

ORIGINAL RESEARCH

Reproductive biology of fringescale sardinella (*Sardinella fimbriata* Valenciennes, 1847) from Malampaya Sound, Palawan, Philippines

JESUSITO A. VICENTE* and HERMINIE P. PALLA

College of Fisheries and Natural Sciences (CFiNS), Western Philippines University, 5300 - Puerto Princesa, Philippines.
ORCID *Jesuito A. Vicente*  <https://orcid.org/0000-0001-5923-5486>, *Herminie P. Palla*  <https://orcid.org/0000-0003-2080-6602>



ABSTRACT. Reproduction is a fundamental biological process that is essential for the continuous survival of fish species. Understanding their early life history and reproductive biology can explain how the population behave over time. A total of 1,238 fish samples were examined to determine the reproductive patterns and period of fringescale sardinella (*Sardinella fimbriata*) from Malampaya Sound, Palawan, Philippines. Monthly sampling from April 2023 to March 2024 revealed a 1:1 sex ratio. Gonadal examination of the fish revealed the presence of spawning individuals throughout the study period. The minimum size of matured fish observed was 11.0 cm and 11.1 cm for male and female *S. fimbriata*, respectively. The peak of spawning was April as indicated by the highest calculated GSI of 7.62% and fecundity of 18,465. A smaller peak was again observed in the month of September. The length at maturity was estimated to be 11.4 and 8.8 cm for males and females, respectively. Fecundity ranged between 2,700 to 36,067 eggs per spawn for size class between 11.1-14.8 cm and weight 13.07-31.93 g. Regression analysis between fecundity and morphometric characteristics such as body length, weight, eviscerated weight, and gonad weight revealed a positive correlation. Very low coefficients of determination were computed, ranging between 0.0028-0.1233. A significant association between fecundity and the morphometric variable gonadal weight was observed, as shown by the p-value of 0.0000. These outcomes are valuable data in the formulation of conservation and management strategies for the area. Implementation of appropriate conservation measures, monitoring of environmental parameters, strict enforcement of fishery regulation, coupled with increased environmental awareness and community participation will guarantee the long-term sustainability of the fringescale sardinella population and the preservation and sustainable use of marine biodiversity in Malampaya Sound.



*Correspondence:
jesuito.vicente@gmail.com

Received: 4 August 2024
Accepted: 19 October 2024

ISSN 2683-7595 (print)
ISSN 2683-7951 (online)

<https://ojs.inidep.edu.ar>

Journal of the Instituto Nacional de
Investigación y Desarrollo Pesquero
(INIDEP)



This work is licensed under a Creative
Commons Attribution-
NonCommercial-ShareAlike 4.0
International License

Key words: Fecundity, fish reproduction, gonadal development, reproductive seasonality, spawning behavior.

Biología reproductiva del tunsoy (*Sardinella fimbriata* Valenciennes, 1847) del Estrecho de Malampaya, Palawan, Filipinas

RESUMEN. La reproducción es un proceso biológico fundamental que resulta esencial para la supervivencia continua de las especies de peces. Comprender su ciclo vital temprano y su biología reproductiva puede explicar cómo se comporta la población a lo largo del tiempo. Se examinaron un total de 1.238 muestras de peces para determinar los patrones reproductivos del tunsoy (*Sardinella fimbriata*) del Estrecho de Malampaya, Palawan, Filipinas. El muestreo mensual de abril de 2023 a marzo de 2024 reveló una proporción sexual de 1:1. El examen gonadal de los peces mostró la presencia de individuos reproductores durante todo el período de estudio. El tamaño mínimo de los peces maduros observados fue de 11,0 cm y 11,1 cm para los machos y las hembras de *S. fimbriata*, respectivamente. El pico de desove fue en abril, como lo indica el mayor GSI estimado de 7,62% y

la fecundidad de 18.465 huevos por puesta. Se observó nuevamente un pico más pequeño en el mes de septiembre. La longitud de madurez se estimó en 11,4 y 8,8 cm para los machos y las hembras, respectivamente. La fecundidad varió entre 2.700 y 36.067 huevos por puesta para la clase de tamaño entre 11,1-14,8 cm y peso 13,07-31,93 g. El análisis de regresión entre la fecundidad y las características morfométricas como longitud corporal, peso, peso eviscerado y peso de las gónadas reveló una correlación positiva. El coeficiente de determinación fue muy bajo y varió entre 0,0028 y 0,1233. Se observó una asociación significativa entre la fecundidad y la variable morfométrica de peso gonadal, como lo demuestra el valor p de 0,0000. Estos resultados constituyen datos valiosos para la formulación de estrategias de conservación y gestión de la zona. La aplicación de medidas de conservación adecuadas, el seguimiento de los parámetros ambientales, la aplicación estricta de la normativa pesquera, junto con una mayor conciencia ambiental y la participación de la comunidad garantizarán la sostenibilidad a largo plazo de la población del tunsoy y la conservación y el uso sostenible de la biodiversidad marina en el Estrecho de Malampaya.

Palabras clave: Fecundidad, reproducción de peces, desarrollo gonadal, estacionalidad reproductiva, comportamiento de desove.

INTRODUCTION

Reproduction is considered a biological process of living organism essential to ensure the continuing survival of the species (Muchlisin 2014). In fisheries, the understanding of reproductive biology of fish can be used as a basis in the formulation of conservation and management strategies (Brewer et al. 2008; Grandcourt et al. 2009), development of culture techniques (Muchlisin et al. 2004), aquaculture diversification (Muchlisin 2013) and environmental impact assessments (Schlosser 1990).

Many small, fast growing fish species like sardines are known to be 'r-strategists' (Pauly et al. 1998). These are species with early maturation, high fecundity, short generation times, and minimal parental investment (Pianka 1970). This attribute is to maximize reproductive output and population growth rate in environments where resources are abundant but unpredictable (Pauly et al. 1998). Sardines are broadcast spawners (Ganias 2014), and fertilization occurs externally once millions of eggs are released into the water (Shapiro and Giraldeau 1996).

Sardines are major component of fish landings from Malampaya Sound. There are at least 6 species of sardines found in the area (Gonzales 2013), of which fringescale sardinella (*Sardinella fimbriata*) is the most common. These ray-finned fishes belonging to Clupeidae Family. They are 11

to 19 cm in length, with moderately slender bodies, found in the coastal waters of the Indo-west Pacific, from Kuwait to southern India and the Bay of Bengal to the Philippines (Whitehead 1985; Dalzell and Ganaden 1987). Fringescale sardinella can be distinguished from other species by its elongated and streamlined body, with a silvery coloration on the sides and a darker back (Sivasubramaniam et al. 2020).

There have been many studies conducted on the reproductive biology and early life history of sardines. However, there has been very few studies reported for fringescale sardinella, particularly in the Philippines and Malampaya Sound. Significant studies by Ganias et al. (2003), Rohit and Bhat (2003), Tsikliras and Antonopoulou (2006), Bellier et al. (2007), and Ghosh et al. (2013) highlights that oceanic variability influences the reproduction of fringescale sardinella and related species. Temperature, salinity, and food availability can impact the timing of spawning seasons (Basilone et al. 2021), and because of this spatial and temporal variation occurs. Natural and anthropogenic pressures like climate change, overfishing, pollution and habitat destruction can also change their reproductive timing and success (Silva et al. 2006; Hunnam 2021). In the study conducted by Baali et al. (2017), they found out that *Sardinella aurita* and *S. maderensis* have distinct spawning seasons. While *S. longiceps* exhibits seasonality that spawns in June to August (Kripa et al. 2018). For fringescale sardinella, it has been reported to spawn throughout the year.

In the Philippines, it occurs during the southwest monsoon season (Willette et al. 2011) and with varying peaks depending on the locality (Guanco et al. 2009; Rivera et al. 2017).

The study focused on the fringescale sardinella of Malampaya Sound. Malampaya Sound is a protected inlet composed of complex sheltered bays, coves, estuaries, and islands at the northwestern tip of Palawan Island. It was considered as one of the important and richest traditional fishing grounds and termed as 'fishbowl of the Philippines' (Gonzales et al. 2017) as it constitutes to 19% of the total national municipal landings in the 1970s (Estudillo et al. 1987). However, due to the natural causes, amplified by anthropogenic stresses, the marine environment deteriorated, and the fish population declined (Pauly et al. 2002, 2005). The area was so overfished that commercial fisheries is prohibited in 1973 (Ronquillo and Llana 1987). It was declared a protected landscape and seascape in 2000 to conserve its remaining resources while allowing sustainable utilization of the area.

This study aims to determine the reproductive patterns and period of fringescale sardinella. Specifically, this investigation will ascertain the go-

nadal development, sex ratio, gonadosomatic index (GSI), length at maturity and fecundity of the said species found in Malampaya Sound, Palawan. Data from this study can be used as an input in the management interventions that can be implemented in the area.

MATERIALS AND METHODS

Fringescale sardinella samples were collected every month between April 2023 to March 2024 from Barangay Pancol, Taytay, Palawan (Figure 1). It is one of the densely populated areas along the coast of the Inner Sound and one of the fish landing sites for artisanal fisheries in the area. Fish bought from the landing site were brought to the Western Philippines University, Puerto Princesa City. Samples were randomly selected from the fish catch. Processing included measurement, weighing, sex determination, dissection and microscopic analysis. The ratio between male and female was determined and evaluated using the chi-square goodness-of-fit test (Zar 2001). Reproductive or-

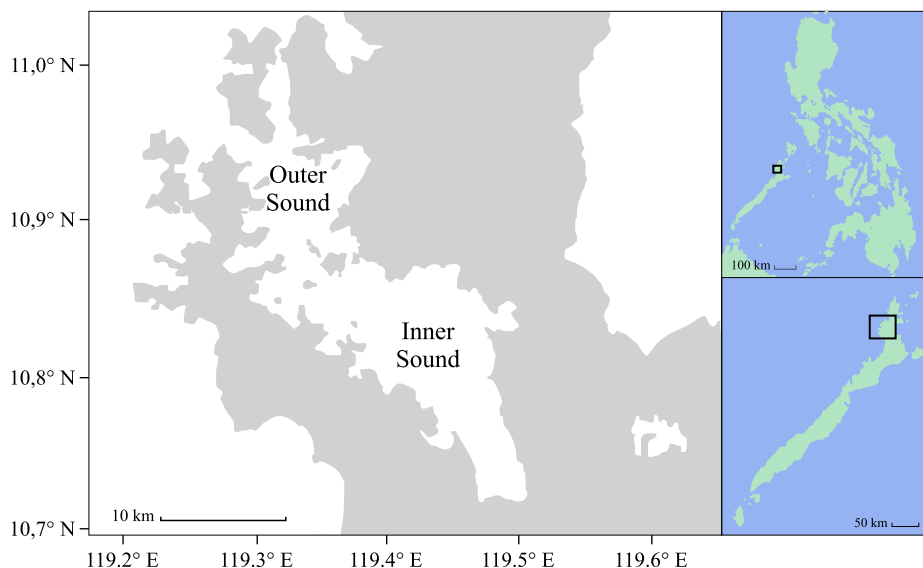


Figure 1. The map of Malampaya Sound, Palawan, Philippines.

gans from each specimen were carefully set aside, weighed and sampled. Maturity stages were assessed based on morphological characteristics of gonads (Brown-Peterson et al. 2011). Random samples were subjected to histological evaluation to confirm correct staging and documentation. Ovaries in spawning capable stage were placed in plastic vials and immediately fixed in 10% buffered formalin for 24 h, and then they were transferred in 70% ethanol for storage.

Total lengths (TL) were measured at the nearest 0.1 cm, from the tip of the snout to the end of the tail. Whole body weight and gonad weight were measured to the nearest 0.01 g. Resulting values were used to compute the Fulton condition factor (K) (Froese 2006) and gonadosomatic index (GSI) (Gaikwad et al. 2009) with the following formulas:

$$K = 100 * \text{Weight}/\text{length}^3$$

$$\text{GSI} (\%) = \frac{\text{Weight of gonad}}{\text{Total weight of fish}} \times 100$$

Gonadosomatic index of all the fish samples were computed throughout the sampling period and was used as a tool to identify the spawning season. The GSI of small (= mean length – standard deviation) and large (= mean length + standard deviation) females were also determined. The proportion of mature individuals in each size class were determined and calculated. Fish was considered matured when they were in spawning capable, regressing and, regenerating stages (Brown-Peterson et al. 2011). The length at maturity (L_{m50}) was the size where 50% of fish are already sexually mature (Willoughby and Tweddle 1978). Fish were clustered into 1.0 cm size class. The L_{m50} was calculated using the following formula (Fontoura et al. 2009):

$$P = \frac{A}{1 + e^{(-r(L-L_{m50}))}}$$

where P is the proportion of reproductive females, A is the curve asymptote, r is the slope and L is the length of the fish.

Fecundity determination was done using the volumetric method described by Bagenal and Braum (1978). A gonad was placed in a container with a known volume of water. Clumps of adhering eggs were broken up and eggs were carefully separated using a dissecting needle. The bottle was homogenized before a subsample was taken for analysis. Three subsamples were taken from each gonad for counting. The number of hydrated oocytes in the subsample were counted under a stereo microscope. Note that the ovaries with postovulatory follicles were not included as it is an indication that the fish has already spawned. Fecundity (F) was calculated using the formula (Murua et al. 2003):

$$F = \frac{\text{Total volume S}}{\text{Volume Ss}} \times \text{no. of hydrated ova Ss}$$

where S is the sample and Ss is the subsample.

The relationship between fecundity and morphometric variables such as length, weight, eviscerated weight and gonad weight were determined using the General Linear Model and Regression Analysis.

RESULTS

Sex ratio and gonadal development

A total of 1,238 fish samples were examined throughout the study period, where 50.6% and 52.9% were identified as male (n = 626) and female (n = 612), respectively (Table 1). Monthly proportion between sexes varied. Despite this, no significant difference was observed except during the month of May. This was verified by the chi-squared (χ^2) values computed which revealed no significant difference between the two.

Table 1. Monthly sex ratio with the corresponding chi-square (χ^2) values, percentage of mature individuals, and Fulton's condition factor (K) of fringescale sardinella from Malampaya Sound, Palawan from April 2023 to March 2024, n = 1,238. Note: the asterisk indicates significant difference observed between the number of sexes based on the computed p-values at 0.05 level of significance.

Month	Male				Female				Sex ratio male:female	χ^2
	n	%	%Mature	K	n	%	%Mature	K		
April 2023	49	49.0	71.4	0.929	51	51.0	84.3	0.985	1:1	0.04
May	39	38.2	51.3	1.025	63	61.8	76.2	1.015	1:1.6	5.65*
June	57	55.9	33.3	0.927	45	44.1	68.9	0.930	1:0.8	1.41
July	54	52.4	63.0	0.938	49	47.6	87.8	0.955	1:0.9	0.24
August	46	44.2	52.2	1.028	58	55.8	86.2	1.009	1:1.3	1.38
September	57	54.8	56.1	0.981	47	45.2	87.2	0.992	1:0.8	0.96
October	48	46.2	85.4	0.968	56	53.8	96.4	0.947	1:1.2	0.62
November	59	56.7	59.3	0.926	45	43.3	88.9	0.914	1:0.8	1.88
December	56	53.8	66.1	0.932	48	46.2	87.5	0.911	1:0.9	0.62
January 2024	53	51.5	49.1	0.940	50	48.5	66.0	0.955	1:0.9	0.09
February	59	56.7	61.0	0.969	45	43.3	93.3	0.971	1:0.8	1.88
March	49	47.1	65.3	0.906	55	52.9	89.1	0.905	1:1.1	0.35
Total	626	50.6	59.3	0.956	612	49.4	84.3	0.958	1:1	0.16

Gonadal examination of fish revealed presence of spawning capable individuals throughout the study period (Figures 2-4). However, very few mature fish were observed during the months of June and January. The minimum size of matured fish measured were 11.0 and 11.1 cm for male and female fringescale sardinella, respectively.

Spawning season determination

The gonadosomatic index of all the samples for the entire period of study showed that males had relatively lower GSI than females (Figure 5). It was further revealed that male GSI was relatively more stable fluctuating slightly between 1.19% and 3.93%, whereas for females, it started at the highest of 7.62% in April 2023 and then abruptly decreased to 2.47% the following month. From

May 2023 onwards, it was observed that the GSI was almost constant between 1.98% to 4.2%. Generally, larger females have higher GSI than small females except in the months of April, June and October (Figure 6).

Length at maturity (L_{m50})

Gonads classified as spawning capable, regressing, and regenerating were considered matured. High frequencies of sexually matured fish were observed in all size classes between 10.7 to 15.8 cm. The length at maturity, where 50% of the fish already reached sexual maturity, was estimated to be 11.4 and 8.8 cm for males and females, respectively. The smallest mature fish sample that was collected for this study was 11.0 cm for males and 11.1 cm for females.

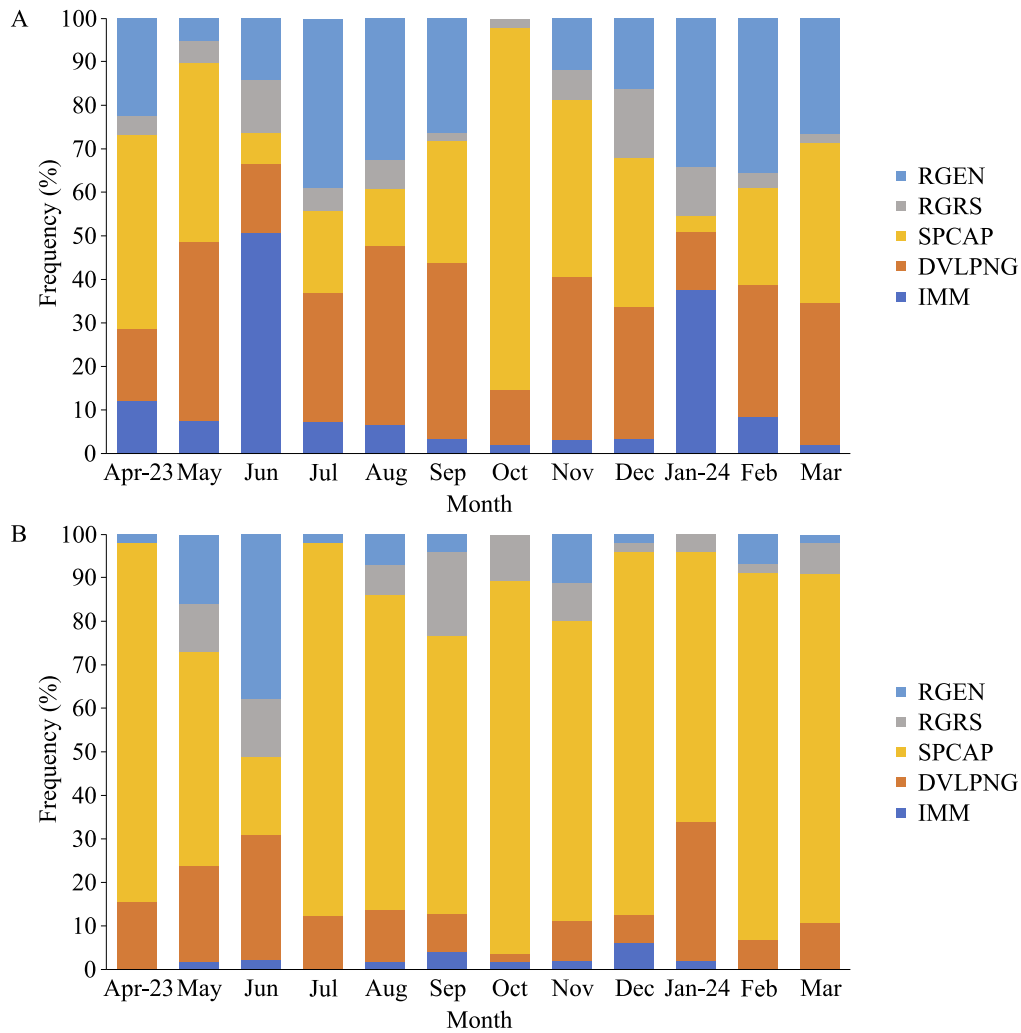


Figure 2. Distribution of different maturity stages of fringescale sardinella from Malampaya Sound, Palawan from April 2023 to March 2024. A) Male. B) Female. IMM: immature, DVLPNG: developing, SPCAP: spawning capable, RGRS: regressing, RGEN: regenerating.

Fecundity

A total of 400 sexually mature females were subjected for fecundity counting. Analysis revealed that the fecundity ranged between 2,700 and 36,067. The mean fecundity was calculated as 12,679 eggs per spawn for size class between 11.1-14.8 cm and weight between 13.07-31.93 g. Monthly fecundity fluctuates, however, the highest count was recorded in April (Figure 7). A smaller

peak was also observed in September. Regression analysis revealed a positive correlation between fecundity and the morphometric characteristic body length, weight, eviscerated weight, and gonad weight (Figure 8). A very low coefficients of determination were computed ranging between 0.0028 and 0.1233. However, further analysis revealed that only the gonadal weight had a significant association with fecundity with a p-value of 0.0000.

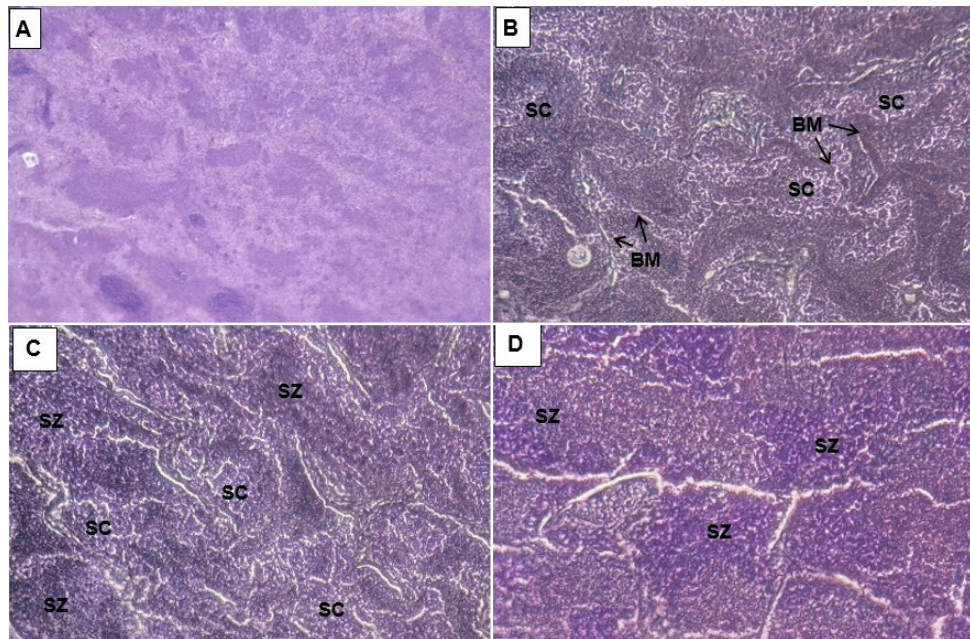


Figure 3. Histology of fringescale sardinella testis at various stages. A) Immature. B and C) Developing. D) Spawning capable. BM: basement membrane of seminiferous tubule, SC: spermatocytes, SZ: Spermatozoa.

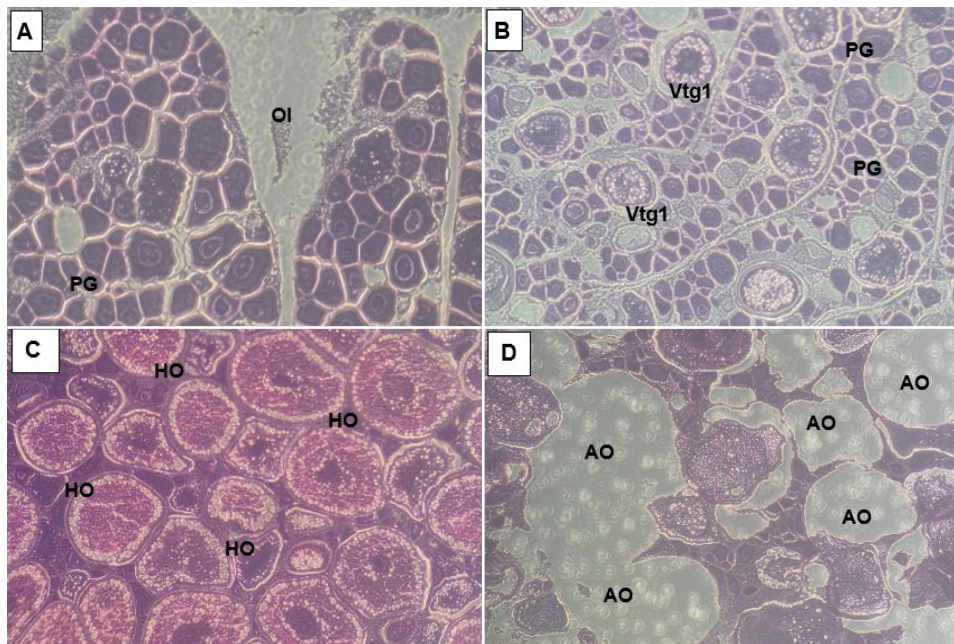


Figure 4. Histology of fringescale sardinella ovary at various stages. A) Immature. B) Developing. C) Spawning capable. D) Regressing. OI: ovarian lamella, PG: oocyte of primary growth, Vtg1: developing ovary with cells in initial vitellogenesis, HO: hydrated oocytes, AO: atretic oocytes.

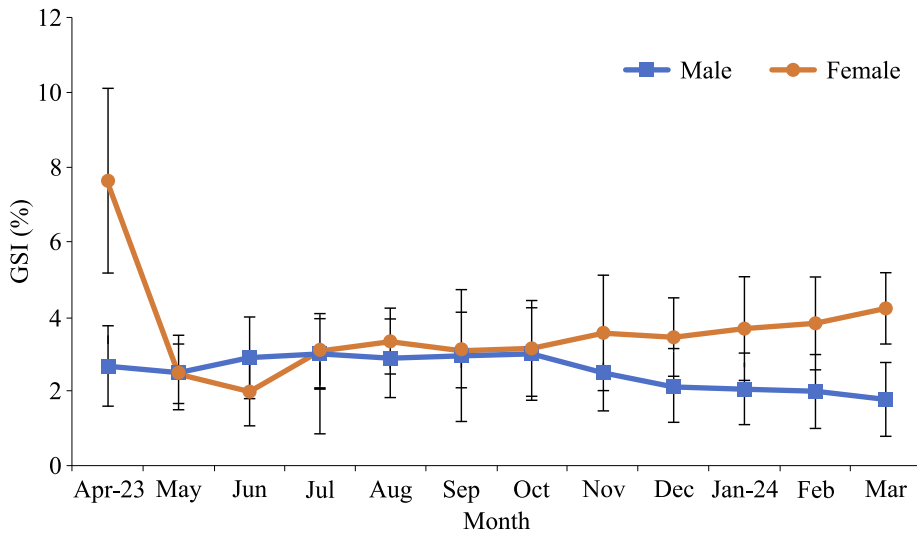


Figure 5. Monthly gonadosomatic index (GSI) of fringescale sardinella from April 2023 to March 2024.

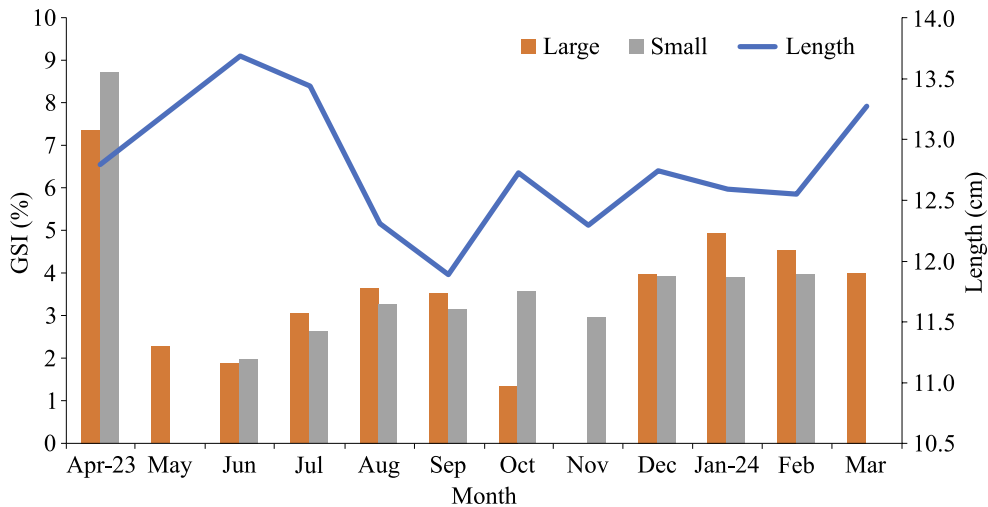


Figure 6. Average length per month sampled and the gonadosomatic index (GSI) between large and small female fringescale sardinella.

DISCUSSION

Studying the sex ratio of fringescale sardinella is an essential element of its management and conservation. A balanced ratio of male and female is essential for reproductive success. In the present

study, despite monthly variations, no significant difference between sexes were observed except during the month of May. The total ratio was calculated as 1:1. According to Chen et al. (2022), a disproportionate population can result in a reduced reproduction rate and may impact the overall population size. It can even lead to severe evolutionary consequences if left unchecked (Raymond et al.

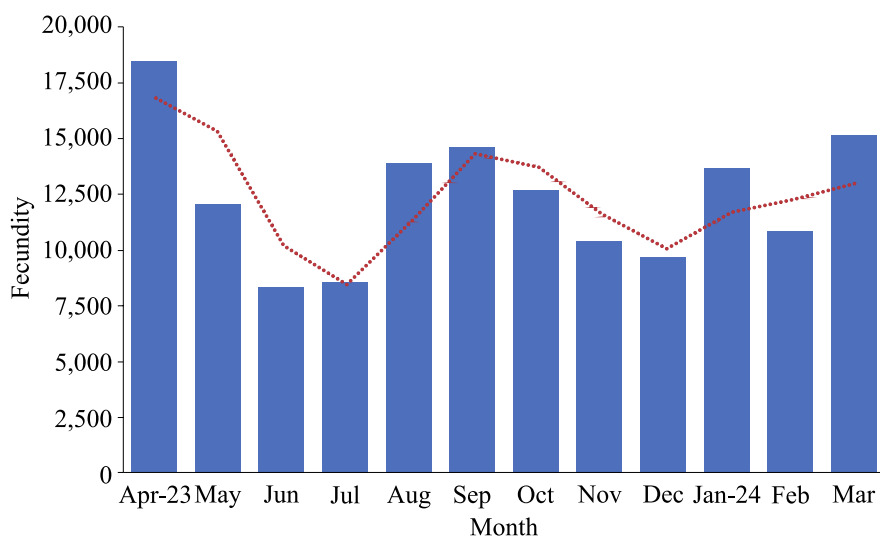


Figure 7. Monthly fecundity of fringescale sardinella from April 2023 to March 2024.

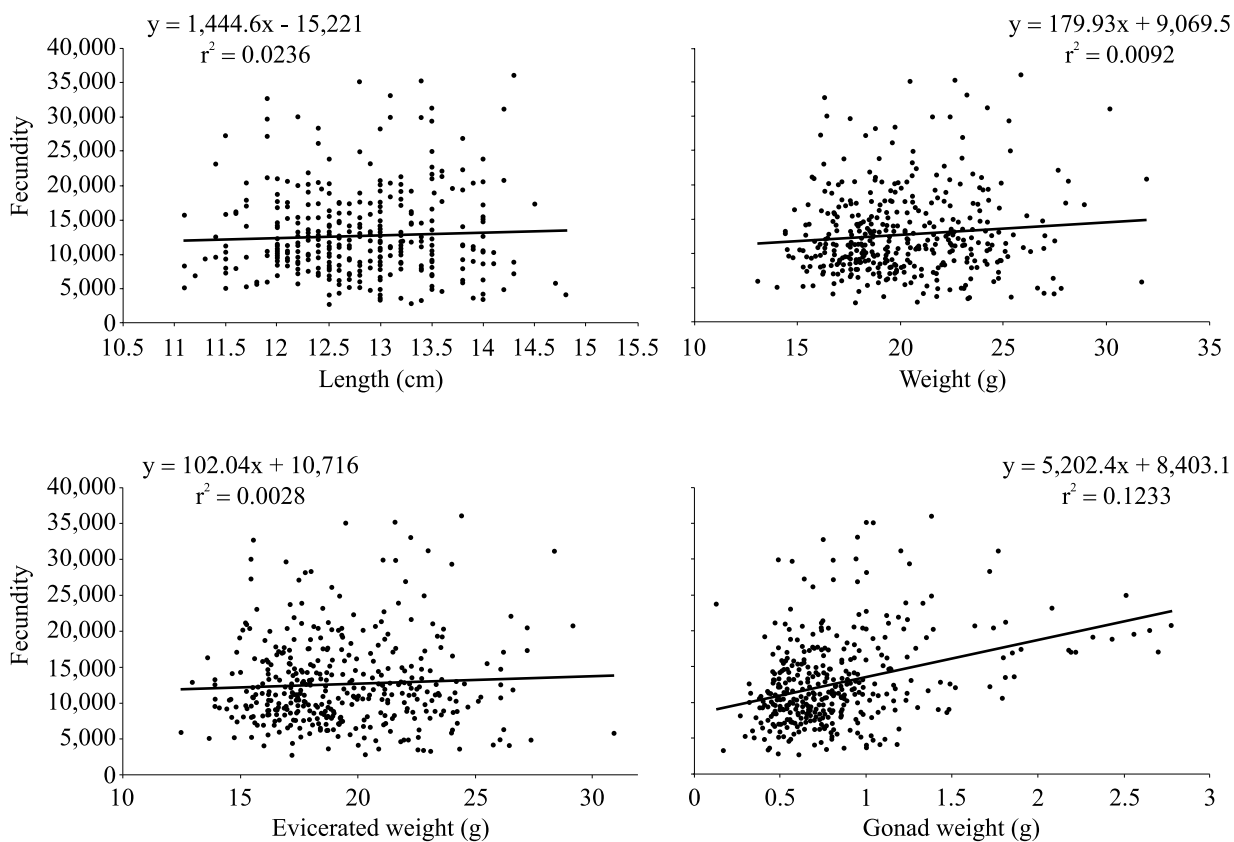


Figure 8. Relationship between fecundity and some morphometric characteristics of fringescale sardinella.

2023), resulting in a reduction in genetic diversity (Martinez et al. 2023). Consequently, the fish are becoming less resistant to diseases and struggle adjusting to slight changes on environmental condition.

Variations in sex ratio across can be a result of fishing practices (Robinson et al. 2017). Selective fishing and high fishing pressure, which is common to Malampaya Sound decades ago, can skew the sex ratio that can change the age and size structure of the fish populations. However, we do not discount the fact that this is also a natural occurrence because sex ratio is also influenced by environmental conditions, predation, diseases, and individual growth rates (Chen et al. 2022). Thus, continuous monitoring and practicing sustainable fishing are essential to maintain healthy fish populations. Behavioral patterns must also be considered when analyzing male to female ratio as some tends to exhibit seasonal aggregation that can create potential biases during sampling (Reichard et al. 2014). It is documented that species of sardines aggregate during spawning seasons or go to specific spawning grounds to increase reproductive potential (Ganias 2008; de Souza Moraes et al. 2012).

Most of the species in the Family Clupeidae spawns throughout the year. In the Philippines, it occurs during the southwest monsoon season (Willette et al. 2011). The fringescale sardinella studied in major fishing grounds in the country found to spawn throughout the year (Guanco et al. 2009; Rivera et al. 2017). This same observation was also seen in Malampaya Sound. Examination of the gonads revealed high presence of hydrated oocytes every month, indicating potential year-round spawning. The peak of spawning was April as indicated by the highest calculated GSI of 7.62% and fecundity of 18,465. A smaller peak was again observed in the month of September. According to Mukhopadhyay et al. (2020), the GSI values correlate with the maturation of the gonads. This result is similar to the study conducted by Rivera et al. (2017) in Manila Bay with the peak of spawning observed from February to May. However, in

Visayan Sea, the peak was observed from July to September (Guanco et al. 2009). According to studies, spawning season varies between and amongst localities (Winemiller and Rose 1992; Murua and Saborido-Rey 2003; Morgan 2008). This can be attributed to environmental and anthropogenic factors such as water temperature, salinity, dissolve oxygen levels, nutrition and feeding, stress, pollutants, population density and fishing intensity (Cushion 2010; Canosa et al. 2023). These variables can make epigenetic modifications during sex differentiation and alter its expression which can also affect several generations (Hattori et al. 2020).

In general, spawning is driven mainly by environmental variations. However, the size of the fish is another contributing factor that can affect reproductive ability (Slesinger et al. 2021; Dominguez-Petit et al. 2022). Larger females have more intense and prolonged spawning episodes compared to smaller females. This is clearly seen in the monthly GSI of fringescale sardinella except in the months of April, June, and October. Having smaller individuals with high GSI is uncommon but likely can happen due to species-specific habitat adaptation (Jonsson and Jonsson 2011; van Overzee and Rijnsdorp 2014).

The length at maturity of the samples were calculated as 11.4 and 8.8 cm for male and female Fimbriated sardines, respectively. Published reports for this species are 12.0-12.3 cm for males, 10.8-13.3 cm for females, and 13.0-14.6 for mixed sexes (Radhakrishnan 1964; Bennet et al. 1992; Ghosh et al. 2013; Rivera et al. 2017; Bintoro et al. 2019; Musel et al. 2022). The samples in Malampaya Sound falls shorter than the given ranges. This is not surprising as the exploitation rate in the area is exceedingly high during the previous years. According to de Roos et al. (2006), fish matures earlier as a genetic and plastic response to fishing pressure.

The highest fecundity recorded for this species was 365,324 in Lawas, Sarawak, Malaysia (Musel et al. 2022). For this study, the average was 12,187 eggs per ovary. The significant association between

fecundity and the gonadal weight only suggest that larger fish with big and heavier gonads tend to be more fecund than smaller fish. This is due to the reason that bigger fish have more body space to accommodate more eggs (Jan and Jan 2017). However, the observed values of the coefficient of determinations are too low and not indicating the same. Accounting other factors other than morphological characteristics will give us a bigger picture of the complex interaction that are not captured by a simple linear model. While gonadal weight is a good indicator of fecundity, there are other factors that may affect its reproductive potential such as species-specific traits (e.g. parental quality, size, condition), resource availability (e.g. food abundance and quality), environmental (e.g. temperature) and evolutionary factors (e.g. stock biomass, fishing pressure) (Witthames et al. 1995; Kjesbu et al. 1998; Murua et al. 2003; Lambert 2008; Hsieh et al. 2011). Moreover, this maybe due also to the small size range of the collected samples. Increasing the sampling size with a wide morphological range will give us a more reliable estimate. As a whole, annual variation in fecundity is expected even within a population (Horwood et al. 1986; Rijnsdorp 1991; Kjesbu et al. 1998).

Identification of the sexual development patterns, combined with gamete production systems and life history traits can explain how reproductive strategies influence reproductive potential over time (Winemiller and Rose 1992) of fringescale sardinella from Malampaya Sound. Together with fecundity, they are important aspects in understanding not just the biology of the said fish species, but also the changes in the population structure overtime. They can predict population trends and can be used as a basis in designing adaptive conservation programs for the area, i.e. setting size limits, quotas, and close seasons for fishing. Continuous monitoring of these parameters, implementation of conservation measures, strict enforcement of regulations and educating local communities is a requisite for the sustainability of not just fringescale sardinella but the entire Malampaya Sound.

To sum, the results of study on the reproductive pattern of fringescale sardinella (*Sardinella fimbriata*) from Malampaya Sound, Palawan, Philippines, gave an important understanding into the species' reproductive biology. The outcomes on sex ratio, gonadal development, length at maturity, and fecundity are important in understanding the population dynamics of the species. The determination of these parameters is essential in adaptive conservation programs, sustainable fisheries management, and attesting the health of the ecosystem. The study highlights the importance of regular monitoring of these parameters and the implementation of appropriate conservation measures. It also emphasizes the need for community education and strict implementation of fishing regulations to guarantee the long-term sustainability of the fringescale sardinella population and the preservation and sustainable use of marine biodiversity in Malampaya Sound.

Author contributions

Jesusito A. Vicente: conceptualization; data gathering and investigation; writing-original draft preparation; writing-review and editing. Herminie P. Palla: conceptualization; analysis; writing-original draft preparation; writing-review and editing; supervision. All authors read and approved the final manuscript.

REFERENCES

- BAALI A, BOURASSI H, FALAH S, ABDERRAZIK W, MANCHIH K, AMENZOU K, YAHYAOU A. 2017. Reproductive biology of *Sardinella* sp. (*Sardinella aurita* and *Sardinella maderensis*) in the South of Morocco. Pak J Biol Sci. 20 (4): 165-178. DOI: <https://doi.org/10.3923/pjbs.2017.165.178>
- BAGENAL TB, BRAUM E. 1978. Eggs and early life history. In: BAGENAL TB, editor. Methods for

- assessment of fish production in fresh waters. IBP Handbook 3. Oxford: Blackwell Scientific Publications. p. 165-201.
- BASILONE G, FERRERI R, ARONICA S, MAZZOLA S, BONANNO A, GARGANO A, PULIZZI M, FONTANA I, GIACALONE G, CALANDRINO P, et al. 2021. Reproduction and sexual maturity of European sardine (*Sardina pilchardus*) in the Central Mediterranean Sea. *Front Mar Sci.* 8: 715846. DOI: <https://doi.org/10.3389/fmars.2021.715846>
- BELLIER E, PLANQUE B, PETITGAS P. 2007. Historical fluctuations in spawning location of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the Bay of Biscay during 1967-73 and 2000-2004. *Fish Oceanogr.* 16 (1): 1-15. DOI: <https://doi.org/10.1111/j.1365-2419.2006.00410.x>
- BENNET PS, NAIR PN, LUTHER G, ANNIGERI GG, RANGAN SS, KURUP KN. 1992. Resource characteristics and stock assessment of lesser sardines in the Indian waters. *Indian J Fish.* 39 (3-4): 136-151.
- BINTORO G, SETYOHADI D, DJOKO LELONO T, MAHARANI F. 2019. Biology and population dynamics analysis of fringescale sardine (*Sardinella fimbriata*) in Bali Strait waters, Indonesia. *IOP Conf Ser Earth Environ Sci.* 391: 012-024. DOI: <https://doi.org/10.1088/1755-1315/391/1/012024>
- BREWER SK, RABENI CF, PAPOULIAS DM. 2008. Comparing histology and gonadosomatic index for determining spawning condition of small-bodied riverine fishes. *Ecol Freshw Fish.* 17 (1): 54-58.
- BROWN-PETERSON NJ, WYANSKI DM, SABORIDO-REY F, MACEWICZ BJ, LOWERRE-BARBIERI SK. 2011. A standardized terminology for describing reproductive development in fishes. *Mar Coast Fish.* 3: 52-70. DOI: <https://doi.org/10.1080/19425120.2011.555724>
- CANOSA LF, BERTUCCI JI. 2023. The effect of environmental stressors on growth in fish and its endocrine control. *Front Endocrinol.* 14: 1109461. DOI: <https://doi.org/10.3389/fendo.2023.1109461>
- CHEN X, LIU B, LIN D. 2022. Sexual maturation, reproductive habits, and fecundity of fish. In: CHEN X, LIU B, editors. *Biology of fishery resources*. Singapore: Springer. p. 113-142.
- CUSHION N. 2010. Growth, reproductive life-history traits and energy allocation in *Epinephelus guttatus* (red hind), *E. striatus* (Nassau grouper), and *Mycteroperca venenosa* (yellowfin grouper) (Family Serranidae, Subfamily Epinephelinae) [dissertation]. Miami: University of Miami.
- DALZELL P, GANADEN RA. 1987. A review of the fisheries for small pelagic fishes in Philippine waters. *Tech Pap Ser Bur Fish Aquat Resour (Philipp)*. 10 (1). 58 p.
- DE ROOS AM, BOUKAL DS, PERSSON L. 2006. Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proc R Soc B Biol Sci.* 273 (1596): 1873-1880. DOI: <https://doi.org/10.1098/rspb.2006.3518>
- DE SOUZA MORAES LE, MARCOLINO GHERARDI DF, KATSURAGAWA M, TAVARES PAES E. 2012. Brazilian sardine (*Sardinella brasiliensis* Steindachner, 1879) spawning and nursery habitats: spatial-scale partitioning and multiscale relationships with thermohaline descriptors. *ICES J Mar Sci.* 69 (6): 939-952. DOI: <https://doi.org/10.1093/icesjms/fss061>
- DOMÍNGUEZ-PETIT R, GARCÍA-FERNÁNDEZ C, LEONARDUZZI E, RODRIGUES K, MACCHI GJ. 2022. Parental effects and reproductive potential of fish and marine invertebrates: cross-generational impact of environmental experiences. *Fishes.* 7 (4): 188. DOI: <https://doi.org/10.3390/fishes7040188>
- ESTUDILLO RA, GONZALES CL, ORDONEZ JA. 1987. The seasonal variation and distribution of zooplankton, fish eggs and fish larvae in Malam-paya Sound. *Philipp J Fish.* 20 (1-2): 1-43.
- FONTOURA NF, BRAUN AS, MILANI PCC. 2009. Estimating size at first maturity (L_{50}) from Gonadosomatic Index (GSI) data. *Neotrop Ichthyol.* 7: 217-222.

- FROESE R. 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *J Appl Ichthyol.* 22 (4): 241-253. DOI: <https://doi.org/10.1111/j.1439-0426.2006.00805.x>
- GAIKWAD MV, MORE VR, SHINGARE SM, HIWARALE DK, KHILLARE YK. 2009. Study on gonado-somatic and fecundity relationship in air breathing fish *Channa gachua* (Ham.) from Godavari near Aurangabad. *Afr J Basic Appl Sci.* 1 (5-6): 93-95.
- GANIAS K. 2008. Ephemeral spawning aggregations in the Mediterranean sardine, *Sardina pilchardus*: a comparison with other multiple-spawning clupeoids. *Mar Biol.* 155: 293-301. DOI: <https://doi.org/10.1007/s00227-008-1027-7>
- GANIAS K, SOMARAKIS S, MACHIAS A, THEODOROU AJ. 2003. Evaluation of spawning frequency in a Mediterranean sardine population (*Sardina pilchardus sardina*). *Mar Biol.* 142: 1169-1179. DOI: <https://doi.org/10.1007/s00227-003-1028-5>
- GANIAS K, SOMARAKIS S, NUNES C. 2014. Reproductive potential. In: GANIAS K, editor. *Biology and ecology of sardines and anchovies*. Boca Raton: CRC Press. p. 79-121.
- GHOSH S, RAO MVH, SUMITHRUDU S, ROHIT P, MAHESWARUDU G. 2013. Reproductive biology and population characteristics of *Sardinella gibbosa* and *Sardinella fimbriata* from northwest Bay of Bengal. *Indian J Geo-Mar Sci.* 42 (6): 758-769.
- GONZALES BJ. 2013. *Field guide coastal fishes of Palawan*. Manila: Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security (CTI-CFF) Secretariat.
- GONZALES BJ, MATILLANO MVD, ALUDIA G, MIGUEL JA, CLIMATICO RB. 2017. CPUE of fishing gears in Malampaya Sound, western Taytay, Palawan, Philippines. *World Wildlife Fund, Palawan-Philippines and Western Philippines University.* 22 p. DOI: <https://doi.org/10.13140/RG.2.2.21164.67207>
- GRANDCOURT EM, AL ABDESSALAAM TZ, FRANCIS F, AL SHAMSI AT, HARTMANN SA. 2009. Reproductive biology and implications for management of the orange-spotted grouper *Epinephelus coioides* in the southern Arabian Gulf. *J Fish Biol.* 74 (4): 820-841. DOI: <https://doi.org/10.1111/j.1095-8649.2008.02163.x>
- GUANCO MR, MESA SV, BELGA PB, NUNAL DRM. 2009. Assessment of the commercial fisheries of western and central Visayan Sea. *BFAR NFRDI Tech Pap Ser.* 12: 1-44.
- HATTORI RS, CASTAÑEDA-CORTÉS DC, ARIAS PADILLA LF, STROBL-MAZZULLA PH, FERNANDINO JI. 2020. Activation of stress response axis as a key process in environment-induced sex plasticity in fish. *Cell Mol Life Sci.* 77 (21): 4223-4236. DOI: <https://doi.org/10.1007/s00018-020-03532-9>
- HORWOOD JW, BANNISTER RCA, HOWLETT GJ. 1986. Comparative fecundity of North Sea plaice (*Pleuronectes platessa* L.). *Proc R Soc B Biol Sci.* 228: 401-431.
- HSIEH HY, LO WT, WU LJ, LIU DC, SU WC. 2011. Comparison of distribution patterns of larval fish assemblages in the Taiwan Strait between the northeasterly and southwesterly monsoons. *Zool Stud.* 50 (4): 491-505.
- HUNNAM K. 2021. The biology and ecology of tropical marine sardines and herrings in Indo-West Pacific fisheries: a review. *Rev Fish Biol Fish.* 31 (2): 1-36. DOI: <https://doi.org/10.1007/s11160-021-09649-9>
- JAN M, JAN N. 2017. Studies on the fecundity (F), gonadosomatic index (GSI) and hepatosomatic index (HSI) of *Salmo trutta fario* (Brown trout) at Kokernag trout fish farm, Anantnag, Jammu and Kashmir. *Int J Fish Aquat Stud.* 5 (6): 170-173.
- JONSSON B, JONSSON N. 2011. *Ecology of Atlantic salmon and brown trout; habitat as a template for life histories*. Fish & Fisheries Series. 33. Dordrecht: Springer. 708 p. DOI: <https://doi.org/10.1007/978-94-007-1189-1>
- KJESBU OS, WITTHAMES PR, SOLEMDAL P, WALKER MG. 1998. Temporal variations in the fecundi-

- ty of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *J Sea Res.* 40: 303-321. DOI: [https://doi.org/10.1016/S1385-1101\(98\)00029-X](https://doi.org/10.1016/S1385-1101(98)00029-X)
- KRIPA V, MOHAMED KS, KOYA KPS, JEYABASKARAN R, PREMA D, PADUA S, KURIAKOSE S, ANILKUMAR PS, NAIR PG, AMBROSE TV, DHANYA AM. 2018. Overfishing and climate drives changes in biology and recruitment of the Indian oil sardine *Sardinella longiceps* in southeastern Arabian Sea. *Front Mar Sci.* 5: 443. DOI: <https://doi.org/10.3389/fmars.2018.00443>
- LAMBERT Y. 2008. Why should we closely monitor fecundity in marine fish populations? *J Northw Atl Fish Sci.* 41: 93-106. DOI: <https://doi.org/10.2960/J.v41.m628>
- MARTINEZ V, GALARCE N, SETIAWAN A. 2023. Developing methods for maintaining genetic diversity in novel aquaculture species: the case of *Seriola lalandi*. *Animals.* 13 (5): 913. DOI: <https://doi.org/10.3390/ani13050913>
- MORGAN MJ. 2008. Integrating reproductive biology into scientific advice for fisheries management. *J Northw Atl Fish Sci.* 41: 37-51. DOI: <https://doi.org/10.2960/J.v41.m615>
- MUCHLISIN ZA. 2013. Potency of freshwater fishes in Aceh waters as a basis for aquaculture development program. *J Iktiologi Indones.* 13 (1): 91-96.
- MUCHLISIN ZA. 2014. A general overview on some aspects of fish reproduction. *Aceh Int J Sci Technol.* 3 (1): 43-52. DOI: <https://doi.org/10.13170/aijst.3.1.1355>
- MUCHLISIN ZA, HASHIM R, CHONG ASC. 2004. Preliminary study on the cryopreservation of tropical bagrid catfish (*Mystus nemurus*) spermatozoa; the effect of extender and cryoprotectant on the motility after short-term storage. *Theriogenology.* 62 (1-2): 25-34. DOI: <https://doi.org/10.1016/j.theriogenology.2003.05.006>
- MUKHOPADHYAY A, GIRI S, HAZRA S, DAS S, CHANDA A. 2020. Influence of oceanographic variability on the life cycle and spawning period of *Sardinella fimbriata* in the Northern Part of Bay of Bengal. *Proc Zool Soc.* 73: 285-295. DOI: <https://doi.org/10.1007/s12595-019-00314-5>
- MURUA H, KRAUS G, SABORIDO-REY F, WHITTAMES PR, THORSEN A, JUNQUERA S. 2003. Procedures to estimate fecundity in marine fish species in relation to their reproductive strategy. *J Northw Atl Fish Sci.* 33: 33-54. DOI: <https://doi.org/10.2960/j.v33.a3>
- MURUA H, SABORIDO-REY F. 2003. Female reproductive strategies of marine fish species of the North Atlantic. *J Northw Atl Fish Sci.* 33: 23-31. DOI: <https://doi.org/10.2960/j.v33.a2>
- MUSEL J, ANUAR A, HASSAN MH, MUSTAFA WZW, PAUL PS, SAHIDUN I, CHIBA SUA. 2022. Population dynamics and the spawning season of the commercial dominant species (*Encrasicholina devisi* and *Sardinella fimbriata*) from the northern region of Sarawak. *Aquac Aquar Conserv Legis.* 15 (3): 1162-1177.
- PAULY D, ALDER J, BAKUN A, HEILEMAN S, KOCK KH, MACE P, PERRIN W, STERGIOU KI, SUMAILA UR, VERRIOS M, et al. 2005. Marine fisheries systems. In: HASSAN R, SCHOLLES R, ASH N, editors. *Ecosystems and human well-being: current state and trends.* Washington: Island Press. p. 477-511.
- PAULY D, CHRISTENSEN V, DALSGAARD J, FROESE R, TORRES F. 1998. Fishing down marine food webs. *Science.* 279 (5352): 860-863. DOI: <https://doi.org/10.1126/science.279.5352.860>
- PAULY D, CHRISTENSEN V, GUÉNETTE S, PITCHER TJ, SUMAILA UR, WALTERS CJ, WATSON R, ZELLER D. 2002. Towards sustainability in world fisheries. *Nature.* 418: 689-695. DOI: <https://doi.org/10.1038/nature01017>
- PIANKA ER. 1970. On r- and K-Selection. *Am Nat.* 104 (940): 592-597. DOI: <https://doi.org/10.1086/282697>
- RADHAKRISHNAN N. 1964. Notes on some aspects on the biology of the fringe scale sardine, *Sardinella fimbriata* (Cuvier & Valenciennes). *Indian J Fish.* 11 (1): 127-134.
- RAYMOND S, TODD C, RYALL J, FANSON B, KOEHN J, TONKIN Z, HACKETT G, O'MAHONY J, BERRY K, LIESCHKE J, ROURKE M. 2023. Using density

- estimates, sex ratios and size structure to assess the status of a threatened Australian freshwater crayfish (*Euastacus armatus*) population. *Hydrobiologia*. 850 (19): 4181-4194. DOI: <https://doi.org/10.1007/s10750-023-05289-1>
- REICHARD M, POLAČIK M, BLAŽEK R, VRTÍLEK M. 2014. Female bias in the adult sex ratio of African annual fishes: interspecific differences, seasonal trends and environmental predictors. *Evol Ecol*. 28 (6): 1105-1120. DOI: <https://doi.org/10.1007/s10682-014-9732-9>
- RIJNSDORP AD. 1991. Changes in fecundity of female North Sea plaice (*Pleuronectes platessa* L.) between three periods since 1900. *ICES J Mar Sci*. 48 (3): 253-280. DOI: <https://doi.org/10.1093/icesjms/48.3.253>
- RIVERA E, BENDAÑO A, BOGNOT EDC, GONZALES F, TORRES JR. FSB, SANTOS MD, LOPEZ GDV. 2017. Reproductive biology of common small pelagic fishes in Manila Bay, Philippines. *Philipp J Fish*. 24 (1): 47-60.
- ROBINSON OJ, JENSEN OP, PROVOST MM, HUANG S, FEFFERMAN NH, KEBIR A, LOCKWOOD JL. 2017. Evaluating the impacts of fishing on sex-changing fish: a game-theoretic approach. *ICES J Mar Sci*. 74 (3): 652-659. DOI: <https://doi.org/10.1093/icesjms/fsw222>
- ROHIT P, BHAT UG. 2003. Reproductive biology and population characteristics of *Sardinella gibbosa* and *Sardinella fimbriata* from northwest Bay of Bengal. *Indian J Fish*. 50 (3): 271-278.
- RONQUILLO IA, LLANA MEG. 1987. Biological effects of fishery management measures in the Philippines. Proceedings of the Symposium on the Exploitation and Management of Marine Fishery Resources in Southeast Asia. Darwin, Australia, 16 February 1987. Bangkok: Regional Office for Asia and the Pacific and FAO. p. 244-248.
- SCHLOSSER IJ. 1990. Environmental variation, life history attributes, and community structure in stream fishes: implications for environmental management and assessment. *Environ Manage*. 14 (5): 621-628. DOI: <https://doi.org/10.1007/BF02394713>
- SHAPIRO DY, GIRALDEAU L-A. 1996. Mating tactics in external fertilizers when sperm is limited. *Behav Ecol*. 7 (1): 19-23. DOI: <https://doi.org/10.1093/beheco/7.1.19>
- SILVA A, SANTOS MB, CANECO B, PESTANA G, PORTEIRO C, CARRERA P, STRATOUDAKIS Y. 2006. Temporal and geographic variability of sardine maturity at length in the northeastern Atlantic and the western Mediterranean. *ICES J Mar Sci*. 63 (4): 663-676. DOI: <https://doi.org/10.1016/j.icesjms.2006.01.005>
- SIVASUBRAMANIAM K, RAJAPACKIAM S, FERNANDO AA, FERNANDO WMTB, THIVAKARAN GA. 2020. Length-weight relationships of six commercially important species of fishes from Palk Bay, Southeast Coast of India. *Int J Fish Aquat Stud*. 8 (4): 127-131.
- SLESINGER E, JENSEN OP, SABA G. 2021. Spawning phenology of a rapidly shifting marine fish species throughout its range. *ICES J Mar Sci*. 78 (3): 1010-1022. DOI: <https://doi.org/10.1093/icesjms/fsaa252>
- TSIKLIRAS AC, ANTONOPOULOU E. 2006. Reproductive biology of round sardinella (*Sardinella aurita*) in the north-eastern Mediterranean. *Sci Mar*. 70 (2): 281-290. DOI: <https://doi.org/10.3989/scimar.2006.70n2281>
- VAN OVERZEE HMI, RIJNSDORP AD. 2015. Effects of fishing during the spawning period: implications for sustainable management. *Rev Fish Biol Fish*. 25 (1): 65-83. DOI: <https://doi.org/10.1007/s11160-014-9370-x>
- WHITEHEAD PJP. 1985. FAO species catalogue. Vol. 7. Clupeoid fishes of the world (suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, anchovies and wolf-herrings. Part 1 - Chirocentridae, Clupeidae and Pristigasteridae. *FAO Fish. Synop*. 125 (7/1). 303 p.
- WILLETTE DA, BOGNOT E, MUTIA M, SANTOS M. 2011. Biology and ecology of sardines in the Philippine: a review. *BFAR-NFRDI Tech Pap Ser*. 13 (1). 22 p.

- WILLOUGHBY NG, TWEDDLE D. 1978. The ecology of the commercially important species in the Shire Valley fishery, Southern Malawi. Symposium on river and floodplain fishes in Africa, Bujumbura, Burundi, 21-23 November 1977. CIFA Tech Pap. 5. p. 137-152.
- WINEMILLER KO, ROSE KA. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Can J Fish Aquat Sci.* 49 (10): 2196-2218. DOI: <https://doi.org/10.1139/f92-242>
- WITTHAMES PR, GREER WALKER M, DINIS MT, WHITING CL. 1995. The geographical variation in the potential annual fecundity of dover sole *Solea solea* (L.) from European shelf waters during 1991. *Neth J Sea Res.* 34 (1-3): 45-58. DOI: [https://doi.org/10.1016/0077-7579\(95\)90013-6](https://doi.org/10.1016/0077-7579(95)90013-6)
- ZAR JH. 2001. *Biostatistical analysis*. 4th ed. New Jersey: Pearson Publishing Company.