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Original Article

Reproductive biology of short mackerel, *Rastrelliger brachysoma*, off Pattani Bay, Lower Gulf of Thailand♣

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Abstract

The reproductive biology of short mackerel, *Rastrelliger brachysoma*, which forms spawning aggregation off Pattani Bay was measured by gonadosomatic index (GSI), size at first maturity (L_{50}) and morphometric maturity classification. We found an unbalanced sex ratio between males and females (1.60:1, $p<0.0001$). Two peaks of GSI were coincident with two spawning seasons; the pre-monsoon (February) and the south-west monsoon (May, June, August, and September). The L_{50} was estimated to be 17.8 cm and 18.3 cm (TL) for male and female, respectively. The morphometric classification indicated that 50% of *R. brachysoma* population off Pattani Bay matured at 16.2 cm (TL) and 14.7 cm (FL). Positive relationships were found between fecundity and total length, total weight, and ovary weight. The occurrence of immature and maturing stages found throughout the year indicated that the pattern of catch from this habitat might affect fish recruitment and stock.

Keywords: fecundity, gonadosomatic index (GSI), morphometric maturity, size at first maturity (L_{50}), spawning season

1. Introduction

The reproductive biology of fishery resources is an important prerequisite for management and sustainable use (Fazrul *et al.*, 2018; Fontoura, Braun, & Milani, 2009; Trindade-Santos & Freire, 2015). In fishes, young individuals are distinguished based on the degree of gonadal maturity; however, the main difficulty is separating adolescent individuals from those at the beginning of a new reproductive cycle. Therefore, estimating the size at first maturity (L_{50}) is a useful tool in fish stock assessments (Fontoura *et al.*, 2009). Information of both spawning season and size at first maturity is essential for proper management of fisheries. These data should be collected at both spatial and temporal scales (Trindade-Santos & Freire, 2015). However, it is time consuming to determine maturity stages by histological examination of the gonads or by investigation of secondary

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sexual characteristics. The computer program (MATURE) was introduced as an easy tool to estimate size at sexual maturity from morphometric data (Somerton, 1980) that assigns a 0.5 probability for morphometric maturity to correspond to 50% of the cohort defined to be mature.

Rastrelliger species including *R. brachysoma*, *R. faughni* and *R. kanagurta* are important fisheries resources in Southeast Asian and other Indo-Pacific countries. They are targeted in commercial and artisanal fisheries, typically with the use of purse seines and gill nets except from the central part of the Indo-Pacific Ocean where they are caught within a single fishing net (Mohsin & Ambak, 1996). Short mackerel (*R. brachysoma*) is an important marine fish commodity and is a new candidate species for aquaculture in Thailand (Senarat, Kettratad, & Jiraungkooskul, 2016). Different migration pattern of males and females to and from fishing grounds could result in exploitation of either males or females at a particular time leading to varying of sex ratio (Rao, 1962). Variations of sex ratio and gonadosomatic index (GSI) provide reproductive data for fisheries management and information on fish population affected by fisheries activities (Trindade-Santos & Freire, 2015).

To successfully complete a reproductive cycle, getting a chance at spawning activity and larval survival are crucial. There are a few studies on reproductive biology of *R. brachysoma* including those in India (Roul, Kumar, Ganga, & Rohit, 2017), Indonesia (Sudjastani, 1974), Thailand (Senarat, Jiraungkoorskul, & Kettratad, 2017) and Myanmar (Aye, 2019). However, there is no report on the reproductive and spawning behavior of *R. brachysoma* in Thailand. The present study is aimed to (i) characterize sex-ratio, (ii) estimate monthly changes of gonad maturity, (iii) determine spawning season based on gonadal development stages, (vi) define type of spawning by the frequency distribution of maturity stage, (v) illustrate gonadal maturation by histological approach, (vi) estimate size at first maturation (L_{50}) and morphometric maturity based on fish length, and (vii) determine fecundity and relationships of fish length, fish weight and ovary weight.

2. Materials and Methods

2.1 Fish sampling and laboratory analysis

This study was carried out off the mouth of Pattani Bay, a semi-enclosed, shallow, and estuarine water body at the southern tip of the Gulf of Thailand (Fazrul, Hajisamae, Ikhwanuddin, & Pradit, 2015; Hajisamae & Yeesin, 2014). Monthly sampling of *R. brachysoma* was conducted by mackerel gill net with the mesh sizes of 3.5 cm, 4.0 cm and 4.5 cm at a water depth of 2-6 m off Pattani Bay between February 2019 and February 2020 (Figure 1) (Soe, Pradit, & Hajisamae, 2021). After landing, fish specimens were immediately chilled in iced water and taken to the laboratory at the Faculty of Science and Technology, Prince of Songkla University. Approximately 50 fish samples were randomly selected from the monthly samples and immediately preserved in 10% formalin for four days and thereafter soaked in water for one night and transferred to 70% ethanol for further analyses. Fish samples were recorded for total length to the nearest 0.1 cm, total weight and entire gonad weight to the nearest 0.01g. The macroscopic observation of gonad stage was determined by external appearance as suggested by Rao (1967).

For histological analyse, fresh gonadal tissue were treated based on Roberts, Smail, and Munro (2012). A small piece of tissue was extracted from the middle part of the right side of male and female gonads then preserved in 10% buffered formalin for 24 hours. They were dehydrated in an automatic tissue processor for 24 hours, cut at 3 mm thickness and embedded in paraffin. Thereafter, 5µm width gonad tissue was cut by an automatic microtome (LEICA Mod. 2035 Biocut), stained with Mayer’s haematoxylin and Eosin and photographed under a microscope (NIKON Eclipse E200) attached with a digital camera (NIKON DS Fi2). The criteria to identify the developmental stages of the oocytes was based on the appearance of the most advanced oocytes, post-ovulatory follicles and atretic oocytes (Havimana, Ohtomi, Masuda, & Vazquez, 2020).

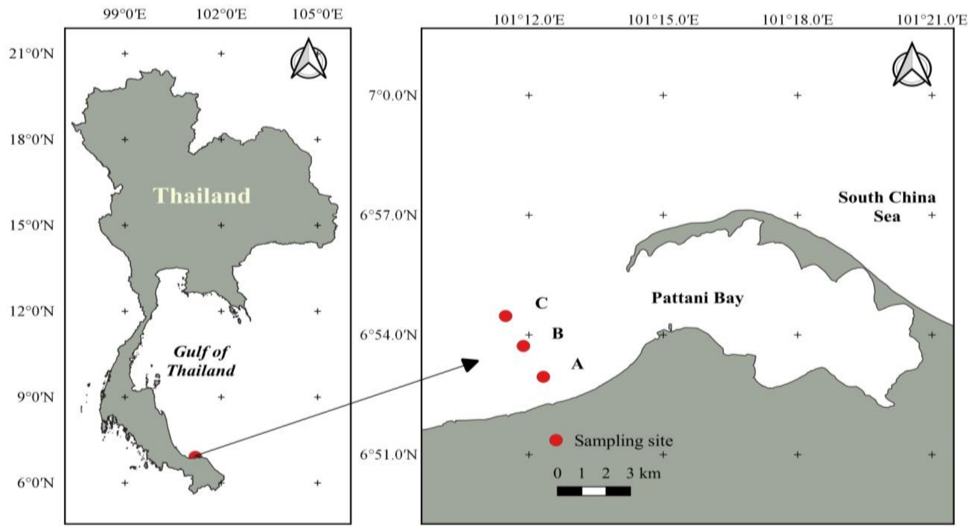

Figure 1. Sampling sites off Pattani Bay. Sites marked ‘A’, ‘B’ and ‘C’ represent water depth contours 2 m, 4 m and 6 m, respectively.

2.2 Data analyse

Based on monthly distribution of males and females, sex ratio was calculated as number of male divided by female. The Chi-square (χ^2) was applied to test for deviation from a 1:1 ration between male and female (Sokal & Rohlf, 1981). The gonadosomatic index (GSI) was used to determine monthly reproductive state. It was estimated as proposed by Adebisi (1987).

GSI= (Gonad weight (g)/ Total weight (g))* 100

Data on reproduction was complemented by total length (cm), monthly spawning frequency and sampling period. To determine spawning season and type of spawner, 623 gonads were defined into five stages including, immature (Stage I), maturation (Stage II), starting maturation (Stage III), maturation with recent spawning (Stage IV), and spent (Stage V) by macroscopic observation. The stage III and above were considered for calculating percentage of gonad maturity as these stages were considered ready to spawn. Spawning period was determined when the proportion of nearly ripe, ripe, and spent ovaries were high (Ghosh, Rao, Mahesh, Kumar, & Rohit, 2016).

Size at first sexual maturity was estimated by logistic estimation of gonad maturity that was run with “sizeMat” package in R program (R Core Team, 2019) between total length (TL) and, sexual maturity character for immature (Stage I and II) and mature (Stage III-V). Then, 50% of sexually matured organisms were estimated by fitting the fraction of mature fish against length interval. The estimated logistic function was as follow:

Y=1/1+exp-(a+b*X)

where, X= allometric variable, Y= stage of sexual maturity, a= Y-intercept and b= slope of the curve. All statistics for each parameter were calculated from each bootstrap sample (median and confidence intervals).

To analyze size at morphometric maturity, the data set was prepared including allometric measures and other attributes (month and sex category) of 623 fish samples. A principle component analysis was performed with two allometric variables: X (total length) and Y (fork length) in log base. Then, PCA analysis and discriminate analysis (linear regression) allocated any individuals into juvenile and adult. These two groups were distributed using hierarchical classification procedure by “Ward D” and “euclidean” based on their loads on the two axes of the PCA (Corgos & Freire, 2006) that was run with “sizeMat” package.

Fecundity of female ovary was measured from three different parts (anterior, middle and posterior) of the ovary under a binocular microscope (Murua *et al.*, 2003). Egg diameter was measured by an ocular meter and determined by gravimetric method as:

F = nG/g

where, n= number of egg in the subsample, G= total weight of the ovary and g= weight of the subsample. Relationship between fecundity (F) and independent variables (X) of total length (TL), total weight (TW) and ovarian weight (OW) were analyzed by linear regression analysis (Gulland, 1983).

$F = aX^b$

where, a = constant and b = regression co-efficient. The results of a and b values from this equation were converted to a linear form by the following equation:

ln Fecundity (F) = ln a + b (ln X)

where, X = TL or TW or OW, a and b = constant values from linear regression analysis and r^2 is the correlation between fecundity (F) and TL or TW or OW were tested at the 0.05 probability level of significance. Fecundity was calculated to a linear form using logarithms and then finally converted to antilog by exp (ln(F)).

3. Results

3.1 Sex ratio

The sex ratio analysis showed that male was predominant in almost all months (Table 1). The observed sex ratio of 1.60:1 (χ^2 = 32.82, p<0.0001) indicate an unbalanced ratio between males and females in this fishing ground (Figure 2).

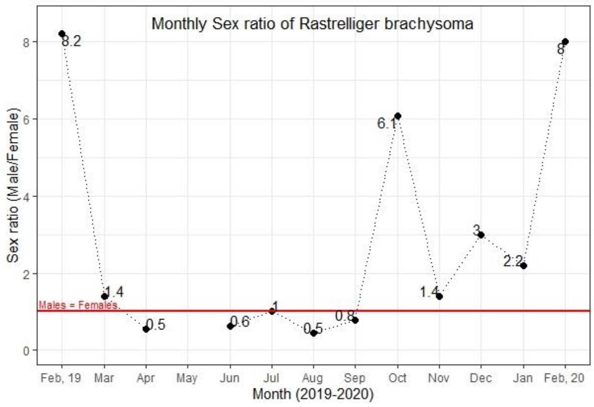

Figure 2. Monthly sex ratio of *Rastrelliger brachysoma* from 2019-2020. Horizontal red line indicating 1:1 sex ratio between male and female

3.2 Gonadosomatic index

Females had higher GSI value than that of males. The maximum GSI value of female was observed in September, whereas the minimum was in December (Table 1). By GSI analysis, active spawning female was found sporadically the entire year round.

3.3 Spawning season and spawner type

According to maturity stage and monthly percentage composition of immature and mature fishes, a general trend of immature fish was observed throughout the year (Figure 3). Partially matured and spawned female was found in May, June, August, September 2019 and February (2020).

Table 1. Sex ratio, gonadosomatic index (GSI) values for males and females of *Rastrelliger brachysoma*

Month	Number of fish		Sex ratio	χ^2	*p* value	Mean GSI (%)	
	♂	♀				♂	♀
Feb, 19	41	5	8.2	28.17*	<0.0001	0.29	0.66
Mar	24	17	1.4	1.19	0.27	0.84	1.44
Apr	19	35	0.5	4.74*	0.029	0.71	1.13
May	0	2	0.0	NA	NA	-	-
Jun	21	33	0.6	2.67	0.10	0.57	1.62
Jul	14	14	1.0	0	1	0.74	0.83
Aug	12	26	0.5	5.16*	0.02	0.78	1.39
Sep	27	35	0.8	1.03	0.31	0.78	2.16
Oct	79	13	6.1	47.35*	<0.0001	0.29	0.92
Nov	42	30	1.4	2	0.16	0.46	0.67
Dec	12	4	3.0	4*	0.05	0.41	0.41
Jan	44	20	2.2	9*	0.003	0.36	0.54
Feb, 20	48	6	8.0	32.67*	<0.0001	0.17	1.63
Overall	383	240	1.60	32.82	<0.0001	0.44	1.23

*(χ^2, p<0.05), (Critical value $\chi^2_{0.95}$= 3.84), NA= not applicable

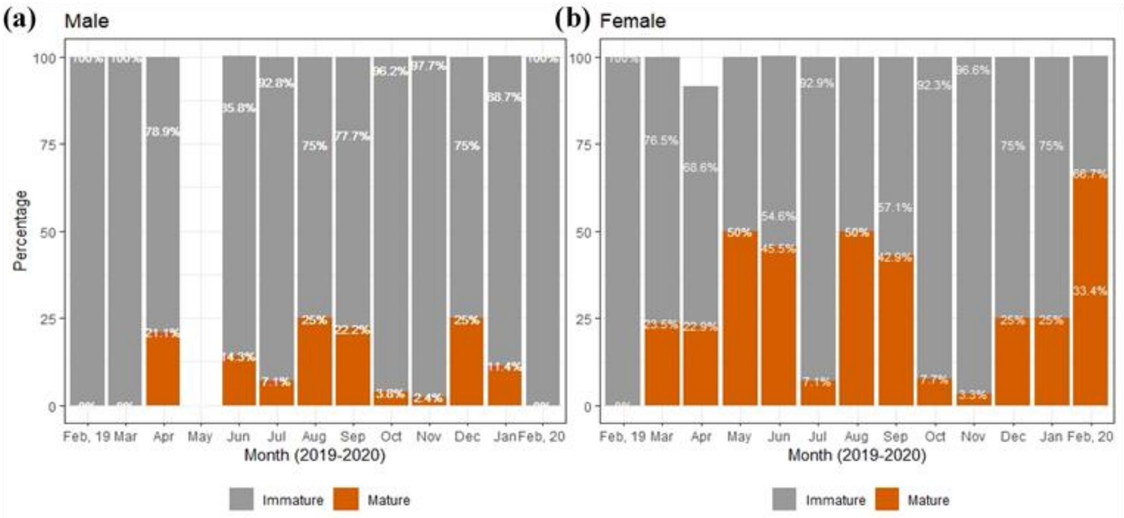

Figure 3. Percentage frequency of maturity stages of *Rastrelliger brachysoma*, (a) male and (b) female

Five maturity stages were determined based on the color pattern and size of gonad occupied in the body cavity (Figure 4) and the appearance of the most advanced oocytes, post-ovulatory follicles and atretic oocytes by microscopic observation (Figure 5). In the stages I-II, immature ova measured up to 20-70 µm representing the general eggs in these ovary stages. From this group, a batch of eggs developed from immature to mature stages (III), with sizes of egg from 50 to 200 µm. For stages IV-V, egg size was between 100-400 µm. Based on histological analysis, *R. brachysoma* had an asynchronous gonad containing oocytes at various stages of development due to multiple spawning during reproductive season (Figure 5f).

3.4 Size at first maturity (L_{50})

The first maturity of *R. brachysoma* was at 17.8 cm and 18.3 cm (TL) for male and female, respectively. Result from statistical analysis, at the confidence interval of 95%, found that sizes at first maturity were between 17.6-18.1 cm and 18.2-18.5 with the b value of 2.30 and 2.03 for male and female, respectively. A strong relationship between proportion of maturity and total length of fish for both sexes was also found (r^2>0.5) (Figure 6).

3.5 Size at morphometric maturity

The size of 50% of morphometric maturity was estimated to be 16.2 cm (TL) and 14.7 (FL) for the pooled sex, 14.7 cm (TL) and 13.5 cm (FL) for male and 18.2 cm (TL) and 16.5 cm (FL) for female of *R. brachysoma* (Table 2 and Figure 7). The b-value was larger in males indicating that males might grow faster than females.

3.6 Fecundity and regression analysis

It was found that fecundity ranged between 6,638 and 37,000 eggs with an average of 18,828 eggs (Figure 8). The highest fecundity was in fish with a total length of 19.5 cm. Results from regression analysis showed a positive

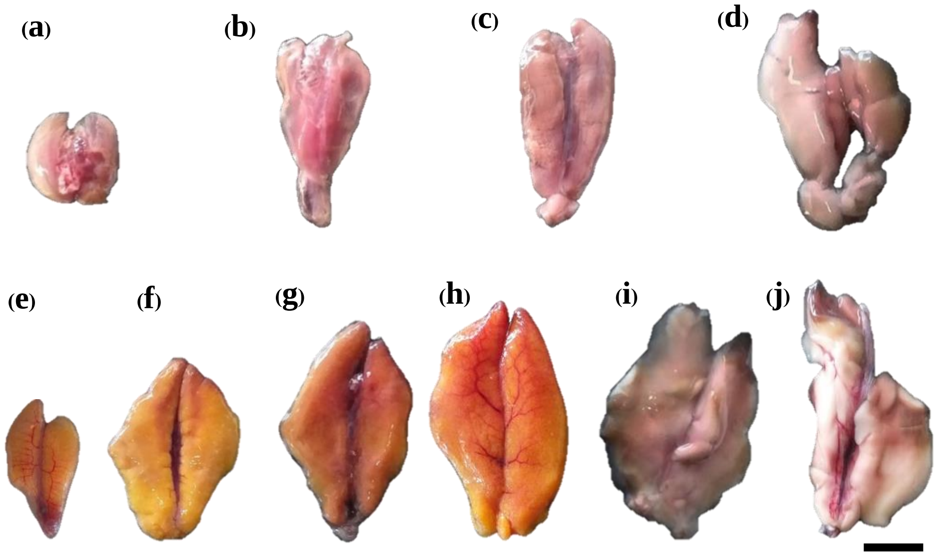

Figure 4. Macroscopic examination of gonad maturity stages of males (a-d) and females (e-j) of *Rastrelliger brachysoma*. (a) immature, (b) maturing (c) start mature and (d) spent stage, (e) immature, (f) maturing, (g) start mature, (h) ripe (ready to spawn) and (i-j) spent stages. Scale bar 1 cm

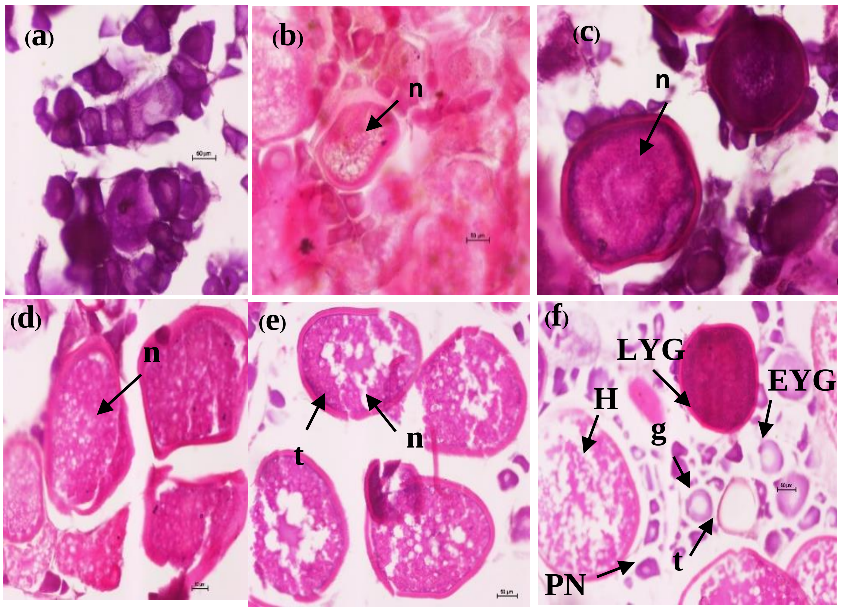

Figure 5. Oocyte developmental stages and post-ovulatory follicle of female *Rastrelliger brachysoma*: (a) peri-nucleolus, (b) pre-vitellogenic, (c) early yolk globule, (d) late yolk globule, and early atretic follicle, (e) late atretic follicle and post-ovulatory follicle and (f) asynchronous oocyte development. ***n:*** Nucleus, ***g:*** granulosa cell layer, ***t:*** thecal cell layer, ***y:*** yolk, ***PN***: Peri-nucleus, ***EYG:*** early yolk globule, ***LYG:*** late yolk globule, ***H:*** hydrated. Scale bars 50 µm

relationship between fecundity and total length, total weight, and ovary weight ($p<0.05$). The computed b value was very high for fecundity and total length (b= 8.27) but low for fecundity to body weight and fecundity to ovary weight (b<2).

4. Discussion

Sex ratio is an important biological aspect to assess changes in structure of populations and their reproductive capabilities (Trindade-Santos & Freire, 2015). Results from this study indicate a trend towards the dominance of males leading to a heterogeneous sex ratio of *R. brachysoma*. Similar finding was reported in Myanmar waters where there was the higher number of males compared to females for most of *Rastrelliger* spp. and the similar trend of sporadic peaks in gill net fishery (Aye, 2019). Normally, the higher sex ratio in spawning population was mainly related to sampling gear, sampling time and age (Ward *et al.*, 2019). Types of fishing

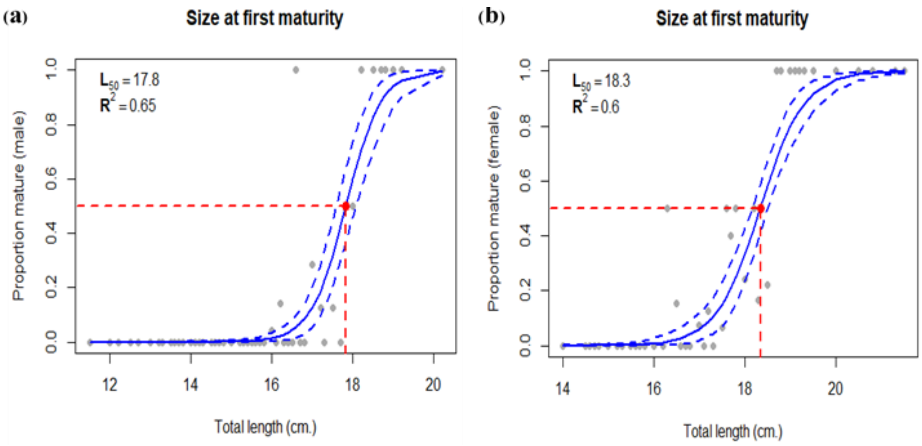

Figure 6. Size at first sexual maturity of *Rastrelliger brachysoma* (a) male and (b) female. L_{50}= size at first maturity in total length (cm) and R^2= correlation coefficient

gear is being responsible for males entering to spawning population more than females (Funk & Sandone, 1990). The gonadosomatic index (GSI) result showed sporadic peaks with that of female higher than male (Table 1). The higher GSI value normally coincides with peak period of spawning, then the onset of the spawning season can be defined (Fontoura *et al.*, 2009; Trindade-Santos & Freire, 2015). Therefore, spawning period can be identified when GSI value is high. Pattani Bay is influenced by the north-east monsoon season from November to February and the south-west monsoon season from May to September. Consequently, high rainfall occurs for seven months (Chaiwanawut, Hattha, & Duangmala, 2005). This study indicates two main spawning seasons of this species which are coincident with pre-monsoon in February and south-west monsoon spawning season in May, June, August, and September (Figure 3). It has been reported that *R. brachysoma* has long spawning season such as May to October in Indonesia (Sudjastani, 1974), and July to December in Myanmar (Aye, 2019). In the upper part of the Gulf of Thailand, a short term breeding season of *R. brachysoma* was reported from December to February (Senarat *et al.*, 2017). This is confirmed by the present study when mature females are found during December to February and the less mature females were observed in October-November. Aye and Tint (2020) reported that the dominance of medium and large size fish throughout the year indicating multiple breeding season of *Rastrelliger* species in Myanmar.

This study found that *R. brachysoma* has an asynchronous ovary containing oocytes at various stages of development supporting a multiple spawning behavior during its reproductive season. The macroscopic stage determination from this study is in agreement with the histological examination for the maturity stages as the immature and mature ova are 20-400 µm. The term “asynchronous” refers to oocytes recruit and ovulate from the yolked oocytes in several batches during each spawning season (Murua & Saborido-Rey, 2003). Batch spawning is an adaptive strategy of fish which will release eggs over a long period which increases survival probability (Lambert & Ware, 1984). Generally, the spawning period is indicated when the female ovaries are translucent (stage IV). Oktaviani, Supriata, Erdmann, and Abinawanto (2014) reported that when there is an overall high percentage of specimens at stage IV and V maturity, it would be considered as a spawning aggregation area. Different sizes of yolked ova in a mature fish indicate prolong spawning behavior with the largest size of yolked ova found during the peak spawning months (Ghosh *et al.*, 2016).

The size at first maturity (L_{50}) was 17.8 cm and 18.3 cm (TL) for male and female, respectively. Maturity rate of male was faster than that of female as indicated by high ‘b’ value of male. In comparison, for fishes in Myanmar, L_{50} was estimated to have 18.1 cm and 19.6 cm in male and female, respectively (Aye, 2019). Compared with this study, maturity stage of fish is smaller than that reported by Aye (2019). By morphometric maturity analysis, the size of 50% of *R. brachysoma* population matured at 16.2 cm (TL) and 14.7 cm (FL) (Table 2). However, Kongseng, Phoonsawat, and Swatdipong (2020) reported that fully mature *R. brachysoma* in the Gulf of Thailand was found at ≥14 cm TL. It can be seen that the size on fish maturity changes with locality. *R. brachysoma* showed a sexual dimorphism, in which males have the shorter bodies and longer caudal fins than females (Sudjastani, 1974). This leads to differences in the calculation of 50% of size at morphometric maturity between males and females by two variables of total length and fork length. Their 50% of size at maturity by morphometric data were calculated as 14.7 cm (TL) in male and 18.2 cm (TL) in female. Therefore, future research should also focus on variation of morphometric characteristics for the separate sexs of fish. In fisheries management, a minimum legal size limit is generally site-specific (Trindade-Santos & Freire, 2015); for this reason, L_{50} information of fish including both sexual and morphometric maturities at local fishing ground is important for local fisheries management. Thus, to ensure sustainable fishery of this stock, fishing activity shall be avoided during their spawning season and the use of nets with suitable mesh sizes should be implemented.

This study confirms that *R. brachysoma* is an intermittent spawner and a prolific breeder due to their high productivity and spawning activity throughout the year. Also, Yohannan and Abdurahiman (1998) reported that Indian mackerel *R. kanagurta* was assumed to be prolific breeder due to their spawning over the year when they have favorable temperature and availability of food for spawning. The

Table 2. Classification of morphometric maturity based on the total length (TL) and fork length (FL) of *Rastrelliger brachysoma*. a = y-intercept, b= slope (where if b= 1 means isometric).

Sex	Sample (n)	Adult growth parameter			Size of 50% maturity (cm)	
		a	b	*p* value	TL	FL
Pooled sex	623	1.95	0.79	< 0.0001	16.2	14.7
Male	383	1.03	0.85	< 0.0001	14.7	13.5
Female	240	2.28	0.78	< 0.0001	18.2	16.5

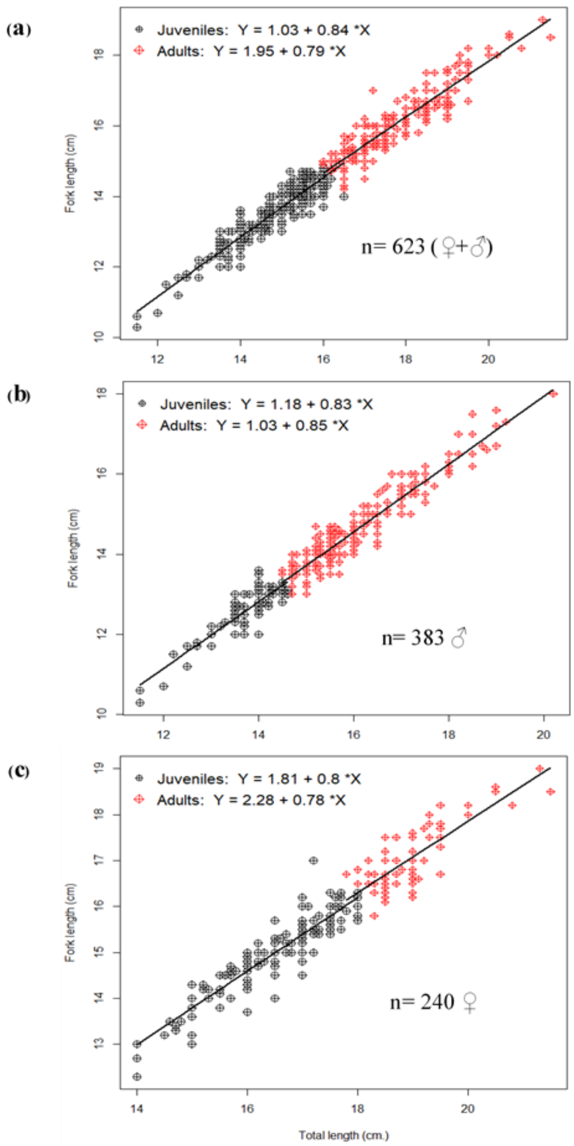

Figure 7. Maturity classification of *Rastrelliger brachysoma* off Pattani Bay, (a) pooled sex, (b) males and (c) females. Black circles represent juveniles and red rectangles represent adults.

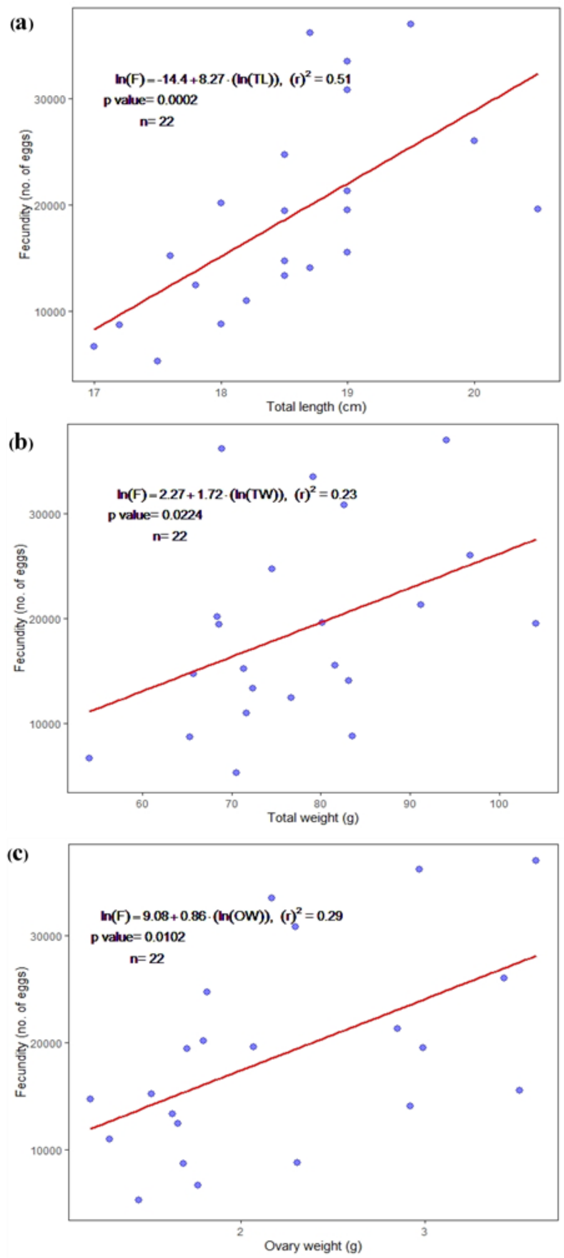

Figure 8. Relationship between fecundity (F) and (a) total length (TL), (b) total weight (TW) and (c) ovary weight (OW) of *Rastrelliger brachysoma*

logarithmic relationships between fecundity and total length, total weight and ovary weight were found to be linear, indicating that fecundity increased with the increases in length, body weight and ovary weight. The disparate b value between total length, total weight and ovaray weight is probably due to an intermittent spawning strategy of *R. brachysoma*. For the calculated fecundity index, the b value is normally close to 3 for teleost fish, whereas it is close to 2 for elasmobranch fish (Holden & Raitt, 1974). However, this value always varied between small and large fish species, the former typically producing proportionately fewer eggs than the latter. Strong relationship between fecundity and total length was found (Figure 8). Santana, Tondato, and Súarez (2019) concluded that the positive relationship between fecundity and length and weight was usually recognized with more energy storage by larger female, intending to invest for reproduction. Bhendarkar, Rathod, and Joshi (2018) stated that ovarian weight and total length were the most important factors in determining fecundity of mackerel fish.

Overall, our finding supports not only the reproductive behavior of short mackerel (*Rastrelliger brachysoma*) but also provides critical information for spawning season and awareness of sustainability on minimal legal sizes limit on this species. In the future, fish size should be limit on at least 16.2 cm (TL) or 14.7 cm (FL) to pave the way for fishes to spawn once in their life before being captured.

5. Conclusions

The present study improves the understanding of short mackerel (*Rastrelliger brachysoma*) reproductive biology in nearshore habitat to support an effective fisheries management program. It is suggested that regulating of a minimum size of capture is important as indicated by data of size at first maturity (L_{50}), morphometric maturity, spawning season and the dominance of immature and maturing stages detected throughout the year. The pattern of catch from this habitat might affect fish recruitment and stock. Thus, appropriate stock management is required for a sustainable utilization of fish resource.

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References

Adebisi, A. (1987). The relationships between the fecundities, gonadosomatic indices and egg sizes of some fishes of Ogun River, Nigeria. *Archiv Fur Hydrobiologie, 111*, 151-156.

Aye, Z. M. (2019). Fishery biology of some scombrid fishes from Palaw and adjacent coastal waters, Taninthayi region. (Doctoral thesis, Mawlamyine University, Myanmar).

Aye, Z. M., & Tint, K. M. M. (2020). Some population parameters of *Rastrelliger* spp. from palaw and adjacent coastal waters, Taninthayi region in Myanmar. *International Journal of Fisheries and Aquatic Studies*, *8*(3), 577-584.

Bhendarkar, M. P., Rathod, R. H., & Joshi, H. D. (2018). Study on the fecundity and gonadosomatic index of *Rastrelliger kanagurta* (Cuvier, 1817) of southern coast of Maharashtra, India. *Journal of Applied and Natural Science*, *10*(1), 107-110.

Chaiwanawut, C., Hattha, K., & Duangmala, P. (2005). Patterns of rainfall in Pattani Province from 1982 to 2001. *Songklanakarin Journal of Science and Technology*, *27*, 116-176.

Corgos, A., & Freire, J. (2006). Morphometric and gonad maturity in the spider crab *Maja brachydactyla*: A comparison of methods for estimating size at maturity in species with determinate growth. *ICES Journal of Marine Science*, *63*, 851-859. doi:10.1016/j.icesjms.2006.03.003

Fazrul, H., Hajisamae, S., Ikhwanuddin, M., & Pradit, S. (2015). Assessing impact of crab gill net fishery to bycatch population in the lower Gulf of Thailand. *Turkish Journal of Fisheries and Aquatic Sciences, 15*, 761-771. doi:10.4194/1303-2712-v15_3_21

Fazrul, H., Hajisamae, S., Ikhwanuddin, M., Aziz, N. A. N, Naimullah, M., & Hassan, M. (2018). Study on the reproductive biology of the blue swimming crab, *Portunus pelagicus* females from Pattani coastal waters, Thailand. *AACL Bioflux, 11*(6), 1776-1791.

Fontoura, N. F., Braun, A. S., & Milani, P. C. C. (2009). Estimating size at first maturity (L_{50}) from Gonadosomatic Index (GSI) data. *Neotropical Ichthyology*, *7*(2), 217-222. doi:10.1590/S1679-62252009000200013

Funk, F., & Sandone, G. J. (1990). Catch-Age analysis of Prince William Sound, Alaska, herring, 1973-1988. Alaska department of fish and game. *Fishery Research Bulletin* No. 90-01. Retrieved from https://www.adfg.alaska.gov/fedaidpdfs/FRB.1990.01.pdf

Ghosh, S., Rao, M. V. H., Mahesh, V. U., Kumar, M. S., & Rohit, P. (2016). Fishery, reproductive biology and stock status of the Indian mackerel *Rastrelliger kanagurta* (Cuvier, 1817), landed along the north-east coast of India. *Indian Journal of Fisheries*, *63*(2), 33-41. doi:10.21077/ijf.2016.63.2.53399-05

Gulland, J. A. (1983). *Fish stock assessment. A manual of basic method* (pp. 1-241). Rome, Italy: Food and Agriculture Organization of the Nations.

Hajisamae, S. & Yeesin, P. (2014). Do habitat, month and environmental parameters affect shrimp assemblage in a shallow semi-enclosed tropical bay, Thailand? *Raffles Bulletin of Zoology*, *62*,107-114.

Havimana, L., Ohtomi, J., Masuda, Y., & Vazquez, M. (2020). The reproductive biology of female crimson sea bream *Evynnis tumifrons* off the southwestern coast of Kyushu, Japan. *Fisheries Science*, *86*, 65-75. doi: 10.1007/s12562-019-01380-6

Holden, M. J, & Raitt, D. F. S. (1974). Manual of fisheries science. Part 2 - Methods of resource investigation and their application. *FAO Fisheries Technical*

Paper, *1*(115rev.1), 1-211. Retrieved from https://agris.fao.org/agris-search/search.do?recordID=XF7600305

Kongseng, S., Phoonsawat, R., & Swatdipong, A. (2020). Individual assignment and mixed-stock analysis of short mackerel (*Rastrelliger brachysoma*) in the inner and eastern Gulf of Thailand: Contrast migratory behavior among the fishery stocks. *Fisheries Research*, *221*, 105372. doi:10.1016/j.fishres.2019.105372

Lambert, T. C., & Ware, D. M. (1984). Reproductive strategies of demersal and pelagic spawning fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *41*(11), 1565-1569. doi:10.1139/f84-194

Mohsin, A. K. M, & Ambak, M. A. (1996). *Marine fishes and fisheries of Malaysia and neighbouring countries* (pp. 1-743). Serdang, Malaysia: Universiti Pertanian Malaysia Press.

Murua, H., & Saborido-Rey, F. (2003). Female reproductive strategies of marine fish species of the North Atlantic. *Journal of Northwest Atlantic Fishery Science*, *33*, 23-31. doi:10.2960/J.v33.a2

Murua, H., Kraus, G., Saborido-Rey, F., Witthames, P. R., Thorsen, A., & Junquera, S. (2003). Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *Journal of Northwest Atlantic Fishery Science*, *33,* 33-54. Retrived from http://digital.csic.es/bitstream/10261/26870/1/murua2.pdf

Muto, N., Alama, U. B., Hata, H., Guzman, A. M. T., Cruz, R., Gaje, A., . . . Ishikawa, S. (2016). Genetic and morphological differences among the three species of the genus *Rastrelliger* (Perciformes: Scombridae). *Ichthyological Research*, *63*, 275-287. doi:10.1007/s10228-015-0498-z

Oktaviani, D., Supriata, J., Erdmann, M., & Abinawanto, A. (2014). Maturity stages of Indian mackerel *Rastrelliger kanagurta* (Cuvier , 1817) in Mayalibit Bay, Raja Ampat, West Papua. *International Journal of Aquatic Science*, *5*(1), 67-76.

R Core Team. (2019). R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. Retrived from https://www.R-project.org

Rao, K. V. (1962). Distribution of the young stages of the mackerel, *Rastrelliger kanagurta* (Cuvier) in the Indian inshore waters. *Proceedings of the Symposium on Scombroid Fishes 1*, 469-482.

Rao, V. R. (1967). Spawning behaviour and fecundity of the Indian mackerel, *Rastrelliger kanagurta* (Cuvier), at Mangalore. *Indian Journal of Fisheries*, *14*(1 & 2), 171-186. Retrieved from http://eprints.cmfri.org.in/id/eprint/2279

Roberts, R. J., Smail, D. A., & Munro, E. S. (2012). Laboratory methods. In R. J. Roberts (Ed.), *Laboratory methods* (pp. 439-481). Oxford, England: Blackwell Publishing.

Roul, S. K., Kumar, R. R., Ganga, U., & Rohit, P. (2017). Length-weight relationship of *Rastrelliger brachysoma* (Bleeker, 1851) and *Rastrelliger faughni* Matsui, 1967 from the Andaman Islands, India. *Journal of Applied Ichthyology*, *33*, 1266-1267. doi:10.1111/jai.13469

Santana, C. A., Tondato, K. K., & Súarez, Y. R. (2019). Reproductive biology of *Hyphessobrycon eques* (Characiformes: Characidae) in southern Pantanal, Brazil. *Brazilian Journal of Biology*, *79*(1), 70-79. doi:10.1590/1519-6984.176273

Senarat, S., Kettratad, J., & Jiraungkooskul, W. (2016). Morpho-histology of the reproductive duct in short mackerel *Rastrelliger brachysoma*. *Advances in Environmental Biology*, *9*(8), 210-215.

Senarat, S., Jiraungkoorskul, W., & Kettratad, J. (2017). Ovarian histology and reproductive health of short mackerel, *Rastrelliger brachysoma* (Bleeker, 1851), as threatened marine fish in Thailand. *Songklanakarin Journal of Science and Technology*, *39*(2), 225-235.

Soe, K. K., Pradit, S., & Hajisamae, S. (2021). Feeding habits and seasonal trophic guilds structuring fish community in the bay mouth region of a tropical estuarine habitat. *Journal of Fish Biology*, 1-16. doi:10.1111/ jfb.14851

Sokal, R. R., & Rohlf, F. J. (1981). *Introduction to biostatistics* (2nd ed.). New York, NY: Dover Press.

Somerton, D. A. (1980). A computer technique for estimating the size of sexual maturity in crabs. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(10), 1488-1494. doi:10.1139/f80-192

Sudjastani, T. (1974). The species of *Rastrelliger* in the Java Sea; their taxonomy, morphology and population dynamics. (Master's thesis, University of British Columbia, Canada).

Trindade-Santos, I., & Freire, K. M. F. (2015). Analysis of reproductive patterns of fishes from three large marine ecosystems. *Frontiers in Marine Science*, *2*(38), 1-10. doi:10.3389/fmars.2015.00038

Ward, E. J., Delgado-nordmann, H., Brenner, R. E., Beaudreau, A. H., Moffitt, S. D., & Shelton, A. O. (2019). Assessing long-term changes in sex ratios of Pacific herring in Prince William Sound, Alaska. *Fisheries Research*, *211*(40), 300-308. doi:10.1016/j.fishres.2018.10.031

Yohannan, T. M., & Abdurahiman, U. C. (1998). Environmental influence on the behaviour of Indian mackerel and their availability to fishing gear along the Malabar coast. *Indian Journal of Fisheries*, *45*(3), 239-247.