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Reproductive Biology and Gonadal Histology of *Decapterus macarellus* (Cuvier, 1833) in Pondokdadap Waters, Indonesia: Implications for Sustainable Fisheries Management

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ABSTRACT

This study investigates the reproductive biology and gonadal histology of *Decapterus macarellus* in Pondokdadap, East Java, to inform size- and season-based fisheries management. Gonadal maturity stages were identified through combined morphological (Cassie) and histological analysis. The length at first gonadal maturity (Lm) was estimated at 21.08 cm, whereas the length at first capture (Lc) was 20.63 cm, indicating that the current fishery predominantly harvests immature individuals (Lc < Lm). Histological examination of the ovaries revealed five oocyte developmental stages (primary growth, yolk vesicle, vitellogenic, maturation, and post-spawning). Most ovaries were dominated by early oocytes (primary growth and yolk-vesicle stages), with only a small proportion of females reaching advanced maturity stages (III–IV). Oocyte diameters increased from 40.84–56.09 µm at early vitellogenesis to an average of 316.25 µm at stage III, and up to 411.80 µm in fully mature oocytes, while post-ovulatory follicles were not observed in the sampled individuals. The coexistence of multiple oocyte stages within the same ovary confirms asynchronous oocyte development characteristic of batch spawners. Our results show that the current fishery mainly exploits pre-spawning fish and that the combination of Lc < Lm and asynchronous spawning necessitates the implementation of a minimum landing size of at least 21.1 cm, together with the identification of peak spawning periods to design temporal fishery closures. These measures would help protect spawning biomass and support the long-term sustainability of *D. macarellus* in Indonesian small pelagic fisheries.

1. INTRODUCTION

The mackerel scad (*Decapterus macarellus*) is a small pelagic fish that plays a vital role in marine ecosystems, serving as a key species in the food web and supporting larger predators such as tunas and sharks [1]. Additionally, this species helps regulate zooplankton populations, which contributes to ecosystem stability [2]. However, excessive fishing pressure and habitat degradation, driven by environmental change and coastal development, threaten *D. macarellus* populations and may disrupt marine biodiversity. The growing demand for this species in the fisheries sector has intensified exploitation, underscoring the need for science-based conservation and management strategies to ensure long-term population sustainability.

Reproductive success in *D. macarellus* is influenced by several factors, including water quality, temperature, and food availability [3]. The size at initial gonadal maturity (Lm) has been reported to vary between 20 and 30 cm, depending on habitat conditions and fishing intensity [4-6]. To develop effective fisheries management strategies, understanding the species' reproductive dynamics is crucial. Reproductive indices such as the gonadosomatic index (GSI) are widely used tools for determining spawning periods and assessing how environmental conditions and energetic status affect reproductive success [7, 8]. The GSI compares gonadal weight to total body weight to estimate energy allocation to gonadal tissue [8, 9]. However, GSI has limitations because it can be affected by factors such as physiological condition, body mass, and spawning cycle, which may lead to misinterpretation of reproductive maturity [10].

The GSI is frequently used to assess reproductive status by comparing gonadal weight to total body weight, thus estimating energy allocation to gonadal tissue [11, 12]. However, the gonadal maturity index has limitations because it can be affected by factors such as physiological condition, body mass, and spawning cycle, which may lead to misinterpretation of reproductive maturity [13]. Therefore, additional methodologies are needed to achieve more accurate assessments of the reproductive stage and spawning potential.

Histological analysis of gonads offers a more precise evaluation of reproductive stages compared to macroscopic methods. It allows detailed identification of cellular structures and gamete development, providing valuable insights into reproductive cycles, oocyte dynamics, and spawning capacity [14]. Combining histological and morphological analyses improves the accuracy of maturity assessments, as histology detects microstructural changes while morphology offers an overview of gonadal size, colour, and texture [15, 16]. Furthermore, histological analysis supports the study of gametogenesis and its relationship with hormonal fluctuations, offering a comprehensive framework for understanding fish reproductive biology [14].

Although several recent studies have examined the reproductive biology of *D. macarellus* in different Indonesian regions (e.g., Sulawesi Sea, Maluku Sea, southern Ambon waters, and the southern waters of western Java), these have mostly relied on macroscopic maturity staging, length-based analyses, or generalized reproductive parameters [2, 4-6, 8]. Despite the economic importance of *D. macarellus* in the small-pelagic fishery of Pondokdadap, there is still no locally derived, histology-based estimate of length at first maturity (Lm) and length at first capture (Lc) for this landing site. Current management and stock assessments in this area, therefore, rely on parameters from other regions or on visual maturity assessments that may misclassify gonadal stages. As a result, it remains unclear whether the present exploitation pattern in Pondokdadap targets predominantly immature or mature individuals, and how this affects the reproductive potential and resilience of the local stock.

Environmental stressors such as water temperature, salinity, pollution, and habitat alteration are known to affect gonadal development and fertility in marine fishes, including small pelagics [15]. Contaminants (e.g., heavy metals) and thermal anomalies can impair gametogenesis, disrupt endocrine regulation, and alter spawning phenology [17-20]. In the present study, we focus on combining morphological and histological analyses to describe the reproductive stages of female *D. macarellus* and to estimate Lm and Lc specifically for the Pondokdadap fishery. By providing locally validated maturity and capture parameters and documenting oocyte developmental patterns, this study supplies key biological inputs for setting minimum landing sizes and designing size- and season-based management measures. Environmental stressors that may influence reproduction are considered in the discussion based on existing literature, but the primary emphasis of this work is on the reproductive parameters required for practical, science-based management of *D. macarellus* in Indonesian small pelagic fisheries.

2. MATERIALS AND METHODS

2.1 Study area and sampling design

Sampling was conducted at the coastal fishing port (PPP) Pondokdadap, Sendangbiru, Malang District, East Java, Indonesia, located at approximately 8°25’59’’ LS - 112°40’55’’ BT (Figure 1). This landing site is one of the main hubs for small pelagic fisheries operating in the southern waters of Java. Fish samples of *Decapterus macarellus* were obtained from commercial landings between December 2023 and March 2024.

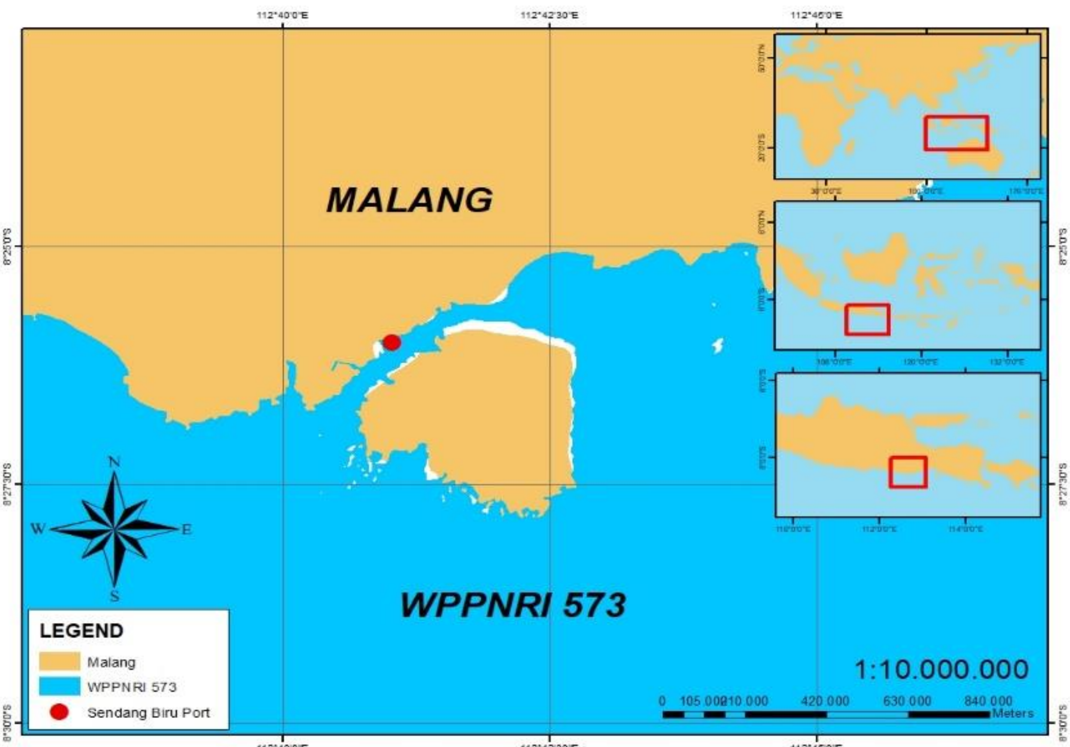

Figure 1. Study area: Pondokdadap fishing port, Sendangbiru, Malang, Indonesia

Specimens were collected from catches of purse seine vessels operating in coastal and oceanic waters off southern East Java. The dominant gear targeting *D. macarellus* in this fishery is a purse seine with a codend mesh size of approximately 2.5 inches, as reported by fishers and vessel records. This information is relevant for interpreting the Lc derived from the length–frequency data. In total, 450 female individuals were analysed in this study, with 125 fish specimens sampled in December, 125 fish in January, 100 fish in February, and 100 fish in March 2024. All specimens were transported on ice to the laboratory for further examination.

2.2 Length measurements and macroscopic gonadal

staging

In the laboratory, each fish was measured for total length (TL) to the nearest 0.1 cm using a measuring board. Body weight (BW) was recorded to the nearest 0.1 g using a digital balance, and the paired gonads were carefully dissected and weighed to the nearest 0.01 g after blotting excess moisture. The abdominal cavity was opened by a ventral incision, and the gonads were removed and examined visually.

The FAO book [21] uses several sources to identify fish species. In addition, fish species identification uses the FishBase website to make comparisons with the latest species morphology data that has been updated. Analysis of maturity observations is visually based on the Cassei method, as shown in Table 1 [22-24].

Table 1. Gonadal maturity level (GMP) based on the Cassie method

GMP	Visual Description	Gonad Morphology Properties
I	Gonads have not yet proliferated (Immature)	Gonads have not yet proliferated (Immature). Gonads are very small, clear, and colourless.
II	Mature gonads (towards maturity)	Gonads begin to enlarge and pale in colour.
III	Mature (maturing) gonads	Gonads are larger and more intensely coloured.
IV	Ripe, which means ready to spawn	Gonads are very large, full of eggs/sperm, ready for spawning.
V	Spent (Post Spawning)	Gonads are smaller, wrinkled, and paler in colour than before.

Macroscopic gonadal maturity was determined following the Cassie method as presented in the FAO species identification guide for fishery purposes. Gonads were classified into five maturity stages (I–V) based on their size, colour, vascularisation, and texture (Table 1). Only female individuals for which the maturity stage could be clearly assigned were used for the estimation of Lm. Our analysis focused on maturity-stage frequencies, Lm, Lc, and histological observations.

2.3 Estimation of length at first maturity (Lm) and length at first capture (Lc)

Lm was estimated using a logistic model fitted to the proportion of mature females by length class. Fish were grouped into 1 cm length classes, and the fraction of mature individuals (stages III–V) within each class was calculated. The relationship between the proportion of mature females (P) and length (L) was modelled as:

$$P(L) = \frac{1}{1 + \exp^{-(a+bL)}}$$

where, a and b are fitted constants.

Lm, defined as the length at which 50% of females are mature, was obtained as:

$$Lm = -\frac{a}{b}$$

Model parameters were estimated by non-linear regression using Microsoft Excel. Lc was estimated from the length–frequency distribution of the catch using a length-converted catch curve approach. The method follows standard procedures described by FAO for tropical small pelagics, where the logarithm of the number of individuals in each length class is regressed against the corresponding mid-length, and the inflexion point of the ascending limb of the curve is used to approximate Lc. The detailed equations used in this study are presented above, with Fc(L) denoting the frequency of fish in each length class, dL the class interval, and the mean and standard deviation of the cohort length distribution.

2.4 Histological processing of ovaries and oocyte measurements

To characterize oocyte development and validate macroscopic maturity stages, a subsample of 10 ovaries was processed for histological analysis. These ovaries were selected from 450 females to represent the various maturity stages that would be observed in the catch. Specifically, three ovaries from each of Cassia's maturity stages I–IV (and V if available) were collected, using random sampling and well-preserved gonads at the macroscopic stage.

Immediately after dissection, one gonadal lobe from each selected female was cut into small pieces approximately 5–10 mm thick and immersed in 10% neutral buffered formalin for a minimum of 24–48 hours to ensure complete fixation. After fixation, tissue samples were rinsed briefly with running tap water and then dehydrated through a graded series of 70% ethanol for 30–60 minutes. The dehydrated samples were cleared in two changes of xylene (25 minutes each) and embedded in paraffin wax at 56–58°C using a tissue embedding system.

Paraffin blocks were sectioned using a rotary microtome to obtain serial sections of 5 µm thickness. Sections were floated on a warm water bath to remove wrinkles, mounted on glass slides, and dried at 45°C overnight. Routine haematoxylin–eosin (H&E) staining was performed following standard protocols: slides were deparaffinised in xylene, rehydrated through descending ethanol concentrations, stained with Harris haematoxylin for approximately 5 minutes, rinsed in running water, differentiated in acid alcohol, blued in alkaline water, counterstained with eosin for 3 minutes, then dehydrated, cleared in xylene, and coverslipped using mounting medium. Histological preparations were examined under a light microscope at 400× magnification. Digital images were captured using a digital camera attached to the microscope. Oocyte diameter was measured along the longest axis using software. For each ovary, at least 50 oocytes per developmental stage were measured in randomly selected, non-overlapping fields of view. These measurements were used to describe the size ranges associated with the different oocyte stages.

3. RESULTS AND DISCUSSION

3.1 Results

3.1.1 Length at first maturity (Lm)

A total of 152 females with clearly assignable gonadal stages were used to estimate Lm. Within this subset, 95 females were classified as mature (stages III–V). TL of these females ranged from 8.2 to 30.0 cm. The logistic model fitted to the proportion of mature females by length class yielded an

Lm of 21.08 cm TL.

3.1.2 Length of first fish caught (Lc)

The Lc, estimated from the length-converted catch curve, was recorded as 20.63 cm TL. Lc and Lm were located in close proximity to the modal length class, with Lc exhibiting a slightly lower measurement than Lm (20.63 cm vs. 21.08 cm). This finding suggests that a significant proportion of the catch comprised females that had not yet attained first maturity. The histological level of gonadal maturity is illustrated in Figure 2. The majority of individuals exhibited a TL ranging from 8.20 to 30.0 cm, with the positions of Lm (21.08 cm) and Lc (20.63 cm).

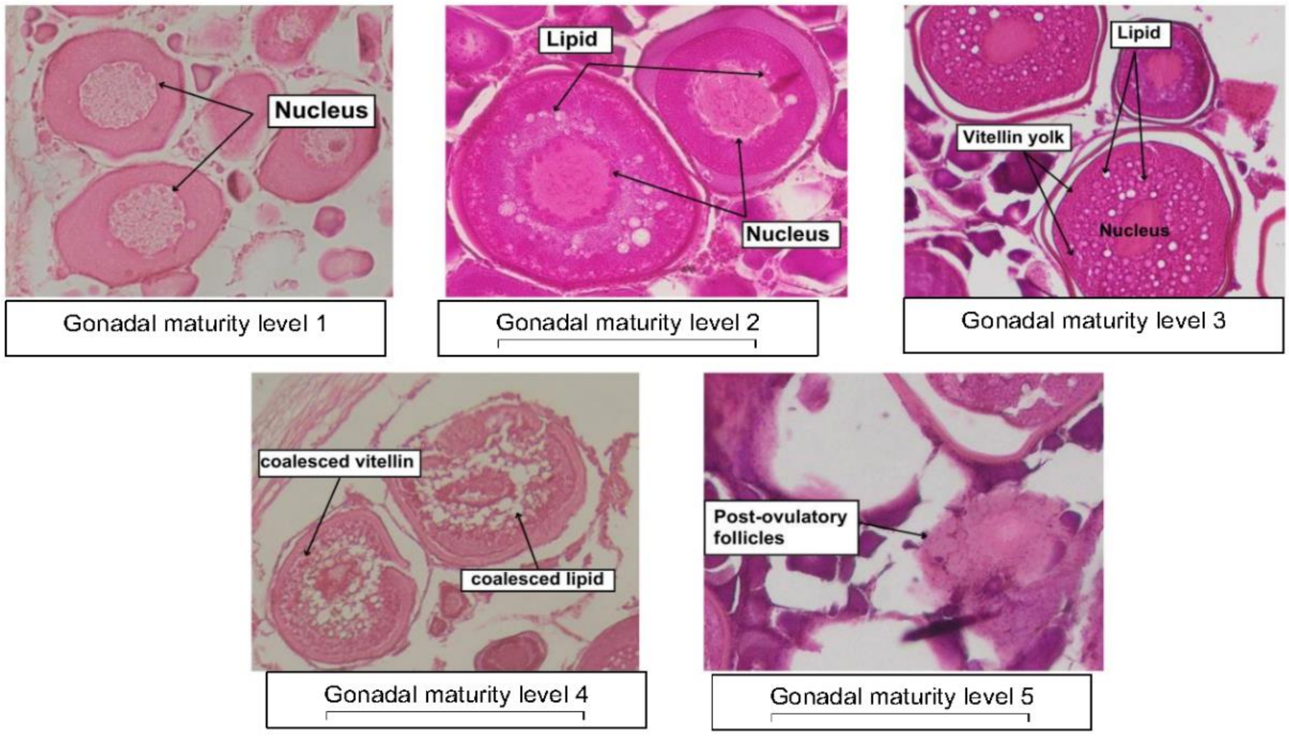

Figure 2. Histological level of gonadal maturity of fish eggs *D. Macarellus*

3.1.3 The gonadal maturity level (GMP)

Histological analysis of a subsample of 10 ovaries revealed the presence of five stages of oocyte development: primary growth, yolk vesicle, vitellogenin, maturation, and post-spawning follicles, following the classification of studies [25, 26]. Most ovaries were dominated by early-stage oocytes (primary growth and yolk vesicle), while only a smaller proportion of females exhibited large vitellogenin or fully mature oocytes.

Oocyte diameters increased consistently across developmental stages. Early vitellogenin oocytes (stage II) ranged from 40.84 to 56.09 µm. Stage III (vitellogenin) oocytes had a mean diameter of approximately 316.25 µm. whereas fully mature oocytes in stage IV reached up to 411.80 µm. post-ovulatory follicles were not detected in the examined sections, suggesting that the sampled females had not recently completed spawning. The simultaneous presence of oocytes at multiple stages within the same ovary indicates asynchronous oocyte development typical of batch spawners.

The five stages of oocyte development in the ovaries of *D. macarellus* follow the description by the study [27], namely primary growth, yolk vesicle, vitellogenesis, maturation, and post-spawning. Histologically, the initial phase is characterized by the presence of a dark cytoplasm with a small nucleolus, followed by the formation of lipid vesicles, and subsequently, the accumulation of uniform vitellin yolk in proximity to the nucleus. During the maturation phase, the vitellin yolk undergoes a process of aggregation, resulting in the formation of large granules, accompanied by a substantial increase in oocyte size. In the post-spawning phase (POF), the ovary exhibits remnants of damaged follicles subsequent to ovulation.

The development of *D. macarellus* oocytes demonstrates that the primary growth and yolk vesicle phases are predominant at the early maturity stage, while the vitellogenesis and maturation phases are more prominent at the late maturity stage. The POF was not detected in the samples observed. The results obtained demonstrate that the majority of fish are in the early stages of development, with only a small number of individuals having reached gonadal maturity stages III and IV.

3.2 Discussion

3.2.1 Gonadal maturity and implications for fisheries management

The estimated Lm of 21.08 cm TL for *D. macarellus* in Pondokdadap falls within the lower range of values. The relatively low Lm reflects faster growth or earlier energy allocation to reproduction in this population but may also be influenced by strong size-selective fishing pressure. Intensive exploitation that preferentially removes larger and older individuals may favor genotypes and phenotypes that mature at smaller sizes, leading to a downward shift in Lm over time. So these findings indicate that most of the fish caught have not reached reproductive maturity, which is a major concern for the sustainability of the species, as well as impacting fishing before reaching adult size can be detrimental, potentially reducing reproductive output and causing depletion of fish stocks in their habitat, preventing stock depletion, especially in reproductively immature species [28-31]. Because the size of fish at the level of sexual maturity is strongly influenced by exploitation pressure and habitat conditions, overfishing can reduce sexual maturity and endanger population sustainability [32-34]. So, healthy habitat conditions are very important in ensuring optimal growth and reproductive success in fish. It is proven that a favorable environment has the capacity to increase GSI and spawning effectiveness [35, 36]. Furthermore, a good environment will provide a framework that supports opportunistic reproductive strategies; suitable habitat, substrate, and structure are very important in protecting fish from external threats [37]. In addition, a positive correlation has been shown between high habitat quality and fish diversity, as well as the ability of fish to reach their full reproductive potential [38]. Therefore, habitat restoration has been identified as an important factor in ensuring the long-term sustainability of fish populations.

The length at first capture (20.63 cm TL) is slightly lower than Lm implies that the fishery routinely retains females that have not yet spawned. Considering that most of the catch falls within the 21.1 cm TL class, a considerable fraction of the spawning potential is harvested before first reproduction. The estimated Lc is consistent with the 2.5-inch mesh size of the purse seine gear used in this fishery, which is sufficiently small to capture individuals near and below Lm. From a management perspective, these results indicate that increasing the minimum mesh size, or enforcing a minimum landing size of at least 21.1 cm TL, Discrepancies between length first caught (Lc) and length first to gonadal maturity (Lm) in certain species, such as *Decapterus macarellus*, indicate unsustainable fishing practices, where immature individuals are caught before they have a chance to reproduce, thus threatening the sustainability of fish stocks [39, 40]. The exploitation of fish before they reach sexual maturity is a crucial issue in fisheries management, as it can lead to population instability, stock declines, and disruptions in the balance of marine ecosystems. Fishing pressure on juvenile fish can diminish their reproductive capacity, prompt evolutionary shifts, and reduce genetic diversity [37, 41-43]. It is imperative to comprehend the multifaceted factors that influence this size determination, including environmental conditions and fishing pressure [44, 45], because an in-depth understanding of the first maturity size can facilitate the management of fish resources and the development of sustainable utilization strategies [46]. The hypothesis that effective and data-driven regulation of minimum catch sizes will stabilise and regenerate fish populations such as *Decapterus macarellus* in the long term has been proven [47, 48]. Consequently, the establishment of minimum catch sizes has been demonstrated to exert a favourable influence on ecosystem health, in addition to ensuring the sustainability of fisheries resources for the communities that are reliant on these sources.

3.2.2 Asynchronous development and management implications

The histological evidence of asynchronous oocyte development, with the coexistence of early and advanced oocytes within the same ovary, indicates that *D. macarellus* in Pondokdadap is a batch spawner capable of multiple spawning events within a reproductive season. This reproductive strategy can buffer the population against occasional adverse environmental conditions during part of the spawning period, because not all reproductive output is concentrated in a single brief event. Furthermore, examination of the histological features of the gonads also provides insight into the maturity, development, and health condition of individual fish in the captured population, suggesting that larger individuals are more likely to contain mature eggs or sufficient sperm. Sexual maturity in fish is subject to variation depending on species, environment, and individual factors, including diet and physiological condition [49, 50]. Utilizing data from studies spanning multiple species, including gonadal growth in tuna and barramundi, it was determined that external factors, such as temperature and contaminants, influence gonadal growth rates and sexual maturity [51, 52].

3.2.3 Histological observations of oocyte development

A histological analysis of *Decapterus macarellus* ovaries identified five distinct stages of gonadal maturity, which is consistent with the classification proposed by studies [53, 54]. The primary growth phase was characterised by the presence of dark cytoplasm and small nucleoli, indicating early-stage oocyte development. At maturity stage II, the diameter of the eggs ranged from 40.84 to 56.09 μm, thus indicating the commencement of the vitellogenesis process. This finding is consistent with previous studies that established a correlation between early vitellogenesis and increased yolk deposition in oocytes [50]. Stage III of gonadal maturity was characterized by increased lipid accumulation in oocytes, with an average diameter of 316.25 μm, reflecting more advanced reproductive development. The proportion of mature oocytes increased significantly at the highest maturity stages (IV and V), with diameters reaching 411.80 μm, signaling readiness for spawning.

The notion that egg size can serve as an indicator of reproductive status has been extensively validated through numerous studies conducted on various fish species. A plethora of research has been conducted on the subject, and the results indicate a positive correlation between egg size and fish health and fertility. This suggests that larger eggs are indicative of the ability to support healthy progeny. For instance, a study [55] demonstrated that gonad size is associated with reproductive success, including observations on post-ovulatory follicles that facilitate the assessment of fish maturity. Furthermore, research [56] illustrated that gonad size and weight are closely related to individual body size, an important parameter for assessing the level of reproductive maturity in fish. This finding suggests that physical size can be utilised as a tool to assess the state of reproduction when individuals are at a certain stage in their life cycle. In certain cases, these indicators have been found to be more reliable than alternative methods.

Furthermore, the study [57] emphasized the pivotal role of hormones in the sexual differentiation process, which can influence gonad size. The study demonstrated that the morphological characteristics of the gonads can function as markers of reproductive status in specific species. Research [58] demonstrated that environmental influences also affect gonad size, indicating that these parameters are not invariably stable and can be impacted by external factors.

In conclusion, the size of the ovum is a significant indicator of reproductive status, especially when combined with other analyses such as gonadosomatic indices and gonadal morphological parameters. This multidimensional approach provides a more comprehensive picture of the reproductive health of the aquatic species studied.

3.2.4 Implications for sustainable fisheries management

The findings of this study emphasise the pressing necessity for fisheries management policies grounded in scientific principles, with the aim of averting the detrimental consequences of overexploitation. The capture of *Decapterus macarellus* prior to its attainment of reproductive maturity poses a significant threat to the sustainability of the population and the disruption of ecosystem equilibrium. A substantial body of research has underscored the significance of incorporating ecological parameters, such as the spawning season and habitat conditions, into fisheries regulations to ensure the long-term viability of the species and the ecosystem as a whole [2, 5]. The implementation of minimum catch size regulations, complemented by seasonal fishing restrictions, has been shown to enhance reproductive success and improve stock replenishment rates. The use of selective fishing gear can also reduce bycatch of immature individuals, thereby improving the overall sustainability of the fishery [58]. Furthermore, the integration of histological assessment with population dynamics modelling will refine conservation strategies, contribute to the long-term viability of the *D. macarellus* fishery, and ensure that policies implemented are based on valid and accurate scientific data. This study also emphasises the necessity of implementing fisheries management policies that are grounded in scientific evidence, with a view to averting the issue of overexploitation. The capture of *D. macarellus* prior to attaining reproductive maturity has the capacity to diminish the population and disrupt the equilibrium of the ecosystem. Studies [59, 60] demonstrated that elevated fishing pressure can modify the reproductive characteristics of species, including a reduction in maturity size, which impacts the success of population regeneration and the ability of species to recover from overexploitation.

As also emphasized by studies [23, 59], science-based management should consider various reproductive traits in order to facilitate a more comprehensive understanding of the productivity of fish populations. This approach is regarded as more efficacious in ensuring species survival and maintaining ecosystem balance. Consequently, the implementation of policies founded upon a scientific understanding of the reproductive capabilities of species is recommended, with the aim of ensuring optimal maintenance of population sustainability and ecosystem balance. Consequently, ongoing monitoring and evaluation are required to ensure that fisheries practices continue to support healthy ecosystems and reduce pressure on target species. The repercussions of inadequate fisheries management have the potential to be deleterious to the sustainability of fish resources and the equilibrium of ecosystems. These include wide-ranging effects on species variation and ecosystem health, including excess exploitation of target species. In the context of marine fisheries, unsustainable management has the potential to cause [59, 60] decline in biomass and habitat destruction, leading to biodiversity loss [60, 61]. In order to ensure that fisheries management is not only sustainable but also able to restore ecosystem balance, this is in line with the principles of adaptive management. Adaptive management practices aim to improve understanding of the consequences of environmental management choices [62].

4. CONCLUSIONS

This study provides locally derived reproductive parameters for female *Decapterus macarellus* in the Pondokdadap small pelagic fishery. The Lm was estimated at 21.08 cm TL, while the Lc was 20.63 cm TL, indicating that the current fishery predominantly exploits females that have not yet spawned. Histological analysis revealed the coexistence of multiple oocyte developmental stages within the same ovary, confirming asynchronous oocyte development characteristic of batch spawners, with oocyte diameters increasing from approximately 40–60 µm in early stages to more than 400 µm in fully mature oocytes.

From a management perspective, the combination of Lc < Lm and asynchronous batch spawning raises concern about the long-term reproductive potential of the stock if current exploitation patterns continue. To ensure that a larger proportion of females can spawn at least once before capture, we recommend implementing a minimum landing size of no less than 22 cm TL, i.e., slightly above the estimated Lm of 21.08 cm TL to provide a precautionary safety margin. This size-based regulation should be aligned with adjustments to the mesh size and selectivity of the dominant fishing gear used in Pondokdadap to reduce the retention of sub-mature individuals.

The asynchronous reproductive strategy implies that *D. macarellus* can spawn in multiple batches over an extended period rather than in a single, brief event. This feature can increase resilience to short-term environmental variability, but it also means that spawning females are vulnerable to fishing over much of the reproductive season. Accordingly, future management should not only adopt minimum size limits but also seek to identify peak spawning periods—using time-series data on gonadal maturity or GSI—and design temporal closures that cover the main spawning peaks. Integrating these size- and season-based measures, supported by continued monitoring of length structure and reproductive parameters, would help maintain spawning biomass and support the long-term sustainability of *D. macarellus* in the Pondokdadap fishery.

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