

Reproductive Biology of the Rivulated Parrotfish (*Scarus rivulatus*) in the Seribu Islands: Fecundity, Sex Ratio, Gonadosomatic Index, and Spawning Patterns

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Abstract

Scarus rivulatus is a protogynous hermaphroditic parrotfish closely associated with coral reefs and plays an important ecological role in maintaining reef health through grazing activities. However, information on its reproductive biology in the Seribu Islands, Jakarta, Indonesia, remains limited, although such knowledge is important for sustainable fisheries management. This study aimed to examine the sex ratio, gonadosomatic index (GSI), fecundity, and spawning pattern of *S. rivulatus*. A total of 2,425 specimens were collected monthly from January to December 2022. Sex identification was based on body coloration and morphology and confirmed by gonadal examination, with individuals classified as female, initial-phase (IP) male, or terminal-phase (TP) male. Total length and body weight were measured, and gonads were analyzed to determine sex, GSI, fecundity, oocyte diameter distribution, and histological characteristics. The overall sex ratio was 1:0.8 (male:female), with females dominating smaller size classes and males occupying larger ones, indicating a protogynous reproductive strategy. GSI values varied throughout the year, with spawning peaks in February, September, and December. Fecundity ranged from 17,013 to 178,813 oocytes and showed positive correlations with total length and body weight. Oocyte diameter distribution and histological observations indicated asynchronous ovarian development, suggesting partial spawning and gradual oocyte release throughout the year. These results underscore the importance of protecting larger individuals and implementing seasonal closures and size-based harvesting regulations to ensure population sustainability. This study provides baseline data that can support future management efforts, and further research should explore sex transition processes and larval recruitment dynamics to strengthen ecosystem-based fisheries approaches.

Keywords: Parrotfish, spawning pattern, sex ratio, fecundity, Seribu Island, gonadosomatic index

Introduction

Scarus rivulatus is a major herbivorous fish in Indo-Pacific coral reef ecosystems and plays a crucial role in maintaining the ecological balance by controlling macroalgal growth and supporting coral recruitment (Welsh and Bellwood, 2012; Gusrin et al., 2020; Lange et al., 2020; Tuwo et al., 2021; Yanti et al., 2023; Nurfajar et al., 2024). This species primarily grazes on the epilithic algal matrix (EAM), thereby playing an essential role in algal removal and reef resilience (Gordon et al., 2015). The ecological role of parrotfishes, including *S. rivulatus*, in regulating algal communities and sustaining ecosystem functions has been widely confirmed in global studies (Abu-Taweel et al., 2023;

Donovan et al., 2023). However, populations of *S. rivulatus* in the Seribu Islands, Indonesia, an ecologically important marine region, are under severe pressure due to habitat degradation, reef fragmentation, pollution, and unregulated fishing (Nurfajar et al., 2024). Since *S. rivulatus* is a protogynous hermaphroditic species, with individuals changing from females to males as they grow larger, size-specific impacts may alter its reproductive dynamics and threaten population sustainability, emphasizing the urgency of studying reproductive biology as a basis for conservation and fisheries management and highlighting the need for detailed reproductive studies to inform conservation and fisheries management strategies. Therefore,

understanding the reproductive characteristics of this species is essential for maintaining its population sustainability and ecological function.

Most studies on parrotfishes have emphasized their feeding ecology, habitat use, and functional roles in promoting reef resilience through grazing and bioerosion, while only few studies are investigating their reproductive biology in detail (Sievers *et al.*, 2020; Lange *et al.*, 2020; Abu-Taweel, 2023; Annandale *et al.*, 2024; Molina and Álvarez, 2024; Randazzo-Eisemann *et al.*, 2024). In particular, studies on the reproductive biology of *S. rivulatus* are limited, especially for Indonesia. Although some local studies have examined aspects of its reproduction, these studies are fragmented and have not provided comprehensive insights into hermaphroditism or the differentiation of male phases into initial phase (IP) and terminal phase (TP) individuals (Gordon *et al.*, 2016; Gusrin *et al.*, 2020; Fatihah *et al.*, 2021; Tuwo *et al.*, 2021; Yanti *et al.*, 2025). Conversely, the reproductive cycles and hermaphroditic traits of several *Scarus* species in coral reef ecosystems worldwide have been studied more extensively, providing valuable insights into spawning seasons, sex-change mechanisms, and reproductive potential. These findings have not only advanced biological understanding but have also informed practical fisheries management strategies, such as temporary seasonal closures to support stock sustainability (Bonaldo and Bellwood, 2008; Suzuki *et al.*, 2010; Taylor and Cruz, 2017; Sievers *et al.*, 2020). Recent global studies have highlighted the importance of understanding parrotfish reproductive biology for maintaining coral reef ecosystem resilience and supporting evidence-based conservation actions (Morgan, 2008; Abu-Taweel *et al.*, 2023).

However, research on the reproductive biology of *S. rivulatus* in Indonesia, particularly in the Seribu Islands, remains scarce and poorly understood. Existing data on key reproductive parameters, including sex ratio, gonadosomatic index (GSI), fecundity, and spawning periodicity, are limited and fragmented, and their associations with habitat quality remain unclear. This paucity of information constrains the formulation of effective, evidence-based conservation and management strategies for this ecologically important species, which contributes significantly to the maintenance of coral reef structure, productivity, and resilience (Morgan, 2008).

The present study represents the first comprehensive investigation of the reproductive biology of *S. rivulatus* in the Seribu Islands, focusing on sex ratio, GSI dynamics, and spawning patterns throughout an annual reproductive cycle. It also

provides a refined classification of males into two distinct reproductive phases—initial phase (IP) and terminal phase (TP)—to enhance the accuracy of interpreting reproductive strategies and sex-change mechanisms through the integration of histological and macroscopic gonad analyses. This combined methodological approach offers deeper insights into the timing and mechanisms of reproduction of *S. rivulatus* inhabiting coral reef systems that are increasingly affected by anthropogenic pressures. Bridging this knowledge gap is expected to advance scientific understanding and inform practical conservation actions, particularly in promoting the sustainable management of reef fish populations and coral reef ecosystems in the Seribu Islands.

This study aimed to comprehensively assess the reproductive biology of *Scarus rivulatus* in the Seribu Islands by analyzing the sex ratio, gonadosomatic index (GSI), and spawning patterns throughout the annual reproductive cycle. Specifically, this study sought to determine the reproductive characteristics and seasonal patterns that underlie the reproductive strategy of this species. The expected outcomes include detailed insights into key reproductive parameters that can serve as baseline data for future ecological and fisheries research. These findings are expected to strengthen the scientific foundation for effective management practices and contribute to the long-term sustainability of reef fisheries and coral reef ecosystems in the Seribu Islands.

Materials and Methods

This study was conducted from January to December 2022 in the waters of the Seribu Islands in the DKI Jakarta Province, Indonesia. Sampling locations were distributed across several islands with shallow coral reef ecosystems that serve as the primary habitat for *S. rivulatus*. Fish samples were collected from five locations (Karang Bongkok Island, Karang Congkak, Semak Daun, Karang Beras, and Air) (Figure 1) using Muroami nets. Sample identification and subsequent gonad histology analyses were performed at the Fisheries Biology Laboratory of the Faculty of Fisheries and Marine Science, IPB University.

Sampling procedure

Monthly sampling was conducted for all size classes (small, medium, and large). For each specimen, the total length (mm) and body weight (g) were measured using a fish measuring board and an analytical balance, respectively. The gonads were subsequently dissected, weighed, and preserved in 10% neutral-buffered formalin to ensure complete tissue submersion for fixation. All procedures adhered to the standard methods described by Effendie (1979).

Sex identification and classification

Sex identification was assessed by macroscopic examination and confirmed through histological verification. Specimens were initially identified based on secondary sexual characteristics (e.g., body coloration and external morphology) and subsequently confirmed by gonadal inspection after dissection of the specimens. The applied criteria were as follows: (1) females, absence of male traits with gonads containing oocytes at various developmental stages; (2) initial-phase (IP) males, external morphology resembling females, but with testes or testicular lobes present upon dissection, often accompanied by residual oogenic tissue indicative of sex transition; and (3) terminal-phase (TP) males, with distinctive male coloration and morphology with fully developed testes (Figure 2). Individuals exhibiting both ovarian and testicular tissues or showing histological evidence of transition were categorized as IP males. The determination of sex characteristics, both macroscopically and histologically, also followed the criteria described by Yanti *et al.* (2023) in their study on sex change and gonad maturity of *S. rivulatus* from the Seribu Islands, Indonesia. Histological preparations were performed according to the protocol described by Longenecker *et al.* (2020).

Sex ratio

The sex ratio was calculated using the following equation:

$$NK = \frac{\sum J}{\sum B} \dots \dots \dots (1)$$

where NK (sex ratio); $\sum J$ (number of male fish (individuals)); and $\sum B$ (number of female fish (individuals)). To determine whether the numbers of males and females were in balance (theoretical ratio 1:1), a chi-square (χ^2) test was applied using the following equation:

$$X^2 = \sum_{i=1}^n \frac{(O_i - E_i)^2}{E_i} \dots \dots \dots (2)$$

where: X^2 (chi-square value); O_i (observed frequency of male or female fish); and E_i (expected frequency of male or female fish 1:1).

Gonadosomatic Index (GSI)

The gonadosomatic index (GSI) was calculated to determine the gonadal maturation level:

$$GSI = \frac{GW}{BW} \times 100 \dots \dots \dots (3)$$

where: GSI (gonado somatic index); GW (gonad weight (g); and BW (body weight of sample fish (g)).

Fecundity

Fecundity was estimated using the gravimetric method. Each gonad was divided into three parts (anterior, median, and posterior). Subsamples were collected from each part, and the number of eggs was counted using a stereo microscope. Total fecundity was calculated using the following equation:

$$F = (G.V.X)/Q \times F \dots \dots \dots (4)$$

where: F (total fecundity); G (weight of all gonads (g); V (suspension volume (ml); X (fecundity of gonadal subsample (oocyte/ml); Q (weight of sample gonads (g)). The relationship between fecundity and body length is expressed by the following equation:

$$F = aL^b \dots \dots \dots (5)$$

where: F (fecundity (oocytes)); L (total length of fish (cm)); a and b are species-specific (constants). The oocyte diameter was defined as the length of the longest axis of the oocyte, measured using a calibrate ocular micrometer.

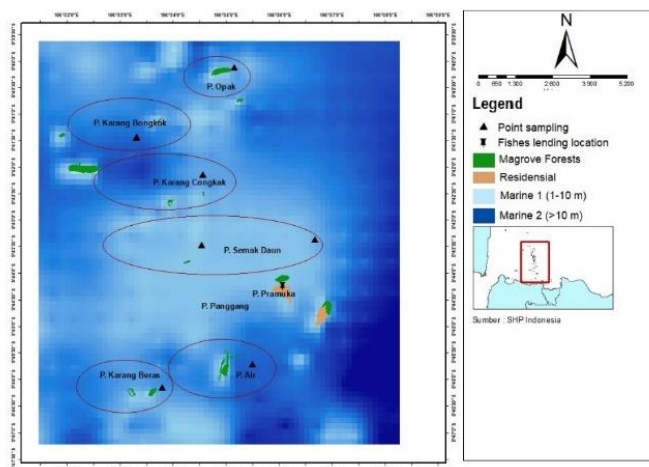


Figure 1. Sampling locations of *S. rivulatus* parrotfish on the Seribu Islands, Indonesia



Figure 2. External morphology of *S. rivulatus* across sex categories. (a) Female; (b) initial-phase (IP) male; (c) terminal-phase (TP) male

Egg diameter

The diameter of the oocytes was measured using a microscope equipped with an ocular micrometer. A total of 150 eggs per specimen were measured to determine the size range and oocyte diameter distribution at gonadal development stage III and IV. Oocyte diameter measurements were performed on GSI III and IV. Reproduction patterns were estimated based on the histological development of oocytes in the gonads and the distribution of egg diameter in GSI III and IV. The results of oocyte diameter measurements were converted into a histogram of oocyte diameter distribution. The pattern of oocyte size diameter distribution was analyzed descriptively by examining the mode of size distribution. The number of oocytes measured was 50 in the anterior, median, and posterior sections. Oocyte diameters were measured under a stereo microscope at 10×10 magnification.

Data analysis

The sex ratio was analyzed using the chi-square test to assess its conformity to a 1:1 ratio. GSI, fecundity, and egg diameter were analyzed descriptively and presented in tables or graphs to illustrate their variations by month and gonadal maturity stages.

Results and Discussion

Sex ratio

A total of 2,425 *S. rivulatus* specimens were collected from January to December 2022. The sample consisted of 1,323 females (54.6%) and 1,102 males (45.4%), including 524 initial-phase (IP) males and 578 terminal-phase (TP) males. Females were mostly found in the smaller size classes, whereas TP males dominated the larger size classes. IP males, representing transitional individuals from females to males, occurred within a total length range of 10.5–23.6 cm (Figure 3). The Chi-Square test showed that the overall sex ratio was 1:0.8 (male:female), which did not differ significantly from a balanced ratio (1:1) ($P > 0.05$). However, size-based analysis revealed a clear pattern, with females prevailing in smaller size classes and males

dominating larger size classes, suggesting protogynous sex change in this species. Specifically, females dominated the small size class (7.8–22.0 cm), IP males were found in the medium size class (9.6–22.0 cm), and TP males dominated the large size class (15.0–29.2 cm) (Figure 4a). The clear difference in body size between females, IP males, and TP males indicates a distinct size structure in the *S. rivulatus* population on the Seribu Islands

The results of this study showed a clear size-related pattern in the sex composition of *S. rivulatus*. This pattern reflects the protogynous characteristics of *S. rivulatus*, where individuals initially mature as females before undergoing a sex change to become males (Sakai et al., 2006; Taylor and Cruz, 2017; Tuwo et al., 2021; Abu-Taweel et al., 2023). The dominance of females in the small size class indicates that most young individuals have not yet undergone sex transition, whereas the dominance of TP males in a larger size class confirms that sex change occurs after reaching a certain size and age (Bonaldo and Bellwood, 2008). Previous studies have shown similar patterns in other tropical parrotfish species. According to Tuwo et al. (2021) and Barba (2010), tropical parrotfish populations typically show female dominance at smaller sizes and male dominance at larger sizes. This pattern underlines the biological mechanism of protogyny in maintaining reproductive balance and reflects how the population structure is linked to growth and maturation processes. This pattern of size-based sex distribution has important implications for the fisheries management of *S. rivulatus*. Understanding the dynamics of sex change can help establish appropriate minimum catch sizes to maintain population balance and ensure reproductive sustainability.

Temporal variations in the sex ratio provide additional insights into reproductive behavior. From January to March, the catches were dominated by males, whereas from April to December, more females were caught, with the sex ratio significantly skewed towards females during the peak spawning season in September. This phenomenon is likely related to spawning aggregation behavior, where females migrate to spawning sites in large numbers during the spawning period, whereas males tend to

maintain territorial areas near these sites. This seasonal shift is consistent with the findings of Welsh and Bellwood (2012), who indicated that during the spawning season, *S. rivulatus*, like many other hermaphroditic fish species, exhibits aggregation behavior, where individuals gather at specific spawning sites. Therefore, the tendency of females to dominate catches during certain months appears to be driven by temporal reproductive movements rather than population imbalance. This behavior often involves females migrating in large numbers to participate in mass spawning, whereas males establish and defend territories in the surrounding area, which can lead to higher visibility of females at aggregation sites (Sadovy and Colin, 2012).

The relatively balanced overall sex ratio in the Seribu Islands differs from the findings from several other locations in Indonesia, such as Spermonde (Tuwo *et al.*, 2021) and Tanjung Tiram (Aswady, 2019), where females are far more dominant. Freitas *et al.* (2019) also reported a sex ratio in *S. trispinosus* reaching 1:8. This contrast suggests possible site-specific influences on the demographic structure of *S. rivulatus*, such as local fishing intensity and habitat conditions. This balance in the ratio may indicate that the local population of *S. rivulatus* in the Seribu Islands still maintains a stable reproductive capacity, as in protogynous hermaphrodite species, even a small number of males can produce enough sperm to fertilize a large number of female eggs (Coscia *et al.*, 2016; Benvenuto *et al.*, 2017). Nevertheless, the lower proportion of large males from April to December may be an early indication of fishing pressure targeting larger individuals, which are generally terminal-phase males and play an important role in successful reproduction.

Protogynous hermaphroditism, where individuals transition from female to male, is influenced by various ecological factors. In tropical parrotfish, factors such as social structure, mating systems, population density, environmental stability, food availability, and predation pressure play important roles in shaping sex ratio variations (Coscia *et al.*, 2016; Pla *et al.*, 2022). These dynamics also apply to *S. rivulatus*, where the balance between females and males is highly dependent on ecosystem conditions and external pressure. Among anthropogenic factors, selective fishing of large individuals is one of the main causes of imbalance, disrupting both the demographic composition and the timing of sex change in the population.

Hamilton *et al.* (2007b) reported in the California sheephead fish (*Semicossyphus pulcher*), exploitation of large individuals led to a decrease in the proportion of terminal-phase males, a shift in the size at which sex transition occurs, and a reduction in

the reproductive productivity of the population. Similar findings were reported by Hawkins and Roberts (2004) in Caribbean parrotfish, where intensive harvesting of large males caused distortion in the sex ratio and lowered fertilization success rates. Furthermore, Taylor (2014) showed that fishing pressure is the dominant factor determining the size at which sex changes occur in various protogynous fish populations. As an adaptive response, smaller individuals may begin to change sex earlier when larger males are removed from the population, but this can reduce genetic diversity and overall fecundity

Pavlowich *et al.* (2018) emphasize that the loss of the largest size classes due to intensive fishing not only reduces long-term reproductive capacity but also alters the reproductive strategies of the population, thereby requiring the implementation of management strategies based on sex-change dynamics such as size limits and seasonal closures. Furthermore, a study by Chong-Montenegro *et al.* (2022) on small-scale fisheries in tropical regions showed that high fishing pressure can distort sex ratios in protogynous fish, reduce fertilization success, and slow population recovery rates. Cumulative evidence indicates that protecting larger males is essential for maintaining reproductive success and preventing demographic collapse in protogynous fish populations.

From a management perspective, these findings have important implications for the sustainability of *S. rivulatus* populations. The dominance of females at smaller sizes and the decreased proportion of large males highlight the need to implement management policies based on minimum catch sizes and the protection of terminal-phase males in the wild. The presence of a balanced sex ratio during the spawning season indicates that the reproductive capacity of the population is still functioning well; however, long-term sustainability could be threatened if the fishing pressure on large males continues to increase in the future. Therefore, management strategies that include seasonal fishing closures during spawning aggregation periods and establishing minimum catch size limits must be implemented to maintain the balance of sex structure and support the resilience of *S. rivulatus* stocks in the Seribu Islands.

Index of gonadal maturity (GSI)

The gonadosomatic index (GSI), a quantitative indicator of gonadal development and reproductive condition, showed clear variation between the sexes and male phases in *S. rivulatus* on the Seribu Islands. Female GSI values fluctuated throughout the year, with a marked increase in February (1.72), September (2.06), and December (1.92) (Figure 5).

Males exhibited a similar pattern, with GSI increases observed in February (IP 2.75%; TP 0.50%), September (IP 3.23%; TP 0.67%), and December (IP 2.85%; TP 0.57%). Throughout the year, the GSI values of the initial-phase (IP) males were

consistently higher than those of the terminal-phase (TP) males. Although variations occurred between sexes and male phases, all groups showed synchronized seasonal fluctuations, with peak gonadal development occurring simultaneously in all groups.

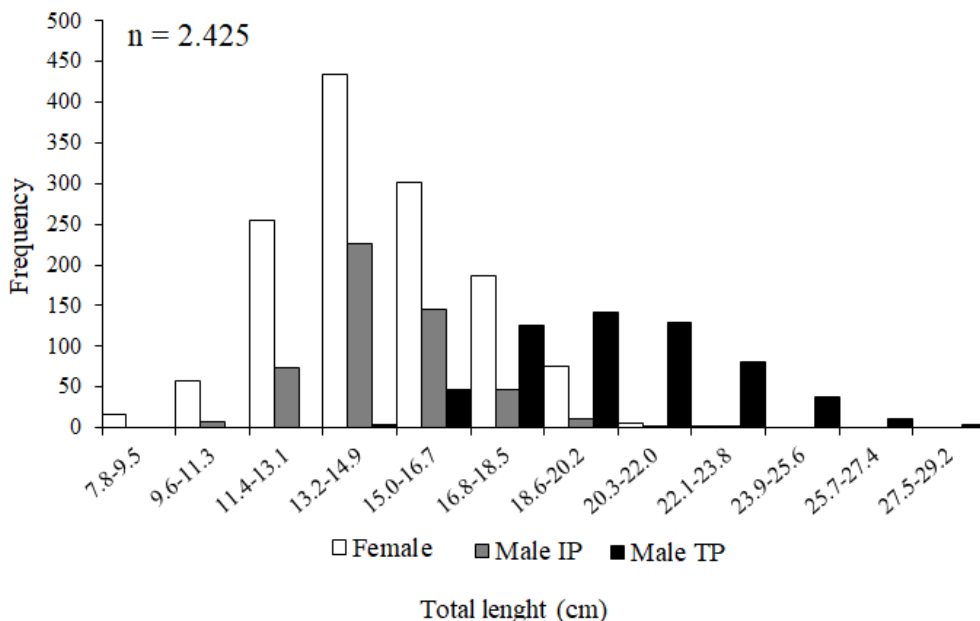


Figure 3. Size distribution of catches of parrotfish *S. rivulatus* collected in the Seribu Islands, Jakarta

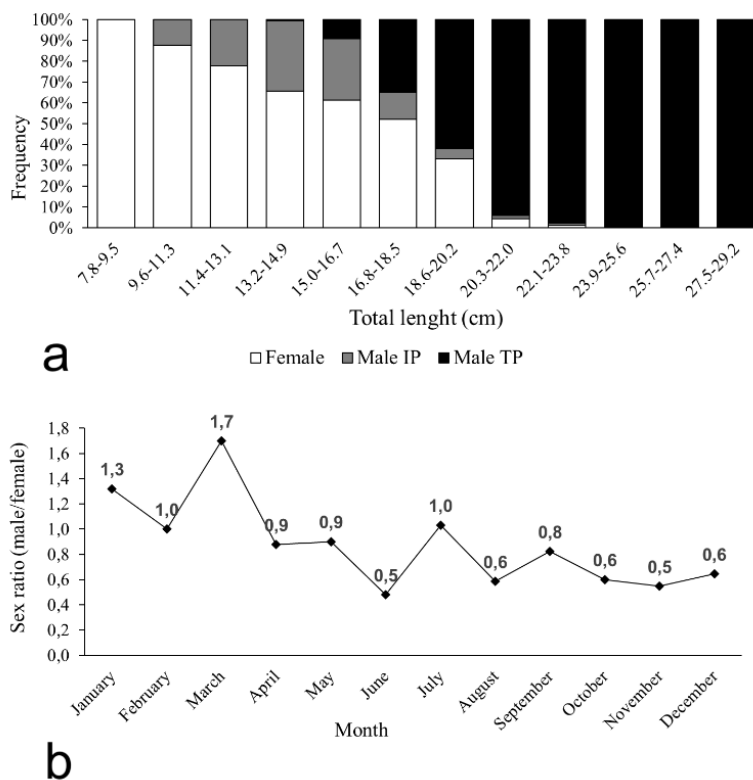


Figure 4. Sex ratio of parrotfish *S. rivulatus* based on a) length class interval and b) study time, collected in the Seribu Islands, Jakarta

Temporal variation in the gonadosomatic index (GSI) clearly illustrated the reproductive cycle of *S. rivulatus* and its adaptation to local environmental changes. The highest GSI values during specific months corresponded to the main spawning peaks. This pattern is consistent with earlier studies of gonad development in *S. rivulatus* in the same region where reproductive activity occurred throughout the year, with the highest intensity at the end and middle of the year (Yanti *et al.*, 2023). These results are also in line with observations from North Sulawesi which showed an increase in the gonadosomatic index (GSI) of parrotfish during the seasonal transition period, indicating synchronization between the gonad maturation cycle and environmental conditions that support successful spawning (Deeng *et al.*, 2022). *Scarus trispinosus* in the Southwest Atlantic display a similar reproductive pattern, with increased spawning activity in February–March and September–December, indicating a seasonal pattern similar to that of *S. rivulatus* in the Seribu Islands (Freitas *et al.*, 2019). A similar pattern was also identified in *Hipposcarus longiceps* in Guam, where GSI values increased, approaching the peak spawning season, and decreased immediately after, reflecting a partial spawning strategy that recurs throughout the year (Taylor and Crush, 2017). Ecologically, this reproductive timing is advantageous because it aligns spawning with periods of high primary productivity and environmental stability, ensuring greater larval survival and recruitment success. The increase in GSI values during these months coincides with the intermonsoon period, which is characterized by relatively calm waters and increased primary productivity, potentially enhancing larval survival through the availability of food and stability of the tropical marine environment (Welsh and Bellwood, 2011).

Throughout the observation period, the gonadosomatic index (GSI) values of the initial phase (IP) males were consistently higher than those of the terminal phase (TP) males, reflecting the characteristic diandric reproductive strategy of protogynous species (Sakai *et al.*, 2006). In this system, IP males often act as “sneakers,” which are small individuals that quickly sneak into the spawning area when females release their eggs and then simultaneously release sperm before being chased away by TP males to maximize fertilization opportunities (Hamilton *et al.*, 2008; Yamauchi, 2002). This behavior represents an alternative reproductive tactic that allows smaller individuals to participate in spawning events despite social hierarchies being present. Sneaker males are generally smaller but have higher GSI values because they invest more energy in sperm production, which is a physiological adaptation that increases fertilization success during the brief spawning period.

This alternative strategy is a form of stable evolutionary adaptation that allows non-dominant individuals to continue contributing to the reproductive success of the population under intense male competition (Ota and Kohda, 2005; Kumawura *et al.*, 2009). Such reproductive flexibility is one of the key mechanisms that maintain population stability in protogynous species, particularly under varying ecological and social conditions.

The results of this study also highlight the importance of considering anthropogenic pressure when interpreting fluctuations in the GSI. Variations in reproductive activity, including changes in GSI values and spawning times, may reflect physiological responses to fishing pressure and changing environmental conditions (Andrade *et al.*, 2003; Lowerre-Barbieri *et al.*, 2023). In the Seribu Islands, where tourism and artisanal fishing are both intensive, the observed GSI fluctuations may not only reflect natural patterns of the reproductive cycle but also physiological responses to environmental pressures. Several studies have shown that selective fishing pressure on large individuals can affect the reproductive dynamics of protogynous hermaphroditic fishes, including parrotfish. Historical exploitation of *Bolbometopon muricatum* led to significant changes in the demographic structure of males, indicating that fishing could alter reproductive strategies and timing (Hamilton *et al.*, (2007a). Similar findings were reported for the Serranidae family, where intensive fishing changed spawning patterns and reduced the peak of the gonadosomatic index (GSI) through the loss of large individuals, who play a critical role in successful fertilization (Freitas *et al.*, 2019). Therefore, interpreting GSI trends requires a combined ecological and anthropogenic perspective to distinguish between natural reproductive seasonality and human-induced changes.

High fishing pressure can also lead to a decrease in body size with sex change (length of sex change) in protogynous parrotfish, reflecting demographic adaptation to overexploitation. This phenomenon shows that individuals in populations experiencing intense fishing pressure can adjust their reproductive strategies to ensure their persistence. For example, fish may undergo earlier gonadal maturation or increased spawning frequency within a single season as a compensatory mechanism against the increased mortality from fishing (Welsh and Bellwood, 2011; Van Overzee and Rijnsdorp, 2014). Such plasticity in reproductive timing and strategy, while beneficial in the short term, may reduce long-term genetic diversity and reproductive potential if a high fishing intensity persists. Thus, changes in body size during sex transition in *S. rivulatus* in the Seribu Islands can serve as an important signal of anthropogenic pressure affecting the reproductive dynamics and population structure of this species.

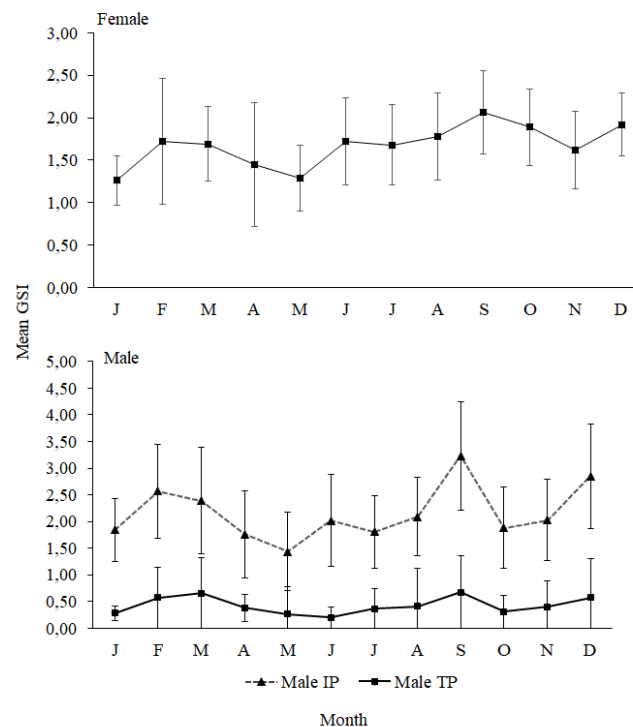


Figure 5. Gonad maturity index of parrotfish *S. rivulatus* collected in Seribu Islands, Jakarta

Reproductive potential

The total fecundity of *S. rivulatus* observed during the study period ranged from 17,013 to 178,813 oocytes, with an average of $71,130 \pm 37,066$. This range correlated with a total fish length of 12.1–23.2 cm and body weight of 35.6–253.2 g. The highest fecundity was recorded in individuals measuring 21.8 cm, and the lowest was found in individuals measuring 12.4 cm. Regression analysis showed a strong positive relationship between fecundity and total length ($F = 24.454$, $L^{2.8365}$; $R^2 = 0.65$) and body weight ($F = 1178.1$, $W^{0.907}$; $R^2 = 0.66$) (Figure 6). These results indicate that larger individuals have higher fecundity within the observed size range studied.

The positive correlation between body size and fecundity in parrotfishes, particularly *Scarus* spp., indicates that larger individuals significantly contribute to population dynamics. Larger individuals can produce more eggs, thereby increasing the chances of larval survival and successful recruitment (Pears *et al.*, 2006; Lavin *et al.*, 2021). Eggs produced by larger females generally contain higher energy reserves, resulting in stronger and more resilient larvae to environmental fluctuations. (Lam, 1994). In addition, large fish usually have a longer reproductive period, allowing sustained contributions to the population and increased fecundity under favorable environmental conditions (Pears *et al.*, 2006).

These findings are consistent with those reported for other coral reef fishes, such as *Plectropomus maculatus* and *Bolbometopon muricatum*, which also show a positive relationship between body size and reproductive output (Lavin *et al.*, 2021; Hamilton *et al.*, 2008a). From a fisheries ecology perspective, large individuals play a critical role in maintaining stability and facilitating population recovery following exploitation. Higher fertility rates in larger fish exponentially increase egg production compared with that in smaller fish (Dietzel *et al.*, 2020; Richards *et al.*, 2012). However, because large individuals are the primary targets of fishing activities, they are more vulnerable to capture, which can significantly reduce overall reproductive productivity and slow the recovery of the population (Dulvy *et al.*, 2004; Abesamis *et al.*, 2014). In the case of *S. rivulatus* in the Seribu Island, protecting large individuals, particularly mature females and terminal-phase males, is an essential management priority. Implementing management policies, such as minimum catch size regulations and seasonal fishing restrictions during spawning periods, can ensure the optimal contribution of large individuals to recruitment while supporting the long-term sustainability of coral reef fish populations exposed to anthropogenic pressure.

Reproduction pattern

The oocyte diameter of *S. rivulatus* in this study ranged from 0.030 to 0.120 mm and exhibited a

bimodal distribution pattern. The first mode was in the 0.051-0.057 mm class interval, and the second mode was at 0.092-0.099 mm size. The size distribution of the oocytes is shown in Figure 7.

Histological analysis revealed multiple stages of oocyte development within a single ovary, ranging from oogonia and primary oocytes to mature oocytes at the vitellogenesis stage (Figure 8).

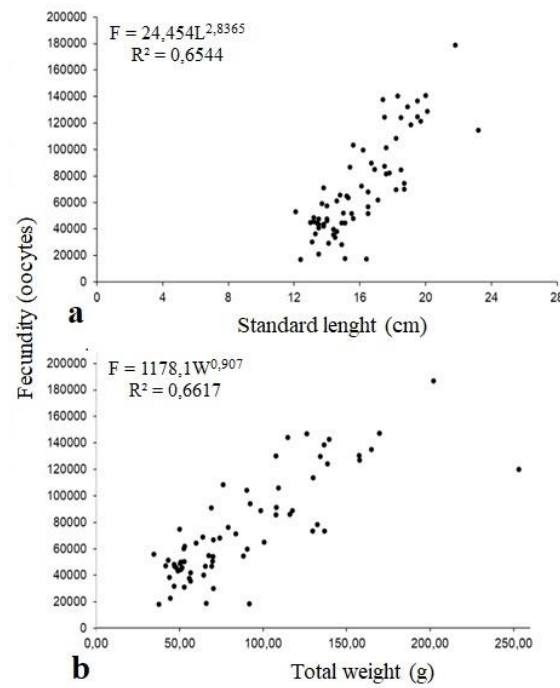


Figure 6. Relationship of fecundity to (a) total length and (b) total weight of parrotfish *S. rivulatus* during the study in the Seribu Islands, Jakarta

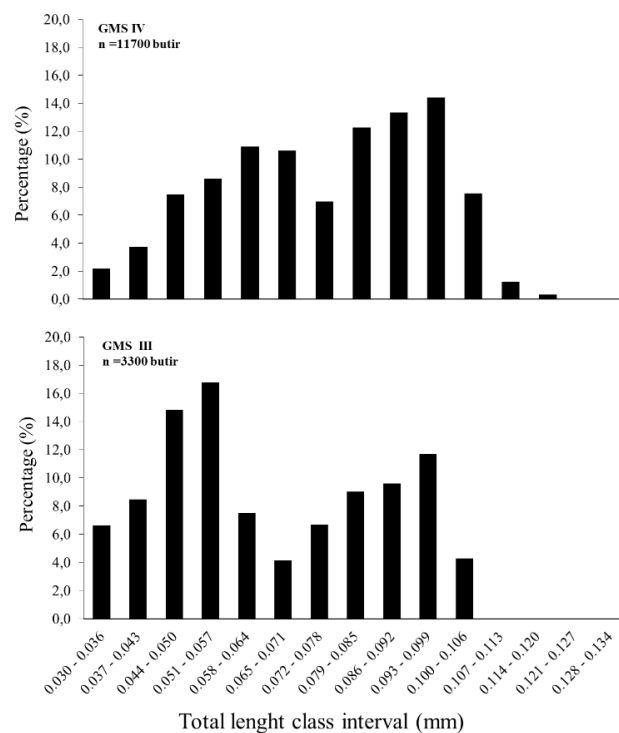


Figure 7. Size distribution of oocyte *S. rivulatus* gonadal maturity stage III and IV in the Seribu Islands, Jakarta

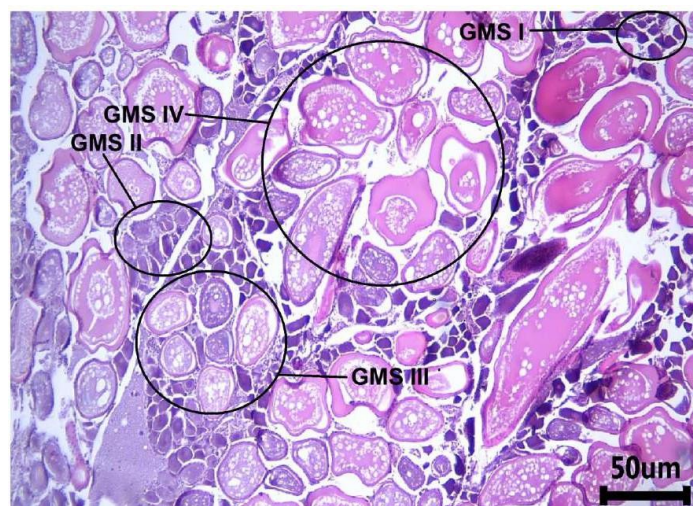


Figure 8. Histological cross-section of female *S. rivulatus* gonads with different levels of oocyte development. GMS=gonadal maturity stage

The reproductive pattern of *S. rivulatus* was examined using a combination of the gonadosomatic index (GSI), histological analysis of oocyte development, and oocyte size-frequency distribution. All three approaches consistently revealed that *S. rivulatus* exhibits year-round spawning activity, characteristic of a partial spawner. The bimodal distribution of oocyte sizes, along with the simultaneous presence of various developmental stages within a single ovary, indicates asynchronous ovarian development, which supports multiple spawning events within a single reproductive cycle. These results are consistent with previous findings in other parrotfish species. Freitas *et al.* (2019), for instance, reported a similar asynchronous oogenesis pattern in *Scarus trispinosus*, marked by the coexistence of oocytes at various developmental stages within a single ovary, consistent with partial spawning behavior. Furthermore, recent studies on *S. rivulatus* shows asynchronous spawning with seasonal variability in spawning peaks (Tuwo *et al.*, 2023; Yanti *et al.* 2023). Overall, the asynchronous gonad development and partial spawning strategy in *S. rivulatus* represent advantageous reproductive adaptations, enabling enhanced reproductive output and better chances of successful recruitment in dynamic coral reef environments. Species with repeated spawning cycles typically inhabit stable tropical and subtropical waters, such as parrotfish and related taxa, which are known for their complex social structures and habitat-specific behaviors (Francini-Filho *et al.*, 2008).

Conclusion

S. rivulatus in Seribu Island has a relatively balanced sex ratio, with females dominating the

smaller size classes and males dominating the larger size classes. This species exhibits a gradual spawning pattern throughout the year, supported by asynchronous ovarian development. These findings highlight the importance of protecting larger individuals to maintain reproductive capacity, and serve as a basis for fisheries management based on size and fishing season

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