35				2		1	1		4
	35–36			1		2				3
	36–37					1				1
	37–38						1			1
	38–39					1	1		3	5
	39–40			1		1		3		5
2016	40–41				1	1	2			4
	41–42				2	1	1	1		5
	42–43		1		2			2	5	10
	43–44			1	1	1		2	4	9
	44–45			1	5		1			7
	45–46					2		1		3
	47–48				1	1		1	1	4
	48–49					1	1	1		3
	49–50				1			1		2
	50–51								1	1
	54–55						1			1
	27–28									
	28–29									
	31–32									
	32–33							1		1
	33–34								1	1
	34–35								1	1
	35–36	1								1
	36–37	1								1
	37–38								2	2
	38–39	3		1						4
2017	39–40			1	2		1		1	5
	40–41					1		1	1	3
	41–42	1		1		2		2	1	7
	42–43	2	1		2	1	1		2	9
	43–44	1							1	2
	45–46	1					1		1	3
	46–47						1			1
	47–48	2								2
	49–50								1	1
	50–51	1								1
	Total	13	3	7	19	21	14	17	27	120

Table 4. Results of the Kruskal–Wallis and Scheirer–Ray–Hare tests for the number of reproductive cells (HO = hydrated oocyte, POF = postovulatory follicle, ATP = atretic oocyte, and ATY = tissue in Atresia) per total length class (TLC) of the *Lutjanus purpureus* specimens obtained from the Amazon continental shelf between April and November in 2016 and 2017. DF = degrees of freedom; SQ = sum of squares. The dashed lines indicate insufficient data for the statistical analysis. Significant *p* values are highlighted in bold type.

Dependent Variable	Factor	DF	SQ	H	*p*
HO	TLC	3	642.1	31.883	0.3635
	Month	7	1815.8	9.016	0.25151
	TLC:Month	17	5778.4	286.919	0.03748
	Residual	93	16,233.0		

Table 4. *Cont.*

Dependent Variable	Factor	DF	SQ	H	*p*
ATY	TLC	3	1562	17.818	0.6189
	Month	7	3419	38.994	0.79129
	TLC:Month	171.243	14.175	0.65468	0.65438
	Residual	93	88,104		
POF	TLC	3	--	5.4868	0.1394
	Month	--	--	--	--
	TLC:Month	--	--	--	--
ATP	TLC	--	--	--	--
	Month	7	--	5.9117	0.5501
	TLC:Month	--	--	--	--

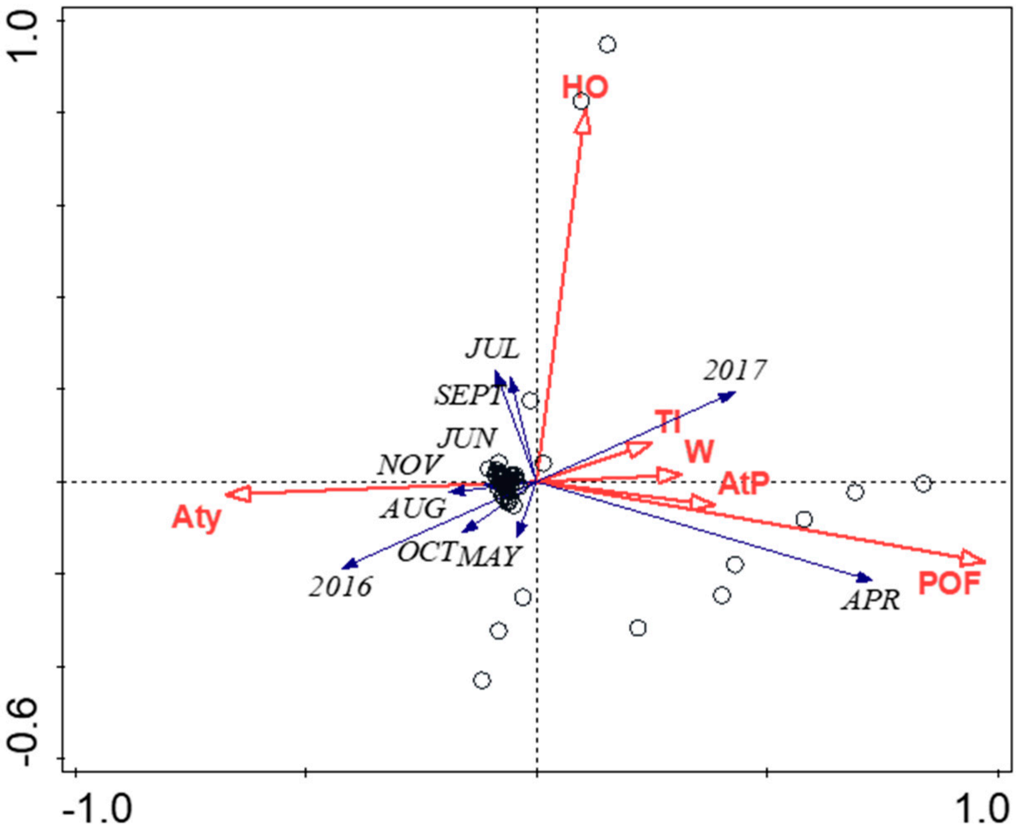

Figure 5. Ordination plot of the cell types indicative of spawning (HO = hydrated oocyte, POF = postovulatory follicle, AtP = Atretic oocyte, and Aty = presence of atresia) and the weight (W in grams) and total length (TL in cm) classes resulting from the redundancy analysis (RDA) of *Lutjanus purpureus* specimens obtained from the Amazon continental shelf in relation to the months of April through November in 2016 and 2017. W1 < 200 g; W2 = 201–500 g; W3 = 501–800 g; W4 = 801–1000 g; W5 > 1000 g; TL1 < 27 cm; TL2 = 28–35 cm; TL3 = 35.1–40 cm; TL4 = 40.1–45 cm, TL5 = 45.1–50 cm.

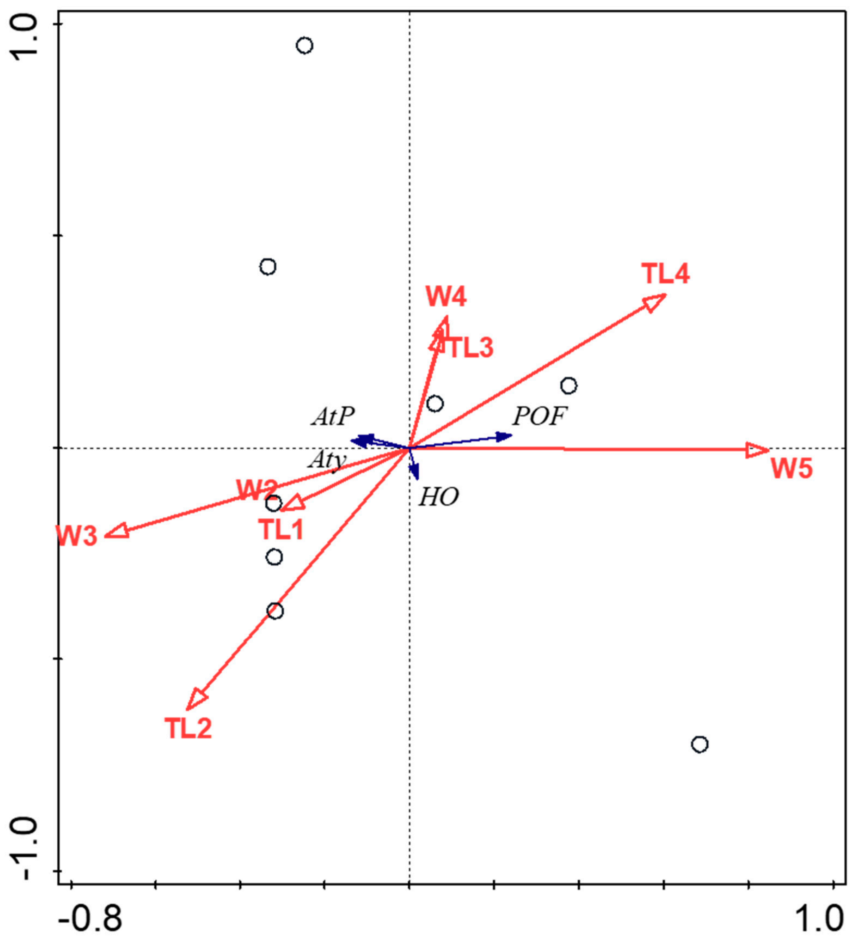

Figure 6. Ordination plot of the spawning cell types (OH, POF, AtP, and Aty) and the weight (W) and total length (TL) classes resulting from the redundancy analysis (RDA) of the *Lutjanus purpureus* specimens obtained from the Amazon continental shelf in 2016 and 2017. W1 < 200 g; W2 = 201–500 g; W3 = 501–800 g; W4 = 801–1000 g; W5 > 1000 g; TL1 < 27 cm; TL2 = 28–35 cm; TL3 = 35.1–40 cm; TL4 = 40.1–45 cm, TL5 = 45.1–50 cm. HO = hydrated oocyte, ATY = atresia, ATP = atretic oocyte, POF = postovulatory follicle.

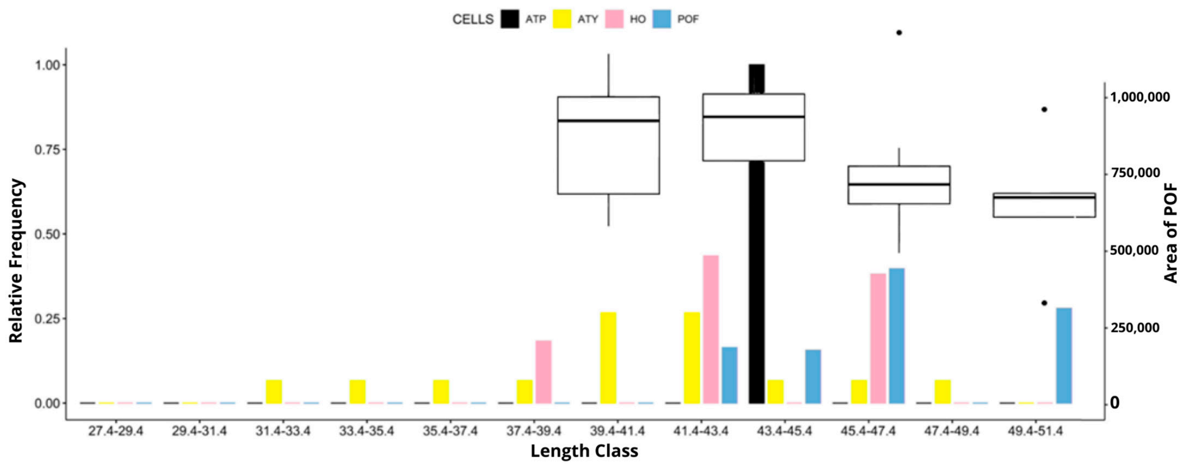

Figure 7. Relative frequency (*y* axis) of the spawning cell types (HO = hydrated oocyte, POF = postovulatory follicle, ATP = atretic oocyte, and ATY = presence of atresia) and the area of the POFs (*z* axis—box plot of the mean, standard deviation, and maximum and minimum values) per total length class (*x* axis) of the *Lutjanus purpureus* specimens obtained from the Amazon continental shelf between 2016 and 2017.

4. Discussion

Fishing bans and minimum size limits for snapper catches have been implemented in Brazil since 1984 [45], albeit with little or no practical effect in terms of the maintenance of spawning stocks or the modification of the fisheries [46,47]. Since the mid-1960s, when snapper fisheries first became established on the Amazon continental shelf, *L. purpureus* has been targeted by regulations, in response to its high commercial value in comparison with the other local species, which induced an exponential growth in fishing effort and catches [1,48–50].

The current scenario of the *L. purpureus* stocks on the Amazon continental shelf reflects ineffective attempts at management (see Supplementary Material) derived from the unique characteristics of the region, the reduced potential for low enforcement, and the frequent opportunities for corrupt actions in the commercial exploitation of snapper stocks. This is not only a threat to the sustainability of these stocks, but also a potential generator of poverty in the region. The migration of the snapper fishing fleet from northeastern Brazil to the Amazon continental shelf has resulted in a major increase in the pressure on the *L. purpureus* stocks in this region [50].

Overall, projections for the snapper fisheries of northern Brazil envisage a gradual but short-term trend of collapse, reflecting a cyclical process given that, even if *Lutjanus purpureus* is listed as a vulnerable species [51], fishing effort is likely to remain intense, with a mean catch size (total length) of 28 cm [3,50] (Figure 7).

The confirmation of the occurrence of reproductive processes in *L. purpureus* during months outside the closed season is of critical importance for the understanding of the life history of the species and its potential adaptability to changes in environmental conditions [52–55]. Despite the limitations of the present study, which was restricted to the official fishing season, the identification of the reproductive continuity of *L. purpureus* was extremely important because it extends beyond the legally sanctioned closed season (December through April).

This emphasizes the need for the integration of alternative approaches for the more reliable assessment of the reproductive dynamics of snappers, given the imminent risk of the collapse of fisheries through the accumulation of both historic and more recent overfishing events in traditional fishing countries, such as China and Indonesia [56–58]. Better controls of the fleets, in particular clandestine operations, would be one potentially effective option, given the irresponsible behavior of these actors, despite legal restrictions, such as the tracking of boats larger than 15 m and annual licensing.

Energetic adjustments that optimize reproductive processes to ensure the continuity of a population appear to be relatively common biological phenomenon in species faced with intense pressure from fisheries. Recently, a mathematical model of productivity "enhancement" has been proposed, based on the predator (fishery)–prey relationship [59–61]. An additional factor is now climate change, which is especially relevant in the case of *L. purpureus*, which is associated with coral reefs, habitats known to be impacted profoundly by increasing temperatures [7,57].

Up until the early 2000s, the approach to the management of *L. purpureus* stocks were still based entirely on macroscopic analyses which, while practical, will tend to overlook ultrastructural processes, such as the continued appearance of POFs after the end of the closed season. Nuñez and Duponchelle [62] and, more recently, Brown-Peterson et al. [26] attempted to reduce the mismatch between the macro- and microscopic observation of the gonads by developing a new scale, which included histological data. Because the follicles are formed and then disappear within a period of around five days [23], a significant amount of spawning may still occur during the fishing season. In addition, the POFs have an even shorter cycle in tropical environments, and are thus even more difficult to detect when water temperatures exceed 27 °C [7,23].

The highest percentage of hydrated oocytes (HOs), which indicate imminent spawning, was recorded in July, in specimens in the 42 cm total length class, even though HOs are found in fish as small as 38 cm. In the present study, the POFs also decreased in size with increasing fish body length, which may reflect a reduction in the reproductive capacity of older individuals, as observed in other bony fish [63]. The shape of the POFs changes allometrically, given that the surface area of the POF along the lamellar epithelium decreases at a slower rate than the total area of the follicle. Over the course of its degeneration, then, the shape of the POF shifts from irregular to semiretangular and, finally, triangular, providing an additional morphological criterion for the determination of the stage of the POF [64].

In addition to the difficulties of detecting ultrastructures in tropical environments, multiple spawning patterns, which are common in *L. purpureus* [65], *L. campechanus* [66–68], *Lutjanus synagris* [69], *Lutjanus peru* [70], *Lutjanus guttatus* [71], and *Lutjanus alexandrei* [72], and include asynchronous oocyte development in the mature (SPW) females, indicate the production of multiple batches of eggs during the spawning period. Snappers typically spawn in reproductive aggregations, which can be monitored and mapped by divers or underwater camera systems, or through the analysis of the variation in catches. Fishing grounds with higher than average catches per unit effort (CPUEs) will likely represent the areas of reproductive aggregations, as observed in *Lutjanus cyanopterus* [73], *Lutjanus cubera* [74], *Lutjanus jocu* and *L. synagris* [75], and *Lutjanus gibbus* [76].

Extensive breeding periods are common in many tropical fish species [68,77–81] and the recognition of the spawning period as a critical moment in the life cycle of these species should be a fundamental consideration in the development of public fishery policies. In the present study, the identification of the POFs and HOs indicates the need for a reappraisal of current regulations, given that a reproductive peak was found in the month of July, in the middle of the official fishing season, threatening stock recruitment. The more effective monitoring and repression of illegal fishing should also be a priority, given that losses may be far greater than those estimated in the most recent estimates. In fact, Freire et al. [50] concluded that the available catch statistics are totally unrealistic, based on a comparison with the records of *L. purpureus* exports published on the official site siscomex.gov.br [5].

Because the present study recorded individuals that were able to reproduce below the L_{50} threshold established for the species, and during the official fishing season, it would be relevant to consider the implementation of new regulations to protect the breeding stock, such as the use of more selective fish traps. The fact that this study reconfirms Freire's [3] findings on the L_{50} further reinforces the need to review the current measures used to limit pressures on *L. purpureus* stocks. The availability of updated data on reproductive rates is a major contribution to the control of impacts on fishery stocks.

In addition to the existing studies of snapper fisheries, interdisciplinary research will likely be important to protect stocks most effectively, including a focus on the social actors, and their motivations and internal factors that drive their fishing activities. One possibility here is the application of vulnerability indices, which can be used to assess the influence of the success of a local fishery, including the ecological, socioeconomic and socioecological vulnerability of a population [82].

In addition to biological research, such as that of the present study, there is a clear need for more detailed scientific studies of the Amazon reef, which is a highly sensitive and vulnerable environment, which is crucial to the stocks of many species, but is also affected by intense fishing activity [7,31]. Microscopic analyses aligned with the macroscopic assessment of the involution period of aquatic organisms are proving to be highly effective [26,78,83,84], although other aspects of the reproductive process also require attention, such as the larval life stage and the influence of the lunar phase on spawning patterns [85,86].

What is clear is that fishing is having damaging effects on the *L. purpureus* stocks of the Amazon continental shelf, reducing their potential for recruitment and, ultimately, their long-term survival [57,58]. Given this, in addition to the existing regulations and a potential extension of the closed season, the more effective control of logbooks and clandestine vessels is clearly needed. Because the snapper fishery is highly socially significant in the region, the vulnerability of this activity to illegal and unsustainable practices must also be carefully considered.

Better controls of the flow of raw materials in the fishing industry, associated with the more systematic use of logbooks, which are already required, may also limit the potential for unrealistic production records. This approach would be complemented by more detailed records of the size distribution of the catches landed at Amazonian ports. As well as identifying spawning grounds and controlling fishing activities, this approach would also help to reduce the damage caused to the species' stocks.

Even so, further research, with more extensive sampling that also covers the closed season, will be needed to provide realistic estimates of current stocks. A more accurate definition of the spawning period will require the collection of samples throughout the year, including the closed season, in order to define the life cycle of the species more reliably [71,72,87]. In the meantime, more effective controls and monitoring of the industry, including fishing licenses and the establishment of quotas according to the capacity of each vessel, would contribute to the regulation of catches, given the current total lack of controls.

5. Conclusions

Spawning structures (POFs) were found in *Lutjanus purpureus* specimens in months outside the closed season, indicating that the species may be reproducing during the fishing season, when there are no controls on catches.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes9040136/s1 Table S1: Brazilian regulations governing the *Lutjanus purpureus* fishery, in chronological order.

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Institutional Review Board Statement: The specimens used in this study were obtained through donations from the fishing industry of dead individuals. During the methodology applied, the authors carefully followed the recommendations of the Ethics Committee on the use of animals.

Data Availability Statement: The data analyzed during the study is not made available to the public, but can be made available to the corresponding author upon reasoned inquiry.

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