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Reproductive biology of the mackerel scad, *Decapterus macarellus* (Cuvier, 1833), in the Sulawesi Sea, Indonesia

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ABSTRACT

Indonesia is the second largest fishery producer in the world, producing many small pelagic fish. To improve information for sustainable fishery management in the Sulawesi Sea, we examined the reproductive biology of the main target species, the mackerel scad *Decapterus macarellus* (Cuvier, 1833). Between May 2020 and March 2021, we collected 1267 mackerel scads from two landing sites in northern Sulawesi. These fish ranged from 13.4 to 38.2 cm in total length, and their sex ratio, length at first maturity (Lm), reproductive periodicity, and potential spawning grounds were studied. An equal male to female (M:F) sex ratio of 0.98:1.00 was osberved. The lengths of males and females at first maturity (Lm) were 22.59 and 21.62 cm, respectively. The mackerel scads spawned throughout the year, peaking in January, March, May, and September. Spawning occurs mainly during the first quarter of the moon's phase. Most mature individuals with a high gonadosomatic index were found near Tumumpa Dua and the northern and western coasts of the Sangihe and Siau Islands, suggesting that there are specific locations where mackerel scads spawn. Fishery managers can use this information to implement temporary and regional fishing closures to develop sustainable fishing practices for small pelagic fish species.

1. Introduction

Small pelagic fishes are a substantial source of income in many developing countries. Of the 84.4 million tons of total marine capture production reported in 2018, finfish accounted for 85%, with small pelagic fish being the leading group, followed by Gadiformes, tuna, and tuna-like species (FAO, 2022). Small pelagic fish comprise diverse species, which refer to fish with body lengths ranging between 10 and 30 cm, or up to 60 cm as adults, schooling primarily within the epipelagic zone (depths of 0–200 m) of the oceans (Fréon et al., 2005). The small pelagic species caught are usually unique between countries or regions; for example, anchoveta or Peruvian anchovy (*Engraulis ringens*) in Peru and Chile, sardines (*Sardinella* spp.) in the tropical waters off Africa and Asia, and scads (*Decapterus* spp.) caught mainly in eastern and south-eastern Asia (Fréon and Misund, 1999). At a global scale, scads (*Decapterus* spp.) were listed as major small pelagic genera of marine capture production globally, with an annual average production of 1199 thousand tons per year (2004–2013) and up to 1336 thousand tons in

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2018, making 2% of the total marine capture fishery production in the world (FAO, 2022).

Indonesia ranks second among the world's marine capture producers after China (FAO, 2022). In Indonesia's national fisheries system, the small pelagic resource potential and total allowable catch are presented as an accumulation of the entire group, without separating it into different species. A total of 17 species were recorded under the small pelagic category, with the predominant species belonging to the groups of mackerels, scads, and trevallies (MMAF, 2016). Mackerel scads were found to be the main species of the small pelagic catch in north Sulawesi, caught primarily by purse seines, and contributed 18% to the total catch in the respective fisheries management area (FMA 716) (MMAF, 2016). Hence, North Sulawesi is well known nationwide for its small pelagic production. Small pelagic fish are one of two groups of important species, in terms of quantity and value, targeted by fishers in the FMA 716, covering the Sulawesi Sea and the northern coast of Halmahera Island (USAID, 2019). Besides fishing in the North Sulawesi waters, fishers from this area often fish in adjacent fishing grounds outside the FMA 716, yet they land their catch at fishing ports across the North Sulawesi region. If stock and fishing grounds are not clearly defined, this is a concern for fishery managers when developing a fishery harvest strategy.

Studies related to mackerel scads in Indonesia have been undertaken to reveal their size distribution, growth patterns (Silooy et al., 2019), reproductive biology, population dynamics (Nur et al., 2017; Pattikawa et al., 2018; Silooy et al., 2021; Zamroni et al., 2019), population genetics (Zamroni et al., 2014; Zamroni and Suwarso, 2011), exploitation rate (Hariati, 2011), and habitat (Rahmadi and Puspasari, 2015). As a biological mechanism for transmitting genetic information from generation to generation, reproduction in teleosts is affected by changes in the environment and timing, with the latter ensuring adequate food during the reproductive cycle. Various approaches have been used to study the reproductive biology of mackerel scads in Indonesia, such as length-based life history parameters (Bintoro et al., 2020; Fadila et al., 2016; Iksan and Irham, 2009) and production models based on catch data (Fadhilah et al., 2021).

Knowledge of reproductive biology can inform fishery managers of the actual stock conditions of the respective resources and possible management measures to be taken. This study investigated the reproductive biology of mackerel scad (*Decapterus macarellus*) in the Sulawesi Sea to support sustainable fishery management. Reproductive seasonality, lunar periodicity, and potential spawning grounds were examined, and management measures for sustainable resource use were suggested.

2. Materials and methods

2.1. Study sites and sample collection

Fish were sampled from a commercial catch from May 2020 to March 2021 at two landing sites, Tumumpa Dua, and Bitung (Fig. 1), in North Sulawesi, Indonesia (due to logistical constraints, samples were not available in November and December 2020). Fish were collected for up to six days during each moon phase to estimate lunar pattern of spawning periodicity (see Section 2.3. Data analysis). During the study, fishers were interviewed to gather information about the fishing grounds. The information was collected using participatory mapping techniques. The total length (TL) and body weight (BW) of the fish were measured to the nearest millimeter and grams, respectively (Table 1).

2.2. Sample dissection and gonad identification

Fish gonads were macroscopically examined for sex identification by dissecting the gonads, following West (1990) and Diouf (1981). The shape and color of the testes and ovaries were used to assign the sex and gonadal maturity of the fish. In females, mature ovaries have a typical flaccid appearance and are empty, often bloodshot, or contain a small number of remnants, ripe eggs (West, 1990; Diouf, 1981). In males, the testes develop a whitish to pinkish color and are enlarged with conspicuous superficial blood vessels; when regressing, the testes are flaccid and bloodshot (Diouf, 1981). Gonad weight (*GW*) was measured to the nearest 0.1 g to calculate the gonadosomatic index (GSI) as a proxy for reproductive activity (Flores et al., 2019), using the formula GSI $= GW/BW \times 100$, where *GSI* is the gonadosomatic index, *GW* is the weight of the gonad, and *BW* is the body weight of the individual fish.

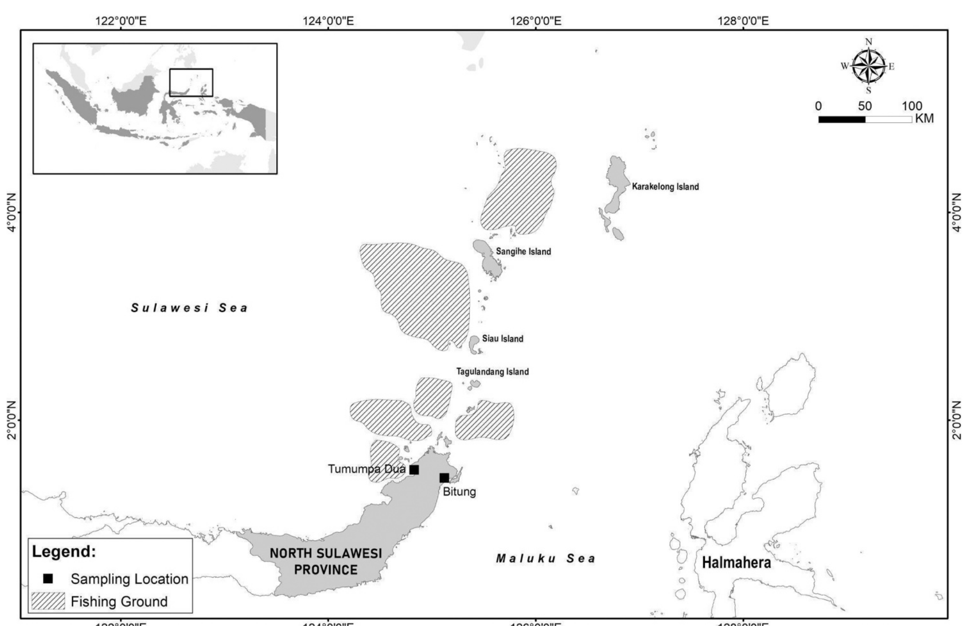

Fig. 1. Samples of *Decapterus macarellus* were collected from two landing sites (Tumumpa Dua and Bitung) in the mainland of the North Sulawesi province. Information on fishing grounds shown in the map was obtained from local fishers who landed their catch in Tumumpa and Bitung.

Table 1
Mean length (cm) and weight (g) of immature and mature individuals of the mackerel scad (*Decapterus macarellus*) caught in northern Sulawesi based on its sex (male, female). The range of length and weight of the samples are presented in the bracket.

Male							
Year	**Month**	**Immature**			**Mature**		
		n	**Length**	**Weight**	**n**	**Length**	**Weight**
2020	May	1	23.00 (NA)	113.39 (NA)	24	28.03 (22.50–38.20)	240.38 (104.89–555.65)
2020	Jun	7	19.80 (15.80–21.60)	77.76 (34.02–104.89)	66	25.59 (21.90–30.40)	172.07 (102.06–303.34)
2020	Jul	71	18.20 (14.00–23.00)	60.33 (22.67–119.06)	33	23.6 (19.80–27.10)	134.61 (79.37–198.45)
2020	Aug	32	21.98 (17.50–25.10)	105.77 (45.35–155.92)	95	25.32 (22.90–30.40)	163.89 (119.06–292.0)
2020	Sep	24	23.16 (20.50–26.00)	125.33 (82.21–184.27)	50	25.30 (19.40–29.60)	165.34 (73.71–252.31)
2020	Oct	82	20.57 (15.60–24.40)	92.83 (36.85–150.25)	6	24.93 (22.20–26.90)	164.43 (113.4–215.46)
2021	Jan	36	24.08 (18.00–25.30)	140.45 (48.48–160.74)	47	28.21 (22.00–32.50)	227.04 (102.06–331.97)
2021	Feb	14	24.29 (20.00–26.20)	147.09 (73.71–173.5)	23	26.55 (24.20–30.90)	201.53 (140.61–299.37)
2021	Mar	3	21.27 (18.70–24.20)	94.97 (53.58–148.83)	26	30.62 (27.50–35.00)	298.70 (193.34–454.16)
Female							
Year	**Month**	**Immature**			**Mature**		
		n	**Length**	**Weight**	**n**	**Length**	**Weight**
2020	May	2	24.70 (22.60–26.80)	157.34 (110.56–204.11)	15	25.49 (23.10–28.50)	171.79 (116.23–232.46)
2020	Jun	29	20.06 (14.60–23.10)	81.23 (31.18–121.9)	62	25.54 (22.40–29.30)	173.48 (113.40–277.83)
2020	Jul	95	18.00 (13.40–23.40)	57.97 (22.67–130.4)	50	23.70 (17.30–28.20)	139.50 (56.69–229.63)
2020	Aug	23	21.27 (17.40–23.60)	95.27 (48.19–133.24)	83	24.90 (22.60–28.30)	158.72 (113.39–238.13)
2020	Sep	8	22.41 (19.00–23.70)	117.65 (68.04–144.58)	58	24.97 (20.00–27.50)	161.59 (76.54–223.96)
2020	Oct	66	20.84 (15.50–24.50)	96.60 (39.69–158.76)	18	19.96 (17.20–27.50)	90.56 (48.19–223.96)
2021	Jan	18	23.81 (19.70–25.00)	139.51 (68.89–161.31)	43	27.48 (24.00–30.70)	214.94 (142.31–305.89)
2021	Feb	10	24.43 (23.00–25.00)	153.85 (129.56–170.95)	20	26.05 (24.00–30.00)	190.05 (152.80–312.98)
2021	Mar	2	24.5 (24.00–25.00)	156.07 (150.54–161.59)	25	29.36 (27.60–32.50)	272.13 (232.75–361.46)

2.3. Data analysis

Length at first maturity (Lm) was analyzed following Tokai and Mitsuhashi (1998) by maximizing the likelihood of binomial distribution in the logistic curve using the "SOLVER" tool in Excel. The percentage of mature individuals and GSI were plotted against fishing ground information, which was used to identify the potential reproductive areas and spawning grounds of mackerel scads in the Sulawesi Sea.

The sex ratio of the mackerel scads was estimated and tested for significant differences in the proportion of males and females for a theoretical 1:1 relationship using a chi-square (X^2) equation (Kenney and Keeping, 1951). Size differences between males and females were examined using the Kolmogorov-Smirnov (KS) test. All statistical analyses were performed using the RStudio software (R Core Team, 2022; RStudio Team, 2020). Seasonal spawning patterns were estimated using the monthly proportions of mature individuals. The lunar periodicity of spawning was calculated using the proportion of mature individuals during each moon phase. The equation describing the moon phase was based on the data presented in Koenig et al. (2016)). The moon phases are described as follows: New Moon = NM ± 3.5 d; First Quarter (Q1) = NM + 3.5 to NM + 11.5 d; Full Moon = FM ± 3.5 d; Third Quarter (Q3) = FM + 3.5 to FM + 11.5 d. Differences in the proportion of mature gonads for each female and male individual were compared among moon phases (NM, Q1, FM, and Q3) using the Proportion Z-test. Similarly, differences in GSI for each female and male individual were compared among moon phases using one-way ANOVA followed by Tukey's HSD post hoc test for pairwise comparisons.

3. Results

3.1. Morphometric characteristics and sex ratio

A total of 1267 individuals of mackerel scad with a mean total length of 23.25 cm (range = 13.4–38.2 cm) and mean weight of 138.37 g (range = 19.84–555.65 g) were collected. We observed 640 males (270 immature and 370 mature individuals) and 627 females (253 immature and 374 mature individuals). The immature male fish size ranged between 14.00 and 26.20 cm (22.67–184.27 g), while the immature female size ranged between 13.40 and 26.80 cm (22.67–204.11 g) (Table 1). We observed that the mature male individuals ranged from 19.40 to 38.20 cm (73.71–555.65 g), while the mature female individuals ranged from 17.20 to 32.50 cm (48.19–361.46 g) (Fig. 2). A significant difference was found between the length frequencies of male and female individuals (Kolmogorov–Smirnov test, H = 10.139, *p*-value = 0.014). The sex ratio was 0.98:1.00 (M:F), and the observed proportion was statistically insignificant (X^2 = 0.154, p = 0.6944). Each month, we found that the proportion range for males and females was 41.6–60.5 and 39.5–58.4, respectively. The length at first maturity (Lm) for females and males were 21.62 and 22.59 cm, respectively (Fig. 3).

3.2. Spawning periodicity

From 2020–2021, mature female and male gonads were found in all sampling months (Fig. 4), indicating that mackerel scads spawned year-round. The mean monthly gonadosomatic index (GSI) ranged from 0.35% to 2.20% and from 0.54% to 2.78% for male and female individuals, respectively (Fig. 5), demonstrating a similar presence of premature and mature fish in the same area. For both female and male individuals, the highest mean GSI was found in May and September 2020, and January and March 2021, indicating that the peak spawning season of the mackerel scad in the Sulawesi Sea occurred during these months.

Mature female and male gonads were observed during all the moon phases (Fig. 6). For female individuals, the proportion of mature gonads was found to be significantly high (91.7%) during the first quarter (Q1) compared to those during the New and Full Moon phases (Proportion Z-test; $p < 0.05$). However, for male individuals, higher proportions of mature gonads were observed during the first quarter (79.6%) and the third quarter (86.2%) of the moon phases, and these proportions were significantly higher than those during the New and Full Moon phases (Proportion Z-test; $p < 0.05$). The highest mean GSI was observed in the first quarter (Q1) of the moon phase in both females and males (Fig. 7). For females, the GSI was found to be significantly higher during the first quarter (Q1) than during the other moon phases (One-way ANOVA; F = 16.54; $p < 0.05$). Likewise, for male individuals, the GSI was found to be significantly higher during the first quarter (Q1) than during the other moon phases (One-way ANOVA; F = 10.26; $p < 0.01$), indicating that peak spawning occurred during this moon phase.

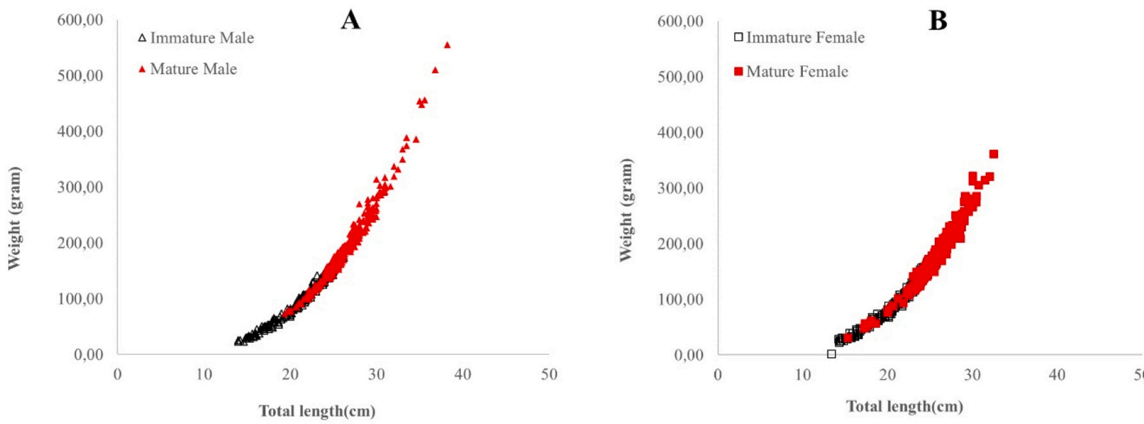

Fig. 2. Morphometrics (length and weight) of the male (A) and the female (B) *Decapterus macarellus* in the Sulawesi Sea.

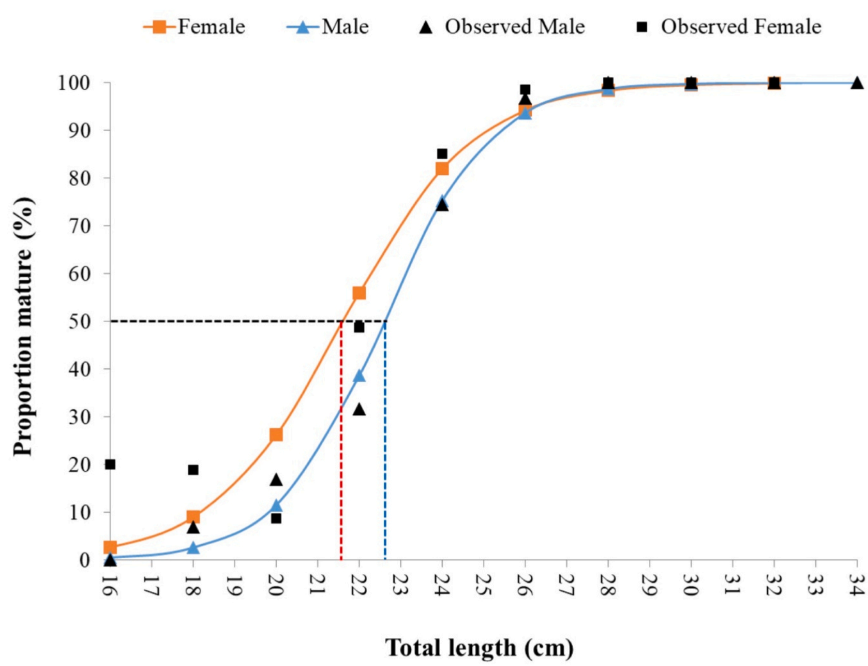

Fig. 3. Length maturity (Lm) model of the female and male *Decapterus macarellus* in the Sulawesi Sea.

3.3. *Potential reproductive area*

Based on the GSI from individual samples of mackerel scad collected from various locations in the Sulawesi Sea, we observed that the highest reproductive potential was found in areas close to the mainland of Sulawesi, around Bunaken and Manado Tua, with the mean GSI of 2.09 (± SD = 1.24, range = 0.03–5.06) (Fig. 8). However, based on the composition of mature and immature individuals, we observed that the highest percentage of mature individuals was found on the northern Sangihe Island and the western Sangihe and Siau Islands, with the percentage of mature individuals being 100% and 97%, respectively (Fig. 9). Based on the mature individuals combined with the high gonadosomatic index, the highest spawning potential was observed off Tumumpa Dua and around the northern and western sides of the Sangihe and Siau Islands, highlighting these areas as distinct spawning grounds for the mackerel scad.

4. Discussion

Herewith, we present the first study on the reproductive periodicity and potential spawning areas of *Decapterus macarellus* in the northern Sulawesi Sea and provided important information for fisheries management of small pelagic fish in the region. Studies on reproductive biology of *D. macarellus* have been carried out in different sites in Indonesia (Table 2). Earlier studies have suggested that the unit stock of mackerel scads in the Sulawesi Sea is most likely different from that in other conspecific populations. The population structure of the mackerel scad in the Sulawesi Sea differs from that of its conspecifics in the Makassar Strait, Bone Bay, Tolo Bay, Flores Sea, Banda Sea, and Maluku Sea (Zamroni et al., 2014). This is supported by a recent study on fish parasites of the mackerel scad, which detected a different pattern of metazoan parasites in this fish in North Sulawesi and North Maluku (Retnoningtyas et al., 2023). Consequently, the reproductive biology of *D. macarellus* in the Sulawesi Sea may be distinct from that of its conspecifics from other locations in Indonesia. However, it is also essential to note that the macroscopic method used to examine gonad maturity in the present study was the least accurate compared to histological studies, especially in distinguishing mature and immature gonads (Klibansky and Scharf, 2015). Studies using microscopic analyses, such as histological analysis for gonad examination, are required in the future.

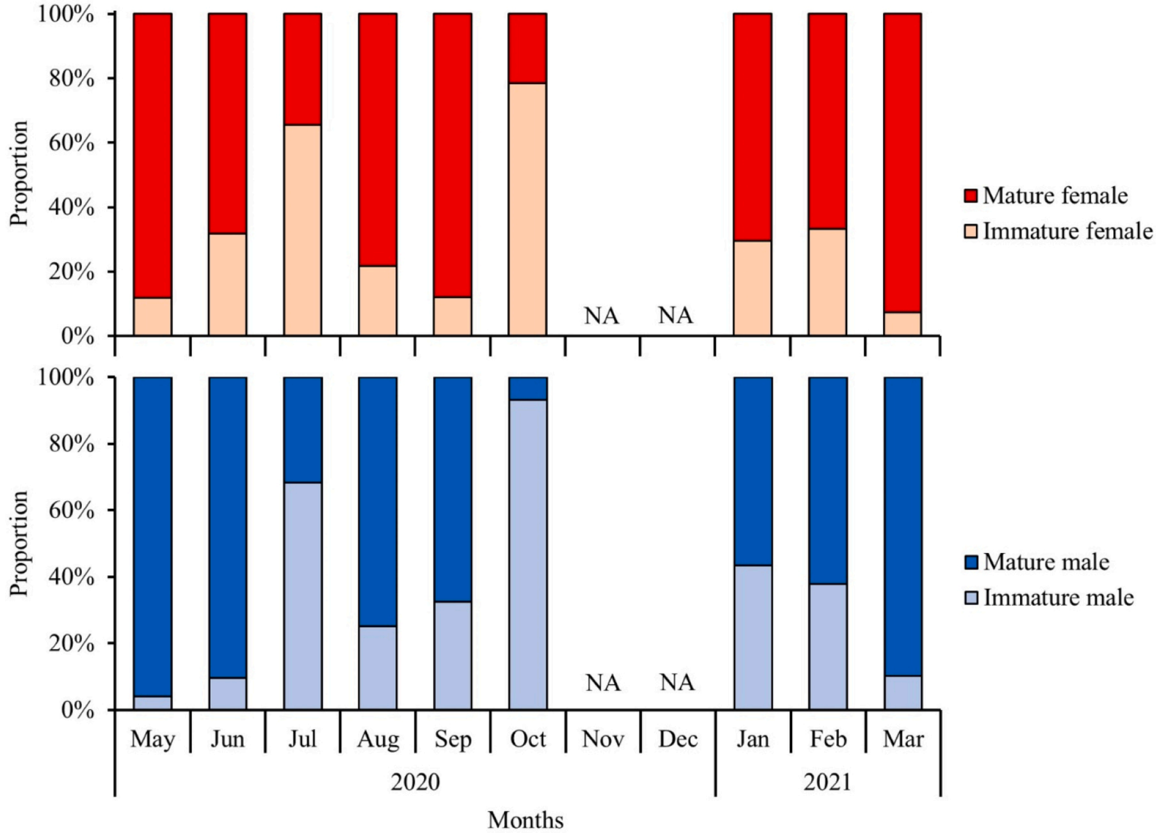

Fig. 4. Temporal changes in the proportion of immature and mature female and male gonads of *Decapterus macarellus* in the Sulawesi Sea between May 2020 and March 2021.

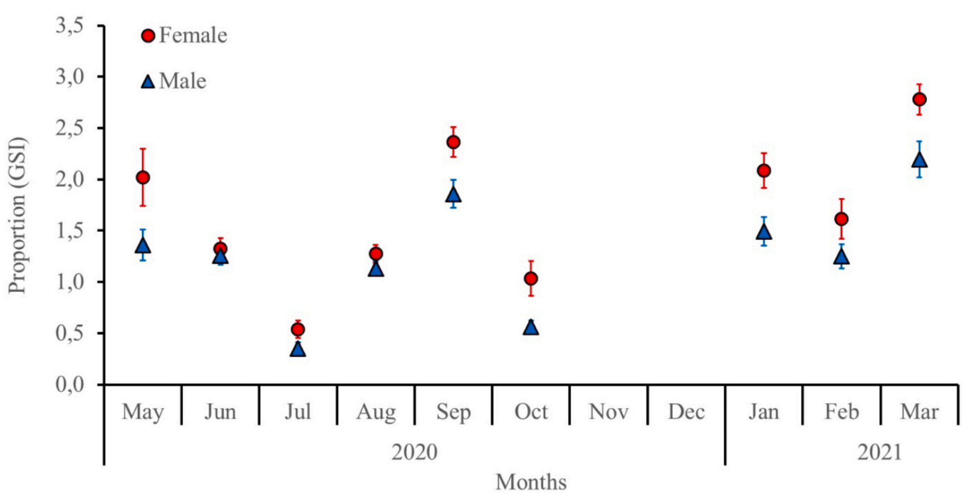

Fig. 5. Temporal changes in the proportion of the female and male gonadosomatic index of *Decapterus macarellus* in the Sulawesi Sea between May 2020 and March 2021.

The length and weight of samples from North Sulawesi waters ranged between 13.4 and 38.2 cm and 2.26–555.65 g, respectively. The size varied from month to month, and larger sizes were found during the spawning months (January, March, May, and September), indicating considerable gonad weight, and that the fish were in the mature stage. We found a similar size range for mackerel scad stocks in the Ambon waters (Silooy et al., 2019). In addition, Silooy et al. (2019) found a more extensive length range in January and September, which corresponds to our findings in North Sulawesi.

The sex ratio of the species was equal between male and female individuals during the study period. Similarly, the sex ratios of conspecifics in the Ambon and Banda Seas were equal (Silooy et al., 2021; Zamroni and Suwarso, 2011). However, male-biased sex ratios have been observed in other conspecific species at different sites in Indonesia. For instance, the sex ratios (M: F) in the Banda Sea (Zamroni and Suwarso, 2011), Sulawesi Sea (Zamroni et al., 2019), Central Sulawesi (Unus, 2009), and Kendari (Fadila et al., 2016) are 1.3:1, 1.96:1, 1.32:1, and 1.31:1, respectively. An equal sex ratio is required to maintain population survival (Gustomi and Sulistiono, 2016; Nasution et al., 2010). Although sex ratio is often treated as a stable population

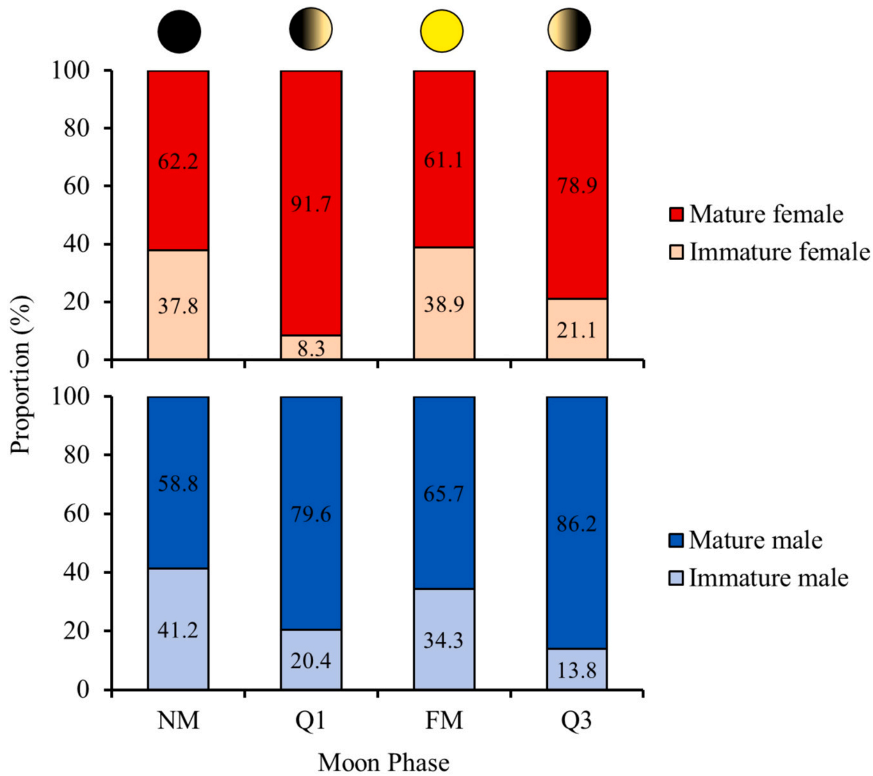

Fig. 6. Lunar periodicity in the proportion of immature and mature female and male gonads of *Decapterus macarellus* in the Sulawesi Sea sampled between May 2020 and March 2021. Description of moon phases are as follows: New Moon = NM ± 3.5 d; First Quarter (Q1) = NM + 3.5 to NM + 11.5 d; Full Moon = FM ± 3.5 d; Third Quarter (Q3) = FM + 3.5 to FM + 11.5 d.

indicator, recent theoretical evidence suggests that it can fluctuate under many conditions (Pettersson et al., 2004). Variations in the sex ratio can be affected by several factors, including behavioral patterns, mortality, and growth rates between male and female individuals; spawning behavior; sexual maturity; length distribution due to depth ranges; and the length (or age) of the individuals (Effendie, 1997; Smith et al., 2018).

The length at first maturity (Lm) of mackerel scad in the Sulawesi Sea was 22.59 and 21.62 cm for male and female individuals, respectively. The Lm values found in this study were lower than those in Ambon (Silooy et al., 2021), Blitar (Wulan, 2017), Kendari (Fadila et al., 2016), Banda Sea (Zamroni and Suwarso, 2011), North Maluku (Iksan and Irham, 2009) and Tomini Bay (Widiyastuti and Zamroni, 2017). However, the Lm found in this study was comparable to that of conspecifics in the central and southern parts of the Sulawesi Sea (Zamroni et al., 2019) and West Sulawesi (Nur et al., 2017). Lm discrepancy can result from the influence of environmental and ecological factors, including nutrient conditions, seawater temperature, irradiation, feeding habits, physiological conditions of fish, and the location of the fishing ground (Rada et al., 2019; Sudarno et al., 2020; Udupe, 1986; Wootton, 1985). Latitudinal differences of more than 5° and the high fishing pressure might also have affected the length at first maturity (Effendie, 1997; Restiangsih and Amri, 2019). For instance, rapid maturation is a strategy used by fish populations to cope with high fishing pressures (Restiangsih and Muchlis, 2019).

Temperature and food availability primarily affect energy allocation for somatic growth and reproduction in fish (Wootton, 1990). Temperature and food availability influence metabolism and surplus energy, thereby affecting the energy allocation for somatic growth and reproduction (Wootton, 1990). Favorable feeding conditions can affect the early maturity of fish individuals (Kjesbu, 1994). Likewise, optimal sea temperatures can also affect the synthesis and secretion of hormones that influence gametogenesis (Pankhurst and van der Kraak, 1997) but can indirectly reduce energy investment in growth and reproduction if the fish are experiencing unfavorable temperature conditions (Jobling et al., 1993). In the present study, we found that the spawning of mackerel scads in the Sulawesi Sea occurs year-round, with peaks occurring annually in January, March, May, and September. The peak spawning season differed among conspecifics in other areas. For instance, the spawning peaks of mackerel scad occur in January, March, May, and November at the eastern of North Sumatera (Fadhilah et al., 2021), in June–August at Banda Sea (Zamroni and Suwarso, 2011), in April–July at the South China Sea (Shiraishi et al., 2010), in August–November at Tomini Bay (Widiyastuti and Zamroni, 2017), in June at West Sulawesi (Nur et al., 2017), in March and July at Cape Verde (Costa et al., 2020), and in August and September at Tanzania (Sululu et al., 2022). This peak spawning discrepancy may be explained by the genetic diversity of the fish, water temperature regimes, and food availability (Yoneda and Wright, 2005). At higher latitudes, the spawning season occurs over shorter periods and mostly coincides with warmer sea temperatures (Sanchez-Ca and Arreguin-S, 2012), whereas at lower latitudes, some tropical fishes exhibit longer spawning seasons (Craig, 1998; Johannes, 1978). Since it can be assumed that the sea temperature in Indonesia has less variability and the ocean is warm and quite similar among different areas within the country, food availability might have affected the peak of the spawning season.

A very high percentage of mature individuals (97–100%) was observed on the northern and western sides of Sangihe and Siau Islands. In contrast, a high gonadosomatic index (GSI) distribution was observed around the North Sulawesi Peninsula. In the case of gonad maturity data, note must be taken for the data of mature individuals observed, because we used the least accurate method to determine gonad maturity. However, gonadal maturity data are sufficient to determine gonadal development patterns (West, 1990). Both enabled the potential spawning grounds of the mackerel scad in the North Sulawesi Sea to be clearly defined. The mackerel scad has specific spawning grounds with

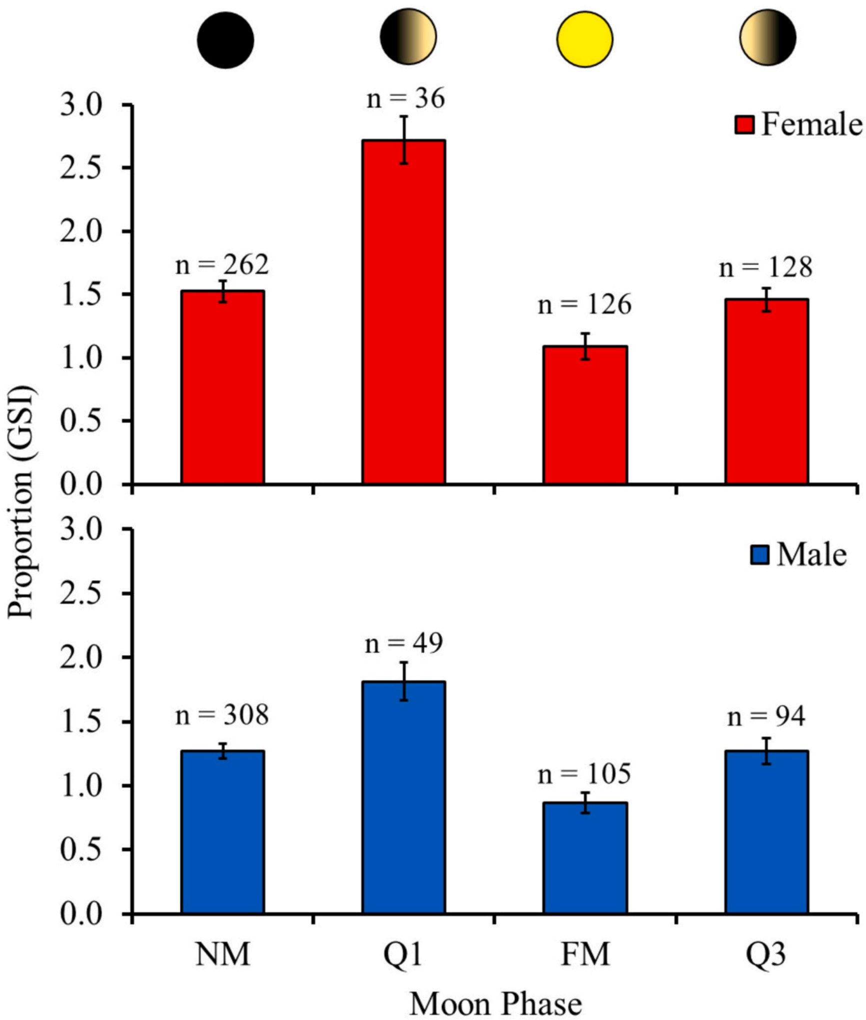

Fig. 7. Lunar periodicity of the female and male gonadosomatic index of *Decapterus macarellus* in the Sulawesi Sea sampled between May 2020 and March 2021. Description of moon phases: New Moon = NM ± 3.5 d; First Quarter (Q1) = NM + 3.5 to NM + 11.5 d; Full Moon = FM ± 3.5 d; Third Quarter (Q3) = FM + 3.5 to FM + 11.5 d.

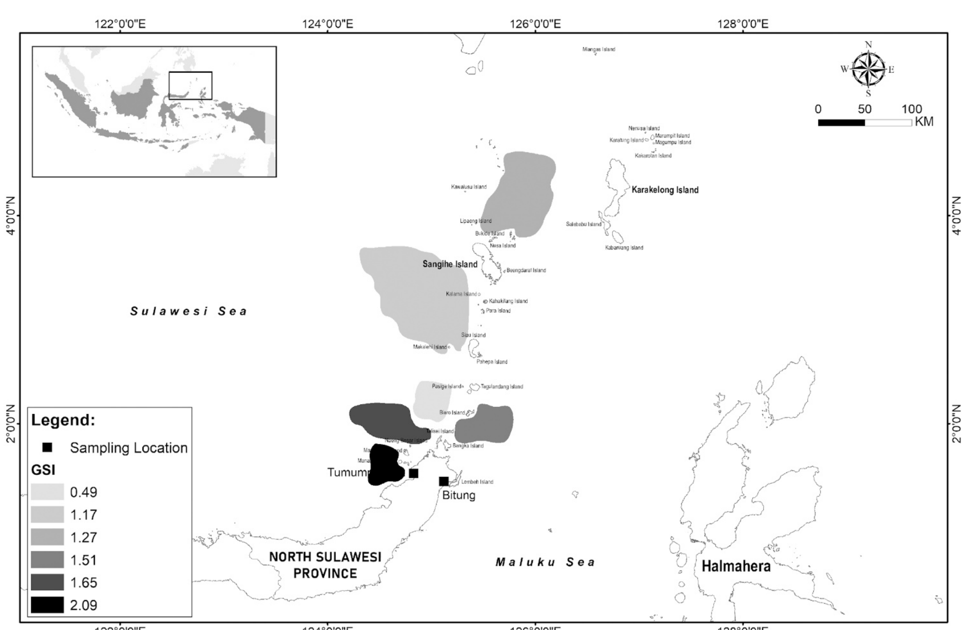

Fig. 8. Distribution of the gonadosomatic index (GSI) of *Decapterus macarellus* in the Sulawesi Sea.

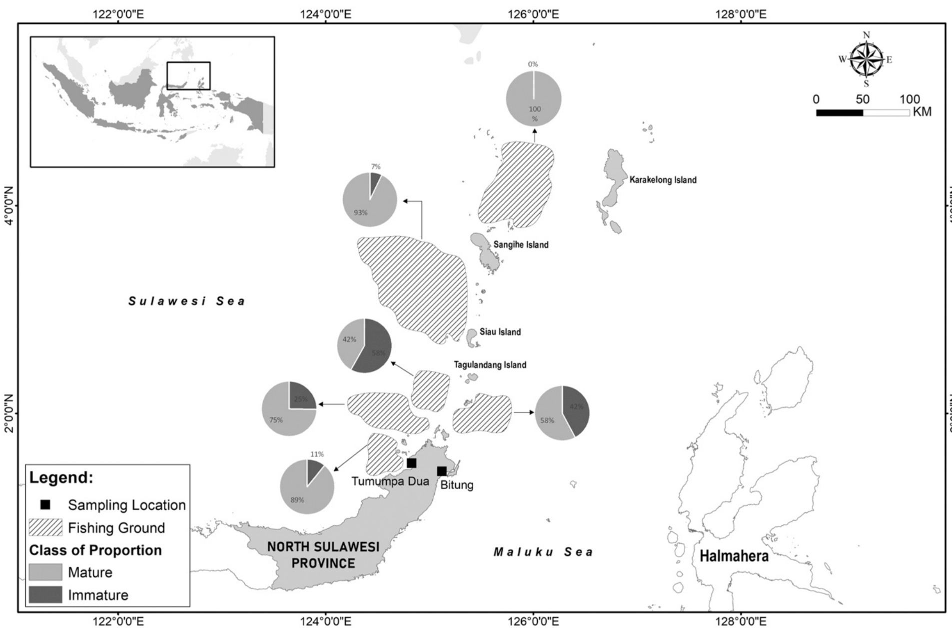

Fig. 9. Potential spawning grounds of the mackerel scad, *Decapterus macarellus*, in the Sulawesi Sea, as indicated by the proportion of matured individuals.

Table 2
Sex ratio, Lm, range of gonadosomatic index, and reproductive season of the mackerel scad (*Decapterus macarellus*) recorded from different geographic locations. Lm estimation uses total length except stated otherwise (FL: fork length), (*) indicates mean, (**) indicates mean of each stage of maturity (see Costa et al., 2020), M: male, F: female.

Sites	Sex ratio (M: F)	Lm (cm)	Range of Gonadosomatic Index (%)	Reproductive Season	Source
Ambon, Indonesia	NA	NA	0.54–1.78	NA	Pattikawa et al. (2018)
Ambon, Indonesia	1:1.02	24.9 (M), 24.8 (F)	NA	NA	Silooy et al. (2021)
Banggai, South East Sulawesi	1.32:1.00	NA	NA	NA	Unus (2009)
Blitar, East Java, Indonesia	NA	26.11 FL	NA	NA	Wulan (2017)
Kendari, Indonesia	1.31:1	25.7 FL	NA	NA	Fadila et al. (2016)
Banda Sea, Indonesia	1.3:1	26.6 FL	0.96 *	Jun–Aug	Zamroni and Suwarso (2011)
Sulawesi Sea, Indonesia	1.96:1	20.7 FL	0.08–7.2	Feb, Mar	Zamroni et al. (2019)
Eastern side of South China Sea	NA	NA	NA	Apr–Jul	Shiraishi et al. (2010)
North Maluku, Indonesia	1:1.8	25.8	NA	NA	Iksan and Irham (2009)
Prigi, Trenggalek, Indonesia	1:1.1	24.03 (M), 23.93 (F)	1.41 *	NA	Bintoro et al. (2020)
Tomini Bay, Indonesia	NA	26.94 FL	2.09 *	Aug–Nov	Widiyastuti and Achmad Zamroni, 2017
West Sulawesi, Indonesia	1:1.01	22.4 (M), 18.8 (F)	0.03–5.29 (M); 0.06–5.06(F)	Jun	Nur et al. (2017)
Likupang, Indonesia	NA	17.7	NA		Pratasik et al. (2020)
Southern Kyushu, Japan	NA	25.8	> 2	Apr–Jul	Shiraishi et al. (2010)
Cabo Verde	1:3.3	26.6 FL (M), 24.1 FL (F)	0.04–4.64 * *	Mar–Apr, Jul–Oct	Costa et al. (2020)
Tanzania	1:1.03 (Tanga); 1:1.2 (Bagamoyo)	14.6 (M), 15.3 (F) at Tanga; 15.0 (M), 15.7 (F) at Bagamoyo	0.17–2.30 (M), 0.34–4.30 (F) at Tanga; 0.20–3.62 (M), 0.26–3.77 (F) at Bagamoyo	Aug (Tanga); Sep (Bagamoyo)	Sululu et al. (2022)

optimal spawning conditions throughout the year. Since the mackerel scad is a planktivorous fish, the plankton distribution around these areas might be higher than that in other areas of the Sulawesi Sea. Findings on phytoplankton distribution around this region were confirmed by Rozirwan et al. (2021), who observed high phytoplankton abundance in the southern part of Sangihe Islands and around Sulawesi mainland as well as Maluku Channel off of Bitung. This study covered less than one month in October, which did not coincide with the peak spawning seasons of fish in the present study (January, March, May, and September). Tumumpa Dua, which accommodates five river mouths passing through Manado City and directly facing Manado Bay, supports the possibility of a high nutrient input that boosts phytoplankton growth and fertility in this area and subsequently becomes a potential fishing ground for mackerel scads. Further research regarding plankton distribution across the Sulawesi Sea is needed to confirm its correlation with the spawning grounds of mackerel scads, as spawning potentially occurs where food is readily available.

Moon-related cycles have been known to influence the reproductive activities of many fish species (Takemura et al., 2010). However, studies have yet to report the lunar spawning of mackerel scads. In the present study, we found that the most mature mackerel scads in the Sulawesi Sea spawned during the first quarter of the moon's phase. Studies on the lunar spawning cycle have been reported for reef fishes of the families Serranidae and Siganidae (Colin et al., 1987; Park et al., 2006; Rahman et al., 2000; Samoilys and Squire, 1994). The groupers *Epinephelus guttatus* and *E. striatus* begin their reproductive activities several days before the full moon (Colin et al., 1987), whereas *Plectropomus leopardus* was observed before the new moon (Samoilys and Squire, 1994). Spawning in siganids is synchronous around the new moon for *Siganus spinus* (Park et al., 2006) and around the first quarter for *S. guttatus* (Rahman et al., 2000). It has been suggested that cues from the moon are associated with the synchrony of the adult reproductive rhythm (Colin et al., 1987) and may consequently increase reproductive success (Ferreira, 1995). Periodicity in moon-related cues, such as moonlight intensity, time of moonrise, and solar cycle, has been hypothesized as a cue for fish reproductive activity (Leatherland, 1993). For instance, moonlight intensity has been suggested to be a cue for melatonin production in fish, triggering lunar-synchronized spawning of siganids (Rahman et al., 2003; Takemura et al., 2010). In addition, gravitational (tidal) and geophysical forces due to changes in the moon's position relative to the Earth and the sun may influence fish reproductive activity. These factors might have indirectly affected the reproductive activities of the mackerel scad in the present study, synchronizing spawning around the moon's first quarter. However, the exact cues for the moon-related cycles, observed for the first time in the mackerel scad, must be better understood and warrant further investigation.

Mackerel scad is an important fishery resource in Indonesia, particularly in the eastern part of Indonesia, including Sulawesi. There is a significant demand for this species as food, which could lead to overfishing. However, data on production and fishing efforts still need to be improved. Without proper management measures, fishing threatens the sustainability of fish stocks. However, the recorded year-round spawning and the proximity of several spawning nuclei make this fish stock less vulnerable to overfishing. To optimize sustainable resource use, our data suggest the following measures to be taken: **a.** optimize fishing gear to local fish stock, in which the size of fish at first capture (Lc) is supposed to be larger than the length at first maturity (Lm), to ensure that the fish spawn at least once before being captured; **b.** restrict the critical spawning areas around the northern and western sides of the Sangihe and Siau Islands as pelagic marine protected areas; **c.** introduce regular temporary fishing closures. Closure periods can be applied during the peak of the spawning season around January, March, May, and September or narrowed down to the first quarter of the moon phase. Such temporary fishing closures positively affect the rebuilding of stock populations (Bartlett et al., 2009; Januchowski-Hartley et al., 2013).

5. Conclusion

The present study examined the reproductive biology of mackerel scads in the Sulawesi Sea, particularly its reproductive periodicity and potential spawning area. We found that this species had an equal sex ratio between males and females, with a length at first maturity (Lm) being 22.59 and 21.62 cm, respectively. Most importantly, we found that the spawning peaks of the species occurred annually in January, March, May, and September during the first quarter of the moon phase. We also identified distinct spawning areas for the species off Tumumpa Dua and around the northern and western sides of the Sangihe and Siau Islands. This will enable temporary and regional fishing closures by fishery managers to develop sustainable fishing practices for small pelagic fish species in the future.

CRediT authorship contribution statement

Heidi Retnoningtyas: Conceptualization, Investigation, Methodology, Formal analysis, Writing – original draft. **Siska Agustina:** Investigation, Methodology, Formal analysis, Visualization, Writing – original draft. **Mohamad Natsir:** Conceptualization, Formal analysis, Writing – review & editing. **Prayekti Ningtias:** Conceptualization, Investigation, Writing – original draft. **Amehr Hakim:** Writing – review & editing. **Arya Kusuma Dhani:** Investigation, Formal analysis. **Intan Destianis Hartati:** Methodology, Formal analysis. **Jessica Pingkan:** Visualization. **Charles P. H. Simanjuntak:** Conceptualization, Investigation, Methodology, Writing – original draft. **Budy Wiryawan:** Conceptualization, Investigation, Methodology, Writing – review and editing. **Am Azbas Taurusman:** Validation, Writing – review & editing. **Ari Purbayanto:** Validation, Writing – review & editing. **Harry W. Palm:** Validation, Writing – review & editing. **Rian Prasetia:** Conceptualization, Methodology, Formal analysis, Visualization, Writing – original draft. **Irfan Yulianto:** Conceptualization, Investigation, Methodology, Formal analysis, Visualization, Writing – original draft. All authors have read and agreed to the published version of the manuscript.

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Data Availability

Data will be made available on request.

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