Aus der Professur für Aquakultur und Sea-Ranching

der Agrar- und Umweltwissenschaftlichen Fakultät

Stock delineation of pelagic fish in Indonesian waters for a better management of sustainable fisheries, including parasitological studies of *Decapterus macarellus* (Cuvier, 1833) and *Scomberomorus commerson* (Lacepède, 1800)

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"Everyone's got their own battles and their own ways of fighting them.

What's important is that we keep moving forward."

Richardus F. Kaswadji

5 April 1945 – 21 February 2013

(A loving memory of an honorable teacher and my lifetime inspiration)

Zusammenfassung

In dieser Studie wurden biologische Aspekte kommerziell genutzter pelagischer Fischarten in Indonesien untersucht, wobei das Hauptaugenmerk auf der Scad-Makrele-, *Decapterus macarellus*, Cuvier 1833 und Spanischen Makrele, *Scomberomorus commerson*, Lacepède, 1800 lag, einschließlich der Verwendung von Parasiten als Indikator zur Separation der Bestände beider Arten in verschiedenen Fanggebieten. Die Biologie von *D. macarellus*, d. h. das Geschlechterverhältnis, die Länge bei der ersten Geschlechtsreife, der lunare Reproduktionszyklus und die Verteilung des gonadosomatischen Index in verschiedenen Fanggebieten, wurden untersucht, um die Populationsdynamik zu verstehen und zu ermitteln, wie die Fischerei die Reproduktionsmerkmale dieser Art beeinflussen kann. Die Untersuchung ergab, dass *D. macarellus* in den Gewässern von Nordsulawesi das ganze Jahr über laicht, mit Hochzeiten im Januar, März, Mai und September. Forschungen über den Mondzyklus, insbesondere bei pelagischen Fischen, sind noch selten. Die Ergebnisse dieser Arbeit zeigen, dass *D. macarellus* hauptsächlich im ersten Viertel der Mondphase laicht. In den Gewässern von Nordsulawesi wurden mehrere Laichplätze identifiziert, was die Vermutung nahelegt, dass *D. macarellus* in diesem Gebiet viele lokale Bestände bildet. Das Vorhandensein lokaler Bestände ist für die Erhaltung und nachhaltige Nutzung von *D. macarellus* als Fischereiressource von großer Bedeutung, insbesondere um die mit der Überfischung verbundenen Risiken zu mindern. Dadurch bietet sich die Grundlage für ein wirksames Fischereimanagement. Ein Vergleich zwischen dem fischereilichen Druck und der Reifegröße von *D. macarellus*, die in der Sulawesi-See und der Maluku-See gefangen werden, zeigt, dass der fischereiliche Druck eine frühere Reifung dieser Art fördern kann. Zur Erklärung dieses Ergebnisses wurde die Theorie der fischereibedingten Evolution herangezogen, wonach der höhere Fischereidruck auf *D. macarellus* in der Maluku-See im Vergleich zu anderen Artgenossen in der Sulawesi-See zu einer früheren Reifung dieser Art geführt haben könnte. Diese Studie unterstreicht die Bedeutung von lebensgeschichtlichen Parametern und der Überwachung des Fischereidrucks für kommerziell genutzte Bestände, um Nachhaltigkeit zu erreichen.

Parasitenuntersuchungen ergaben unterschiedliche Bestände von *D. macarellus* in den Gewässern von Nordsulawesi und Nord-Maluku. Diese Bestandsunterschiede stimmen mit molekularen Analysen aus der Literatur überein. Das Fehlen von Anisakidae-Nematoden deutet darauf hin, dass sich die beprobten Makrelenbestände in Nordsulawesi und Nord-Maluku wahrscheinlich von denen in Java, Bali und Papua-Neuguinea unterscheiden.

Außerdem wurden die beiden Arten, *Pseudodiclidophora decapteri* und *Allopseudodiclidophora opelu*, zum ersten Mal in *D. macarellus* aus indonesischen Gewässern nachgewiesen und ergänzen somit die bestehende Checkliste der Fischparasiten aus indonesischen Meeresgewässern. Auf ähnliche Weise wurde die Bestandsstruktur von *S. commerson* mit Hilfe dieses parasitologischen Ansatzesuntersucht, wobei unterschiedliche Bestände in Nordjava, Südjava und Sulawesi festgestellt wurden. Unterschiede in der Parasitenzusammensetzung, wie z. B. *Callitetrarhynchus gracilis* und *Gotocotyla acanthura*, halfen bei der Identifizierung dieser Bestände. Das Auftreten von *S. commerson* in der Javasee während der Regenzeit lässt auf eine Wanderung während des Nordwestmonsuns schließen. Obwohl die Migrationsroute noch unklar ist, stützen die Ergebnisse anderer Studien die These, dass die Fische wahrscheinlich durch das Südchinesische Meer, die Javasee und die Bali-See wandern. Die Fische in Sulawesi hingegen bildeten einen anderen Bestand und waren nicht mit dem Java-Bestand verbunden. Die in dieser Arbeit vorgestellten Ergebnisse zeigen, dass es immer noch ein breites Spektrum an fehlendem Grundlagenwissen über die heute bedenkenlos genutzten Fischereiressourcen gibt. Die Ergebnisse machen deutlich, wie wichtig es ist, für jeden Bestand geeignete Bewirtschaftungsstrategien zu entwickeln, um den Fortbestand von *S. commerson* in indonesischen Gewässern langfristig zu sichern.

Summary

This study investigated biological aspects of commercially exploited pelagic fish species in Indonesia, primarily focusing on the mackerel scad (*Decapterus macarellus*) and the narrow-barred Spanish mackerel (*Scomberomorus commerson*), including the use of parasite fauna as proxy to delineate the stocks of mackerel scad and the narrow-barred Spanish mackerel across different fishing grounds. The biological aspects of mackerel scad, i.e., sex ratio, length at first maturity, lunar reproduction cycle, and distribution of gonadosomatic index over different fishing grounds, were explored to understand the population dynamics and how fishing may affect the reproductive characteristics of this species. The research revealed that the mackerel scad in the northern Sulawesi Sea spawns year-round, with spawning peaks in January, March, May, and September. Research on the lunar reproduction cycle, particularly for pelagic fish, was still rare; nevertheless, the present study revealed that the fish spawns mainly during the first quarter of the moon phase. Several spawning grounds were identified in northern Sulawesi waters, supporting the notion of many local stocks of the mackerel scad around this area. The presence of local stocks is of great importance for the conservation and sustainable use of mackerel scad as a fisheries resource, particularly to mitigate the risks associated with overfishing. It provides a foundation for effective fisheries management. A comparison between fishing pressures and maturation sizes of the mackerel scad caught in the Sulawesi Sea and Maluku Sea shows that the fishing pressure may drive the earlier maturation of this species. A theory of fisheries-induced evolution was used to explain this result, where higher fishing pressure on *D. macarellus* in the Maluku Sea has plausibly caused earlier maturation of this species, compared to its conspecific in the Sulawesi Sea. This study emphasizes the importance of life history parameters and fishing pressure monitoring for commercially exploited stocks to achieve sustainability.

Parasite examinations identified distinct stock units of the mackerel scad in North Sulawesi and North Maluku waters. These stock differences also align with molecular analyses. The absence of Anisakidae nematodes indicated that the sampled fish stocks of mackerel scad from North Sulawesi and North Maluku are likely distinct from those of Java, Bali, and Papua New Guinea. On another note, two parasite species, *Pseudodiclidophora decapteri* and *Allopseudodiclidophora opelu*, were recorded for the first time in *Decapterus macarellus* from Indonesian waters; therefore, add to the existing checklist of fish parasites from Indonesia's marine waters. Similarly, the stock structure of the narrow-barred Spanish mackerel was examined by using a parasite approach, revealing distinct stocks in northern Java, southern Java, and Sulawesi. Differences in parasite compositions, such as a trypanorhynch cestode *Callitetrarhynchus gracilis* and a monogenean *Cathucotyle cathuaui*, helped identify these stocks. The occurrence of the narrow-barred Spanish mackerel in the Java Sea during the rainy season suggests migration during the northwest monsoon. Although the migration route is still unclear, findings from other studies support the argument that the fish are likely to move along the South China Sea, the Java Sea, and the Bali Sea. The fish in Sulawesí, on the other hand, formed a different stock and was not connected to the Java stock. As an outcome of the results presented in this thesis, there is still a wide range of missing basic knowledge concerning nowadays unquestioned used fisheries resources. These findings emphasize the importance of adopting appropriate management strategies specific to each stock to ensure the long-term sustainability of the narrow-barred Spanish mackerel in Indonesian waters.

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Abbreviations

BW	Body weight
COFI	Committee on Fisheries of FAO
DAAD	Deutscher Akademischer Austauschdienst (German Academic Exchange Service)
DIC	Differential interference contrast
EAF	Ecosystem approach to fisheries
EAFM	Ecosystem approach to fisheries management
F	Fishing mortality
FAO	Food and Agricultural Organization
FMA	Fisheries management area
FMP	Fisheries management plan
g	gram
GSI	Gonadosomatic index
GT	Gross tonnage
GW	Gonad weight
I	Intensity
indet.	Indetermined
IOD	Indian Ocean Dipole
K	Growth parameter
Komnas Kajiskan	*Komisi Nasional Pengkajian Sumber Daya Ikan* (Indonesia's National Committee on Fish Stock Assessment)
L_∞	Asymptotic length
Lc	Length at first capture
Lm	Length at first maturity
M	Natural mortality
mA	Mean abundance
MDS	Multi-dimensional scaling
mI	Mean intensity
MMAF	Ministry of Marine Affairs and Fisheries
n	Number of sample
NWG	National working group
P	Prevalence
SE	Standard error
SEAFDEC	Southeast Asian Fisheries Development Center
SIMPER	Similarity percentage
Sitaro	Siak Tagulandang Biaro
SPR	Spawning potential ratio
t_0	Theoretical age at length = 0
TL	Total length
t_{max}	Maximum age
TW	Total weight
USAID	United States Agency for International Development
WoRMS	World Register of Marine Species
Z	Total mortality

List of Papers

1. Retnoningtyas H, Agustina S, Natsir M, Ningtias P, Hakim A, Dhani AK, Hartati IH, Pingkan J, Simanjuntak CPH, Wiryawan B, Taurusman AA, Purbayanto A, Palm HW, Prasetia R, Yulianto I. (2024). Reproductive biology of the mackerel scad, *Decapterus macarellus* (Cuvier, 1833), in the Sulawesi Sea, Indonesia. Regional Studies of Marine Sciences 69: 103300. https://doi.org/10.1016/j.rsma.2023.103300

   [Will be referred to as **Retnoningtyas et al. 2024**]

2. Retnoningtyas H, Agustina S, Dhani AK, Wiryawan B, Palm, HW, Natsir M, Hartati ID, Prasetia R, Yulianto I. (2023). Impact of fishing pressure on the reproductive biology of mackerel scad, *Decapterus macarellus* (Cuvier, 1833), in the Sulawesi Sea and Maluku Sea, Indonesia. Asian Fisheries Science 36: 164—170. https://doi.org/10.33997/j.afs.2023.36.3.005

   [Will be referred to as **Retnoningtyas et al. 2023a**]

3. Retnoningtyas H, Yulianto I, Wiryawan B, Kleinertz S, Palm HW. (2023). Stock discrimination of mackerel scad *Decapterus macarellus* (Cuvier, 1833) in eastern Indonesia based on the metazoan fish parasite composition. Regional Studies in Marine Science 61 (2023) 102840. https://doi.org/10.1016/j.rsma.2023.102840

   [Will be referred to as **Retnoningtyas et al., 2023b**]

4. Retnoningtyas H, Yulianto I, Wiryawan B, Ruchimat T, Latama G, Kleinertz S, Palm HW. (20xx). Metazoan ectoparasites of the narrow-barred Spanish mackerel (*Scomberomorus commerson* Lacepède, 1800) across Indonesian waters: a potential proxy for stock discrimination and fisheries management decisions. Manuscript.

   [Will be referred to as **Retnoningtyas et al …(a)**]

Additional publications not fully relevant to this thesis:

5. Retnoningtyas H, Yulianto I, Soemodinoto A, Herdiana Y, Kartawijaya T, Natsir M, Haryanto JT. (2021). Stakeholder participation in management planning for grouper and snapper fisheries in West Nusa Tenggara Province, Indonesia. Marine Policy 128:104452. https://doi.org/10.1016/j.marpol.2021.104452 (referred as **Retnoningtyas et al., 2021**)

6. Kleinertz S, Yulianto I, Kurschat C, Koepper S, Simeon BM, Klimpel S, Theisen S, Unger P, **Retnoningtyas H**, Neitemeier-Duventester X, Barton DP, Damriyasa IM, Palm HW. (2022). Elasmobranchs from Indonesian waters: feeding ecology and trypanorhynch cestode fauna composition to support efforts in shark and ray conservation. Acta Parasitologica 67:1612–1625. https://doi.org/10.1007/s11686-022-00593-7

The authors’ contribution to the single publication

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

Heidi Retnoningtyas: Conceptualization, Investigation, Methodology, Formal analysis, Writing - original draft. **Siska Agustina:** Investigation, Methodology, Formal analysis, Visualization, Writing - original draft. **Mohamad Natsir**: 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.

2. Impact of fishing pressure on reproductive biology of mackerel scad, *Decapterus macarellus* (Cuvier, 1833), in Sulawesi Sea and Maluku Sea, Indonesia

Heidi Retnoningtyas: Conceptualization, Formal analysis, Writing—original draft preparation. **Siska Agustina**: Conceptualization, Methodology, Formal analysis, Data curation, Writing—original draft preparation, Visualization. **Arya Kusuma Dhani**: Methodology, Investigation. **Budy Wiryawan**: Writing—original draft preparation, Supervision. **Harry W. Palm**: Writing—original draft preparation, Supervision. **Mohamad Natsir**: Formal analysis, Data curation, Writing—original draft preparation. **Intan Destianis Hartati**: Methodology, Investigation. **Rian Prasetia**: Conceptualization, Formal analysis, Validation, Data curation, Writing—original draft preparation, Supervision. **Irfan Yulianto**: Conceptualization, Validation, Data curation, Writing—original draft preparation, Supervision.

3. Stock discrimination of mackerel scad *Decapterus macarellus* (Cuvier, 1833) in the eastern Indonesia based on metazoan fish parasite composition

Heidi Retnoningtyas: Conceptualization, Methodology, Formal analysis, Visualization, Writing – Original Draft. **Irfan Yulianto**: Conceptualization, Formal analysis, Writing-Original draft. **Budy Wiryawan**: Writing – Review & Editing. **Sonja Kleinertz**: Conceptualization, Methodology, Writing – Review & Editing. **Harry W. Palm**: Conceptualization, Methodology, Writing- Reviewing and Editing, Supervision.

4. Metazoan ectoparasites of the narrow-barred Spanish mackerel (*Scomberomorus commerson* Lacepède, 1800) across Indonesian waters: a potential proxy for stock discrimination and fisheries management decisions

Heidi Retnoningtyas et al. 2023a: Conceptualization, Investigation, Methodology, Formal analysis, Writing - original draft. **Irfan Yulianto:** Conceptualization, Formal analysis, Writing- Original draft. **Budy Wiryawan**: Writing – Review & Editing. **Budy Wiryawan:** Writing – Review & Editing. **Sonja Kleinertz**: Writing – Review & Editing. **Toni Ruchimat:** Writing – Review & Editing. **Gunarto Latama:** Writing – Review & Editing. **Harry W. Palm:** Conceptualization, Writing- Reviewing and Editing, Supervision.

5. Stakeholder participation in management planning for grouper and snapper fisheries in West Nusa Tenggara Province, Indonesia

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6. Elasmobranchs from Indonesian waters: feeding ecology and trypanorhynch cestode fauna composition to support efforts in shark and ray conservation

Sonja Kleinertz: Conception, writing and editing of manuscript, writing of intro and discussion, partly writing of conservation related text, compilation of all data in tables, writing material and method (m & m) parts 2.3-2.4, Supervision of practical part of the thesis in Indonesia 2009 (C. Kurschat); **Irfan Yulianto**: Performance of statistics and analyses, MDS plots, incl. texts for those (mds parasites and stomach contents, 3.2-3.3), partly writing of conservation related text, correction of fnal draft; **C. Kurschat**: Fish parasite isolation, parasite identification and all analyses (lab work), writing of abstract (as part of her master thesis); **Svenja Koepper**: Correction of manuscript, photo plate development; **Benaya Meitasari Simeon**: Writing of ecological role of elasmobranchs, validation and review of identifcation of all elasmobranch species, partly writing of conservation related text; **Sven Klimpel**: Advisor of master thesis (C. Kurschat), providing of material, correction of fnal draft; **Stefan Theisen**: Writing of m & m part: 2.1–2.2, correction of fnal draft; **Patrick Unger**: Writing of result part: 3.1-3.3, correction of fnal draft, partly writing of discussion; **Heidi Retnoningtyas**: Support of compilation of the tables, writing of MDS result texts; **Xaver Neitemeier-Duventester**: Sighting and (re)identifcation of Trypanorhyncha, correction of manuscript; **Diane P. Barton**: Editing of manuscript, English correction of the final draft; **I.M. Damriyasa**: Providing lab space for the study at UDAYANA University, Bali; **Harry W. Palm**: Advisor and revisor of master thesis (C. Kurschat), providing material, discussion of results, correction of final draft, sighting and (re)identifcation of Trypanorhyncha, editing of manuscript.

1. Introduction

1.1. Marine capture fisheries and its management in Indonesia

Due to a growing human population, increasing fish demand challenges producing countries, companies, and fishers to enhance fish production and improve fisheries management worldwide. In 2020, the production from marine capture and aquaculture fisheries contributed 44% and 19% to the total global production of aquatic animals (FAO, 2022). FAO's fishery and aquaculture statistics recorded that 52% of the world's capture production in marine fishing areas was supplied from Asia alone (FAO, 2021). With the exponential population growth, capture fisheries and aquaculture production are and will be increasingly important.

The growing amount of harvested resources requires serious effort to manage the fishery activities to maintain sustainability. Fisheries managers need to realize that the overexploitation or the irresponsible exploitation of the fisheries resources will lead to negative consequences in the future. FAO defines fisheries management as "*an integrated process of information gathering, analysis, planning, consultation, decision-making, allocation of resources and formulation and implementation, with enforcement as necessary, of regulations or rules which govern fisheries activities in order to ensure the continued productivity of the resources and accomplishment of other fisheries objectives*" (FAO Fishery Resources Division, 1997). This working definition was also applied to Indonesia's context and has been formalized through Law No. 31/2004 regarding Fisheries. In the implementation, the Government of Indonesia adopted the principles of an ecosystem approach to fisheries management (EAFM) and applied specific indicators to monitor and evaluate the performance of fisheries management (NWG EAFM, 2014; Muawanah et al., 2018). The FAO Committee on Fisheries (COFI) has acknowledged the ecosystem approach to fisheries (EAF) as the appropriate and practical way to implement the Code of Conduct for Responsible Fisheries, and the technical guidelines on the EAF have been used worldwide (FAO, 1995, 2023; Bianchi and Skjoldal, 2008). Presently, the fisheries management regime in Indonesia recognizes 11 fisheries management areas (FMAs or *wilayah pengelolaan perikanan*/WPP) (Figure 1.1), employing a fisheries management plan (FMP or *rencana pengelolaan perikanan*/RPP) for each FMA. The content of FMP includes (i) the status of fish stocks in the respective FMA, (ii) management goals, and (iii) recommended management implementation steps (**Retnoningtyas et al., 2021**).

In Indonesia, the marine environment and its biodiversity become increasingly essential resources to promote economic growth and social development. Optimizing fish production is another way to strengthen the domestic economy since increased fish production accelerates national economic development (Purwanto et al., 2022). Indonesia is the second largest marine capture producer after China (FAO, 2022), with an estimated yearly fishery potential of up to 12 million tons (MMAF, 2022a). In each FMA, the marine capture commodities are classified into nine species groups: (1) small pelagic fish; (2) large pelagic fish (excl. tuna and skipjack); (3) demersal fish; (4) reef fish; (5) penaeid shrimp; (6) lobster; (7) crabs; (8) blue swimming crab; and (9) squid. As the national fisheries management authority, the Indonesia Ministry of Marine Affairs and Fisheries estimated the potential production and set the total allowable catch for each group. Large and small pelagic species were estimated to have the highest potential of all groups. They were the most contributors to the production of all eleven FMAs, hence to the national fisheries production (MMAF, 2015, 2017, 2022a). In addition to tuna and skipjack, the large pelagic group comprises sharks, king mackerels, and kawakawa, while the small pelagic group is dominated by scad, mackerel, and sardines. Up to 17 species were covered by the small pelagic category, making this group the most multi-species fishery amongst other fishery groups (USAID Oceans, 2019). While anchoveta dominates the global contribution of small pelagic catch, scads are the main species dominated the in the Southeast Asia under the same category, followed by sardines, mackerels, and anchovies (FAO, 2022). Between the Southeast Asian countries, Indonesia is the main producer of small pelagic, contributed to 44% of the region’s total small pelagic production (SEAFDEC, 2022). The global importance of small pelagic fishes implies that long-term sustainability of this fishery is important for future food security.

Effective fisheries management is essential to conserving marine ecosystems, optimizing resources for global food supply, and employing people directly and indirectly involved in the fisheries sector worldwide (Heidrich et al., 2022). Management failures were most probable when stock spatial dynamics resulted in the stock’s concentration. In these situations, understanding the stock status and the capacity to regulate effort became essential. Using the information on spatial dynamics effects at fine spatial and temporal scales may improve management (Buckworth, 2004). The spatial dynamics of the stock were defined by the number of sub-stocks, the locations of their nursery grounds, and the movements associated with each stock.

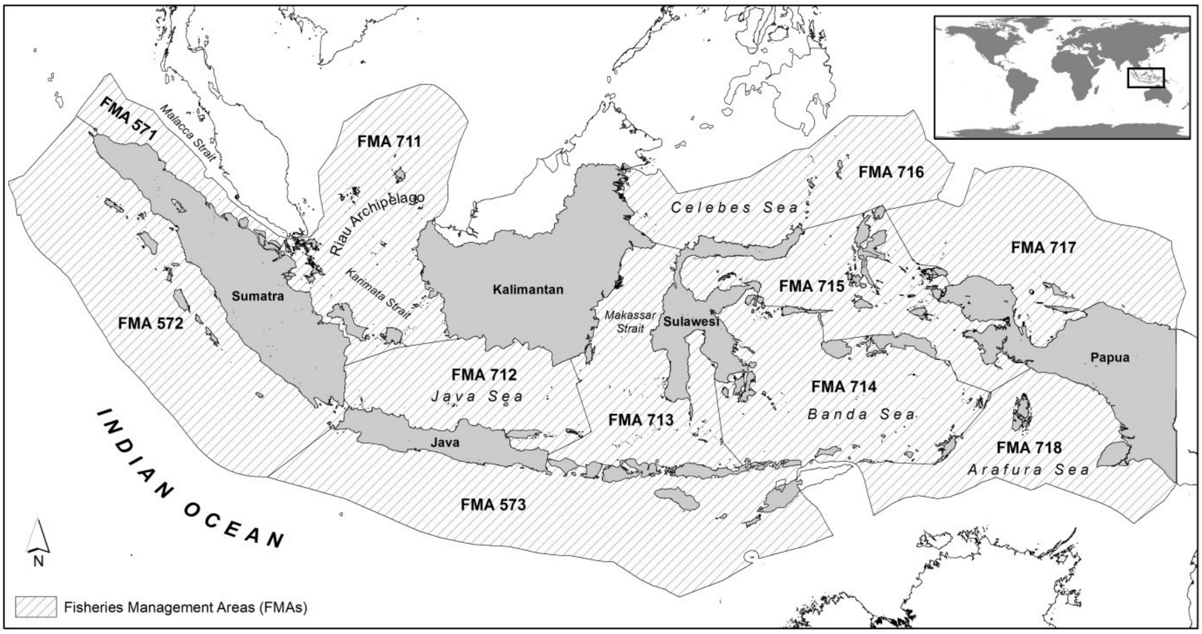

Figure 1-1. Eleven fisheries management areas (FMAs) of the Republic of Indonesia. FMAs 57 indicate areas within the Eastern Indian Ocean, and FMAs 71 within the Pacific Ocean (FAO, 2015).

1.2. Fisheries science to support sustainable resources management

There are fundamental questions that a fishery manager needs to address, such as how many fish are available, how many fishers can fish in a particular fishing ground, and how much catch can be yielded at a particular time (Cochrane and Garcia, 2009). All the answers correlate with the fish's biological and ecological aspects; therefore, understanding the underlying biological and ecological aspects and socio-economic principles is critical to a fishery manager. Developing a fisheries management plan begins with a clear understanding of the stock, including its boundary and status. As an integral component of the biological data, information on the stock structure is collected along with other inputs, i.e., ecological, economic, and social data (Begg et al., 1999; Cochrane and Garcia, 2009). In the stock assessment process, the data is processed to generate parameters on the population dynamics, such as growth, mortality, stock-recruitment relationship, and stock structure (Hoggarth et al., 2006). However, determining the stock structure of fish is challenging due to their variability and instability (Fréon et al., 2005), as the distribution might fluctuate at different spaces and times (Izzo et al., 2017).

Sparre and Venema (1998) defined a stock as a subset of a species inhabiting a particular geographical area and having constant growth and mortality parameters throughout its distribution area. Over time, the concept of stock evolves; thus, it can be conditional on the different methodologies and techniques that offer complementary perspectives on population structure (Cadrin et al., 2014). Understanding the stock structure is essential to formulating appropriate fisheries management and regulations for fishing in which several stocks are exploited differently (Ricker, 1981). Fish stock assessment is meant to provide advice to exploit the aquatic living resource optimally; hence, it needs science to estimate key population dynamics parameters that are useful to manage the fisheries resources in a better way (Sparre and Venema, 1998; Cadrin et al., 2014).

1.2.1. Stock identification as the fundament of stock assessment

Stock identification is critical in the stock assessment process as it answers the fundamental question of the scope of assessment. Stock identification is meant to identify the units within species and their boundaries. At the same time, another term often used interchangeably is stock determination, in which the individuals are classified into those units (Waldman, 2005). A particular stock is determined when it shows specific characteristics (e.g., share a common gene pool) that separate them from the adjacent groups. Sparre and Venema (1998) emphasized the importance of undertaking stock assessment for each stock separately, even though the results may subsequently be pooled into a multi-species fishery assessment. A stock has to be explicitly defined in multi-species fisheries, such as in small-pelagic fisheries, maximizing or optimizing the yield for every species at the same time is inapplicable (Cochrane et al., 2009). Mixed stock fisheries with spatially diverse population traits present challenges (Collie et al., 1990). When multiple stocks, each having varying stock productivities, are considered as one, stock recruitment analysis tends to overestimate the appropriate harvest rate and underestimate the ideal escapement levels (Hilborn, 1985).

In Indonesia's fisheries management, a guideline for stock assessment was established by the National Committee on Fish Stock Assessment Indonesia (*Komnas Kajiskan*). The technical guidelines used two methods to estimate fish biomass: (1) acoustic survey and (2) trawling/swept area. Statistical analysis is further undertaken to obtain information on the biological aspects, i.e., growth and reproduction. Fisheries in Indonesia are generally poor data as time series data of catch and effort at the species level is rarely available (Duggan and Kochen, 2016; Jaya et al., 2022). One of the approaches suggested for poor-data fisheries is length- or age-based catch data analysis (Hordyk et al., 2015a; Hordyk et al., 2015b; Hordyk et al., 2016). For management purposes, biological reference points such as spawning potential ratio (SPR) are applied to describe the reproductive capacity and determine the appropriate size at first capture to maintain resource sustainability.

1.2.2. Identification of stock boundaries and management implication

Identification of fish stock boundaries, which can be based on based on biological, genetic, geographical, or ecological factors, is a critical aspect of fisheries science and management. The delimitation of adjacent populations presents several challenges, particularly in the sea where no obvious geographic limits exist, making it difficult to identify stocks (Quetglas et al., 2012). Essentially, stock boundaries determine who holds the management authority and the right to access fisheries resources; therefore, stock delineation can be political (Berger et al., 2021; Cadrin et al., 2023). Furthermore, Cadrin et al. (2023) highlight that certain populations can be clearly defined by geographical factors, especially when closely linked to specific seafloor habitats or consistent oceanographic characteristics, and exhibit gaps in their distribution compared to other populations. On the other hand, some populations are more geographically fluid, share unclear borders with neighboring populations, or might have some interaction with them. Further complexity in depicting the spatial structure of populations arises from the precision and reliability of the detailed spatial data employed in stock evaluation. Nevertheless, despite these obstacles, stock identification must determine stock boundaries and are designed to encircle populations in a way that aligns with the standard assumptions of stock assessment models.

Identification of stock boundaries may bring some implications to management. Firstly, different stocks might react differently to environmental changes (Pinsky et al., 2013; Tolimieri et al., 2018; Malick et al., 2020); therefore, managers must adapt their strategies. Secondly, managers can tailor harvest strategies by understanding these differences according to each stock's health and abundance (Sloan et al., 2014; Collie et al., 2021). Individually managing each stock is crucial not only for preventing overfishing but also for preserving biodiversity. Preventing overfishing or stock collapse is essential as the consequences extend beyond environmental impacts. Overfishing can profoundly affect food security and the economy locally and potentially on a broader scale (Dyck and Sumaila, 2010; Srinivasan et al., 2010, 2012). Furthermore, the complexity of managing fish stocks increases when stocks cross territorial boundaries. Identifying these stocks requires collaboration and coordination among regulatory bodies (Sibert and Hampton, 2003; Satria and Sadiyah, 2018).

In defining the stock boundaries, Indonesia's fisheries management authorities refer to the FMA system; thus, every species within the same FMA is treated as a single stock. However, this conventional point of view is changing as more studies on stock identification have been undertaken, both between different FMAs and within the same FMA. Many of Indonesia's fisheries are multi-species, where different species are caught by a single fishing gear (Humphries et al., 2019; Wijayanto et al., 2020; Harlyan et al., 2022). In addition to general morphometry (Ardi, 2018), genetics and otolith morphometry have been widely used in stock identification for different fish species in Indonesia (Zamroni, 2012; Suwarso and Zamroni, 2013, 2014; Wujdi et al., 2017, 2022; Manginsela et al., 2020) while the use of parasite is still limited (Latama, 2006; Heirina et al., 2021; **Retnoningtyas et al., 2023b**).

1.3. Fish parasites as biological indicators

Markert et al. (2003) define bioindicators as organisms, or parts of organisms or communities of organisms, that contain information on the quality of the environment or a part of the environment; thus, the aim of using organisms as bioindicators is basically to help describe the natural environment. In aquatic ecosystems, fish can become bioindicators to investigate the hosts' identification, phylogeny, and systematic position (Palm and Klimpel, 2007; Palm et al., 2009) and their environment (Williams and Mackenzie, 2003; Marcogliese, 2004, 2005; Sasal et al., 2007; Biswas and Pramanik, 2016; Morris et al., 2016; Ashmawy et al., 2018), they have been used to study environmental pollution and to evaluate compound and complex structural properties of the environment as well (Chovanec et al., 2003). Furthermore, Biswal and Chatterjee (2020) evaluated the utilization of parasites in modern multidisciplinary methods to monitor and assess the health of aquatic ecosystems, as well as its significance and prospects, involving the field of parasitologists and ecotoxicologists.

In its early application, parasite fauna was used as biological indicators for investigating feeding behavior (Palm, 1999), population, and stock separation of the hosts (Herrington et al., 1939; Lester, 1990; Moser, 1991; Williams et al., 1992), as parasites prevalence and abundance are closely related to their hosts' distribution, migration, and population. Certain parasites infect their hosts at specific ages or within certain regions, and their abundance should vary across different areas, enabling the tracking of the original site of infection (Palm, 2011). In addition to stock identification, these traits can assess the risk of food-borne zoonotic diseases in fish and indicate the health of the host population. Parasites' sensitivity to environmental changes can directly affect their survival in the hosts' body, as well as their reproduction and distribution. Climatic factors, such as temperature, can directly affect the distribution of parasites and pathogens in an aquatic ecosystem (Marcogliese, 2008; Palm, 2011). Additionally, parasites will react to shifts in other abiotic factors, which indirectly influence the distribution and abundance of their hosts (Marcogliese, 2001). As climate changes, parasite populations may shift their distribution, expand into new areas, or decline in certain regions. Although much less studied, changes in dissolved oxygen concentration, salinity, and ocean acidification induced by climate change affect the host-parasite distributions and further affect parasitism and disease (Byers, 2021).

Parasites are incredibly diverse and can infect a wide range of hosts, and consequently, parasites can influence and modify the structure and biodiversity of their hosts (Mouritsen and Poulin, 2002). Changes in parasite diversity may indicate alterations in the ecosystem's overall biodiversity and ecological balance. In the trophic system, parasites influence food web structure by regulating the abundance of dominant host species (Marcogliese, 2002). Parasite species with low host-specificity will be transferred according to the host-feeding ecology. For cultured fish, parasites can be transferred from their wild habitat to the aquaculture system and humans as consumers (Palm and Overstreet, 2000). Therefore, parasite fauna can be used to assess the aquaculture system's quality (Truong et al., 2017; Kleinertz et al., 2022b). Regarding the hosts' feeding ecology, parasite fauna has been studied to investigate deep-sea fish and their environment. Due to food accessibility and subsequent feeding behaviors, meso-, bathypelagic, and demersal fish exhibit varied habits, and this should also be evident in their parasite species and diversity (Klimpel et al., 2006; Palm and Klimpel, 2008).

1.3.1. Selection of parasites as biological indicators

Choosing parasite species as biological markers requires an in-depth understanding of the dynamics between hosts and parasites. A parasite's affinity for its host is essential; some are exclusive to a single host type, while others exhibit a more comprehensive range (Esch and Fernández, 1993). This affinity offers insights into specific host groups and their wellness. The geographic distribution of parasites also matters (Klimpel et al., 2019). A region-specific parasite might relay distinct ecological insights compared to a globally found species. Some parasites react promptly to environmental cues, while others display prolonged responses. With their intricate life cycles spanning multiple hosts, many parasites offer a glimpse into ecological networks (Poulin, 2010).

As biological indicators, parasites can be used as markers for environmental studies and stock identification (MacKenzie and Abaunza, 2014; Biswal and Chatterjee, 2020). Palm (2011) summarized parasite characteristics to be considered when using parasites, whether as biological, accumulation, or impact indicators. Easy identification is a pivotal aspect in selecting parasite species as biological indicators. Reliable identification is possible when parasites can be distinguished through their morphological features or molecular methods. The ease of obtaining samples is another factor, as certain parasites may be simpler to examine than their counterparts. Established data for a specific organ where the parasites are found helps anchor observations and highlight anomalies. Interactions between a parasite and other organisms, whether predators or competitors, can affect parasite efficacy as a marker. Sensitivity to stress and being easily measured is an essential criterion in choosing parasites as biological indicators, mainly when dealing with environmental stressors (Williams and Mackenzie, 2003). As a result, changes in a parasite's distribution or intensity can indicate ecological health fluctuations under diverse environmental scenarios (Marcogliese, 2005).

1.3.2. Parasites as a proxy for stock delineation

Parasite data can describe the local environmental factors causing variations in parasite infestation and, therefore, can describe the characteristics of the host population wherever the species become established (Cardon et al., 2011). This information will help provide a clear discreteness of fish stocks serving as parasite hosts and is fundamental in identifying distinctive management units to support the conservation of natural populations. A management unit presents entities for monitoring and surveillance mechanisms to regulate the effects of human activities (i.e., fishing) upon the abundance of populations and species. The ability of fisheries management to control fishing intensity in management units will subsequently affect the management effectiveness.

Populations or separate fish stocks of a given species can be defined as a subgroup of specimens with a distinct migration pattern, zoogeographic distribution, and feeding habit. These isolated populations occur naturally, can mix within the exact geographical boundaries, and require separate fisheries management strategies to use this fisheries resource sustainably. Exploration of stock identification techniques has resulted in various approaches, i.e., life-history traits, morphology-morphometry, genetics, artificial tags, and environmental signals, such as otolith microchemistry, fatty acids, and parasites (Cadrin et al., 2014). Using parasites as biological tags has been a popular technique for over 80 years (Herrington et al., 1939). The fundamental idea behind using parasites as markers in fish population research is that fish acquire them only in the region where that specific parasite is prevalent (MacKenzie and Abaunza, 2014). Parasites as biological tags can provide phylogenetic descriptions and clarify ancestral dispersal routes and feeding habits of their hosts (Moser, 1991). Particular advantages of the use of biological tags over artificial tags are they are better suited for studies involving species that might not endure capture, handling, and tagging, and can, therefore, eliminate doubts concerning possible abnormal behavior of artificially tagged hosts (MacKenzie and Abaunza, 1998). Parasites have been widely used as indicator in delineating stocks for different groups of fish species, such as benthopelagic (Henriquez et al., 2011; Klapper et al., 2016), demersal (Blaylock et al., 2003; Abaunza et al., 2008; Braicovich et al., 2017), reef-associated (Villegas-Hernández et al., 2021), and pelagic species (Costa et al., 2013; Weston et al., 2015; Vasconcelos et al., 2017). Cantatore and Timi (2015) summarized the surveys on stock discrimination of fish from South American Atlantic waters, demonstrating the application of parasite approach over diverse fish species.

MacKenzie and Abaunza (2014) provided guidelines for choosing parasite species as biological tags for stock identification. In summary, to be effectively used as biological markers for stock identification, parasites should exhibit varied infection levels in host subjects across the study area, analyzed in terms of prevalence, intensity, and abundance. They should persist in the host for durations suited to the study's objective, with some studies demanding longer parasite lifespans. Simpler parasites with single-host life cycles are preferable, although parasites with complex life cycles can be utilized effectively if adequate information on their transmission factors is available. Infection levels should be consistent annually, but considering variations, multi-seasonal and multi-year sampling is crucial to avoid pseudoreplication. The ideal parasite should be easily detectable, requiring minimal host dissection, and have site-specificity. In addition, using parasites that are harmful pathogens or alter host behavior should be avoided.

1.4. Host characteristics

The mackerel scad *Decapterus macarellus* and the narrow-barred Spanish mackerel *Scomberomorus commerson* are marine pelagic species. Mackerel scad is a small pelagic species, while the narrow-barred Spanish mackerel is larger in size and categorized as a tuna-like species. The following descriptions contain information on the general characteristics of each species, including the taxonomy, morphology, feeding ecology, habitat, and distribution, and the fisheries activity involving the respective species, both in the global and Indonesian context.

1.4.1. *Decapterus macarellus* Cuvier, 1833

Superclass	Actinopteri
Class	Teleostei
Order	Carangiformes
Family	Carangidae

Body elongated, slender, and nearly round in cross-section, color in life bluish green above and silvery below, the black blotch on the margin of opercula near the upper edge; caudal fin yellow-green, both jaws without teeth and the posterior end of the maxilla is convex and round, caudal fin yellow-green and dorsal fin lobe sometimes dark distally. Feed on smaller planktonic invertebrates, the adults typically favor clear ocean waters, often surrounding islands, and usually in schools that move fast along the reef edges near deep water. The family of Carangidae is mainly marine, often far offshore, and rarely brackish. The mackerel scad is a small pelagic-oceanic species with a maximum length of 32 cm (Smith-Vaniz, 1999) to 46 cm (Jiménez-Prado and Béarez, 2004). As a pelagic fish, this species inhabits the 0—400 m depth range but is generally caught between 40—200 m depth. This species' distribution is circumtropical throughout the tropical Indian Ocean, including the Red Sea but not the Persian Gulf; in the Indo-West Pacific to the Marquesas Islands, north to southern Japan and south to Australia (Smith-Vaniz, 1999; Zhang et al., 2020; Froese and Pauly, 2023). In temperate and tropical climates, pelagic mackerel-like species of the Carangidae family are significant components of coastal pelagic ecosystems (Clarke and Privitera, 1995).

Scads (*Decapterus* spp.) make up to 2% of the total marine capture production in the world (FAO, 2022). Aside from providing affordable protein sources, particularly for coastal communities, longline tuna fishers commonly use scads as fish bait. Scads are migratory fish that are widely distributed. Little is known about the fishing season of scads, but generally, this species group is available all year round. However, certain species at certain localities occur only in a certain period.

Seven of eleven scads species distributed worldwide have been documented at prominent fishing sites in Indonesia. They are typically available year round, namely

Decapterus macarellus (mackerel scad), *D. kurroides* Bleeker, 1855 (redtail scad), *D. macrosoma* Bleeker, 1851 (shortfin scad), *D. russelli* Rüppel, 1830 (Indian scad), *D. tabl* Berry, 1968 (roughear scad), *D. akaadsi* Abe, 1958 (red scad), and *D. smithvanizi* Kimura, Katahira & Kuriiwa, 2013 (slender red scad) (Atmaja and Sadhotomo, 2005; Kimura et al., 2013). The mackerel scad *D. macarellus* is the main species of scads caught in the eastern Indonesian waters. Most catches were caught by purse seine, and the other fishing gears were seine net, trawl, lift net, gill net, trap, and hook and line. The mackerel scad is commonly marketed fresh and salted or dried.

1.4.2. *Scomberomorus commerson* Lacepède, 1800

Superclass	Actinopteri
Class	Teleostei
Order	Scombriformes
Family	Scombridae

Family Scombridae consists of mackerels, tunas, and bonitos. The narrow-barred Spanish mackerel has an elongated body that is moderately strongly compressed, teeth in jaws intense and compressed, and the lateral line abruptly bent downward below the end of the second dorsal fin. The color of the back is iridescent blue-grey, and the sides are silver with bluish reflections, marked with numerous thin, wavy vertical bands from 20 to 65 bands depending on body length (Collette and Russo, 1984). The narrow-barred Spanish mackerel is a pelagic fish that dwells the continental shelf's edge and in shallow coastal waters, often where there is reduced salinity and high turbidity. They are also seen near drop-offs, shallow or gently sloping reef, and lagoon waters. With main diet consists of small fishes, this fish typically hunts alone and frequently swims in shallow water along coastal slopes. This species is found in the Indo-West Pacific from the Red Sea and South Africa to Southeast Asia, north to China and Japan, south to southeast Australia, and Fiji (Kailola et al., 1993). It is an immigrant to the eastern Mediterranean Sea through the Suez Canal, which can be found westward to at least Tunisia (Collette and Nauen, 1983; Ben Souissi et al., 2006). In the southeast Atlantic, it has been reported from St. Helena as a vagrant (Collette et al., 2011). The narrow-barred Spanish mackerel is classified as a neritic species that lives primarily in shallow coastal waters, yet the adults are seasonally migrating along the extensive longshore

(Collette and Russo, 1984). However, several studies show that narrow-barred Spanish mackerel are effectively resident on a small spatial scale (Buckworth et al., 2007; Newman et al., 2009).

Scomberomorus commerson is one of the important commercial species in the Indian Ocean and the Indo-West Pacific region, supporting the fisheries in the Persian Gulf (Niamaimandi et al., 2015), Arabian Sea (Ben Meriem et al., 2006), and Bay of Bengal (Radhakrishnan et al., 2018). This species is also distributed in the Mediterranean Sea along the northern African countries (Ben Souissi et al., 2006; Juan-Jordá et al., 2013). Data of marine capture fishery in the Southeast Asian countries (SEAFDEC, 2022) recorded catch from hook and lines of Indonesia contributed to the highest production (28.3%), with 6.6% of the total catch composition consisting of *S. commerson*. Meanwhile, this species also contributed 9.1% of the total catch from gillnets as the second most productive fishing gear. The narrow-barred Spanish mackerel supports commercial, recreational, and artisanal fisheries. Commercial fishing mainly uses gears such as trawl nets, purse seines, falling nets, and gill nets to catch this species. In 2019, the narrow-barred Spanish mackerel contributed 39% of the total tuna-like production in Southeast Asia (SEAFDEC, 2022). It is primarily sold fresh or as dried-salted, also popularly processed into fish balls and available in frozen, smoked, and canned products.

Indian Ocean, as the primary fishing grounds for the narrow-barred Spanish mackerel, is why Indonesia is a member country of the Indian Ocean Tuna Commission (IOTC). The majority of the catch of the narrow-barred Spanish mackerel was attributed to vessels flagged to Indonesia. Along with the Indo-Pacific king mackerel *Scomberomorus guttatus*, the narrow-barred Spanish mackerel has long been an essential commodity to the national and global fishery (Widodo, 1989). In the national fishery management, *Scomberomorus* is categorized as a large pelagic catch found in all fisheries management areas (MMAF, 2015), indicating the wide distribution of this species across the Indonesia archipelago.

1.5. Study areas

This study was undertaken in two primary locations: (1) the Sulawesi Sea and the northern Sulawesi peninsula for the mackerel scad, and (2) the northern and southern coast of Java for the narrow-barred Spanish mackerel. Samples of the mackerel scad were all collected from a fishing port in Sulawesi. However, some samples originated from the Maluku Sea, which is situated in different administrative areas. For the narrow-barred

Spanish mackerel analysis, I compared the parasite records from Java coastal waters with those from Sulawesi waters (Latama, 2006).

1.5.1. Sulawesi Sea and northern Sulawesi peninsula

Sulawesi Sea is well-known for its pelagic fishing grounds nationwide (Amri et al., 2015). With a large and deep basin structure, the Sulawesi Sea is dominated by oceanic water mass and is an important passage for Indonesian Throughflow (Susanto et al., 2012). Sangihe Ridge, in the northern part of Sulawesi mainland, is the first deep topographic barrier (1350 m deep) encountered by the Pacific water, providing access to the Sulawesi Sea prior to entering the Makassar Strait (Gordon et al., 2003). The productivity of the Sulawesi Sea, in terms of fish resources, is highly influenced by oceanographic events, such as vertical mixing and coastal upwelling. During the southeast monsoon, the sea surface temperature in the Sulawesi Sea is much warmer than in the Maluku Sea, and the upwelling was weak.

Nevertheless, the wind gap between Gorontalo and the North Sulawesi mountains allows the southerly wind to pass into the Sulawesi Sea and generate vertical mixing (Wirasatriya et al., 2019). Coastal upwelling, on the other hand, was detected in the Sulawesi Sea through a positive anomaly of chlorophyll-a and a negative anomaly of sea surface temperature and sea level during the northwest monsoon (Wirasatriya et al., 2021). Both vertical mixing and coastal upwelling lead to nutrient enrichment in the surface layer and subsequently increase the primary production of the sea.

Besides large pelagic fish, small pelagic species such as the mackerel scad stand out as the most important group targeted by fishers in the Sulawesi Sea in terms of both quantity and value (USAID Oceans, 2019; Zamroni et al., 2019). Apart from fishing in North Sulawesi waters, fishers from Sulawesi frequently venture for fishing into the FMA 715, which covers the Halmahera Sea and the Maluku Sea, however, they land their catch at fishing ports in the North Sulawesi mainland. Tumumpa Fishing Port, the largest fishing port in North Sulawesi, is the primary landing site for pelagic catch from FMA 716. In contrast, Bitung Fishing Port, the second largest, received not only catch from FMA 716 but also from the adjacent FMAs, i.e., 715 and 717 (Zamroni et al., 2019). It becomes a concern for fisheries managers in developing the harvest strategy as the stock unit must be clearly defined, whether or not the stocks from different FMAs belong to one stock.

1.5.2. Northern and southern Java coasts

The Java Sea, situated north of Java Island, is characterized by shallow water and low salinity water, as numerous rivers empty into it (Hamzah et al., 2020), and is strongly affected by the Asia-Australia monsoon system's local climate (Potemra et al., 2016; Susanto et al., 2016). The sea surface temperature was generally highest in April—May and November, while the lowest was in February and August (Sulistya et al., 2007). Java Island is stretched between Karimata Strait in the west and Makassar Strait in the eastern part. The water mass of Karimata Strait is characterized by the low-salinity, warm water of the South China Sea (Gordon et al., 2012), while the Makassar Strait, as the major passage of the Indonesian Throughflow, is characterized by the low-temperature-high-salinity Pacific waters. As an important fishing area for small-scale fishers, the production of the Java Sea mainly comprises demersal and pelagic fishes (Purwanto et al., 2014; Syamsuddin et al., 2018). Pelagic fishing in the Java Sea began in 1970 when the purse seine was introduced (Nurhakim et al., 1987). According to Hadinoto (*pers. comm.*, 2019), the narrow-barred Spanish mackerel usually appear in the Java Sea, particularly in the waters off of North Jakarta, between November and December every year, coinciding with the northwest monsoon or the rainy season. During this period, the salinity of the Java Sea decreased due to rainfall flowing from the rivers to the sea.

The southern part of Java Island, which faces the Indian Ocean, also receives part of the Indonesian Throughflow through the Timor Sea, which not only cools its surface layer while warming it beneath the thermocline, while also causing negative temperature deviations on the sea surface across the Indian basin (Song, 2004; Song et al., 2004). The characteristics of the Indian Ocean, in general, are affected by several oceanographic events, such as equatorial currents (Philander and Pacanowski, 1980), monsoon (Clemens et al., 1991), Indian Ocean Dipole (IOD) (Saji et al., 1999), and upwelling (Susanto et al., 2001). The southern Java coast, situated in the eastern part of the Indian Ocean, is mainly influenced by the Asian-Australian monsoon. Upwelling, which is generated by this monsoon system as a response to the regional wind, is likely to occur from June to October, with the extent of the upwelling area increasing from month to month (Wyrtki, 1962; Susanto et al., 2001; Purba and Khan, 2019). As it brings the nutrient from the water column upward to the surface layer, upwelling drives the productivity of the ocean that supports rich marine biodiversity and fish resources, i.e., pelagic (Nurani et al., 2015; Ma'mun et al., 2017), deep sea and demersal fish (Badrudin et al., 2017), and other seafood such as shrimps and lobsters (Saputra et al., 2013; Milton et al., 2014).

1.6. Objectives

The overall objective of this study is to explore and examine the biological aspect of two economically important pelagic species in Indonesian fisheries that support the stock assessment process. Biological and ecological data are essentially required in the stock assessment, and this study aims to provide insights into the required data that can be obtained and utilized. As pelagic fishes often move beyond the administrative boundaries set by the fisheries authorities, determining stock structure and unit can be complicated. This study also focuses on using parasites as biological tags to understand the stock delineation and migration of pelagic fish and the utilization of length and gonadal data to obtain more information on the reproductive strategy of the small pelagic species.

1. To examine the reproductive biology and distribution of potential spawning areas of the mackerel scad *Decapterus macarellus* around the Sulawesi Sea.
2. To investigate the correlation between fishing pressure and the maturity size of the small pelagic fish *Decapterus macarellus* and how this supports evidence for the fishing-induced evolution theory.
3. To investigate stock delineation of the mackerel scad *Decapterus macarellus* in the Sulawesi Sea and the adjacent waters using metazoan parasites as a proxy.
4. To investigate the metazoan parasite composition of the narrow-barred Spanish mackerel *Scomberomorus commerson* from the Java coasts to identify its association with the narrow-barred Spanish mackerel from Sulawesi waters. Furthermore, the information may provide a general idea of the narrow-barred Spanish mackerel migration route across the Indonesian archipelago.

1.7. Thesis structure

This thesis is composed of seven chapters. **Chapter 1** consists of a general introduction to the marine capture fisheries in Indonesia, including general information on the management implementation, the use of parasites in stock identification as part of fisheries science to support sustainable fisheries management, general characteristics of the mackerel scad and the narrow-barred Spanish mackerel as the focus species in the study, study areas, and the working hypotheses. **Chapter 2** describes the reproductive biology of the mackerel scad in the Sulawesi Sea, its reproductive periodicity, and its potential spawning area; **Chapter 3** demonstrates how fishing pressure, as indicated by the total mortality, affects the maturity size of the mackerel scad. The findings support the fisheries-induced evolution hypothesis and provide evidence from Indonesian tropical fish stock and region that fishing pressure affects fish reproductive biology. **Chapter 4** describes the metazoan parasite composition as a proxy for the mackerel scad *Decapterus macarellus* stock discrimination in the Sulawesi Sea and the Maluku Sea; **Chapter 5** investigates the metazoan parasite composition of the narrow-barred Spanish mackerel *Scomberomorus commerson* and how it can explain the migration route across the northern and southern coast of Java and Sulawesi waters. **Chapter 6** provides a general discussion of the findings from Chapter 2 to Chapter 5, elaborates on five sub-chapters: (1) reproductive biology and spawning behavior of commercially exploited pelagic fish in Indonesia; (2) understanding the impact of fishing on the biology of the exploited species; (3) parasites as indicator for stock delineation and connectivity, (4) the development of parasites studies and its expanding implementation in Indonesia, and (5) management and conservation of fisheries resources in Indonesia. The last part, **Chapter 7**, summarizes the outlook for future application and research activities that can be undertaken to improve stock assessment studies to support the management of fisheries resources in Indonesia.

1.8. Working hypothesis

The working hypotheses are:

1. The reproductive biology of mackerel scad *Decapterus macarellus* allows identification of spawning behavior and potential spawning areas around the Sulawesi Sea, Indonesia
2. Pressure from fishing affects the maturity size of the mackerel scad *Decapterus macarellus* in tropical eastern Indonesia
3. It is possible to discriminate different mackerel scad stocks in the two adjacent waters (Sulawesi Sea and Maluku Sea) based on the metazoan fish parasites
4. The metazoan fish parasites fauna allows identification of the population structure of the narrow-barred Spanish mackerel *Scomberomorus commerson* across the Indonesian archipelago
5. Knowledge of marine fish parasites in Indonesia contributes to develop further methodological approaches in fisheries science in order to support a better sustainable fisheries management in future

2. Reproductive biology of the mackerel scad, *Decapterus macarellus* (Cuvier, 1833), in the Sulawesi Sea, Indonesia[1]

Abstract

Indonesia is the second largest fisheries producer in the world, landing also many small pelagic fish. To improve information for sustainable fisheries management in the Sulawesi Sea, we examined the reproductive biology of the main targeted species, the mackerel scad *Decapterus macarellus* (Cuvier, 1833). A total of 1,349 individuals from 13.4 - 38.2 cm total lengths were collected from two landing sites in North Sulawesi between May 2020 to March 2021, studying the sex ratio, length at first maturity (Lm), reproductive periodicity, and potential spawning grounds. Of those samples, 93.9% (1,267 individuals) had visible gonads with an equal M:F sex ratio of 0.98:1.00. The length at first maturity (Lm) for males and females was 22.59 and 21.62 cm, respectively. *D. macarellus* spawned throughout the year, with spawning peaks in January, March, May, and September, mainly during the first quarter of the moon phase. Most mature individuals combined with a high gonadosomatic index were found off Tumumpa Dua and around the northern and western sides of Sangihe and Siau Islands, indicating distinct spawning grounds of *D. macarellus* in these areas. This enables temporary and regional fishing closures by fisheries managers in order to develop appropriate fishing practices for this small pelagic fish species in future.

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2.1. Introduction

Small pelagic fish provide a substantial source of income for 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 as the main group, followed by gadiformes, and tuna and tuna-like species (FAO, 2022). Small pelagic fish comprises diverse species which refer to fish with a body length range of 10 to 30 cm, or up to 60 cm, as adults, schooling mostly within the epipelagic zone (depths of 0–200 m) of the Oceans (Fréon et al., 2005). The small pelagic species being primarily caught is usually unique between countries or regions, for example, anchoveta or Peruvian anchovy (*Engraulis ringens*) in Peru and Chile, sardinellas (*Sardinella* spp.) in tropical waters off Africa and Asia, and scads (*Decapterus* spp.) which are caught mainly in eastern and southeastern 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 1,199 thousand tons per year (2004—2013) and up to 1,336 thousand tons in 2018, making 2% of the total marine capture fisheries production in the world (FAO, 2022).

Indonesia ranked the second of the world marine capture producers behind China (FAO, 2022). In Indonesia's national fisheries system, small pelagic resource potential and its total allowable catch was 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 (USAID Oceans, 2019). Mackerel scad was found as the main species of the small pelagic catch in North Sulawesi, caught primarily by purse seine, and contributing 18% to the total catch in the respective fisheries management area (FMA 716) (MMAF, 2016a). Hence, North Sulawesi is well-known for its small pelagic production across the nation. Small pelagic fish is one of the 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 Oceans, 2019). Besides fishing in North Sulawesi waters, fishers from this area often fish in the adjacent fishing grounds outside FMA 716, yet they land their catch in fishing ports across the North Sulawesi region. It is a concern for fisheries managers while developing a fisheries harvest strategy, if the stock and fishing ground are not clearly defined.

Studies related to mackerel scad in Indonesia have been undertaken to reveal their size distribution and growth pattern (Silooy et al., 2019), reproductive biology and population dynamics (Nur et al., 2017; Pattikawa et al., 2018; Zamroni et al., 2019; Silooy et al., 2021), population genetics (Zamroni, 2012; Zamroni et al., 2014; Zamroni and Suwarso, 2017), exploitation rate (Hariati, 2011), and habitat (Rahmadi and Puspasari, 2015). As a biological mechanism for transmitting genetic information from one generation to the next, reproduction in teleosts is affected by changes in the environment and the best timing, the latter ensuring adequate food during the reproductive cycle. Various approaches have been undertaken to study the reproductive biology of mackerel scads in Indonesia, such as length-based life history parameters (Iksan and Irham, 2009; Fadila et al., 2016; Bintoro et al., 2020) and production models based on catch data (Fadhilah et al., 2021).

Knowledge on reproductive biology can inform fisheries managers on the actual stock condition of the respective resource and possible management measures to be taken. This study aims to investigate the reproductive biology of the mackerel scad (*Decapterus macarellus*) in the Sulawesi Sea in order to support sustainable fisheries management. The reproductive seasonality, lunar periodicity, and potential spawning grounds were examined, and management measures for ensuring the sustainable use of resources are suggested.

2.2. Materials and Methods

2.2.1. Study sites and sample collection

A total of 1,349 individuals of *Decapterus macarellus* 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 monthly from two landing sites in North Sulawesi, namely Tumumpa Dua and Bitung (Figure *2-1*), from May 2020 to March 2021. Due to logistical constraints, samples were not collected in November and December 2020. The samples were commercially caught by purse seine fishers who caught the fish inside the North Sulawesi Sea, Indonesia. Every month, 52 to 273 individuals were collected from one to six days of sampling. In each sampling, the fishers were interviewed for information on the actual fishing ground by participatory mapping. The fish samples were measured to the nearest millimeter in total length (*TL*) and to the nearest gram of body weight *(BW*) (Appendix 1)**.**

2.2.2. Sample dissection and gonad identification

Of 1,349 individuals, 1,270 individuals were examined for gonad identification since the remaining samples (79 individuals) had no visible gonad to be examined. Each sample of *D. macarellus* was dissected for morphological gonad identification following (West, 1990) and Diouf (1981). The sex of each individual sample was determined through macroscopic examination of the gonads after dissection, whereby the shape and the color of the testis and ovaries were used to assign sex and the gonadal maturity of the fish. For female individuals, the mature gonads have the characteristics typical of typical of flaccid, empty, often bloodshot in appearance, or containing a small number of remnant ripe eggs (West, 1990; Diouf, 1980). For male individuals, testes are well developed; whitish – pinkish colour; enlarged with conspicuous superficial blood vessels, and when regressing, the testes are flaccid and bloodshot (Diouf, 1980). The gonad weight (*GW*) was measured to the nearest 0.1 g to calculate the gonadosomatic index (GSI), as a proxy of reproductive activity (Flores et al., 2019), using the formula of GSI = GW/BW x 100, where *GSI* is the gonadosomatic index, *GW* is the weight of the gonad, and *BW* is the body weight of the individual fish.

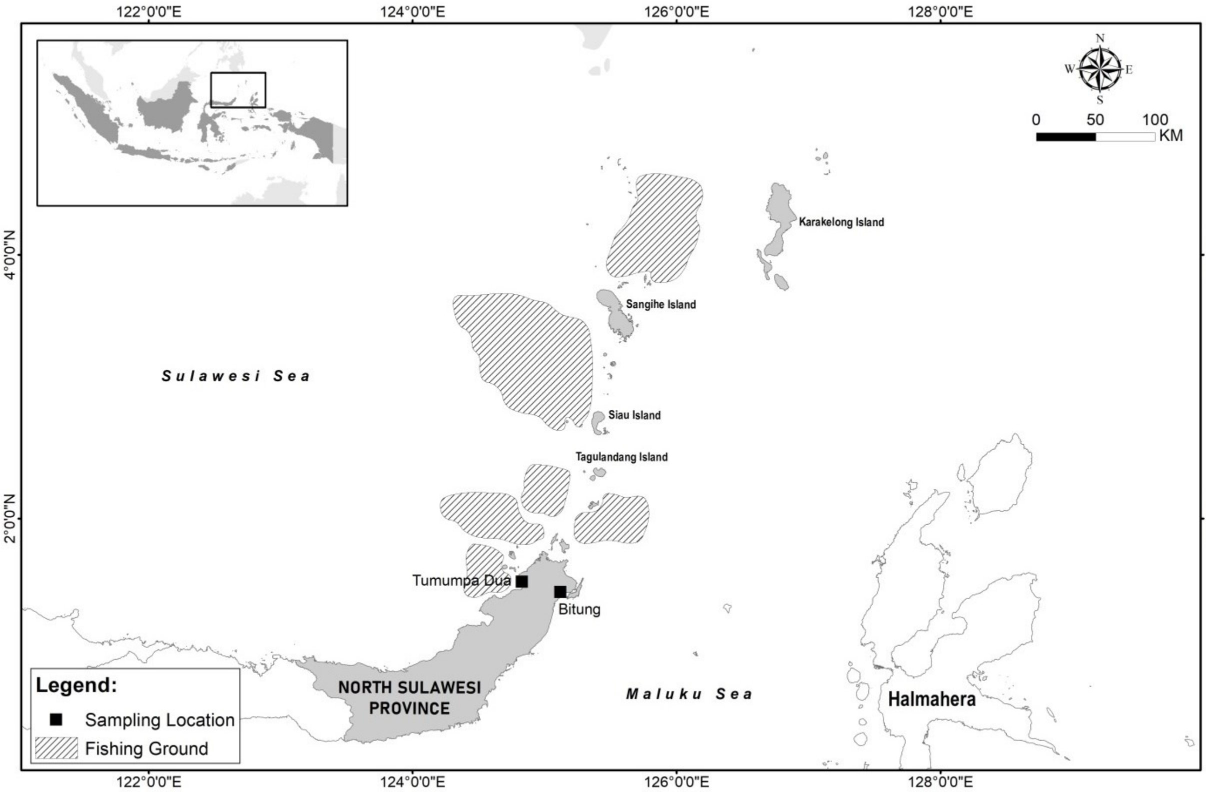

Figure 2-1. Samples of *Decapterus macarellus* were collected from two landing sites (Tumumpa Dua and Bitung) in the mainland of the North Sulawesi province. Information on fishing grounds shown in the map was obtained from local fishers who landed their catch in Tumumpa and Bitung.

2.2.3. Data analysis

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

The sex ratio of *D. macarellus* was estimated and tested for significant differences in the proportion of males and females for a theoretical 1:1 relation using a Chi-square (X^2) equation (Kenney and Keeping, 1951). Size differences between males and females were examined using Kolmogorov-Smirnov (KS) tests. All statistical analyses were performed using RStudio (R Core Team, 2022). Seasonal patterns of spawning were estimated using the monthly proportion of mature individuals. The lunar periodicity of spawning was estimated using the proportion of mature individuals in each moon phase. Description of the 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. Differences in the proportion of mature gonads for each female and male individuals were compared among moon phases (NM, Q1, FM, Q3) using the Proportion Z-test. Likewise, differences of GSI for each female and male individual were compared among moon phases using one-way ANOVA followed by Tukey HSD post hoc for pairwise comparison.

2.3. Results

2.3.1. Morphometric characteristics and sex ratio

A total of 1,270 individuals of *Decapterus macarellus,* or 94.1% of the samples, showed visible gonads. Within those samples, we observed 640 males, consisting of 270 immature and 370 mature individuals, and 627 females, consisting of 253 immature and 374 mature individuals. The immature male fish size ranged between 14.00–26.20 cm (22.67–184.27 g), while the immature female size ranged between 13.40–23.10 cm (2.26–204.11 g) (Appendix 1). We observed that the mature male individuals ranged from 19.4 to 38.2 cm (73.7 - 555.7 g), while the mature female individuals ranged from 17.2 to 32.5 cm (48.2 - 361.5 g) (Figure *2-2*). A significant difference was found between the length frequency of male and female individuals (K-S test, H = 10.139, *p*-value = 0.014). The sex ratio of male to female was 0.98:1.00, and the observed proportion was statistically insignificant (X^2 = 0.154, p-value 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 males and females was 22.59 and 21.62 cm, respectively (Figure *2-3*).

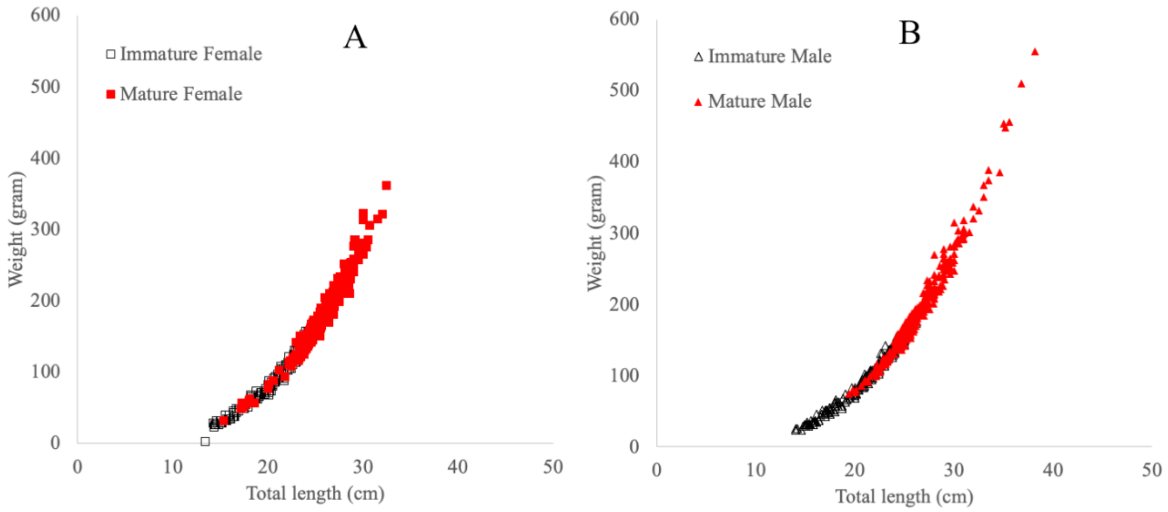

Figure 2-2. Morphometrics (length and weight) of the female (A) and male (B) of *Decapterus macarellus* in the Sulawesi Sea

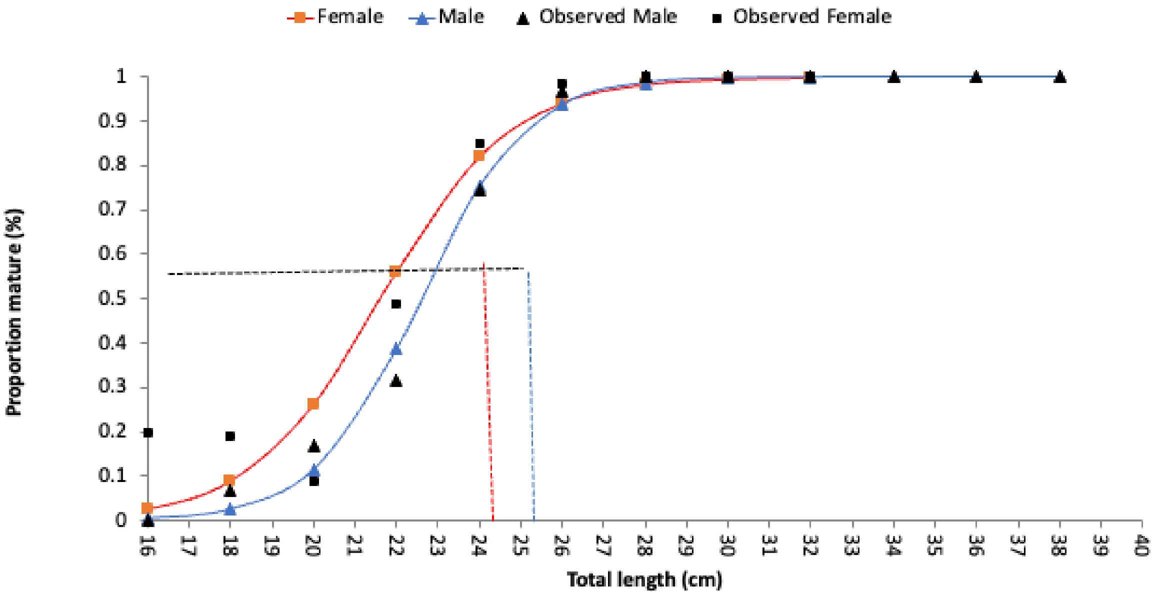

Figure 2-3. Length at first maturity (Lm) model of the female and male *Decapterus macarellus* in the Sulawesi Sea

2.3.2. Spawning periodicity

During the period of sampling months from 2020 to 2021, mature female and male gonads were found in all sampling months (Figure *2-4*), indicating that *D. macarellus* spawns all year round. The mean monthly gonadosomatic index (GSI) ranged from 0.35 to 2.20 %

and from 0.54 to 2.78 % for female and male individuals, respectively (Figure *2-5*), demonstrating the likewise 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 of the spawning season of the *D. macarellus* in the Sulawesi Sea occurred in these months.

Mature female and male gonads were found during all moon phases (Figure *2-6*). For female individuals, the proportion of mature gonads was found 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 the proportions were significantly high 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 both for female and male individuals (Figure *2-7*). For female individuals, the GSI was found significantly high during the first quarter (Q1) among other moon phases (One-way ANOVA; $F = 16.54$; $p < 0.05$). Likewise, for male individuals, the GSI was found significantly high during the first quarter (Q1) among other moon phases (One-way ANOVA; $F = 10.26$; $p < 0.01$), indicating that the peak spawning occurred during this moon phase.

2.3.3. Potential reproductive area

Based on the GSI from individual samples of *D. macarellus* 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) (Figure *2-8*). However, based on the composition of mature and immature individuals, we observed that the highest percentage of mature individuals was found in the northern Sangihe Island and the western Sangihe and Siau Islands, with the percentage of mature individuals of 100 and 97%, respectively (Figure *2-9*). Based on the mature individuals combined with the high gonadosomatic index, highest spawning potential was observed off Tumumpa Dua and around the northern and western sides of Sangihe and Siau Islands, highlighting these areas as distinct spawning grounds of *D. macarellus*.

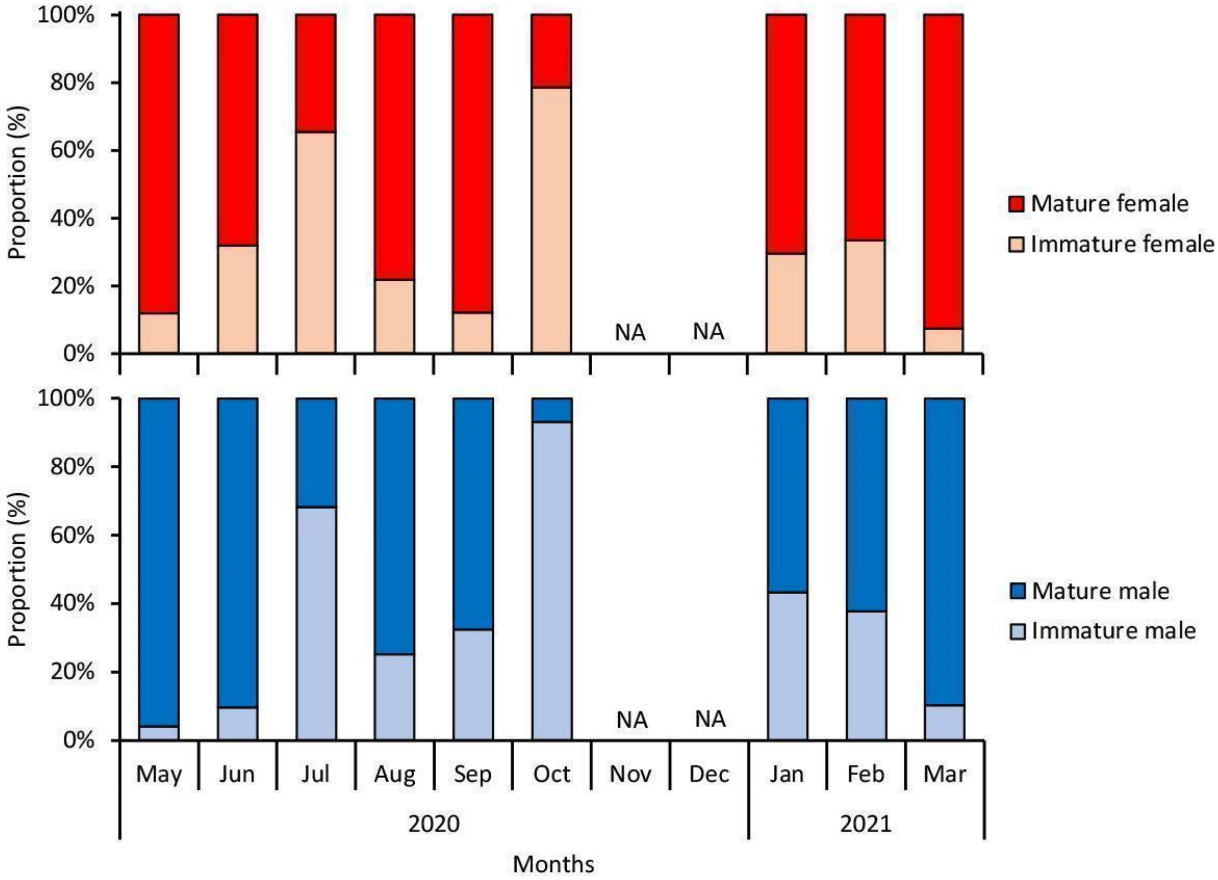

Figure 2-4. Temporal changes in the proportion of immature and mature female and male gonads of *Decapterus macarellus* in the Sulawesi Sea between May 2020 and March 2021

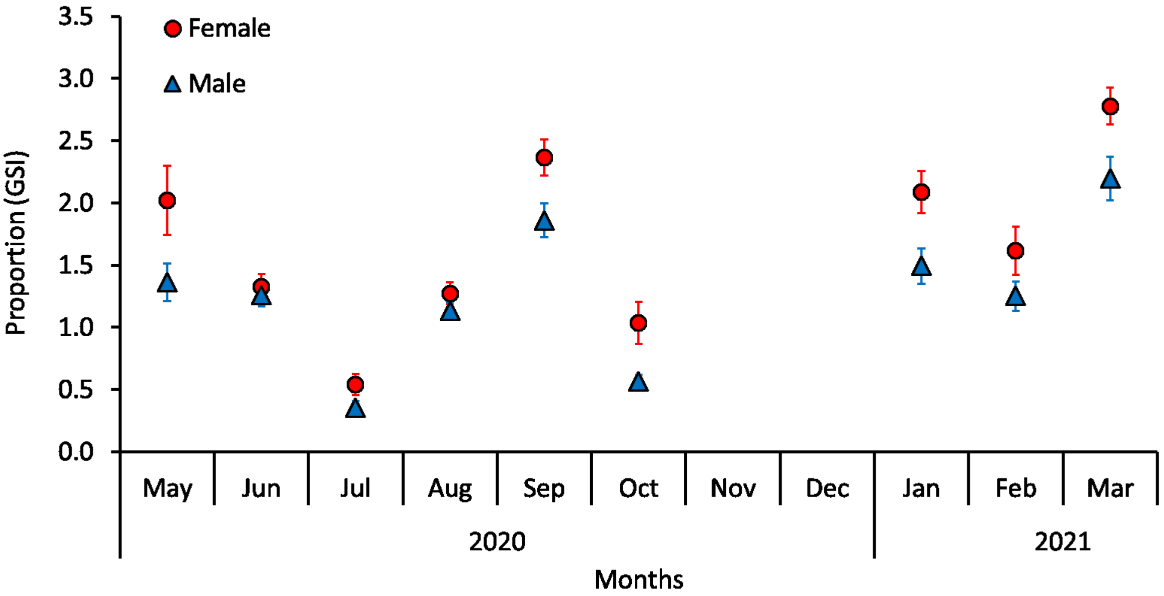

Figure 2-5. Temporal changes in the proportion of female and male gonadosomatic index of *Decapterus macarellus* in the Sulawesi Sea between May 2020 and March 2021

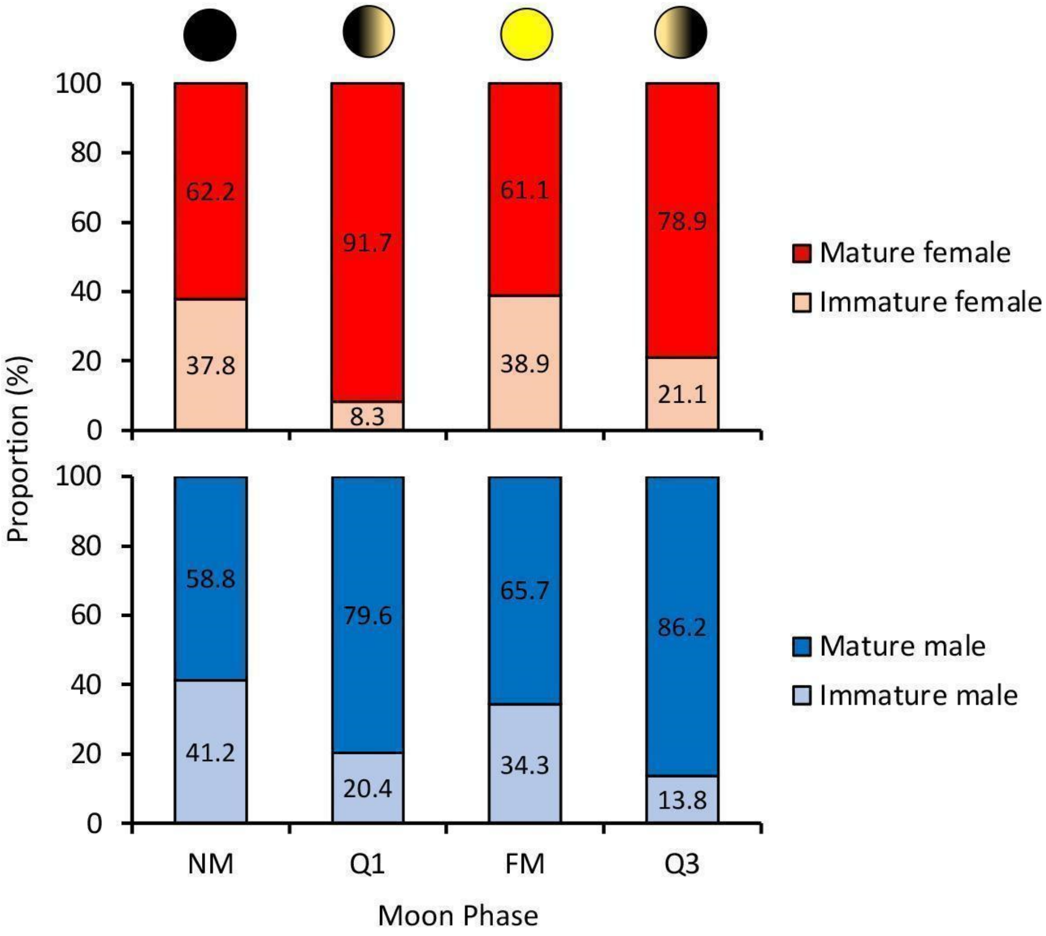

Figure 2-6. Lunar periodicity in the proportion of immature and mature female and male gonads of *Decapterus macarellus* in the Sulawesi Sea sampled between May 2020 and March 2021. Description of moon phases are as follows: New Moon = NM ± 3.5 d; First Quarter (Q1) = NM + 3.5 to NM + 11.5 d; Full Moon = FM ± 3.5 d; Third Quarter (Q3) = FM + 3.5 to FM + 11.5 d

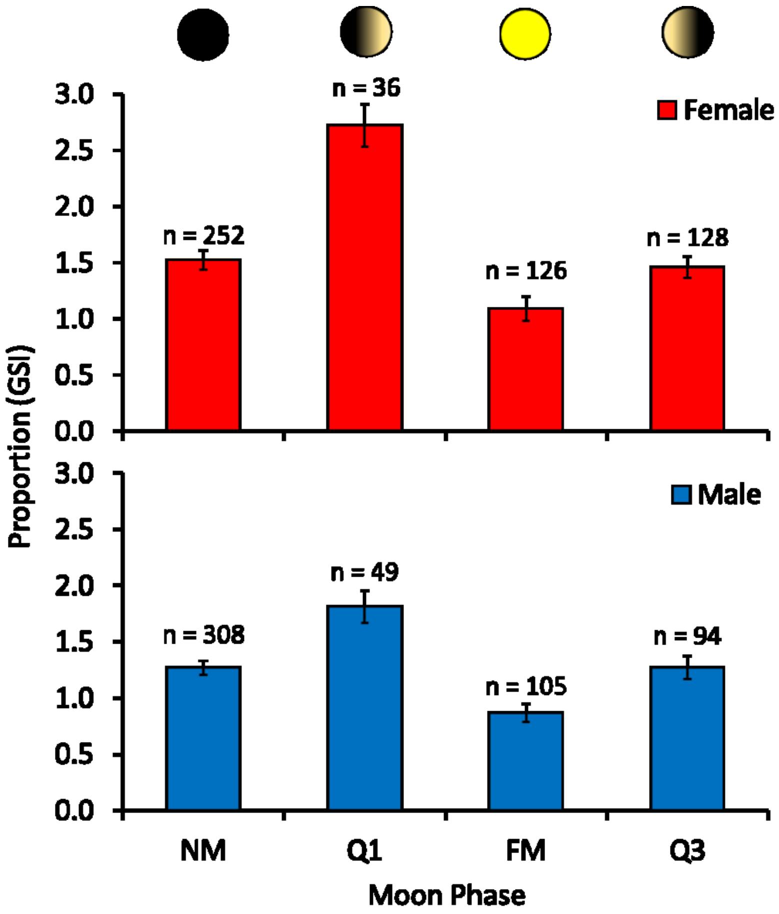

Figure 2-7. Lunar periodicity of female and male gonadosomatic index of *Decapterus macarellus* in the Sulawesi Sea sampled between May 2020 and March 2021. Description of moon phases as follows: New Moon = NM ± 3.5 d; First Quarter (Q1) = NM + 3.5 to NM + 11.5 d; Full Moon = FM ± 3.5 d; Third Quarter (Q3) = FM + 3.5 to FM + 11.5 d

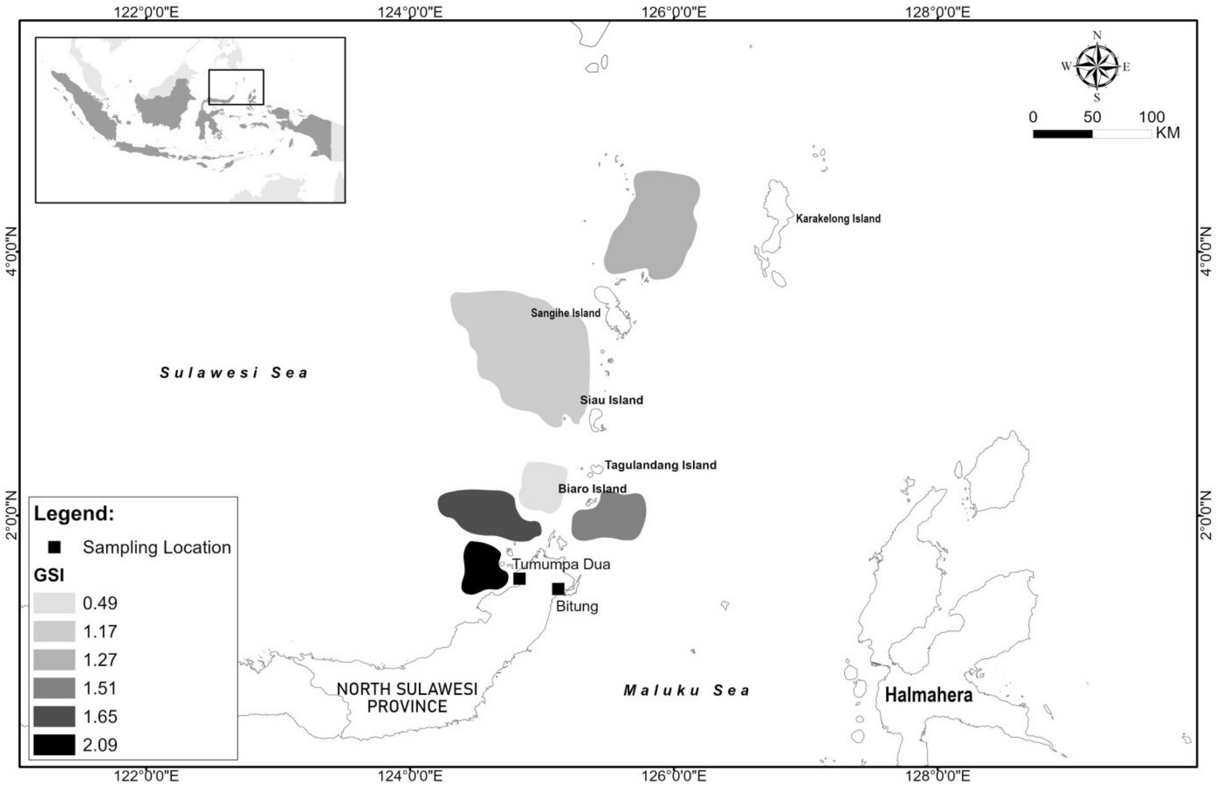

Figure 2-8. Distribution of gonadosomatic index (GSI) of *Decapterus macarellus* in the Sulawesi Sea

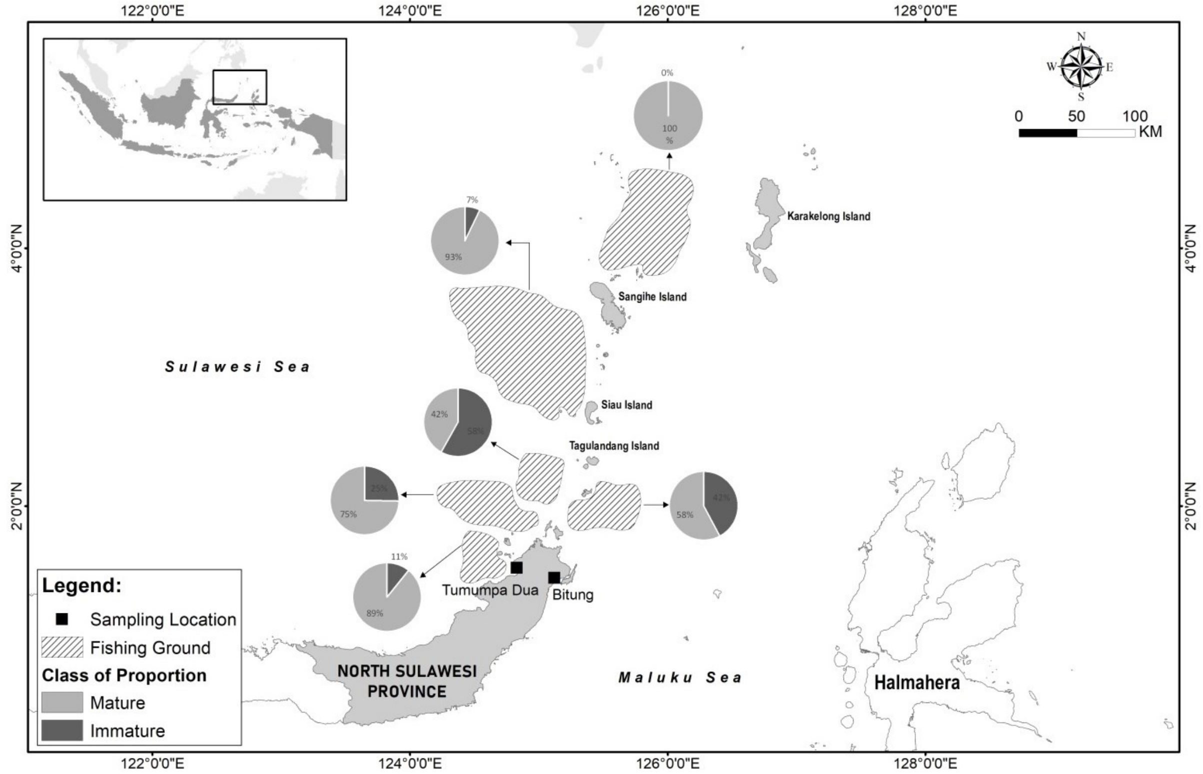

Figure 2-9. Potential spawning grounds of the mackerel scad (*Decapterus macarellus*) in the Sulawesi Sea as indicated by the proportion of mature individuals

2.4. Discussion

Reproductive biology studies of *Decapterus macarellus* have been carried out at many different sites in Indonesia (Appendix 2). However, we herewith present the first study on the reproductive periodicity and potential spawning areas of this species in the northern Sulawesi Sea. We also provide valuable information for the fisheries management of small pelagic fish in the region. Earlier studies have suggested that the unit stock of *D. macarellus* in the Sulawesi Sea is most likely different from other conspecific populations next to it. The population structure of *D. macarellus* in the Sulawesi Sea differed from conspecifics in Makassar Strait, Bone Bay, Tolo Bay, Flores Sea, Banda Sea, and Maluku Sea (Zamroni et al., 2014). This finding is supported by a most recent result from fish parasites of *D. macarellus,* which detected a different pattern of metazoan parasites on this fish in North Sulawesi and North Maluku (**Retnoningtyas et al., 2023b**). Consequently, the reproductive biology of *D. macarellus* in the Sulawesi Sea might also be distinct compared with conspecifics from other locations in Indonesia.

The length and weight of samples from North Sulawesi waters ranged between 13.4 – 38.2 cm and 2.26 – 555.65 g, respectively. The size ranges changed from month to month, and the larger size was found during the spawning months (January, March, May, and September), indicating a larger gonad weight and that the fish were in the mature stage. We found a similar size range *of D. macarellus* stocks in Ambon waters (Silooy et al., 2019). In addition, Silooy et al. (2019) also found a larger length range in January and September, which corresponds to our finding in North Sulawesi. The length at first maturity (Lm) of *D. macarellus* in the Sulawesi Sea was 22.59 and 21.62 cm for male and female individuals, respectively. The Lm found in the present study was lower than the conspecific 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 Achmad Zamroni, 2017). However, the Lm found in this study was comparable to the conspecifics in the central and southern parts of the Sulawesi Sea (Zamroni et al., 2019) and West Sulawesi (Nur et al., 2017). The Lm discrepancy can be a result of the influence of environmental and ecological factors, including the nutrient conditions, seawater temperature, irradiation, feeding habits and physiological conditions of fish, and 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 was a strategy of fish populations to cope with high fishing pressure (Restiangsih and Muchlis, 2019).

The energy allocation to somatic growth and reproduction in fish is affected mainly by temperature and food availability (Wootton, 1990). Temperature and food availability influence metabolism and surplus energy, affecting energy allocation to 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 could reduce energy investment in growth and reproduction indirectly if the fish are experiencing unfavorable temperature conditions (Jobling et al., 1993). In the present study, we found that the spawning of *D. macarellus* in the Sulawesi Sea occurs all year round, with the peak occurring in January, March, May, and September annually. The peak of the spawning season is different among conspecifics in different areas. For instance, the spawning peaks of *D. macarellus* 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 Achmad 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 of spawning discrepancy may be explained by the genetic diversity of the fish and the water temperature regimes and food availability (Yoneda and Wright, 2005). In higher latitudes, the spawning season occurs in shorter periods and mostly coincides with warmer sea temperatures (Sanchez-Cardenas and Arreguin-Sanchez, 2012), while in 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 little variability and the Ocean is warm and is quite similar among different areas within the country, food availability might have affected the peak of the spawning season.

We found that the sex ratio of the species was equal between male and female individuals throughout the one-year study. Similarly, the sex ratio of the conspecifics in the Ambon and Banda Sea was equal (Silooy et al., 2021; Zamroni and Suwarso, 2011). However, the male-biased sex ratio was observed for other conspecific species in other sites within Indonesia. For instance, the sex ratio (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) was 1.3:1, 1.96:1, 1.32:1, and 1.31:1, respectively. An equal sex ratio is needed to maintain the survival of a population (Gustomi et al., 2016; Nasution et al., 2010). Although the sex ratio is often treated as a more or less stable population indicator, recent theoretical evidence suggests that the sex ratio can fluctuate under many conditions (Pettersson et al., 2004). Variations in the sex ratio can be affected by several factors, including behavior patterns, mortality, and growth rates between male and female individuals, spawning behavior, sexual maturity, length distribution due to its depth ranges, and the length (or age) of the individuals (Effendie, 1997; Smith et al., 2018).

A very high percentage of mature individuals (97 - 100%) was observed in the northern and western sides of Sangihe and Siau Islands. In contrast, the distributions of high gonadosomatic index were observed around the North Sulawesi peninsula. Both enable the potential spawning grounds of *D. macarellus* in the North Sulawesi Sea to be clearly defined. It appears that *D. macarellus* has certain spawning grounds where spawning conditions throughout the year are optimal. Since *D. macarellus* is a planktivorous fish, plankton distribution around these areas might be higher than in other areas in 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 a month in October, which does not coincide with the peak spawning seasons of the fish in the present study (January, March, May, and September). On the other hand, Tumumpa Dua, which accommodates five river mouths passing through Manado City and directly facing Manado Bay, supports the possibly high nutrient input which boosts phytoplankton growth and fertility in this area and subsequently becomes a potential fishing ground for *D. macarellus*. Further research regarding the plankton distribution across the Sulawesi Sea is needed to confirm its correlation to the spawning grounds of *D. macarellus* since, potentially, spawning 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, none of the studies has reported the lunar spawning of *D. macarellus.* In the present study, we found that most matured *D. macarellus* in the Sulawesi Sea spawned during the first quarter of the moon phase. Studies on the lunar spawning cycle have been reported in reef fishes from the family of 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* start their reproductive activities several days before the full moon (Colin et al., 1987), while *Plectropomus leopardus* was observed before the new moon (Samoilys and Squire, 1994). For siganids, synchronous spawning was observed around the new moon for *Siganus spinus* (Park et al., 2006) and around the moon's first quarter for *S. guttatus* (Rahman et al., 2000). It has been suggested that the cues from the moon are associated with the synchrony of the adult reproductive rhythm (Colin et al., 1987) and may consequently increase its reproductive success (Ferreira, 1995). Periodicity in moon-related cues, such as moonlight intensity, time of moonrise, and solar cycle, have been hypothesized to be the cues for fish reproductive activities (Leatherland, 1993). For instance, moonlight intensity has been suggested as a cue for melatonin production in fish, triggering the lunar-synchronized spawning in 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 the fish reproductive activity. These factors might have indirectly affected the reproductive activities of *D. macarellus* in the present study, synchronizing the spawning around the moon's first quarter. However, the exact cues for the moon-related cycles, observed for the first time for *D. macarellus*, remain poorly understood and warrant further investigations.

Mackerel scad *D. macarellus* is a vital fisheries resource in Indonesia, especially in the eastern part of Indonesia, including Sulawesi. There is a significant demand for this species as food, which could lead to overfishing, yet the data on production and fishing efforts is still lacking. Without proper management measures, fishing may threaten the fish stock's sustainability. However, the all-year-round spawning and several spawning nuclei close to each other recorded from this present study make this fish stock less vulnerable to overfishing. In order to optimize sustainable use of resources, 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), in order to ensure that the fish has spawned at least once before being captured; **b.** restrict the critical spawning areas around the northern and western sides of Sangihe and Siau Islands as a pelagic marine protected area; **c.** introduction of regular temporary fishing closures. The closure periods can be either 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. Temporary fishing closure is known to impact the rebuilding stock population positively (Bartlett et al., 2009; Januchowski-Hartley et al., 2013).

2.5. Conclusion

The present study examined the reproductive biology of the mackerel scad, *Decapterus macarellus,* in the Sulawesi Sea, particularly investigating the species' reproductive periodicity and potential spawning area. We found that the species had an equal sex ratio between male and female individuals, with the length at first maturity (Lm) being 22.59 and 21.62 cm, respectively. Most importantly, we found that the species' spawning peak occurs in January, March, May, and September annually, during the first quarter of the moon phase. We also identified distinct spawning areas of the species off Tumumpa Dua and around the northern and western sides of the Sangihe and Siau Islands. This finding enables temporary and regional fishing closures by fisheries managers to develop appropriate fishing practices for this small pelagic fish species in the future.

Acknowledgments

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Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

3. Impact of fishing pressure on reproductive biology of mackerel scad, *Decapterus macarellus* (Cuvier, 1833) in Sulawesi Sea and Maluku Sea, Indonesia[2]

Abstract

The high fishing pressure may cause species evolutionary changes toward smaller maturation sizes. In this context, the fishing practices of mackerel scad, *Decapterus macarellus* (Cuvier, 1833), in tropical eastern Indonesia provide an excellent opportunity to examine this hypothesis. Two distinct fishing grounds, the Sulawesi Sea and Maluku Sea, were selected to explore this phenomenon. Samples of *D. macarellus* caught by purse seine fishers operating were sourced from the two fishing grounds. Analysing the total length and maturity stage of each *D. macarellus* specimen from the two stocks were made to estimate key parameters such as the length at first maturity (Lm) and total mortality (Z). The results revealed that total mortality, used as an indicator of fishing pressure, was higher in the Maluku Sea (5.3 year^{-1}) than in the Sulawesi Sea (3.7 year^{-1}) and other areas. Additionally, the Lm of *D. macarellus* in the Maluku Sea was remarkably lower (22.9 cm) than in the Sulawesi Sea (23.9 cm), which can be attributed to the higher fishing pressure. These findings support the fisheries-induced evolution hypothesis, particularly within Indonesian tropical fish stocks and their respective regions, adding new growing evidence that fishing pressure affects fish reproductive biology. The length at first maturity may serve as a valuable proxy for assessing the intensity of fishing pressure on fish stocks.

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[2] This article was published as: Retnoningtyas H, Agustina S, Dhani AK, Wiryawan B, Palm, HW, Natsir M, Hartati ID, Prasetia R, Yulianto I. (2023). Impact of fishing pressure on the reproductive biology of mackerel scad, Decapterus macarellus (Cuvier, 1833), in the Sulawesi Sea and Maluku Sea, Indonesia. Asian Fisheries Science 36: 164—170. https://doi.org/10.33997/j.afs.2023.36.3.005

3.1. Introduction

Fishing activities have been recognised to affect the species composition within marine ecosystems. The common practice in many fisheries is to target larger individuals. A healthy structure of fish stocks is often characterised by a high proportion of large, sexually mature fish. However, the selective removal of target species over time can lead to changes in the size structure of the population. Trends toward earlier maturation are frequently seen in fish stocks that are commercially exploited (Trippel, 1995), and evidence suggests that fishing pressure may have caused evolutionary changes, resulting in smaller maturation sizes (Heino et al., 2015).

Indonesia ranked second among the top seven fisheries capture producers globally, with China leading the list, followed by Peru, India, the Russian Federation, the United States of America, and Vietnam (FAO, 2022). In the context of the top ten national fish production commodities in 2021, scads (*Decapterus* Bleeker, 1851) were the second-highest recorded catch behind bullet tuna *Auxis rochei* Risso, 1810 (7.79 %) (MMAF, 2022b). This proportion highlights the significant role of small pelagic fish, including scads, in contributing to nationwide fish production, complementing the production of tuna (*Thunnus* South, 1845), skipjack (*Katsuwonus pelamis* Linnaeus, 1758), and tuna-like species, such as *Scomberomorus* Lacepède, 1801. Among the seven identified *Decapterus* species recorded from the landing records in Indonesia (Atmaja and Sadhotomo, 2005; Kimura et al., 2013; Zamroni, 2012), *Decapterus macarellus* Cuvier, 1833 stands out as the main species caught in the Sulawesi Sea, contributing 58 % to the total production of small pelagic groups in the respective area (MMAF, 2015). Mitochondrial markers have revealed distinct stock units between the Sulawesi Sea and Maluku Sea (Zamroni et al., 2014), later confirmed by a parasite investigation (**Retnoningtyas et al., 2023b**).

The use of length at first maturity (Lm), in addition to the mean length in the catch (Lc), may serve as a proxy for assessing the intensity of fishing pressure on a stock (Lappalainen et al., 2016; Ramírez-Amaro et al., 2020; Yanti et al., 2020). This study aims to demonstrate how fishing pressure affects the length at first maturity of mackerel scad *D. macarellus* in tropical eastern Indonesia. To achieve this, comparative analyses were made for the maturity lengths of *D. macarellus* and the corresponding fishing pressures between the distinct fishing areas in the Sulawesi and Maluku Seas.

3.2. Materials and Methods

Study sites and sample collection

Decapterus macarellus were collected from landing sites in North Sulawesi, Indonesia, from September 2019 to March 2022. Samples representing the Maluku Sea were collected from two landing sites in Sulawesi, namely Kema Tiga and Tumumpa Dua, after confirming the fishing ground through consultations with local fishers (Figure *3-1*). A total of 22,497 and 10,493 individuals were measured at the landing sites where the fish were caught from the Sulawesi Sea and the Maluku Sea, respectively. The total length of each individual was measured to the nearest millimetre. For gonad measurement, a macroscopic examination was performed following the dissection of 483 individuals from the Sulawesi Sea (52 % female, 48 % male) and 211 individuals from the Maluku Sea (44 % female, 55 % male, 1 % unidentified) all collected during July - August 2020. The shape and the colour of the testis and ovaries were used to assign gonad maturity levels (i.e., mature and immature) following the method outlined by West (1990).

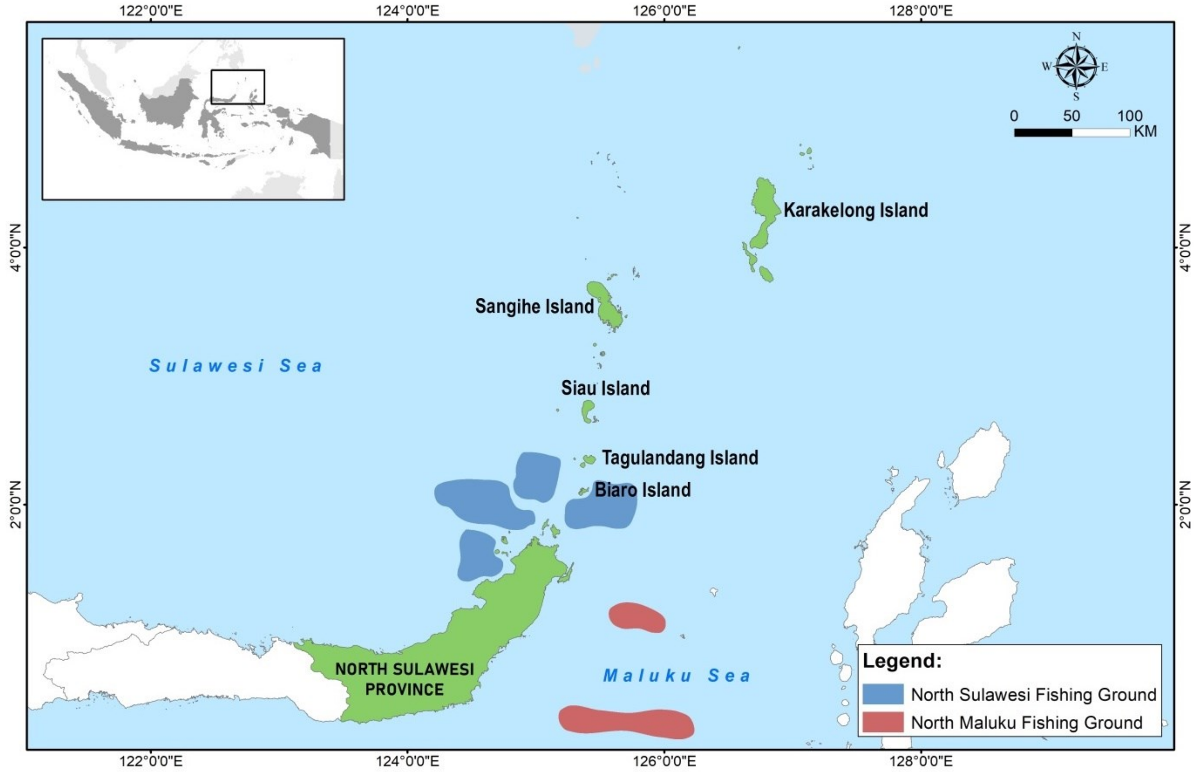


Figure 3-1. Fishing grounds in the Sulawesi Sea (blue polygon) and in the Maluku Sea (red polygon). All fish samples were collected from landing sites in North Sulawesi Province (green polygon)

Data analysis

Total length and maturity stages were used as key parameters to estimate length at first maturity (L_m) and length at first capture (L_c) of *D. macarellus*. The determination of the length at first maturity (L_m) of of each unit stock (Sulawesi Sea and Maluku Sea) was analysed following the methodology by Tokai and Mitsuhashi (1998). This involved maximising the likelihood of binomial distribution in the logistic curve, using a process facilitated through the "SOLVER" tool in Excel.

The life-history parameters essential for calculating the total mortality of *D. macarellus* in each unit stock encompassed asymptotic length (L_∞), growth coefficient (K), and natural mortality (M). The growth coefficient (K) and asymptotic length (L_∞) were estimated according to the von Bertalanffy growth model (Sparre and Venema, 1998). The parameter t_0 was computed using the equation formulated by Pauly (1979). For natural mortality, a combination of various sources was employed. Specifically, the length equation was from Pauly (1980), the joint equation from Hoenig (1983), the t_{max} equation from Then et al. (2015) , and the growth equation from Then et al. (2015) (Table *3-1*).

Table 3-1. Life history parameters of *Decapterus macarellus* in the Sulawesi Sea and Maluku Sea

Parameter	**Label**	**Unit**	**Value**	
			Sulawesi	**Maluku**
Asymptotic length	$L\infty$	cm	38.80	37.53
Growth coefficient	K	$year^{-1}$	0.87	0.86
Theoretical age at length = 0	t_0	year	-0.17	-0.18
Natural mortality	M	$year^{-1}$	1.11	1.11

Total mortality was calculated using length-converted linearised catch curves following Pauly (1984). Length at first capture was also estimated from a detailed analysis of the ascending part of this curve, which expressed the length at which fish have a 50 % probability of getting caught. Life-history parameters, total mortality, and length at first capture were estimated using the "TropFishR" package in RStudio (Mildenberger et al., 2017; Taylor and Mildenberger, 2017). All statistical analyses were performed in RStudio (R Core Team, 2022).

3.3. Results

The total lengths of the *D. macarellus* in the Sulawesi Sea ranged from 7.7 to 38.3 cm, while in the Maluku Sea ranged from 8.1 to 38.3 cm (Figure *3-2*). The length at first maturity (Lm) of this species was higher in the Sulawesi Sea (23.9 cm) than in the Maluku Sea (22.9 cm) (Figure *3-3*), while the length at first capture (L_c) was higher in the Maluku Sea (21.6 cm) than in the Sulawesi Sea (19.6 cm). Total mortality (Z) of the *D. macarellus*, as a proxy for fishing pressure, was lower in the Sulawesi Sea (3.7 year^{-1}) than in the Maluku Sea (5.3 year^{-1}) (Figure *3-4*).

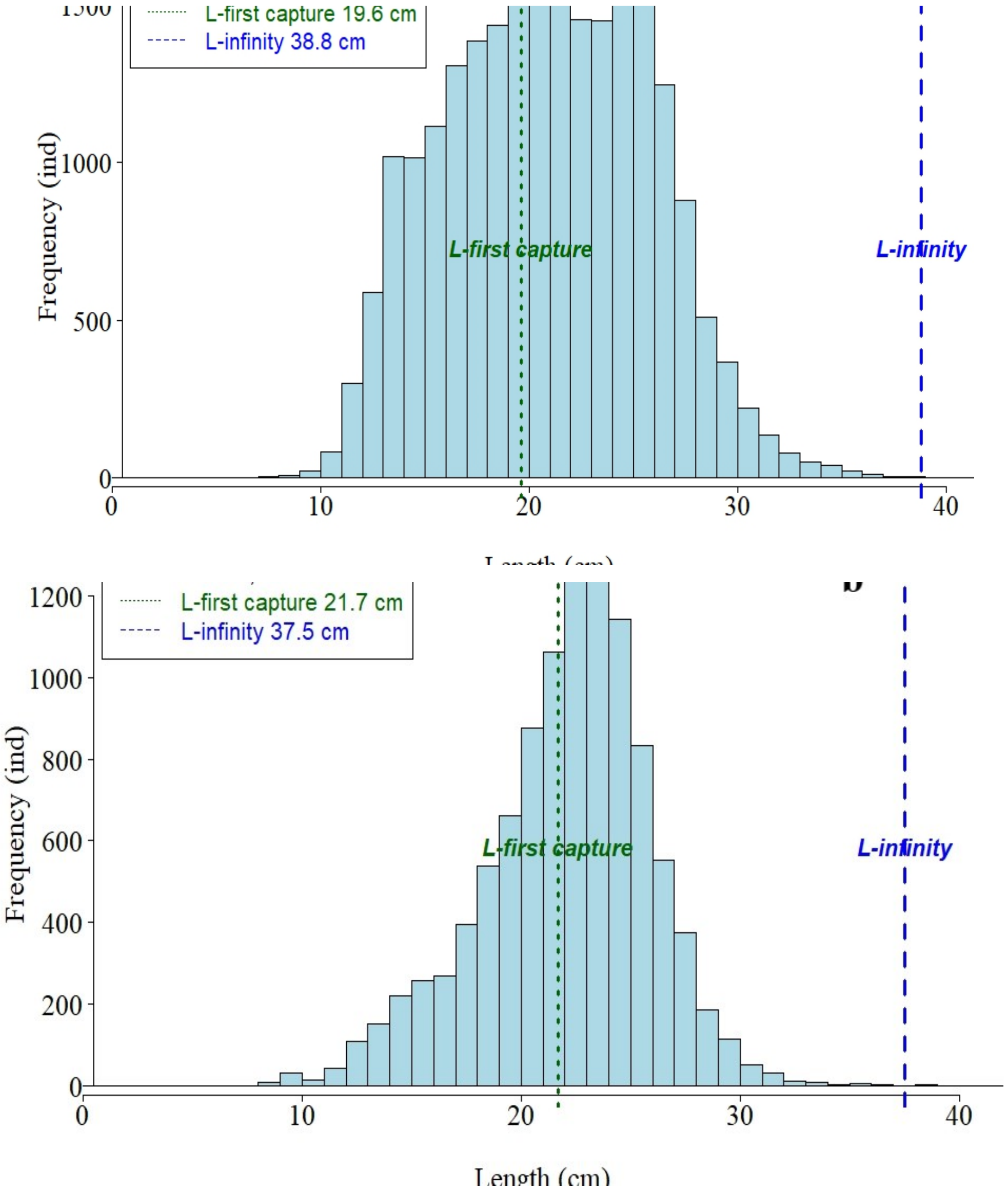


Figure 3-2. Length frequency distribution of *Decapterus macarellus* sampled from (a) Sulawesi Sea and (b) Maluku Sea from September 2019 to March 2022

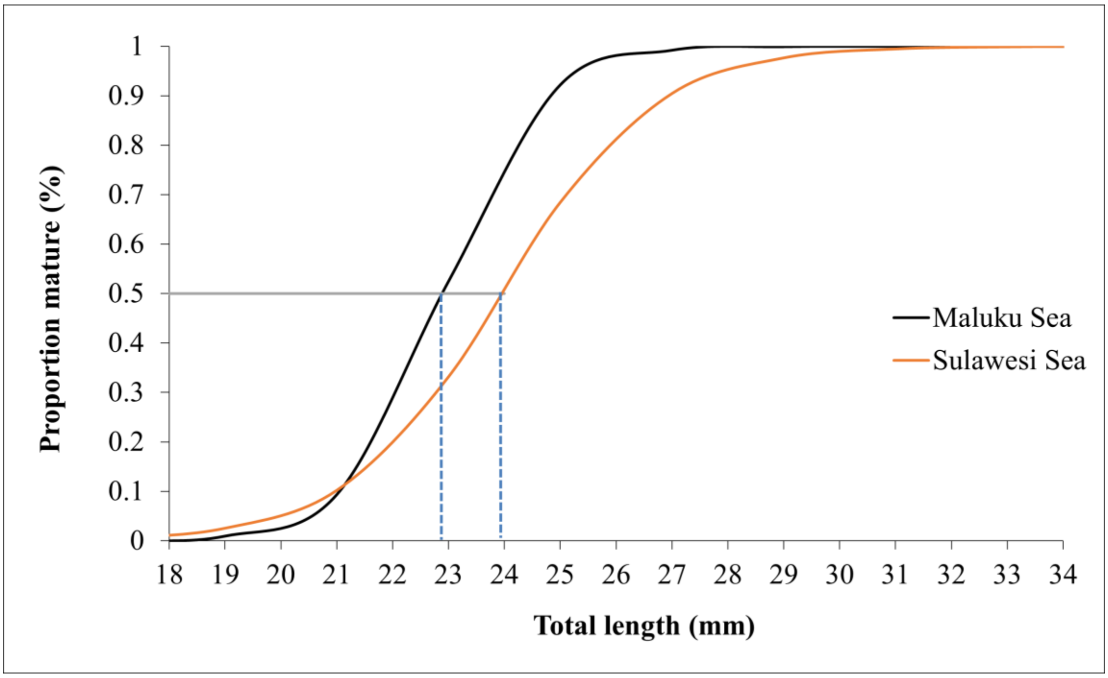
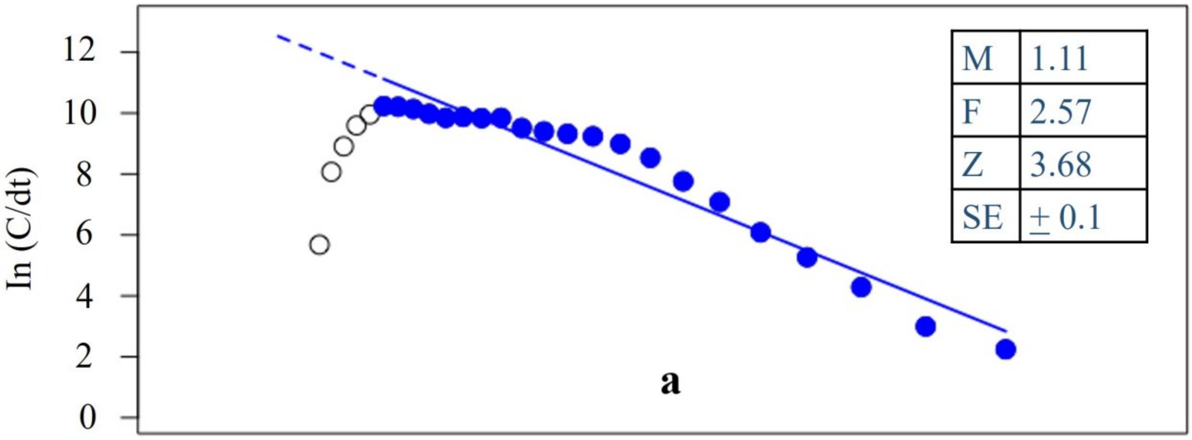


Figure 3-3. Length at first maturity model of the mackerel scad *Decapterus macarellus* in the Maluku Sea (black line) and the Sulawesi Sea (red line) generated by the length-converted linearized catch curves. The curves show that *D. macarellus* in the Maluku Sea matured at a smaller size compared to those in the Sulawesi Sea



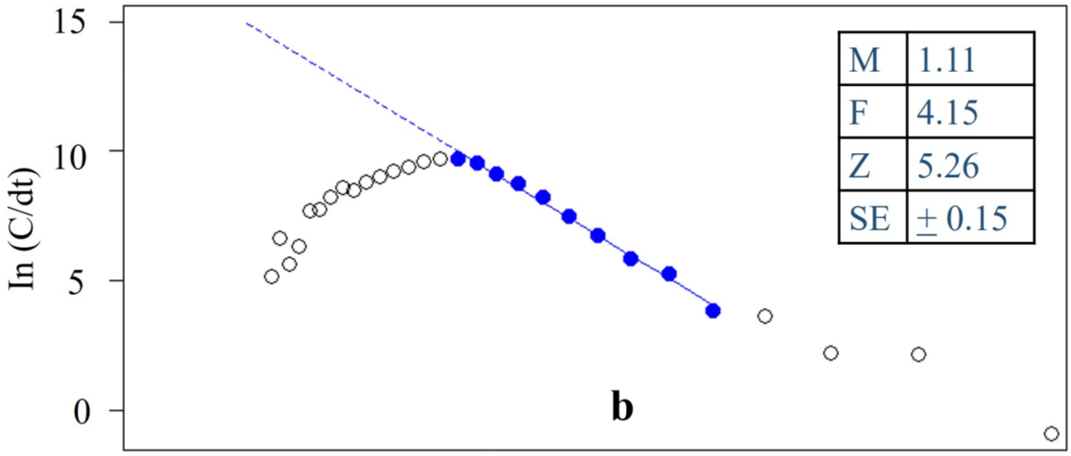


Figure 3-4. Length-converted linearised catch curve was applied to estimate the total mortality (Z) of *Decapterus macarellus* in the (a) Sulawesi Sea and (b) Maluku Sea

Fishing fleets targeting small pelagic fish in the Sulawesi and Maluku Seas were dominated by mini purse seines with one-inch (2.54 cm) mesh size. Following Indonesia's national regulation, the size of fishing vessels is categorised into three groups according to their capacity in gross tonnage (GT), i.e., large (>30 GT), medium (10–30 GT), and small (<10 GT). In both the Sulawesi and Maluku Seas, medium-size vessels were dominant, i.e., 48 % and 62 %, respectively. However, of all vessels operating in the Sulawesi Sea, a significant part of large-sized and medium-sized vessels, i.e., 88 % and 56 %, respectively, also operated in the Maluku Sea, contributing to higher fishing pressure in the respective waters.

3.4. Discussion

Total mortality can be used as a proxy of fishing pressure (Piet et al., 2007; Froese et al., 2015), and, therefore, prompting an investigation of whether fishing pressure varies between the Sulawesi Sea and the Maluku Sea for the target species, *Decapterus macarellus.* Total mortality of *D. macarellus* in the Sulawesi Sea (3.7 year^{-1}) was comparable to those already recorded from other sites in Prigi, Indian Ocean (3.0 year^{-1}; Bintoro et al., 2020), Cabo Verde, the coast of Africa (3.23 year^{-1}; Vieira, 2019), and even within the Sulawesi Sea (2.34 year^{-1}; Zamroni et al., 2019). In contrast, the total mortality of *D. macarellus* in the Maluku Sea was relatively higher than in other locations. This suggests that the fishing pressure of *D. macarellus* in the Maluku Sea was relatively higher than in the Sulawesi Sea and other regions.

Fishing shifts the life history traits of some fish species are well documented (Jennings et al., 1998; Law, 2000). The shift has been for the first time demonstrated for North Sea plaice, *Pleuronectes platessa* Linnaeus, 1758 (Rijnsdorp, 1993) and Atlantic cods, *Gadus morrhua* Linnaeus, 1758 (Hutchings and Myers, 1995), but most recently also for pikeperch, *Sander lucioperca* (Lappalainen et al., 2016) and chondrichthyans (Ramírez-Amaro et al., 2020). The present study demonstrates for the first time such a shift for *D. macarellus* in tropical Indonesia, where the size at maturity in the Maluku Sea was smaller than in the Sulawesi Sea and other areas. This result is most likely caused by differences in fishing pressure on the two examined fish stocks. Consequently, high fishing pressure in a specific region is presumed to have a distinct effect on the local populations of *D. macarellus*. High fishing efforts might induce a lower proportion of mature individuals (spawners) in the Maluku Sea, prompting them to mature at smaller sizes and younger ages as part of fish adaptation (Enberg et al., 2010; Neuheimer and Taggart, 2010).

Fishing pressure and life history traits can contribute to early maturation. Fishing pressure that happened for a long time may alter life history parameters, but the historical data on fishing pressure in the Sulawesi and Maluku Seas are unfortunately unavailable. The stock of *D. macarellus* from the Sulawesi Sea and Maluku Sea is known to be distinct from each other, as confirmed by genetics (Zamroni et al., 2014) and a parasite study (**Retnoningtyas et al., 2023b**). Genetic differences caused or enhanced by exploitation pressure may indicate different lengths and reproductive parameters (De Croos and Pálsson, 2012). In the present study, the life history parameters between Sulawesi Sea and Maluku Sea stocks were similar. Direct environmental variations may also affect maturation probability (Barot et al., 2005).

According to Pauly (2021), a lower relative oxygen supply induces sexual maturation, as the distribution and concentration of dissolved oxygen have a more significant influence on the development of the life of most fish and aquatic invertebrates than food availability (Kramer, 1987). This theory, known as the Gill Oxygen Limitation Theory (GOLT), predicts that maturation and reproduction are induced when a fish reaches a critical ratio of oxygen supply-demand related to the scaling of gill surface area (Chen et al., 2021). As a case study by Amarasinghe and Pauly (2021) showed how stressful environmental conditions prompted the early spawning of tilapia, reducing their growth and the size at which maturity commences.

According to the theory of fisheries-induced evolution, fishing serves as an artificial selection process that can affect the change of life history traits, where the most prominent impact of fishing is on the fish's reproductive biology, such as earlier maturation (Enberg et al., 2010; 2012). This research is the first evidence of fisheries-induced evolution detected for small pelagic fish in tropical Indonesia, particularly on how fishing influences the fish reproductive biology of an essential Indonesian fisheries resource. Fisheries-induced evolution remains underexplored in Indonesia since many species are currently facing overfishing and fully exploited conditions (MMAF, 2022a). Such conditions can shift fish biology and ecology, including habitat choice, diet choice, social behaviour, maintenance, immune defence, neural development and cognition, morphology, migration, energy storage, somatic growth, reproduction, and phenology (Neuheimer and Taggart, 2010). It is suggested that size and age at first maturity must be monitored regularly since these parameters are essential for the stock assessment. Precise calculations are crucial, as an incorrect conclusion on the length at first maturity can lead to an incorrect assessment of the fish stock condition (e.g., spawning potential ratio). The risk of overexploitation is one of the most immediate effects of inaccurate assessments. Suppose stocks are erroneously believed to be healthier than reality, this could lead to higher quotas and excessive fishing, thereby depleting the stock beyond its recovery capacity.

Moreover, the different lengths at first maturity caused by different fishing pressures in the Sulawesi Sea and Maluku Sea implies that a precautionary approach should be strongly encouraged in formulating the harvest strategy for *D. macarellus*. Under the current management framework, the fisheries management area (FMA) 716 covers the Sulawesi Sea and some parts of the Maluku Sea. Bitung Fishing Port, located in North Sulawesi, is a landing site not only for fish caught in the Sulawesi Sea but also from the Maluku Sea. Consequently, separate management measures are necessary given the differentiated stock unit of *D. macarellus* between the Sulawesi Sea and Maluku Sea.

This study aimed to highlight the current fishing conditions and the mackerel scads' maturity sizes in two different yet adjacent fishing grounds, i.e., the Sulawesi Sea and the Maluku Sea, which appeared to be different. More studies are needed to investigate whether the early maturation is caused by long-term fishing pressure, different life history parameters due to distinct stock units, or environmental factors such as oxygen limitation. Such studies will contribute to the knowledge of the fisheries-induced evolution processes in Indonesia's fishery resources and provide valuable insights for more effective and sustainable fisheries management practices.

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Declaration of competing interest

The authors declare no conflict of interest.

Institutional Review Board Statement: Not applicable. No live animals were involved in this study.

4. Stock discrimination of mackerel scad *Decapterus macarellus* (Cuvier, 1833) in the eastern Indonesia based on metazoan fish parasite composition[3]

Abstract

Mackerel scad *Decapterus macarellus* (Cuvier, 1833), a small pelagic species, is the major catch, particularly in the eastern Indonesia. Despite a high catch volume, its utilization status is relatively unknown since stock assessment is mostly conducted for the entire small pelagic group without separating the species. Studies on population biology and stock distribution of mackerel scad in Indonesia so far involved catch-based production models, growth parameter analyses, otoliths, and fish genetics. We herewith discriminate eastern Indonesian fish stocks of *D. macarellus* by comparing the respective metazoan parasite community. We collected 105 specimens of mackerel scad from three closely connected fishing grounds representing two Indonesian fisheries management areas. Recorded metazoan parasites belonged to the Monogenea (4 species), Digenea (8 species), Acanthocephala (1 species), and Crustacea (2 species), with the two Monogenea *Allopseudodiclidophora opelu* (Yamaguti, 1965) and *Pseudodiclidophora decapteri* (Yamaguti, 1965) being the most prevalent. A multidimensional scaling analysis revealed the clustering pattern of the hosts based on the parasites, identifying two major fish stocks, the North Sulawesi group and the North Maluku group. The strength and weaknesses of the so far applied stock assessment methodologies for this small pelagic fish in Indonesia are discussed.

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[3] This article has been published as Retnoningtyas H, Yulianto I, Wiryawan B, Kleinertz S, Palm HW. (2023). Stock discrimination of mackerel scad Decapterus macarellus (Cuvier, 1833) in eastern Indonesia based on the metazoan fish parasite composition. Regional Studies in Marine Science 61 (2023) 102840. https://doi.org/10.1016/j.rsma.2023.102840

4.1. Introduction

Understanding the dynamics of exploited fish populations begins with an identification of their biological identity, preferably through a comprehensive stock assessment. Although being a confusing subject in fisheries science, stock identification is one of the most basic prerequisites for fisheries managers and decision-makers in formulating fisheries management plans (Cadrin et al., 2014). Determination of fish stock structure is challenging since the distribution of fish might fluctuate at different space and time (Izzo et al., 2017), thus their variability and instability is high (Freon et al., 2005). In terms of management purposes, stocks are treated as individual units where each stock can be exploited independently, and catches can be attributed to the stock of origin (Cadrin et al., 2014).

Indonesia, the largest capture fisheries producer behind China (FAO, 2022), is developing management plans for certain priority groups of fish, including small pelagic species. The potential of this species group is up to 800.000 tons and the exploitation rate varied from moderate to over-exploited in different fishing management areas (FMAs) across Indonesia (MMAF, 2022a). In 2020, four small pelagic species groups contributed to the top ten of total fish production nationally, namely scads (8.95%), mackerels (5.59%), sardines (3.73%), and anchovy (3.60%), with scads being the second-highest of all recorded catch after bullet tuna (MMAF, 2022b). At the global scale, scads (*Decapterus* spp.) made up to 1.265 Mio. tons or 2% of the total marine capture production in 2020 (FAO, 2022). Seven species of these widely distributed migratory fish have been recorded from major fishing sites in Indonesia and are generally available throughout the year, namely *Decapterus macarellus* (mackerel scad), *D. kurroides* Bleeker, 1855 (redtail scad), *D. macrosoma* Bleeker, 1851 (shortfin scad), *D. russelli* Rüppel, 1830 (Indian scad), *D. tabl* Berry, 1968 (roughear scad), *D. akaadsi* Abe, 1958 (red scad), and *D. smithvanizi* Kimura, Katahira and Kuriiwa, 2013 (slender red scad) (Atmaja and Sadhotomo, 2005; Kimura et al., 2013). *Decapterus macarellus* is the main species of scads caught in the fisheries management area (FMA) 716, which covers the Sulawesi Sea and the northern coast of Halmahera Island, contributing 18% to the total fish production in the respective area (MMAF, 2015). Despite its wide distribution across the Indonesian archipelago, movement patterns and stock structures of mackerel scads are still poorly understood.

A wide variety of approaches for stock identification have been explored, i.e., life-history traits, morphology-morphometry, genetics, artificial tags, and environmental signals, such as otolith-microchemistry, fatty acids, and parasites (Cadrin et al., 2014). The use of parasites as tags for stock identification has been recognized as having certain advantages (MacKenzie and Abaunza, 2014). They are more appropriate for studies of species that are unlikely to survive capture, handling, and tagging, and reduce the sampling costs (MacKenzie, 2002). Studies of parasites as stock markers have been undertaken for fish inhabiting various types of environments, such as estuarine (Moore et al., 2012), coastal and nearshore (Latama, 2006), deep-sea (Marcogliese et al., 2003; Santos et al., 2009), and oceanic waters which involved pelagic, wide-ranging fish species (Zischke et al., 2013; Moore et al., 2019). The main idea behind using parasites as tags in fish population studies is that fish can only become infected with a parasite if they live in the parasite's endemic area (MacKenzie and Abaunza, 2014). Parasites with short residence times provide information on recent location history and those with extended residence durations on long-term location history (Lester and MacKenzie, 2009; Lester and Moore, 2015).

Biological aspects, population dynamics, and exploitation levels of mackerel scads in Indonesia have been studied through approaches such as the catch-based production model (Sadhotomo and Atmaja, 2012; Triharyuni et al., 2014) and length-based life history parameters (Desmawanti et al., 2013; Zamroni et al., 2019; Bintoro et al., 2020). Despite its importance as a pre-requisite for stock assessment, studies on stock identification, however, are rarely undertaken. To date, methods such as general morphometry (Ardi, 2018) and otolith measurements (Manginsela et al., 2020) have been applied for mackerel scad, in addition to genetic approaches (Zamroni, 2012; Suwarso and Zamroni, 2013, 2014; Zamroni et al., 2014). Multidisciplinary is considered the most efficient where different techniques can be compared and used to complement one another (Abaunza et al., 2008). This study investigates possible mackerel scad stock discrimination between two adjacent fisheries management areas, namely FMA 716 (North Sulawesi Province) and FMA 715 (North Maluku Province), based on the metazoan fish parasite community. The strength and weaknesses of the so far applied methods for *D. macarellus* stock identification are discussed.

4.2. Materials and Methods

4.2.1. Study area, fish sample collection, and parasites isolation

Samples were collected from three fishing grounds, namely, (1) Siak Tagulandang Biaro (abbr. Sitaro) and (2) Sangihe in the North Sulawesi Province, and (3) West Halmahera in the North Maluku Province (Fig. 4.1). A total of 105 specimens of *D. macarellus* were collected, 35 from Sitaro (17 February 2020), 35 from Sangihe Islands (15 April 2020), and 35 from West Halmahera (06 May 2020). After verification from the fishermen that the fish were caught in the respective areas, each fish was separately wrapped inside a plastic bag and stored in the freezer (-20°C) until dissection. In the laboratory, total length and total weight were measured for each fish. The occurrence of metazoan ectoparasites was scanned from the eyes, nasal and buccal cavities, fins, opercula, and gills. Gills were excised and placed in a Petri dish filled with saline solution (NaCl 0.9%). To collect metazoan endoparasites, the body cavity was opened from anterior to posterior and internal organs were removed and separately placed in Petri dishes filled with saline solution. The gut wash technique was applied following Cribb and Bray (2010) to examine parasites inhabiting the gastrointestinal tract. Examination for ecto- and endoparasites was carried out under a dissecting stereo microscope Olympus SZ61 and the parasites were collected and fixed in 4% formaldehyde (for Monogenea and crustacean Isopoda) or 70% ethanol (for Digenea, Acanthocephala, and crustacean Copepoda).

4.2.2. Parasite examination

Following the isolation, parasite specimens, particularly Monogenea and several specimens of Digenea, were stained using Mayer-Schuberg's acetic-carmine technique and mounted in Canada balsam (Palm, 2004). Acanthocephala and crustacean Copepoda were not stained and directly mounted in glycerin, while crustacean Isopoda, due to its size, was neither stained nor mounted on the microscope slide. Identification of parasite taxa was made according to morphological characteristics to the nearest taxonomic level based on original literature and identification keys, e.g., Yamaguti (1965) for Monogenea; Gibson et al. (2002), Parukhin (1966) and Yamaguti (1970) for Digenea; Martin (2013) and Martin et al. (2015) for Crustacean Isopoda; Cressey and Cressey (1980) for Crustacean Copepoda, and Golvan (1969) and Amin et al. (2011) for Acanthocephala. In addition to the original descriptions, we also cross-checked our findings with the annotated checklist of Indonesian marine fish parasites by Theisen (2019) to compare parasite species that have been recorded previously from this host. Measurements and photographs were taken by Olympus BX53 upright microscope with DIC connected to an Olympus DP74 camera.

4.2.3. Parasitological data and statistical analyses

Calculation of parasitological parameters followed Bush et al. (1997), including prevalence, mean intensity, and mean abundance. Environmental data obtained from random sampling, including the number of parasites in fish hosts, are known to be non-normally distributed; however, the normality was tested based on Shapiro and Wilk (1965). Kruskal-Wallis H test was employed to identify whether or not the parasite distribution was significantly different between sites (results expressed in H and p), and the Mann-Whitney Wilcoxon test was undertaken to compare the mean intensity and mean abundance (values expressed in W and p) between species which show a significant difference in their distribution. Since prevalence is a function of proportion (Bush et al., 1997), the difference between sites was tested by Two-Proportion Z-Test (values expressed in z and p). Kruskal-Wallis H Test and Mann-Whitney U Test were conducted in RStudio (R Core Team, 2022), while Two-Proportion Z-Test was calculated manually.

To investigate patterns of host distribution based on the composition of the parasite communities, analyses using multidimensional scaling (MDS) were conducted based on Bray-Curtis dissimilarities. MDS seeks to interpret the entries in the resemblance matrix as actual distances so that samples with distance/dissimilarity are placed at a distance in the ordination plot (Clarke and Gorley, 2015). Goodness-of-fit of the statistic in MDS is shown by the stress value (between 0 to 1), where a value near 0 indicates a better fit. In addition to the MDS plot, cluster analysis was used to show the hierarchical relationship between samples and locations, as well as similarity percentage (SIMPER) to identify the contribution of taxa to the observed value of the Bray-Curtis dissimilarity. Analyses of the MDS plot, cluster diagram, and SIMPER were undertaken using PRIMER Version 7.0.

4.3. Results

4.3.1. Biometric data of hosts

Fish samples from all locations were collected during the transition period between rainy to dry seasons (mid-February to early May 2020). Host samples from Sitaro consisted of 34% female, 60% male, and 6% unidentifiable specimens. Fish from Sangihe consisted of 60% female, 3% male, and the rest (37%) were juveniles. Fish samples from West Halmahera were mostly juveniles (83%). Total length and weight of the fish collected from all locations were significantly different ($H(6) = 68.91$, $p = 1.086\text{e-}15$), $H(6) = 71.51$, $p = 2.964\text{e-}16$, respectively). The mean total length and weight of fish from West Halmahera were smaller compared to samples from Sitaro and Sangihe (Table 1).

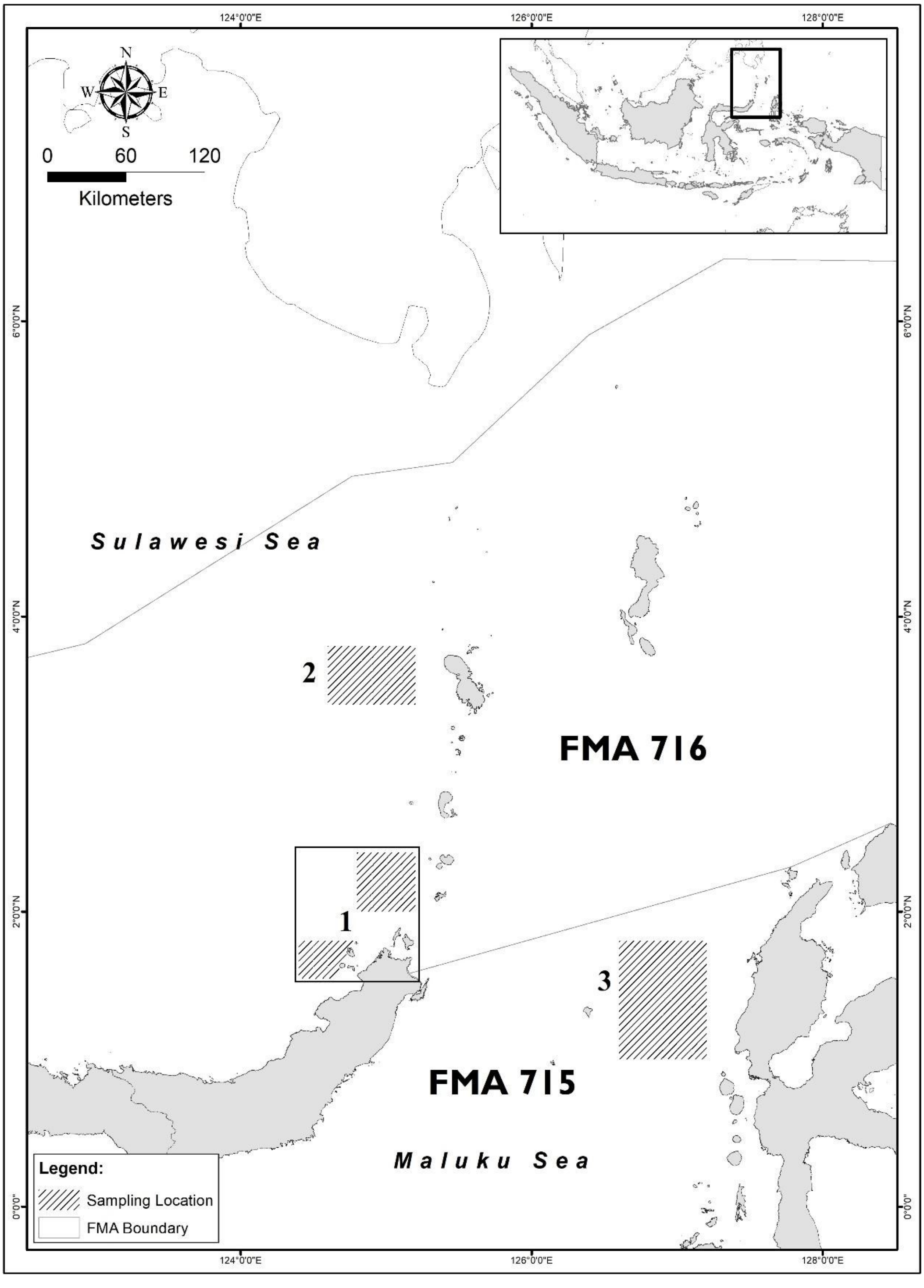


Figure 4-1. Fishing grounds where the fish were collected (shaded areas) with numbers showing the localities. Two sites, Sitaro (1) and Sangihe (2) are part of FMA 716 (North Sulawesi Province) while (3) West Halmahera is part of FMA 715 (North Maluku Province)

Table 4-1. Individuals (n = 35 for each species) collected from three localities presented with mean length, mean weight, and respective standard deviation, as well as sex (F: female; I: indeterminate; M: male). Ranges of total length and total weight are given in brackets

Fishing ground	Sex			Total Length (cm)	Total Weight (g)
	F	I	M		
Sitaro	12	2	21	25.82±0.82 (24.6-27.7)	176.11±17.96 (148.9-218.7)
Sangihe	21	13	1	25.05±0.68 (23.5-26.5)	151.23±13.67 (118.8-181.9)
West Halmahera	3	29	3	19.95±2.72 (16.4-26.1)	84.86±39.66 (43.5-188.5)

4.3.2. Parasite identification

A total of 15 parasite taxa were detected from *D. macarellus* from all locations, consisting of four Monogenea [*Allopseudodiclidophora opelu* (Yamaguti, 1965), *Pseudodiclidophora decapteri* (Yamaguti, 1965), *Pseudaxine* cf. *trachuri* (Yamaguti, 1968), and Polyopisthocotylea indet.], eight Digenea [*Ectenurus selari* (Parukhin, 1966), *Neonotoporus trachuri* (Yamaguti, 1938), *Pseudopecoeloides opelu* (Yamaguti, 1970), Tergestiinae indet., Didymozoidae indet., and three unidentifiable taxa], one Acanthocephala (*Rhadinorhynchus* sp.), and two Crustacea [*Ceratothoa carinata* (Bianconi, 1869) and *Caligus* sp.].

4.3.3. Taxonomic remarks

Ectoparasitic Monogenea *Allopseudodiclidophora opelu* and *Pseudodiclidophora decapteri* (Pseudodiclidophoridae) are commonly known from *Decapterus*. Yamaguti (1965) described both species from *D. pinnulatus* (orig. name for *D. macarellus*) caught off the Hawaiian coast (Palm and Bray, 2014). Both taxa can be recognized based on the symmetrical opisthohaptor and the presence of an anchor-bearing caudal appendage in *A. opelu*, while *P. decapteri* has an asymmetrical opisthohaptor with no anchor-bearing caudal appendage. The length of adult *A. opelu* ranged between 3.1 to 3.4 mm, while juveniles ranged between 0.6 to 0.9 mm. The length of *P. decapteri* ranged between 1.2 to 2.4 mm. Most key characteristics were within the range of *P. decapteri* by Yamaguti (1965), such as the lanceolate body (2.97 mm long, 0.9 mm wide), the haptoral appendage slightly tapering towards its truncate end, the unilateral and hatched-shaped opisthohaptor (1.01 mm), and 32 clamps (46-52µ wide) with flattened, paired, accessory pieces.

Digenea was the most diverse taxon found with five identifiable taxa. *Ectenurus selari* is small (1.9—2.6 mm), having a retractable ecsoma, a subterminal oral sucker, and a well-developed abdominal sucker as wide as the body width (Fig. 4.2A). Compared to other members of *Neonotoporus*, the specimen found in *D. macarellus* from eastern Indonesia has the closest characteristics to *N. opelu* (Yamaguti, 1970) in terms of body length and the ovary shape (sub-globular), while this specimen has a very round ovary. Considering the testes' shape (oval/non-lobed) and its position within the body, which was less posterior compared to *N. opelu*, the authors were confident to identify this specimen as *N. trachuri* (Yamaguti, 1938) (Figure 4.2B). *Pseudopecoeloides opelu* (Fig. 4.2C) was found in Sitaro and West Halmahera with a slender subcylindrical body (3.9 mm), terminal oral sucker (0.15 x 0.18 mm) with subterminal aperture, acetabulum or ventral sucker pedunculate, elliptical testes and in tandem position (anterior testes at the junction of middle, posterior testes at a third of body), and numerous eggs (Yamaguti, 1970). Tergestiinae indet. (Fig. 4.2D) was recognized by the presence of six muscular flanges (collarettes) on each lateral surface at about the level of the pharynx. Body elongated (3.3 mm), cylindrical, with a terminal oral sucker. The intestinal bifurcation was unclear, preventing further identification. Larval Didymozoidae indet. (Fig. 4.2E) were transparent and had an elongated body (3.6—4.5 mm) that narrows anterior. Oral sucker and ventral sucker were found at the anterior part.

Two Crustacea were identified as *Cerathotoa carinata* (Isopoda) and *Caligus* sp. (Copepoda). *Cerathotoa carinata* (length 1.3-2.4 cm) was characterized by the triangular head or cephalon being concaved on the anterolateral margin, and an antennule length subequal to the antenna. *Caligus* sp. was characterized by the caligoid shape of the body and clear distinction of body parts.

Seventeen acanthocephalan specimens were found and all belonged to the genus *Rhadinorhynchus* with the following characteristics: relatively long trunk (6.06—15.45 mm), slender and elongated proboscis (0.64—2.08 mm), and few spines found mostly on the anterior part of the trunk. The specimens had 14 to 16 longitudinal rows of hooks and 38 hooks per row. The closest resemblances to this species are *R. lintoni* Cable & Linderoth, 1963 (14—16 rows of 28—32 hooks each) and *R. katsuwonis* Harada, 1928 (18—22 rows of 28—40 hooks each).

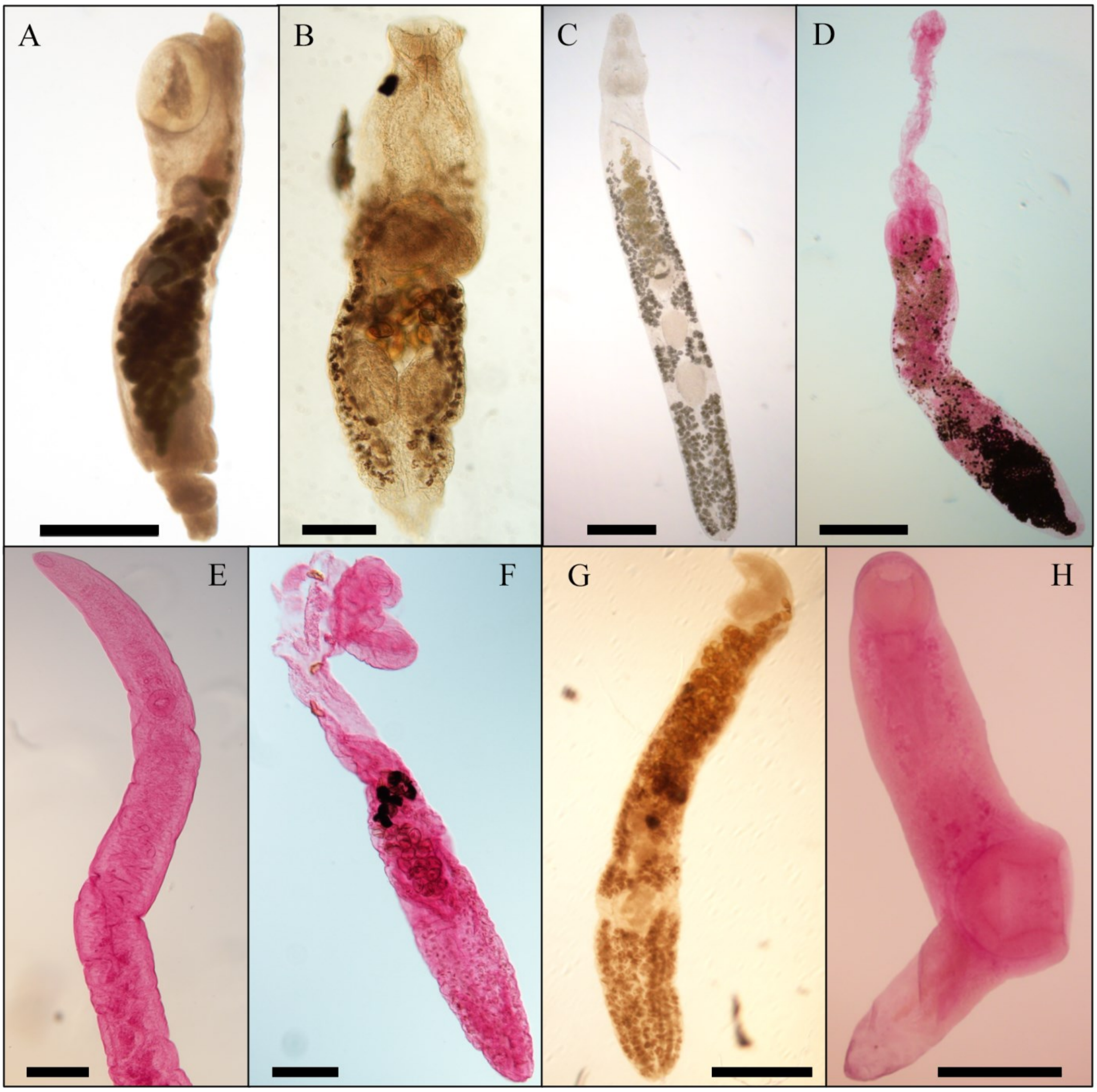


Figure 4-2. Microscope images of eight Digenea taxa found in *Decapterus macarellus* from eastern Indonesia. Five taxa were identifiable to at least family level (**A**: *Ectenurus selari*; scale bar 500 nm, **B**: *Neonotoporus trachuri*; scale bar 500 nm, **C**: *Pseudopecoeloides opelu*; scale bar 500 nm, **D:** Tergestiinae indet.; scale bar 100 nm, **E**: Didymozoidae indet. larva; scale bar 200 nm), and three unidentifiable taxa (**F**: Digenea indet. 1; scale bar 200 nm, **G**: Digenea indet. 2; scale bar 500 nm, **H**: Digenea indet. 3; scale bar 500 nm)

4.3.4. Prevalence, mean intensity, and frequency distribution between sites

Two species of Monogenea (*A. opelu* and *P. decapteri*) were mostly collected from the gill filaments of the hosts and were the most prevalent taxa. Other two monogenean species (*Pseudaxine* cf. *trachuri* sp. and Polyopisthocotylea indet.) were also found at all sites, however, their prevalence and mean abundance were low. Of all Digenea, only *Ectenurus selari*, *Neonotoporus trachuri*, and larval Didymozoidae indet. were present in samples from all sites. The presence of *E. selari* was also indicated in *D. macrosoma* (Theisen, 2020), suggesting *Decapterus* to be common hosts for this species. The endoparasites were collected mostly from the gut wash remnants, indicating the infection site was either inside the stomach or the intestine. Contrasting to monogeneans, the prevalence and mean abundance of crustacean ectoparasites was very low (Appendix 3).

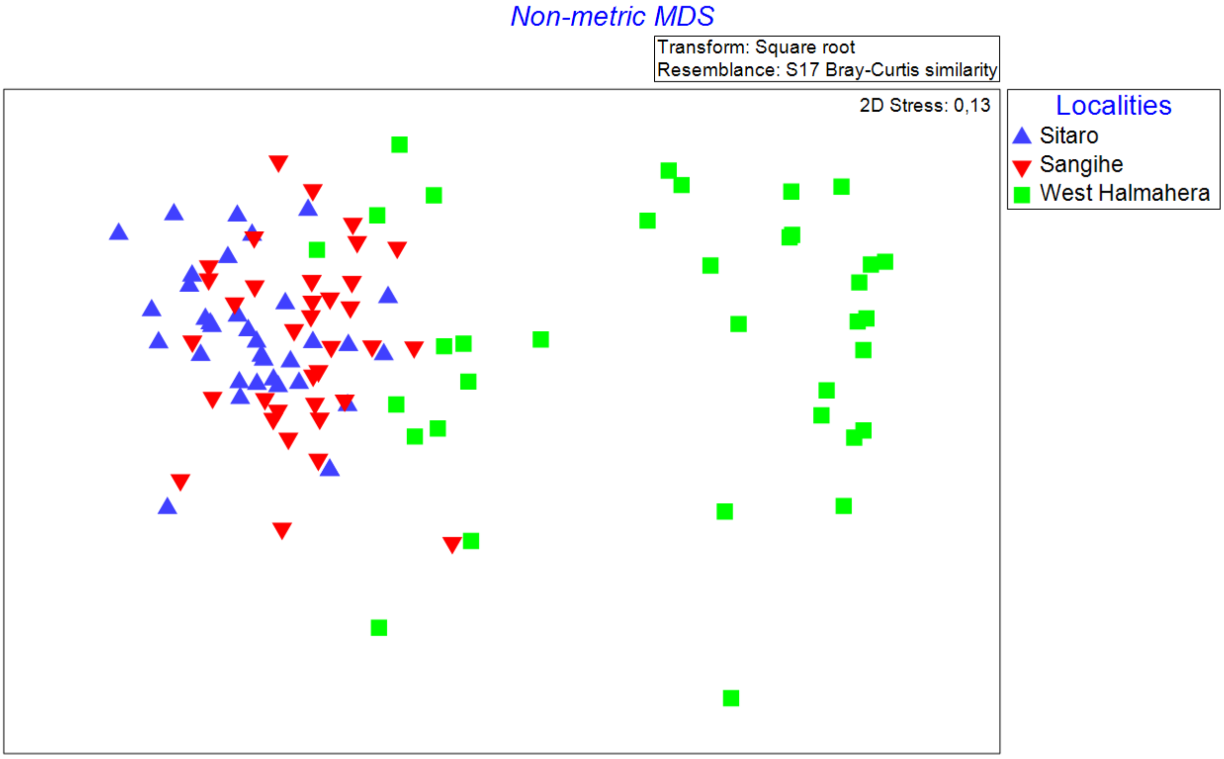
Following the results of $p< 0.005$ from the Kruskal-Wallis H test, post-hoc tests were applied for *A. opelu*, *P. decapteri*, *E. selari*, *Neonotoporus trachuri*, Didymozoidea indet. (larva), and *C. carinata*. Despite the relatively high prevalence at all sites, the mean abundance of *A. opelu* is significantly higher in North Maluku (West Halmahera) compared to North Sulawesi sites (Sitaro and Sangihe), while the mean abundance of *P. decapteri* in North Sulawesi is higher than in North Maluku. The difference in mean abundance and prevalence of *E. selari*, Didymozoidea indet. (larva), and *C. carinata*, however, was not significantly different between the two regions. The mean abundance of *Neonotoporus trachuri* in Sitaro was higher than in Sangihe as well as the prevalence, however, a high infection with 16 individuals was only found in one single host, hence affected the prevalence and mean abundance. The Isopoda *Cerathotoa carinata* was recorded with a low prevalence in samples from Sangihe and West Halmahera, and the difference was observed between Sitaro and West Halmahera by the mean abundance and prevalence (Appendix 4 and Appendix 5).

4.3.5. Similarity analysis and possible discrimination of host population

Visualization by using abundance data of the isolated metazoan parasite taxa showed relatively distinct groups of the examined localities, where fish of North Sulawesi (Sitaro and Sangihe) showed mixed grouping patterns and were rather separated from West Halmahera/North Maluku samples (Fig. 4.3A). The ordination showed a relatively good fit with a stress value of 0.13.

The cluster diagram showed degrees of similarity between samples and locations. In the cluster diagram for samples (Fig. 4.3B), fish from West Halmahera (North Maluku group) formed a randomly distributed yet separated pattern from Sitaro and Sangihe (North Sulawesi group), indicating different parasite characteristics of both site groups and thus leading to the probability of different stocks between locations. Of 35 samples, 12 fish from North Maluku shared similarities with fish from North Sulawesi as seen on the left side of the diagram. A combination of locations generated by a hierarchical cluster analysis showed a similarity value of 85.61 for Sitaro and Sangihe samples, and the combination of these sites with North Maluku resulted in 53.5 similarity (Fig. 4.3C).

The result from SIMPER showed that both in Sitaro and Sangihe, *P. decapteri* contributed 81.09% and 74.56%, respectively, to the similarity of each site (avg. similarity of Sitaro group 77.08, avg. similarity of Sangihe group 74.12), while in West Halmahera, the contribution was made by *A. opelu* (percent contribution 79.62%, avg. similarity 55.79). Interestingly, Sitaro and Sangihe formed a group with a dissimilarity of 26.68% which was contributed by *P. decapteri* (34.33%), *A. opelu* (18.59%), *E. selari* (13.14%), and Didymozoidae indet. (12.30%).



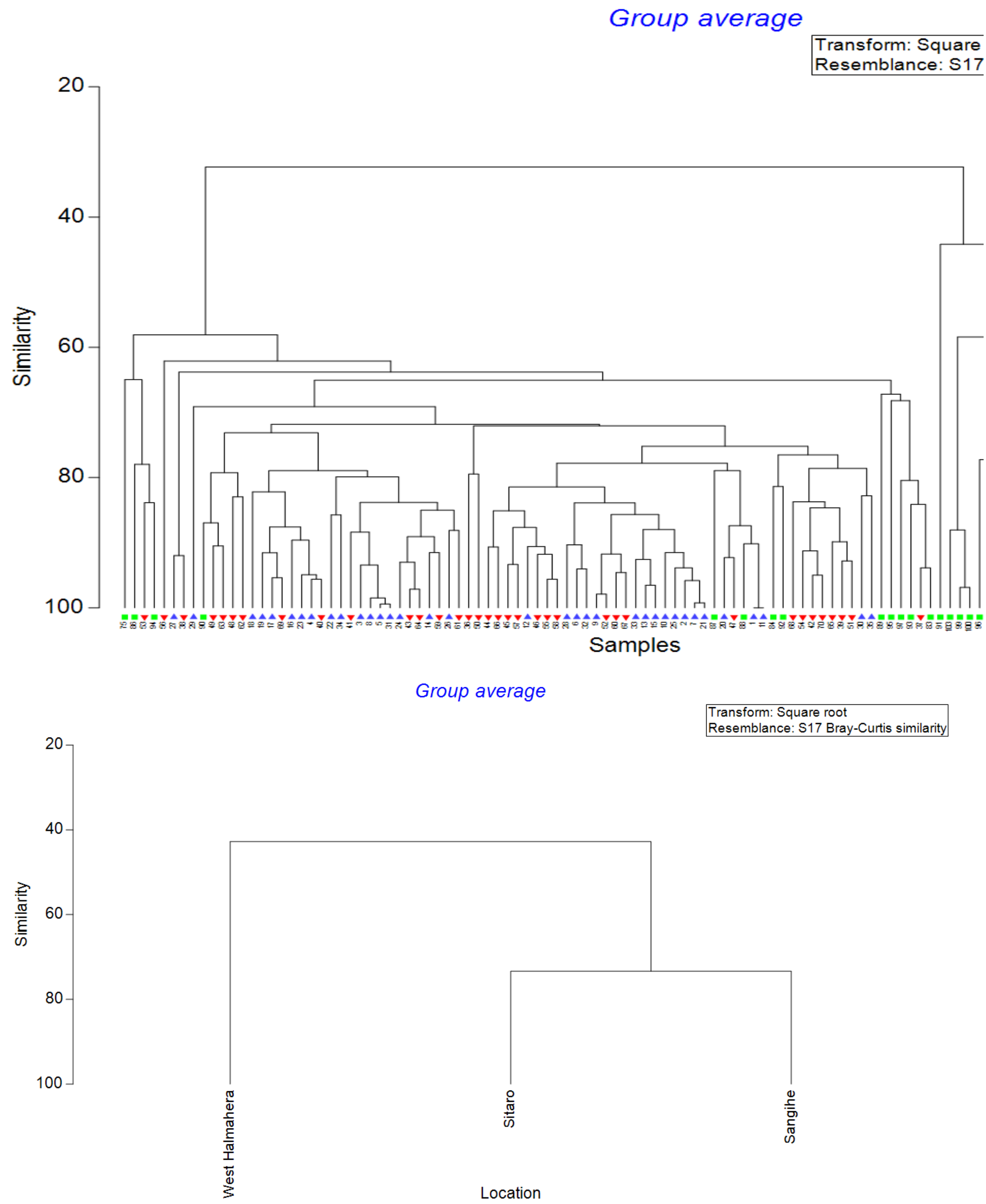


Figure 4-3. Multi-dimensional scaling (MDS) plot based on Bray-Curtis dissimilarities calculated from the square-rooted data of parasite abundance of *Decapterus macarellus* from three localities in the eastern Indonesia; **B**: Dendrogram resulted from clustering analysis of samples showing which samples were mixed; **C:** Group average of localities shows the degree of similarity between sampling sites. Symbols used in the graphs are blue triangle for Sitaro, red triangle for Sangihe, and green square for West Halmahera

4.4. Discussion

North Sulawesi, as part of the FMA 716, is well-known for its small pelagic fish production across Indonesia. In addition to large pelagic, small pelagic fish such as mackerel scad *Decapterus macarellus* are the most important species group, in terms of quantity and value, targeted by fishermen in this region (USAID, 2019). Besides fishing in North Sulawesi waters, fishermen from this area often fish in Halmahera Sea and Maluku Sea, which administratively belong to North Maluku, yet they land their catch in fishing ports across the North Sulawesi mainland. In this study, we demonstrate that the fish hosts from three adjacent fishing grounds belong to two distinct stocks, separated from each other by the characteristics of fish parasite fauna. We also record *Allopseudodiclidophora opelu* and *Pseudodiclidophora decapteri*, considered common parasite species for scads (Yamaguti, 1970), for the first time from *D. macarellus* from Indonesia. Apart from *Ectenurus selari*, previously recorded from *D. macrosoma* by Theisen (2019), the other parasite records are new from Indonesian marine waters in general and for *Decapterus* species in particular. It is interesting to note that Theisen (2019) recorded many nematodes, particularly the Anisakidae, in *Decapterus* from Indonesian waters, suggesting the Anisakidae can be considered a common fish parasite of scads. Palm et al. (2017) listed anisakids found in *D. kurroides* from Java, *Anisakis typica* Diesing, 1860 and *A. t. indonesiensis* from *D. table* from Bali, *Anisakis* sp. from *D. russelli* from Bali and Java, and *A. t. indonesiensis* from *D. macarellus* from Papua New Guinea and *D. macrosoma* also from Bali. Anisakid nematodes were already used for stock discrimination by e.g. Marcogliese et al. (2003) and Klapper et al. (2015). We did not find any nematodes inside the host samples from all studied sites, however, because of the large body size of the third-stage *Anisakis* larvae, overlooking this species in our samples can be excluded. *Anisakis* might therefore also be used as a stock distinguishing taxon for scads when comparing the different Indonesian localities. This suggests that the herewith two sampled fish stocks of *Decapterus macarellus* from Sulawesi and North Maluku both are distinct from those of Java, Bali and Papua New Guinea. The sampling of Theisen (2019) mainly focused on sites off South Bali and South Java (Indian Ocean) compared to the herein investigated central Indonesian Maluku Sea and Sulawesi Sea, where the final hosts of *Anisakis*, namely dolphins, might be less abundant.

We demonstrate discrimination between stocks of *D. macarellus* from North Sulawesi and North Maluku waters. Of all parasites, the monogeneans were the most prevalent parasite group, particularly *A. opelu* and *P. decapteri*. Both species inhabit gills and the oral cavity as their microhabitat with blood as their primary diet. Despite having a high prevalence, the mean abundance of *A. opelu* in North Sulawesi sites was 3-6 times lower than it was in North Maluku, which is an interesting finding. The use of monogeneans as markers for fish stock separation has been recorded in earlier studies (Stanley et al., 1992; Reimer, 1993; Oliva and Ballón, 2002; Timi, 2003; Valdivia et al., 2007; Baker et al., 2007; Campbell et al., 2007). Monogeneans have a direct life cycle that does not involve any intermediate host, and due to morphological adaptations to specific host organs, most monogeneans are highly host-specific (Klimpel et al., 2019), also in Indonesia (Theisen et al., 2017; Theisen, 2019). Since they are generally highly host-specific, the distribution of particular species tends to correspond closely to the distribution and migratory abilities of their hosts and populations (Hayward, 2005). Monogeneans such as *A. opelu* and *P. decapteri* tend to show strong host specificity for one or a few closely related fish species, which, in part, is caused by the specialized swimming activity of the larva of each species (Hayward, 2005) as well as the attachment apparatus that supports their firm attachment to the hosts' gill morphology (Theisen et al., 2017). Our data suggest that both monogeneans are useful as fish stock bioindicators in Indonesian coastal waters.

Aside from the distinguishing species, we also noted parasite species which were found in all sites and responsible for the similarity between stocks, i.e., *Pseudaxine* cf. *trachuri* and *Ectenurus selari*. Monogenean *P. trachuri* is reported to be a widely dispersed species and is an ectoparasite species commonly found in Carangids, i.e., *Trachurus trachurus* (Llewelyn, 1962; Campbell, 2008; Shawket et al., 2018), *Carangoides malabaricus*, *Caranx* sp., and *Decapterus* sp. (Truong et al., 2022), as well as Sparids, i.e., *Boops boops* (Bouguerche et al., 2020). The distribution of the hosts over different regions indicates that this parasite species might be cosmopolitan, which was slightly different with the hosts' distribution of *E. selari*. As an endoparasite, *E. selari* is known to infect different host family, i.e., Carangidae [*Atule mate*, *Selar crumenophthalmus, Megalaspis cordyla*, and *Decapterus macrosoma* (Theisen, 2019; Arthur and Te, 2006), as well as *D. macarellus* which was found in the present study] and Serranidae [*Epinephelus bruneus, E. sexfasciatus,* and *E. tauvina* (Arthur and Te, 2006)]. All of these species, however, were mostly distributed in tropical regions, thus the distribution of *E. selari* was likely to be restricted in tropical regions as well. Given the number of species used as their host, both *P. trachuri* and *E. selari* potentially have low host-specificity, hence unsuitable to be used as indicator for stock determination.

Parasites with a long lifespan such as anisakid nematodes (see above) may have advantages for identifying fish stocks, yet such characteristics can also be a disadvantage if the parasites grow along with the growth of the host, causing ontogenetic alterations of the parasite community structure, a phenomenon that has been documented in the literature (Poulin, 2000, 2004; Poulin and Valtonen, 2001). There is no documentation on the life span of both *A. opelu* and *P. decapteri*, however, an experiment showed that monogeneans can survive from less than one year to more than two years (Chubb, 1977). The longevity of parasite life cycles is one of the major factors that highly correlates with the zoogeographical distribution (Palm and Bray, 2014). Although monogeneans are known to cause obvious harm to heavily infected fish, they usually have very little impact on wild host populations and remain stable over time (Mosquera et al., 2003). According to Stanley et al. (1992), the selection of monogeneans was based on a clear trend in infection rate across the study area as well as morphological aspects which support the selection: the haptoral clamps and the protected environment in the gill filaments imply that it would not be dislodged during capture. In the present findings, *A. opelu* and *P. decapteri* were easy to detect and identify, and like other monogeneans, both species are assumed to have a direct life cycle, thereby eliminating the need for complicated life cycle studies.

The presence of different fish stocks in the sampled region strongly corresponds with the molecular analysis that detected two different stocks of mackerel scad in Sulawesi and Maluku (Suwarso and Zamroni, 2014). The first group consisted of a population from the Sulawesi Sea, in the northern part of the North Sulawesi peninsula, while the second group consisted of populations from areas situated in the southern part of the North Sulawesi peninsula. The authors claimed that the genetic difference between the two groups indicated gene flow originating from the Indian Ocean to the Sulawesi Sea, while the population of the second group was influenced by the South Pacific Thermocline from Maluku Sea to Banda Sea and Flores Sea, and is distributed to other adjacent waters including Bone Bay, Tolo Bay, and Tomini Bay. A subpopulation of Tomini Bay and Makassar Strait was detected within the second group which was likely caused by water mass mixing rather than a genetic break between marine species in the Pacific Ocean with the Indian Ocean as suggested by Williams et al. (2002). In the present study, the fishing grounds of Sitaro and Sangihe, located in the Sulawesi Sea, were compared with West Halmahera in the Maluku Sea. Both seas are known as the main pathways of the Indonesian Throughflow, in which water masses from the North Pacific Ocean enter the Indonesian archipelago to make their way into the Indian Ocean. The Sulawesi Sea also receives inflow from the Sulu Sea, which is considered a secondary inflow portal and is of importance in terms of freshwater inflow (Gordon, 2005; Susanto et al., 2012). Hence, there is the possibility of mixing between the North Pacific Ocean waters and the Sulu Sea waters. On the other hand, the Maluku Sea receives additional inflow from the South Pacific, which supplies relatively saline lower-thermocline water. Although the degree of mixing between different water masses is not investigated in this study, we suggest that the different oceanographic characteristics of the habitat of *D. macarellus* in North Sulawesi and North Maluku are the main factor of stock discrimination. Studies on parasites as biological tags for stock identification already showed that physical features of the waters, such as bathymetry (Brickle et al., 2006), currents (Latama, 2006), temperatures (Timi, 2007), salinity (Rückert et al., 2009), and combination of those (Esch and Fernández, 1993; Timi, 2003) affected the parasite composition in the hosts. Suwarso and Zamroni (2014) also found an interesting stock unit separation of Indian scads *D. russelli* and shortfin scads *D. macrosoma* between the western and eastern parts of Indonesia. The population of Indian scads from the Java Sea (west) and Banda Sea (east) were slightly separated and fell into one clade, while for shortfin scads, the subpopulation from the Java Sea was significantly different from those from the Banda Sea, indicating the role of the Wallace Line as a potential geographic barrier for the migration of this species. This might correspond to the absence of anisakid nematodes in the present study, that would probably separate the stocks of Mackerel scad in the western Indonesia from the eastern Indonesia as happened to the shortfin scads.

The present study presents a promising opportunity of using fish parasites as an approach to undertake stock identification for mackerel scads. Compared to other approaches, parasites study for stock identification and especially in Indonesian waters was rarely considered. The morphometric approach, which includes general morphometry and individual features (i.e., otolith), has been widely used in Indonesia, not only for finfish (Fitriyah, 2017; Ardi, 2018; Kusumaningrum et al., 2021; Wujdi et al., 2017; Mogea et al., 2019; Manginsela et al., 2020; Wujdi et al., 2022) but also for bivalves (Qonita et al., 2015) and crabs (Pramithasari et al., 2017). Factors that might complicate the morphometric analysis for stock discrimination are the high variation in fish phenotypes as well as morphometric changes during spawning, thus requiring large sample sizes (Pawson and Jennings, 1996). Otolith shape is more stable to short-term alterations caused by changes in fish condition or environmental variations, thus being a more reliable tool for demonstrating a phenotypic method of stock identification (Ihssen et al., 1981). However, the otolith shape is highly influenced by its chemical composition, thus it is essential to include otolith microchemistry in the identification of stocks (Nazir and Khan, 2021; Kerr and Campana, 2014). Preparing a single otolith for shape and size observation can be laborious and timeconsuming (Brophy, 2014), while analysis of otolith chemistry is another different task involving elemental and isotopic analysis where contamination or modification is of particular concern. Molecular analysis is, to date, the most popular method to undertake stock identification. Genetic studies have gained considerable popularity since it was first introduced into fisheries science (Mariani and Bekkevold, 2014). The procedures of genetic analysis can be technically more complicated as require advanced technology. In Indonesia, this approach is still rarely used also due to the costs that are still a constraint to fisheries managers.

Parasite studies, on the other hand, can also be time- and labor-consuming at the beginning as preliminary studies might be needed to screen potential parasites species to be used as stock markers, but in the long run, they are more cost-effective. A parasite approach needs only statistically-acceptable sample sizes to infer the statistical significance between samples or locations. The validity of the results from morphometric methods alone is questionable, requiring complementary data such as environmental parameters (e.g., depth, salinity, temperature) and even molecular analyses. For parasites, intensive lab work is not always necessary as mounting and staining of the specimens can be carried out in batches of parasite individuals at a time, being another advantage of this method. Another advantage of biological tagging is that parasites can often be used to identify subpopulations that genetic investigations may not be able to detect (MacKenzie, 2002). There are, however, limitations on knowledge and resources that might cause the unfamiliarity of using a parasite approach in stock identification, where results can be difficult to interpret as the taxonomy and life history are often poorly understood (Pawson and Jennings, 1996). So far, most fish parasitological investigations in Indonesia focused either on cultured fish or on commercially important species (Kleinertz et al., 2022b), limiting the knowledge of other groups. In the context of fisheries management, the combination of different methods is ideal because the results of different techniques can be compared and complement one another (MacKenzie and Abaunza, 2014; Begg and Waldman, 1999).

4.5. Conclusion

The present research demonstrates the use of parasites as an approach that is almost neglected in studying stock discrimination in Indonesia, as well as parasites species (*Allopseudodiclidophora opelu* and *Pseudodiclidophora decapteri*) recorded for the first time from mackerel scad *Decapterus macarellus* from Indonesia. For pelagic species such as mackerel scad, hydro-oceanographic features are likely to be factors affecting larval movement and food availability, which can explain the possible background of stock separation and the development of regional subpopulations. Reflecting our sampling scheme which was only undertaken one time in one particular season, the extent of this study is limited to a preliminary investigation to identify parasite species that vary in prevalence, abundance, or intensity within the study areas. To obtain a more conclusive and reliable understanding of the stock distribution pattern, as well as evidence of possible mixing between different parts within the study areas, this study needs to be followed up with sampling data over different seasons and years, as well as taking environmental parameters that drive the stock separation into account.

Data availability

Data will be made available on request.

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

5. Metazoan parasites of the narrow-barred Spanish mackerel (*Scomberomorus commerson* Lacepède, 1800) across Indonesian waters: a potential proxy for stock discrimination and fisheries management decisions[4]

Abstract

The narrow-barred Spanish mackerel *Scomberomorus commerson* Lacepède, 1800, is a pelagic species distributed mainly in tropical waters, including the Indonesian archipelago. Despite being commonly known as migratory, this species also signals local stock formation, as reported by parasite studies. This study aims to investigate the metazoan parasite composition of *S. commerson* in the northern and southern Java coasts and compare the results with the past study conducted in four sites within the Sulawesi waters to suggest further possible stock separation within Indonesian waters. A total of nine parasite species were selected as the means of comparison. Of all species groups, Monogenea was commonly found to be prevalent at all sites. The parasite composition of host samples from Seribu Islands, located off the northern Java coast, and Palabuhanratu, off the southern Java coast, indicated different population groups also separated from the Sulawesi group. The trypanorhyncha *Callitetrarhynchus gracilis* Pintner, 1931 was highly abundant only in Seribu Islands, which differs from the other sites. However, the seasonal occurrence of *S. commerson* in the Seribu Islands indicates that the species was in the course of migration and was not permanently inhabiting the area. The present study demonstrates that the formation of local stocks across the archipelago is likely to occur; thus, a comprehensive stock assessment of this species within and between fisheries management area(s) is necessary. While molecular and otolith isotopes inform the gene pool and recruitment cohort, parasite faunas may provide insight into the movement and migration of the fish.

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[4] Manuscript prepared for publication

5.1. Introduction

The scombrid group is a highly migratory species that moves across large distances. The narrow-barred Spanish mackerel *Scomberomorus commerson* Lacepède, 1800, is a pelagic species that can undertake lengthy longshore migrations (Collette and Nauen, 1983; McPherson, 1992), but populations that permanently reside in certain areas also seem to exist (Collette et al., 2011). The distribution of this species is globally widespread, with most concentrating on the tropical regions, such as the Indo-West Pacific, including the Red Sea, South Africa, Southeast Asia, north to China and Japan, Australia, and Fiji. At the same time, the introduction to the Mediterranean Sea, which extended eastward to Tunisia, resulted from northward immigration from the Red Sea through the Suez Canal (Ben-Tuvia, 1978; Ben Souissi et al., 2006). The narrow-barred Spanish mackerel inhabits the pelagic-neritic zone of the tropical ocean near the edge of the continental shelf to shallow coastal waters, as well as in drop-offs, shallow or gently sloping reef, and lagoon waters, often of low salinity and high turbidity. The depth range is up to 200 m, but they are frequently caught in depths less than 100 m (Pauly et al., 1996; Collette, 2001; Collette et al., 2011).

Molecular studies have been undertaken to investigate the distribution of the narrow-barred Spanish mackerel populations across different regions, revealing different stock units in Australia (Buckworth et al., 2007, 2012; Newman et al., 2009), Indo-Malay-Papua (Sulaiman and Ovenden, 2010; Fauvelot and Borsa, 2011; Habib and Sulaiman, 2016), Persian Gulf-Gulf of Oman-Arabian Seas (Hoolihan et al., 2006; Abedi et al., 2012), and Indian Ocean and (Habib and Sulaiman, 2017; Radhakrishnan et al., 2018; Feutry et al., 2020). Among those studies, it is interesting that different genetic clades were observed within the Indonesian archipelago. In contrast, only a single genetic stock was identified from the Persian Gulf-Gulf of Oman-Arabian Sea area across a relatively similar distance. Fauvelot and Borsa (2011) concluded that this species might maintain its geographic isolation through philopatry despite the long-distance migration ability.

The signals of how the narrow-barred Spanish mackerels formed local unit stocks have been previously demonstrated by Lester et al. (2001) and Moore et al. (2003) through parasites study, which revealed the different parasites composition of Broome and Torres Strait despite its genetic homogeneity with other northern Australia sites. However, the different conclusions between parasites and molecular studies results can be understood as an indication of subpopulation existence that genetic investigations may not detect (MacKenzie, 2002). Some parasite species that were picked up by the fish during their juvenile stage and stay for a long time (long-lived parasites) can provide information about their hosts' seasonal migrations and migration habits, while short-lived parasites can provide information about their recent environment (Lester, 1990; Palm, 2004). Hosts from the same species inhabiting different environments will likely accumulate parasite species as they encounter different prey.

Stock assessment is fundamental for formulating a fisheries strategy to ensure resource sustainability. In the stock assessment process, the data is processed to generate parameters on the population dynamics, such as growth, mortality, stock-recruitment relationship, and stock structure (Hoggarth et al., 2006). Despite the continuing exploitation of the narrow-barred Spanish mackerels, no regular stock assessment is available for the said stock within Indonesian waters. The narrow-barred Spanish mackerel has long been an essential commodity in Indonesia's fishery (Widodo, 1989). In the national fishery management, *Scomberomorus* is categorized under neritic or tuna-like species found in all fisheries management areas (FMAs), indicating the wide distribution of this species across the Indonesia archipelago (MMAF, 2015). In the Southeast Asian countries, recorded catch from hook and lines of Indonesia contributed to the highest production (28.3%), with 6.6% of the total catch composition consisting of the narrow-barred Spanish mackerels. This species also contributed to 9.1% of the total catch from gillnets as the second most productive fishing gear (SEAFDEC, 2022). The present study investigates the metazoan parasites of *S. commerson* from the northern and southern coast of Java, Indonesia. It compares the findings with earlier studies from Sulawesi (Latama, 2006) to investigate the population structure of the narrow-barred Spanish mackerel within the Indonesian archipelago. The possibility of the narrow-barred Spanish mackerels of Java and Sulawesi coasts forming different stocks from Kupang and Australian stocks is observed. Possible factors responsible for the observed stocks and the implications for future management strategies are discussed.

5.2. Material and Methods

Host samples from Seribu Islands (northern Java; n = 34) were collected during the rainy season in December 2018, and samples from Palabuhanratu (southern Java; n = 35) were collected at the end of the rainy season and entering the transition period of the northwest monsoon March 2020. Total length, standard length, and total weight were recorded, followed by an examination for metazoan ectoparasites of the skin, fins, nasal capsules, and buccal and branchial cavities by the naked eye (Palm and Bray, 2014). Metazoan endoparasites were examined and collected by opening the body cavity from anterior to posterior. Internal organs were removed and placed separately in Petri dishes filled with saline solutions, while the gastrointestinal tract was examined by gut wash technique following Cribb and Bray (2010). Measurements and photographs of parasite specimens were taken by an upright microscope (Olympus BX53) with differential interference contrast (DIC) connected to an Olympus DP74 camera. Monogenean parasites were fixed in 4% formalin, while Crustacea, Digenea, Cestoda, and Nematoda were fixed in 70% ethanol. Monogenea, Digenea, and Cestoda were stained using Mayer-Schuberg's acetic-carmine technique and mounted in Canada balsam (Palm, 2004), while Crustacea and Nematoda were not stained and directly mounted in glycerin. Identification of parasites considered the original descriptions: Yamaguti (1965), Tripathi (1956), Hayward and Rohde (1999a; 1999b), and Rohde and Hayward (1999) for Monogenea, Cressey and Cressey (1980) and Helna et al. (2016; 2018) for Crustacea, Gibson et al. (2002) for Digenea, Palm (2004) for Cestoda, and Williams Jr. and Bunkley-Williams (1996) for Nematoda.

We compared our data with the parasite records in Sulawesi waters (Latama, 2006), selecting only parasites identified to species level except for the nematodes. We selected four Sulawesi sites, i.e., Sangkarang Islands, Bone Bay, Tolo Bay, and Tomini Bay, to be compared with the present study. The available raw data from Latama (2006) allowed us to calculate the prevalence, mean intensity, and mean abundance according to (Bush et al., 1997). Multi-dimensional scaling (MDS) plot was applied to visualize the distribution of hosts based on parasites' mean abundance. The goodness-of-fit of the statistics in an MDS plot is shown by the stress value (0 to 1), where a value near 0 indicates a better fit. From the MDS plot, we observed that the samples from Sulawesi sites tend to form a separated assemblage; thus, we group those samples into one cluster ("Sulawesi"), and the similarity percentage was generated for Seribu Islands, Palabuhanratu, and Sulawesi. Shapiro-Wilk was applied to test the normality of the total length and weight.

In contrast, the Kruskal-Wallis H test was applied to identify the significant difference in the parasite distribution between sites. The difference in the mean abundance was tested using Mann-Whitney Wilcoxon. The significance level was set at $p < 0.05$ for all statistical tests. All significance tests were run in R Studio Version 1.2.5042 (R Core Team, 2020), and similarity percentages and the visualization of the MDS plot and cluster diagram were made using PRIMER Version 7.0.

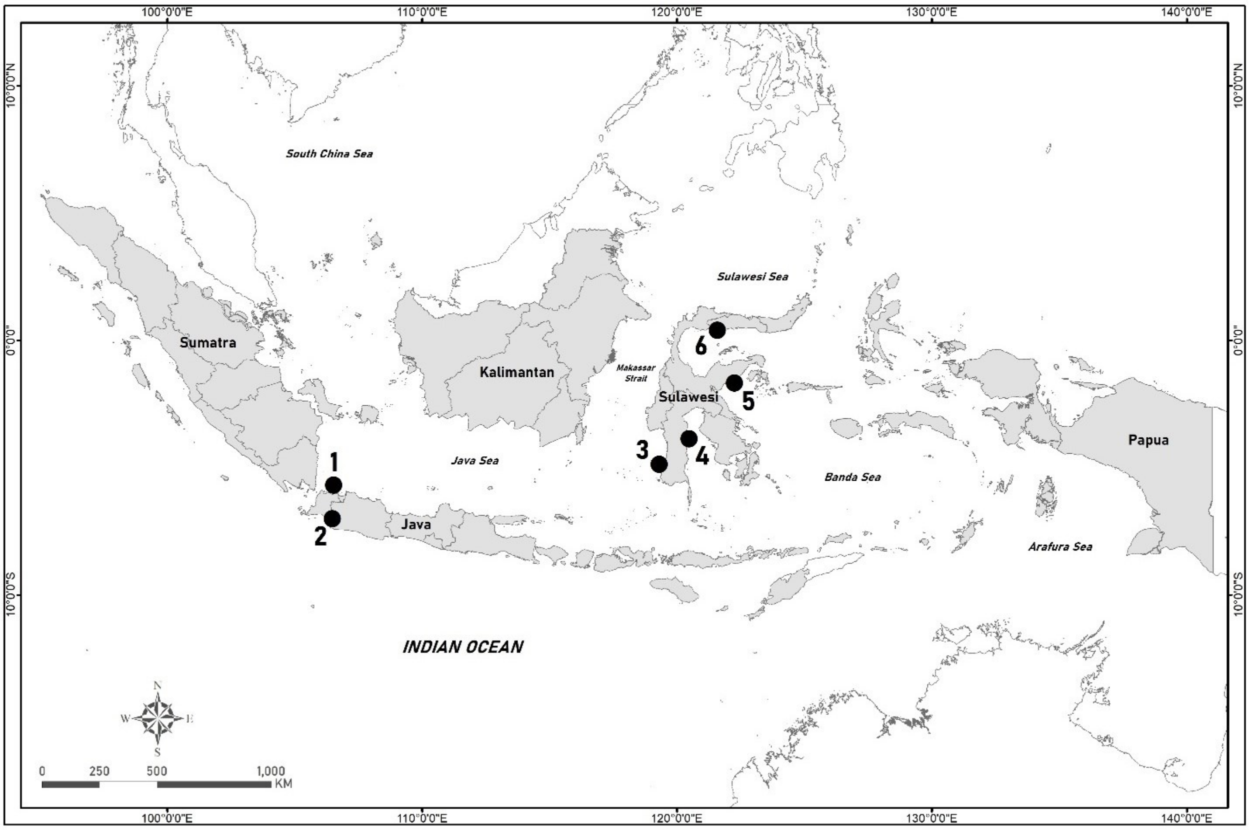


Figure 5-1. Parasite examination of the present study was conducted for the narrow-barred Spanish mackerel *Scomberomorus commerson* collected from Seribu Islands in the northern Java coast (1) and Palabuhanratu in the southern Java coast (2), and the results were compared to parasites records from Sulawesi waters (Sangkarang Islands [3], Bone Bay [4], Tolo Bay [5], and Tomini Bay [6]) examined by Latama (2006)

5.3. Results

Total length and total weight showed normal distribution according to the Saphiro-Wilk test ($W = 0.95$, $p < 0.001$ and $W = 0.82$, $p < 0.001$, respectively). Kruskal-Wallis test showed that the total length and total weight were significantly different between sites ($H = 80.21$, df = 5, $p < 0.001$ and $H = 64.22$, df = 5, $p < 0.001$) (Table 1). Little is known about the spawning season of *Scomberomorus commerson* in the northern and southern Java coasts, but local fishermen in Palabuhanratu catch this species all year round. In Seribu Islands, however, this species tends to be abundant during the rainy seasons only (Martin Hadinoto, *pers. comm.*), probably in the course of migrating, yet the direction is unknown. Host samples from Sulawesi were collected from December 2004 to August 2005, and according to Latama (2006), the fishing of *S. commerson* in Sulawesi waters also occurs all year round.

Table 5-1. Biometrics of *Scomberomorus commerson* from Java (Seribu Islands and Palabuhanratu) and Sulawesi (Sangkarang, Bone Bay, Tolo Bay, and Tomini Bay; R= rainy season, D= dry season, n= number of individuals, TL= total length, TW= total weight). Samples from Sulawesi were collected by Latama (2006). The mean and standard deviation are given in brackets.

Fishing ground	n	TL range (cm)	TW range (g)
Seribu Islands	34	64.0 – 97.7 (72.77±6.33)	1582.0 – 5034.0 (2205.50±672.16)
Palabuhanratu	35	54.2 – 85.2 (67.97±6.36)	1055.0 – 3700.0 (2047.29±593.31)
Sangkarang (R)	40	59.5 – 101.0 (77.28±12.33)	1100.0 – 8350.0 (3171.25±1743.87)
Sangkarang (D)	40	68.0 – 79.0 (72.75±3.49)	2000.0 – 2900.0 (2416.25±303.48)
Bone Bay	40	53.0 – 100.5 (76.26±12.66)	1100.0 – 6000.0 (2626.25±1249.20)
Tolo Bay	14	71.0 – 114.5 (90.57±14.64)	2200.0 – 9500.0 (4521.43±2432.92)
Tomini Bay	40	70.0 – 126.5 (93.47±12.55)	2000.0 – 13200.0 (5030.00±2383.40)

Parasite identification and taxonomical remarks

Before comparing the parasite records, we re-examined the specimens through the microscopic images provided by Latama (2006). We cross-checked it and its original descriptions in the World Register of Marine Species (WoRMS) database. We noticed two parasite species Latama (2006) found need to be revised: *Bivagina australis* Murray, 1931, and *Gotocotyla secunda* Tripathi, 1954. According to the current taxonomy, *B. australis* is now accepted as *Polylabroides australis* Murray, 1931. However, the microscopic images of *B. australis* in Latama (2006) did not fit the original description of *P. australis* (Roubal, 1981; Byrnes, 1985). We compared our findings to the original description and confirmed that *B. australis* in Latama (2006) fit the original description of *Gotocotyla bivaginalis* Rohde, 1976 instead. *Gotocotyla bivaginalis* has an elongated body, symmetrical triangular haptor, paired dorsal vaginae, and numerous clamps with robust lateral sclerites. The paired vaginae and triangular haptor are two characteristics that distinguish this species from the congeners. The specimen has a body length of 7.7 mm and a haptor length of 2 mm, clamp width is 28-33 µm, and clamps are 71 pairs. *Gotocotyla secunda* is currently accepted as *Gotocotyla acanthura* Meserve, 1938; however, we found that the microscopic images and description of *G. secunda* from Latama (2006) fit the description of *Cathucotyle cathuaui* Lebedev, 1958 rather than *G. acanthura*. The genera *Gotocotyla* Ishii, 1936 and *Cathucotyle* Lebedev, 1968 belong to the family of Gotocotylidae Yamaguti, and they both contain species with single or paired vaginae, as well as species having clamps with either elliptical discs or curved bars. *Gotocotyla acanthura* has a single dorsomedial vagina, male copulatory organ with pectinate spines, and clamps with curved bar ribs. Specimens of *G. acanthura* had a body length of 6.6 mm, haptor length of 2.6 mm, clamp width of 40-64 µm, and 60 pairs of clamps. Specimens of *C. cathuaui* had a body length of 7.5-8.7 mm, haptor length of 4.3-6 mm, clamp width of 52-61 µm, and 244 pairs of clamps. While the clamp of *G. acanthura* had a single row of curved bars, *C. cathuaui* had clamps with two rows of flat, elliptical ribs.

Of all parasite specimens isolated from the hosts from both Java coasts, we selected certain species that corresponded to the metazoan parasite species in Sulawesi collected by Latama (2006) to compare the parasitological parameters, i.e., prevalence, mean abundance, and mean intensity. A total of nine parasite species were selected, consisting of five Monogenea (*Pricea multae* Chauhan, 1945; *Pseudothoracocotyla ovalis* Tripathi, 1956; *Gotocotyla acanthura*, *G. bivaginalis*, and *Cathucotyle cathuaui*), a Crustacea (*Cybicola armatus* Bassett-Smith, 1898), two Cestoda (*Callitetrarhynchus gracilis* Pintner, 1931 and *Parotobothrium balli* Palm, 2004), and one genus of Nematoda (*Terranova* sp.). In addition, we found certain parasite species that Latama (2006) did not, and vice versa. In his study, Latama recorded Monogenea *Bivagina alcedinis* Yamaguti, 1963 and Cestoda *Grillotiella branchi* (= *Grillotiella exilis* Palm, 2004) from Sulawesi waters, which were not detected in our samples, while we found Nematodes *Camallanus* sp. and *Hysterothylacium* sp. which were not found in all Sulawesi sites. In total, 13 parasite species were included in the comparison between hosts from Java and Sulawesi (Table 1). Digenea found in the present study was excluded in the comparison as we could not confirm the taxonomy to the species level, and we doubted that the species corresponds to *Lecithochirium neopacificum* Velasquez, 1962 (= *Erilepturus hamati* Manter, 1947) which was found by Latama (2006). However, all Nematodes found in this study were included in the comparison as most of the Nematode species recorded from Indonesia are only identified to the genus level (Theisen, 2019).

Parasitological parameters and frequency distribution between sites

Of all monogeneans, two species showed more than 70% prevalence at all sites in Java and Sulawesi, namely *Pricea multae* and *Cathucotyle cathuaui*. The prevalence of *Pseudothoracocotyla ovalis* was also relatively high, except in Palabuhanratu and Sangkarang Island-rainy season. All parasite species showed significant differences in distribution between locations ($p < 0.05$). After the corrections were made for species names in Latama's original work, all hosts from Sulawesi showed no presence of *Gotocotyla acanthura,* and the distribution of *G. acanthura* in Seribu Islands was higher (P = 88%, mA = 5.6 ind/fish) than Palabuhanratu (37%). *Bivagina alcedenis* was found at all sites in Sulawesi with a relatively high prevalence (> 70%), except in the Sangkarang-dry season. In contrast, it was not found in both Seribu Islands and Palabuhanratu. *Gotocotyla bivaginalis* showed a notable pattern, where the prevalence and mean abundance in Seribu Islands, Palabuhanratu, and Sangkarang, both rainy and dry seasons, was low (≤ 20%) but was comparatively higher in Bone Bay, Tolo Bay, and Tomini Bay. The crustacean *Cybicola armatus* was found in all sites with a prevalence above 60%, as in the case of monogenean *Pricea multae*, *Cathucotyle cathuaui*, and *Pseudothoracocotyle ovalis* in most sites, indicating the commonness of this parasite species for *S. commerson*, however, the distribution of *C. armatus* in Seribu Islands was significantly lower (P = 62%, mA = 2.4 ind/fish) than Palabuhanratu, Sangkarang Island-rainy season, and Tomini Bay. The distribution of trypanorhynch *Callitetrarhynchus gracilis* in Seribu Islands was significantly higher compared to other sites (P = 97%, mA = 13.6 ind/fish), while *Parotobothrium balli* showed moderate prevalence in Tolo Bay (50%) and its overall distribution was significantly different with other sites except with Palabuhanratu. The other trypanorhynch species, *Grillotiella exilis*, was found only in Sulawesi, except in Tomini Bay, yet the prevalence is generally low (2.5 – 26%). Among three Nematoda genera found at the study sites, *Camallanus* sp. was only found in Seribu Islands, thus showing different distribution between Seribu Islands and the rest of the sites, while *Hysterothylacium* sp. did not show any differences between Seribu Islands and Palabuhanratu (Table 2).

Table 5-2. Prevalence (P), mean intensity (mI), and mean abundance (mA) of parasites found in *Scomberomorus commerson* from Java (Seribu Islands and Palabuhanratu) and Sulawesi (Sangkarang Islands, Bone Bay, Tolo Bay, and Tomini Bay). Kruskal-Wallis H test with *p-value* <0.05 (*) indicates parasite species with significantly different distribution between locations. Samples from Sangkarang Islands were collected during the rainy season (R) and dry season (D)

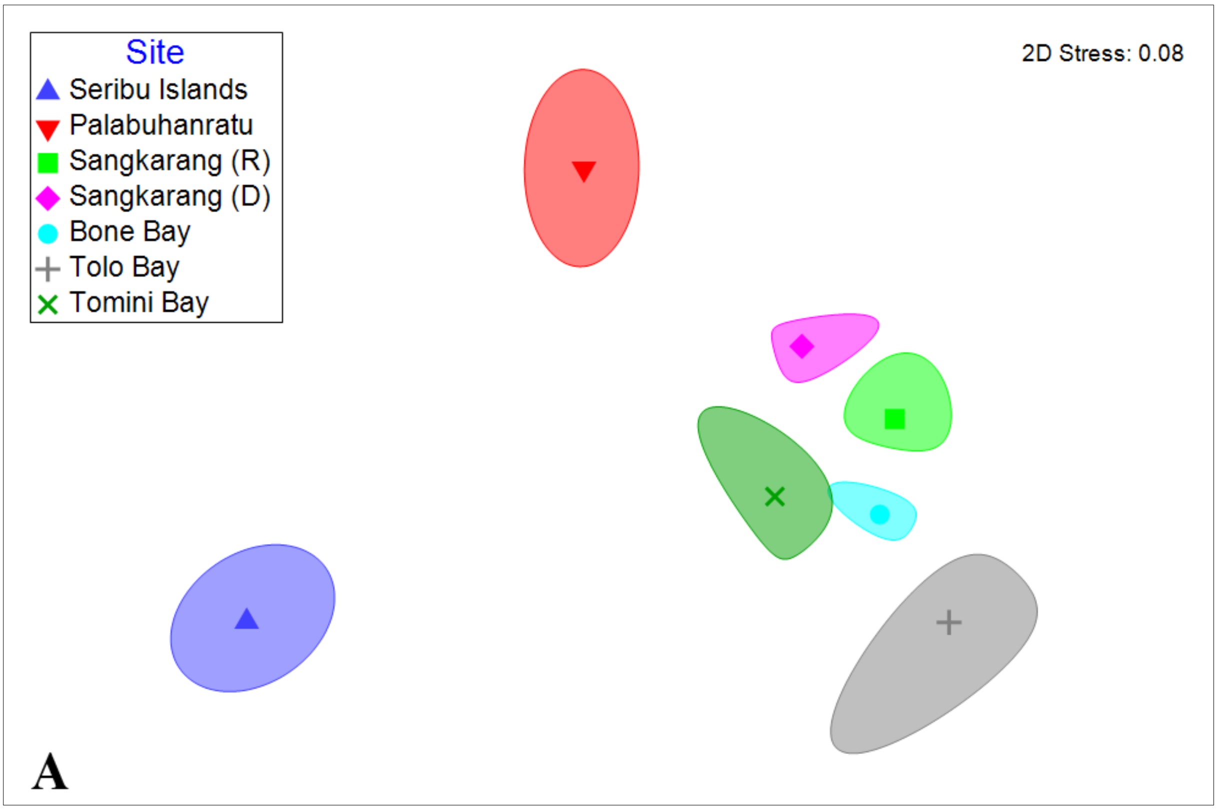
Parasite taxa	**Java**						**Sulawesi**														
	Seribu Islands n = 34			**Palabuhanratu n = 35**			**Sangkarang (R) N = 40**			**Sangkarang (D) n = 40**			**Bone Bay n = 40**			**Tolo Bay n = 14**			**Tomini Bay n = 40**		
	P (%)	**mI**	**mA**	**P (%)**	**mI**	**mA**	**P (%)**	**mI**	**mA**	**P (%)**	**mI**	**mA**	**P (%)**	**mI**	**mA**	**P (%)**	**mI**	**mA**	**P (%)**	**mI**	**mA**
Monogenea																					
Pricea multae	73.5	8.6	6.4	97.1	10.9	10.6	75.0	15.8	11.9	100.0	17.4	17.4	95.0	23.2	22.0	100.0	12.0	12.0	77.5	4.1	3.2
Pseudothoracocotyla ovalis	82.4	11.9	9.8	40.0	3.2	1.3	65.0	6.1	4.0	87.5	6.1	5.4	95.0	12.6	11.9	92.9	14.6	13.6	77.5	6.4	5.0
Gotocotyla acanthura	88.2	6.3	5.6	37.1	3.2	1.2	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0
Gotocotyla bivaginalis	17.6	1.5	0.3	11.4	1.3	0.1	20.0	1.6	0.3	5.0	2.5	0.1	42.5	3.3	1.4	64.3	13.8	8.9	55.0	5.2	2.9
Cathucotyla cathuai	88.2	7.2	6.3	88.6	7.2	6.4	92.5	34.8	32.2	100.0	27.3	27.3	100.0	21.0	21.0	100.0	21.6	21.6	90.0	14.5	13.0
Bivagina alcedenis	0.0	NA	0.0	0.0	NA	0.0	72.5	10.0	7.2	47.5	3.1	1.5	90.0	9.9	8.9	100.0	18.3	18.3	72.5	6.4	4.7
Crustacea																					
Cybicola armatus	61.8	3.9	2.4	94.3	6.6	6.2	92.5	8.5	7.9	90.0	4.8	4.4	72.5	5.0	3.6	85.7	3.8	3.3	77.5	7.9	6.1
Cestoda																					
Callitetrarhynchus gracilis	97.1	14.1	13.6	8.6	3.3	0.3	7.5	1.3	0.1	7.5	1.3	0.1	2.5	1.0	0.0	21.4	12.3	2.6	12.5	2.4	0.3
Parotobothrium balli	8.8	10.7	0.9	25.7	3.9	1.0	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0	50.0	14.3	7.1	5.0	10.0	0.5
Grilliotiella branchi	0.0	NA	0.0	0.0	NA	0.0	2.5	14.0	0.4	12.5	1.4	0.2	2.5	26.0	0.7	21.4	12.3	2.6	0.0	NA	0.0
Nematoda																					
Camallanus sp.	20.6	1.7	0.4	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0
Hysterothylacium sp.	5.9	3.5	0.2	2.9	1.0	0.0	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0
Terranova sp.	0.0	NA	0.0	0.0	NA	0.0	7.5	1.0	0.1	10.0	2.5	0.3	0.0	NA	0.0	0.0	NA	0.0	0.0	NA	0.0

We tested the difference in parasite abundance between Seribu Islands and Palabuhanratu since both are coasts of Java Island with different topography characteristics. According to Mann-Whitney U tests, the abundance of five parasite species were significantly different between these two sites, namely *Pricea multae* ($U = 335$, $p = 0.001$), *Pseudothoracocotyla ovalis* ($U = 190.5$, $p < 0.001$), *Gotocotyla acanthura* (U= 175, $p < 0.001$), *Cybicola armatus* ($U = 311$, $p = 0.001$), and *Callitetrarhynchus gracilis* (U = 41.5, $p < 0.001$). Considering the almost similar distribution of parasites, we put all Sulawesi sites into one group ("Sulawesi"), and Kruskal-Walllis tests were applied to observe the difference between three groups: Seribu Islands, Palabuhanratu, and Sulawesi. The distribution of parasite species were significantly different between site groups: *Pricea multae* ($H = 69.63$, $p < 0.001$), *Pseudothoracocotyla ovalis* ($H = 63.80$, $p < 0.001$), *Gotocotyla acanthura* ($H = 165.46$, $p < 0.001$), *G. bivaginalis* ($H = 54.96$, $p < 0.001$), *Cathuotyla cathuaui* ($H = 69.01$, $p < 0.001$), *Bivagina alcedinis* ($H = 127.22$, $p < 0.001$), *Cybicola armatus* ($H = 20.65$, $p = 0.002$), *Callitetrarhynchus gracilis* ($H = 154.46$, $p < 0.001$), *Parotobothrium balli* ($H = 55.72$, $p < 0.001$), *Grillotiella exilis* ($H = 22.73$, $p = 0.001$), *Camallanus* sp. ($H = 44.11$, $p < 0.001$), and *Terranova* sp. ($H = 15.14$, $p = 0.02$). Only *Hysterothylacium* sp. showed no differences between site groups ($H = 9.96$, $p = 0.176$).

Possible discrimination of host population

The distribution of samples visualized through a non-metric multi-dimensional scaling (MDS) plot following 50-times bootstrap showed a pattern where hosts from Sulawesi are scattered close to each other, while hosts from Seribu Islands and Palabuhanratu were separated (Fig. 3A). Cluster analysis based on Bray-Curtis similarity was performed to see the degree of similarity shared by each site. Bone Bay and Tolo Bay hosts shared 74.63% similarity and 68.08% with Sangkarang Islands (both seasons). Hosts from the Seribu Islands and Palabuhanratu shared a similarity of 52.65%, and both sites shared a similarity of 46.63% with Sulawesi sites (Fig. 3B). To see more clearly how the sites are grouped, a two-dimensional ordination plot was created through overlying nMDS plot with the average cluster groups (Figure 3C). Two major groups are formed with the similarity set at 50%, indicating the separation between Java (Seribu Islands and Pelabuhanratu) and Sulawesi sites. However, when the similarity was set to 60%, four clusters were formed where Seribu Islands and Palabuhanratu are separated, and Tomini Bay is separated from the Sulawesi group.

The similarity percentage (SIMPER) analysis indicated which parasite species contributed most to the differences between the studied sites (Table 3). The average similarity was 57.42% for Seribu Islands with the most contribution (99.22%) from *Callitetrarhynchus gracilis* (27.11%), *Cathucotyla cathuaui* (19.25%), *Pseudothoracocotyla ovalis* (18.44%), *Gotocotyla acanthura* (16.16%), *Pricea multae* (11.33%), and *Cybicola armatus* (6.93%). Samples from Palabuhanratu shared 61.29% similarity, with the contribution from *Pricea multae* (39.96%), *Cybicola armatus* (27.11%), *Cathucotyla cathuaui* (26.45%), *Pseudothoracocotyla ovalis* (2.72%), *Gotocotyla acanthura* (2.3%), and *Parotobothrium balli* (1.19%) made up 99.73% of the group composition. The Sulawesi group shared similarity of 58.95% and the most contribution (99.82%) was composed by *Cathucotyle cathuaui* (35.29%), *Pricea multae* (22.03%), *Pseudothoracocotyla ovalis* (15.09%), *Cybicola armatus* (14.59%), *Bivagina alcedinis* (11.17%), and *Gotocotyla bivaginalis* (1.65%).



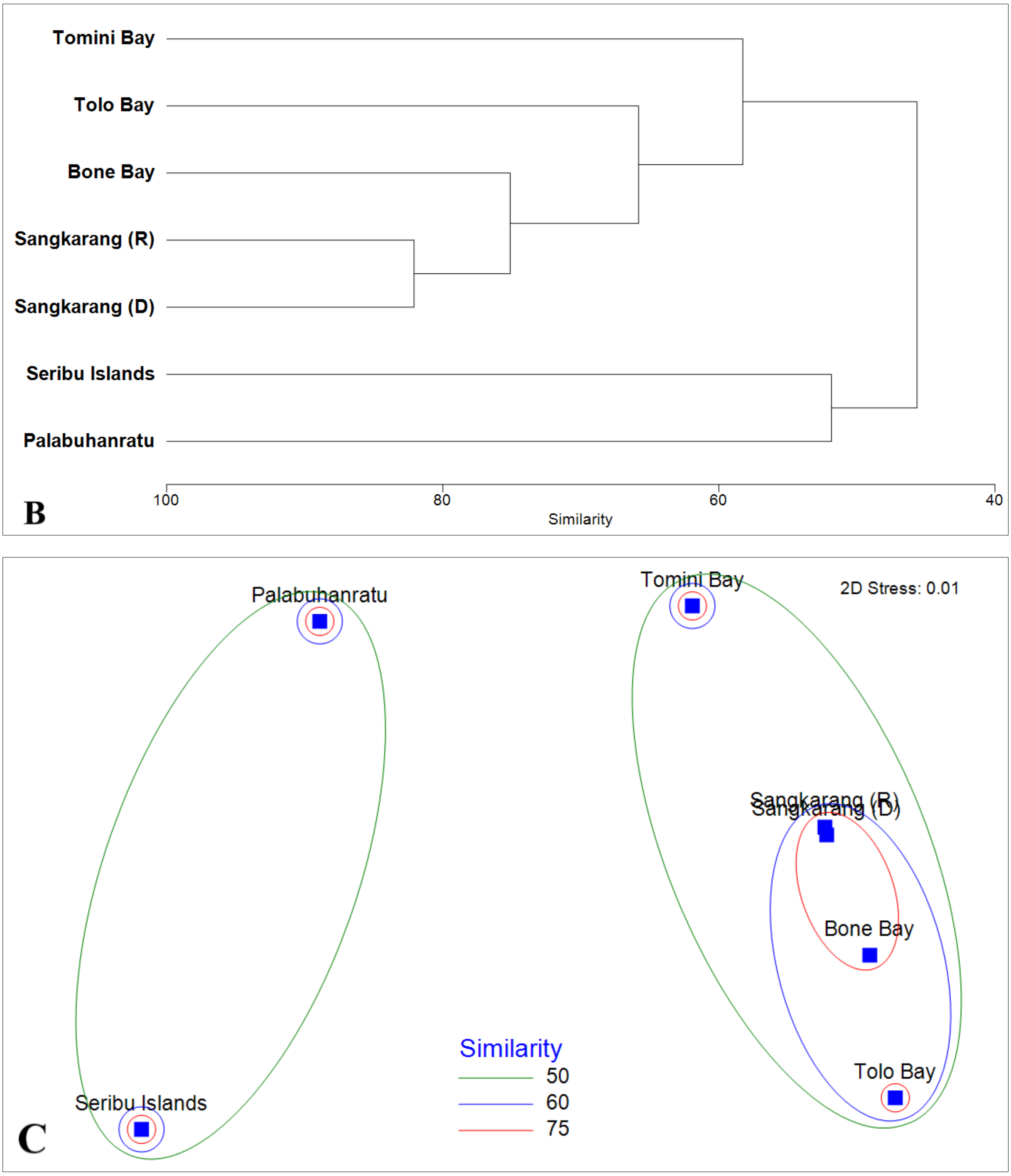


Figure 5-2. Grouping pattern of *Scomberomorus commerson* populations from six sites: Seribu Islands, Palabuhanratu, Sangkarang Islands-R (rainy season), Sangkarang Islands-D (dry season), Bone Bay, Tolo Bay, and Tomini Bay based on metazoan parasites distribution in the host samples shown by a non-metric multi-dimensional scaling (MDS) plot (A), average cluster diagram showing the degree of similarity between sites (B), and (C) two-dimensional ordination resulted from the nMDS overlaid with the site-based average clustering

Table 5-3. Results of SIMPER analysis for similarities of the parasite fauna of the narrow-barred Spanish mackerel, *Scomberomorus commerson*, collected from Seribu Islands (northern Java coast), Palabuhanratu (southern Java coast), and Sulawesi.

Species	Average No. of species	Average similarity	SD of similarity	Contribution (%)	Cumulative contribution (%)
Group Seribu Islands: average similarity = 57.42					
Callitetrarhynchus gracilis	3.13	15.57	1.86	27.11	27.11
Cathucotyle cathuaui	2.23	11.05	1.50	19.25	46.36
Pseudothoracocotyla ovalis	2.54	10.59	1.22	18.44	64.80
Gotocotyla acanthura	2.04	9.28	1.53	16.16	80.96
Pricea multae	1.91	6.51	0.89	11.33	92.29
Cybicola armatus	1.17	3.98	0.70	6.93	99.22
Camallanus sp.	0.26	0.22	0.19	0.38	99.60
Gotocotyla bivaginalis	0.21	0.19	0.15	0.34	99.94
Parotobothrium balli	0.22	0.02	0.07	0.04	99.98
Hysterothylacium sp.	0.11	0.01	0.04	0.02	100.00
Group Palabuhanratu: average similarity = 61.29					
Pricea multae	3.02	24.49	2.44	39.96	39.96
Cybicola armatus	2.22	16.61	2.02	27.11	67.06
Cathucotyle cathuaui	2.22	16.21	1.63	26.45	93.52
Pseudothoracocotyla ovalis	0.63	1.67	0.41	2.72	96.24
Gotocotyla acanthura	0.58	1.41	0.37	2.30	98.53
Parotobothrium balli	0.47	0.73	0.23	1.19	99.73
Gotocotyla bivaginalis	0.13	0.11	0.10	0.18	99.90
Callitetrarhynchus gracilis	0.15	0.06	0.07	0.10	100.00
Group Sulawesi: average similarity = 58.95					
Cathucotyle cathuaui	4.28	20.81	2.15	35.29	35.29
Pricea multae	3.08	12.99	1.35	22.03	57.33
Pseudothoracocotyla ovalis	2.19	8.89	1.22	15.09	72.41
Cybicola armatus	1.92	8.60	1.22	14.59	87.01
Bivagina alcedinis	1.94	6.58	0.92	11.17	98.18
Gotocotyla bivaginalis	0.66	0.97	0.32	1.65	99.82
Callitetrarhynchus gracilis	0.14	0.05	0.08	0.09	99.91
Grilliotiella exilis	0.13	0.02	0.05	0.04	99.95
Parotobothrium balli	0.15	0.02	0.04	0.03	99.98
Terranova sp.	0.05	0.01	0.04	0.02	100.00

5.4. Discussion

In the present study, fish from the Seribu Islands harbored significant trypanorhynch *Callitetrarhynchus gracilis* compared to other sites. Lester et al. (2001) showed that the mean numbers of *C. gracilis* in Australian waters was also low; however, other trypanorhynch species, *Grillotiella branchi* (= *Grillotiella exilis*) and *Otobothrium cysticum* were present in high number, which were not found at all in samples from Java. The presence of different species of trypanorhynch demonstrates the distribution of elasmobranchs as their final hosts (Palm, 2004). Through all three stages of their life cycle, trypanorhynch passes through at least three different hosts and thus is generally considered to exhibit relatively low host specificity at any particular life stage (Palm et al., 1997, 2007; Palm, 2004; Palm and Klimpel, 2007). Grouping patterns of different trypanorhynch genera associated with a particular host characteristic were investigated by Palm et al. (2017). The occurrence of *Grillotia*, for instance, generally characterized the deep-water shark species, while *Callitetrarhynchus* and *Otobothrium* were more associated with pelagic sharks. In terms of shark orders, both *Callitetrarhynchus* and *Otobothrium* characterized the Carcharhiniformes. Carcharhiniformes is an order known to have more than 50 different genera under nine families. Elasmobranch hosts that harbored the adult *O. cysticum* listed by Palm (2004) were all Carcharhiniformes found in Indonesian and Australian waters. The differences in trypanorhynch distribution and abundance correspond to elasmobranch species' distribution and abundance as its hosts. For instance*, Carcharhinus obscurus and Sphyrna zyganea* are the final hosts for *O. cysticum,* found in Australian waters. However, their distribution in Indonesia is limited in certain areas, i.e., Aceh (northern Sumatra), Tanjung Luar (West Nusa Tenggara), and Cilacap (southern Java) (Benaya Simeon, *pers. comm.*).

Little is known about the stock structure of the narrow-barred Spanish mackerel populations in Indonesian waters despite its importance to the country's fish production. As an archipelagic nation, pelagic fish resources in Indonesia ranked first compared to other groups, such as reef and demersal fish (MMAF, 2022a). In this study, we aim to highlight the use of metazoan parasites of *Scomberomorus commerson* from Seribu Islands (northern Java coast), Palabuhanratu (southern Java coast), and Sulawesi waters to provide a general picture of the stock distribution of the narrow-barred Spanish mackerel across different regions in Indonesian waters. The narrow-barred Spanish mackerel *S. commerson* is a migrating species; however, this species also tends to form local stocks (Buckworth et al., 2007). In the present study, the grouping of Sulawesi samples indicated local stock, which also occurred in Australia (Moore et al., 2003) and the Arabian Sea (Habib and Sulaiman, 2017). A local unit might be developed to impact oceanographic conditions, such as water circulation, with which the fish's planktonic stage strongly interacted (Incze and Bailey, 1998). The formation of local stock is influenced by, among others, oceanographic factors and migration patterns. The influence of oceanographic factors might be challenging to associate when the habitat boundary is smaller, such as in estuaries and semi-closed coastal zones. However, this does not mean the possibility of localized stock can be ignored. In Sulawesi, the unique oceanographic condition might likely influence the formation of local stock. Sulawesi Sea, which happens to be one of the crucial pathways for Indonesian Throughflow, creates complex patterns of temperature, salinity, and nutrient levels in the water. Such factors affect the distribution and abundance of prey species, affecting the narrow-barred Spanish mackerel's movement patterns and feeding behavior. The assumption on larval dispersal suggested that the Halmahera and Mindanao eddies and the Indonesian Throughflow play a critical role in maintaining the genetic divergence between demes of pelagic fishes. Indonesia is well known for its high biodiversity and phylogeographic barriers (Majkowski, 2007). The coast's physical characteristics, such as reefs and other structures, can create an attractive habitat for the narrow-barred Spanish mackerel, thereby concentrating local populations. Such barriers support the theory of fish stock delineation in Sulawesi, as shown by the metazoan parasite composition of the mackerel scad *Decapterus macarellus* **(Retnoningtyas et al., 2023**).

Fishing of the narrow-barred Spanish mackerel on the southern Java coast takes place all year round, as stated by the local fishers and confirmed by the six-year record catch data (2014—2019) from Palabuhanratu Fishing Port, showing the highest volume of catch occurred in June to July. However, the narrow-barred Spanish mackerels in Seribu Islands were known to be abundant during the rainy season only, particularly in November-December (Martin Hadinoto, *pers comm.*), which we suspect to be in the course of migration. The different occurrence of fish in Seribu Islands and Palabuhanratu demonstrates the possibility of different migratory patterns of the narrow-barred Spanish mackerel populations; however, it is still unclear how the migration route is taking place. Research on the phylogeny of the commercial mackerels in the Indonesian archipelago showed a genetic subdivision between the western (regions around Sumatera-Java-Flores) and eastern parts (regions around Sulawesi-Maluku-Papua) (Jackson et al., 2014). A molecular study by Habib and Sulaiman (2016, 2017) showed a genetic connectivity between *S. commerson* from the South China Sea, Java Sea, and Bali Sea, supporting the findings. In the case of Australia, parasite faunas were evaluated for evidence of movement and migration (Buckworth et al., 2007), along with molecular and otolith isotope analysis. Lester et al. (2001) have previously concluded that while the stocks of the western coast were mixed, the Broome, Groote Eylandt, and the East Coast populations were more isolated. Parasite fauna also showed that the movement of adult fish from Kupang to Australian waters did not occur, as the adult fish of Australian waters harbored parasite species not found in Kupang.

The narrow-barred Spanish mackerel is a highly exploited pelagic species distributed mainly in tropical waters. Like tuna, research on biological assessment and the fishery of *Scomberomorus commerson* has been undertaken at different locations in the world (e.g., Taghavi Motlagh et al., 2008 [Oman Sea]; Taghavi Motlagh and Ghodrati Shojaei, 2009 [Persian Gulf]; Rohit and Abdussamad, 2013 [India]; Lee, 2013 [Mozambique]; Weng et al., 2020 [Taiwan Strait]; Mohsen et al., 2020 [Egypt]; Tanimoto et al., 2021 [Australian east coast]; and Alrashada, 2022 [Saudi Arabian Gulf]). Despite the importance and the high exploitation level, this species has not been appropriately assessed in Indonesia, and adequate management measures are still lacking. Considering the vast distribution of *S. commerson* across Indonesian waters, available records on the biology and population dynamics of *S. commerson* are still limited (Karimunjawa-Java Sea: Yuliana and Nurhasanah, 2017; Kwandang Bay-northern Sulawesi: Noegroho and Hidayat, 2014; Noegroho et al., 2018; Bone Bay-southern Sulawesi: Mallawa and Amir, 2019). Stock assessment for *S. commerson* at a broader scale has been undertaken for the Indian Ocean as a mandatory contribution of being a country member of the Indian Ocean Tuna Commission (IOTC). For reporting interest, all narrow-barred Spanish mackerel caught off of the Indian Ocean within the Indonesian territory were reported as a single stock unit. Considering the nature of *S. commerson* to form local stocks, fisheries managers should also consider the possibility of different stocks within management area(s). Different stock units imply different migration patterns, growth rates, and susceptibility to fishing pressure; therefore, different harvest strategies and management should be developed for each respective stock unit. The importance of spatial consideration in managing fish stock has long been recognized (Stephenson, 1998; 1999) as the areas traditionally assumed to contain a single stock might have complexities with more than one stock due to mixing. The primary objective is to prevent the loss of spawning amount and spawning areas due to, for instance, overfishing. By defining the boundaries of different populations, fisheries managers can develop specific management strategies based on each stock's unique characteristics and needs. Management measures aimed to ensure the sustainability of the fish stock include the seasonal fishing closures, restriction of certain fishing gears, and the implementation of catch size limits.

Distinguishing fish stock units is one of two fundamental elements in stock identification besides the concept of the stock population structure. For pelagic and migrating fish, in which stock mixing is bound to happen, stock complexity may occur in areas traditionally assumed to contain only a single stock. Therefore, emphasis on fishery management, which considers spatial consideration, is crucially important (Stephenson, 1999). Regarding tuna fisheries, Indonesia has been developing a harvest strategy based on the assessment that estimates tuna stock within Indonesia's Archipelagic Waters (IAW). IAW refers to the fisheries management area (FMA) 713, 714, and 715, which separates from the open ocean FMAs (572 and 573 in the Indian Ocean, and 716 and 717 in the Pacific Ocean) and other archipelagic waters FMAs (571, 711, 712, and 718), and considered some of the most critical areas for tropical tuna catches (Hoshino et al., 2020). The catch within the IAW was estimated to contribute more than 60% of the nationwide tuna production, making these regions a management priority for tuna fisheries in Indonesia. The concept of IAW for tuna harvest strategy assumed of their connectivity between the FMA 713, 714, and 715. Tuna, particularly yellowfin, in the IAW region, is considered a single stock according to the highlight from the WPEA Three Country Stock Assessment Workshop, held in Vietnam in 2015 (Rice et al., 2014). A solid residential behavior was reported by Rice et al. (2014) for skipjack, in which, for assessment purposes, the populations in the western and central Pacific Ocean (WCPO) were considered a single stock (Wild and Hampton, 1993). This concept may also be suitable for the narrow-barred Spanish mackerel as it is most likely distributed across different FMAs. Therefore, more research is needed to investigate the population connectivity between those sites in particular and different regions in Indonesia. Stock identification information helps fisheries managers determine the scope of stock assessment to build further a foundation in formulating fisheries reference points and the harvest strategy. The study on stock delineation may or may not alter the existing stock assessment as new knowledge of stock boundaries is continuously revealed. Studies on stock delineation can also suggest re-evaluating the management scale for fisheries resources in Indonesia, particularly for migrating species such as pelagic fish that reflect regional stock differences.

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6. General Discussion

Pelagic fish species are among the most exploited fisheries resources in the world (FAO, 2022) and also in Indonesia. Many studies have been undertaken to understand their biology, distribution, and population dynamics. However, certain aspects are yet to be explored, such as their spawning grounds, stock structures, and migratory patterns. Under Indonesia’s national fisheries management regulations, small pelagic fish groups comprise more than 15 species. Nevertheless, the total allowable catch and exploitation is stated for the entire group rather than species by species. While focusing on the stock delineation, this study also contributes to the knowledge of reproductive biology and spawning behavior of the mackerel scad *Decapterus macarellus*, which dominates the small pelagic catch, particularly in eastern Indonesia (see **Chapter 2**). A deeper look at the life history traits of this species shows the impact of fishing on their maturity size. The hypothesis of fisheries-induced evolution has been extensively researched and substantiated by several fisheries studies. Consequently, it has emerged as a major concern that demands the attention and awareness of every fisheries manager. The result from this study also sends an alert that too high mortality of important pelagic fish species due to fishing will affect the sustainability of these fisheries resources in the future (see **Chapter 3**).

Stock assessment is fundamental in fisheries management as it provides a comprehensive picture of the fishery's status and condition. To set a management scope, clear boundaries of a unit stock should take place even before starting the stock assessment process. Stock delineation, therefore, is a highly relevant field of research in fisheries sciences. Numerous studies on stock assessment of exploited fish species are published every year all around the world (see review by Hilborn et al., 2020). Stock assessment of pelagic or migratory fish species, in particular, presents numerous challenges due to their unique behavioral patterns, extensive migration ranges, and the dynamic nature of the marine ecosystems in which they exist (Ruzzante et al., 2006; Kerr et al., 2017). In this study, for the first time, local stocks of *D. macarellus* were identified in North Sulawesi waters according to their metazoan parasite fauna (see **Chapter 4**). Parasite study have been demonstrated as a reliable approach to delineate stock units of *D. macarellus*, and further, a similar approach was applied to the narrow-barred Spanish mackerel, *Scomberomorus commerson*. Despite being highly exploited in Indonesia, this tuna-like species receives little attention regarding its stock structures. The narrow-barred Spanish mackerel is known as a migratory species, but they also tend to form local populations. This study (see **Chapter 5**) combines the metazoan parasite fauna of the sampled fish from northern and southern Java coasts with results from Sulawesi waters, concluding possible separation and connectivity of stock units across different regions and the management implications.

6.1. Reproductive biology and spawning behavior of commercially exploited pelagic fish in Indonesia

Biological information helps us to understand the overall life cycles of fish species, including their responses to changes in environmental factors, such as temperature, salinity, ocean acidification, climate change, pollution, and anthropogenic impacts (MacKenzie and Köster, 2004; Rijnsdorp et al., 2009; Casini et al., 2021). One key aspect of understanding fish biology is assessing age, growth, and mortality. Fish age is a significant biological factor in determining growth and mortality rates (Campana, 2001). In fisheries management, accurate age estimation is essential as age-based characteristics, including longevity, sexual maturation age, growth rate, and age-specific reproductive output, offer important insights into the overall life-history strategies of managed species (Newman et al., 2016). Additionally, knowledge of fish mortality rates is essential for population dynamics analysis and implementation of sustainable use of resources (Santos et al., 2022). Reproductive characteristics are another critical aspect of fish biology. Comprehending the reproductive biology of fish species is also critical for determining productivity and providing robust scientific advice in managing fisheries (Morgan, 2008). Reproductive traits such as fecundity and age at sexual maturity provide information on reproductive capacity and spawning behavior (Rochet et al., 2000; Lappalainen et al., 2003).

An understanding of the complete biological aspects of a commercially exploited fish is fundamental to its population equilibrium and successful management (Perera-García et al., 2010). Understanding their biology enables us to evaluate their population size, growth rates, and life history characteristics and further helps determine their sustainability in nature. Incorporating this knowledge into management practices ensures the long-term viability of fish stocks and promotes healthy marine ecosystems. Understanding those aspects is also essential for setting appropriate fishing regulations, such as minimum size limits and harvest quotas, to prevent overfishing and ensure that fish have a chance to reach reproductive age before being harvested. With basic guidelines, we can identify species more or less likely to bounce back from fishing, estimate the size at which sexual maturation occurs, or determine whether species have long lifespans or form spawning aggregations. The latter are particularly at risk if these aggregations are targeted. (Cochrane et al., 2019).

Reproductive biology of commercially exploited fish in Indonesia

Studies on the reproductive biology of commercially exploited fish in Indonesia have been widely undertaken for different species from different localities, ranging from the most lucrative targets, i.e., tuna (Tampubolon et al., 214; Chodrijah et al., 2019; Hidayat et al., 2020), elasmobranchs (White et al., 2006; White, 2007; White et al., 2008), small pelagic (Faizah et al., 2018; Pattikawa et al., 2018; Zamroni et al., 2019; Auliyah and Olii, 2022), demersal and reef fish (Jabbar et al., 2018; Rapi et al., 2020; Khasanah et al., 2019; Fatma et al., 2022; Fadli et al., 2022), and crustacean (Zairion et al., 2015; Hamid et al., 2016), to less lucrative ones, such as ponyfish (Prihatiningsih et al., 2015). Considering the nation's status as the center of marine mega-biodiversity and ranked as the second of the world marine capture producers, the available knowledge on commercially exploited species still needs improvement. Within the group of small pelagic species, for instance, at least 17 different species were listed (USAID, 2017), yet their biological information is very much scattered. In 2020, four small pelagic species groups contributed to the top ten of total fish production nationally, namely scads (8.95%), mackerels (5.59%), sardines (3.73%), and anchovy (3.60%), with scads (*Decapterus* sp.) being the second-highest of all recorded catch after bullet tuna (MMAF, 2022b). Studies related to scads in Indonesia have been undertaken to reveal their reproductive biology and population dynamics (Liestiana et al., 2015; Ongkers et al., 2017; Faizah and Sadiyah, 2019), population genetics (Zamroni et al., 2014; Zamroni and Suwarso, 2014), and exploitation rate (Sururi et al., 2017; Alnanda et al., 2020). The present study by **Retnoningtyas et al. (2024)**; see Chapter 2) contributes to the knowledge of the reproductive biology of the mackerel scad *Decapterus macarellus*, the main species of scads caught in eastern Indonesia, particularly the Sulawesi Sea and the Maluku Sea. In addition to the spawning peaks that many have investigated (Zamroni and Suwarso, 2011; Widiyastuti and Zamroni, 207; Nur et al., 2017; Fadhilah et al., 2021). **Retnoningtyas et al. (2023b)** also suggest potential spawning grounds of the mackerel scad, indicating the presence of local stocks around the northern Sulawesi waters. This finding, therefore, suggests that the stock of *D. maacarellus* in North Sulawesi waters is less vulnerable to overfishing. Nevertheless, further management measures need to be in place to optimize the use of resources.

Spawning pattern of commercially exploited fish

Investigation and monitoring of fish reproductive biology was mainly based on the length and weight of fish specimens and their gonad maturity levels, which were observed either through macroscopic examination or histologically based on the oocyte development criteria. Results from gonad observation provide information on the composition of matured individuals in the population, sex ratio, age at maturity, and spawning pattern. Understanding the timing of spawning can help predict its reproductive cycles and align fishing practices with these cycles to avoid disrupting spawning periods, hence support the population recruitment and preventing overfishing. The moon's cycle, for instance, has long been recognized to influence the spawning cycle of marine organisms in temperate and tropical areas (see Pressley, 1980). However, not much is known about the spawning patterns of marine species based on lunar phases in Indonesian waters. Several examples of gonad maturity and spawning time associated with lunar phase reported from Indonesian waters were mostly corals (Bachtiar, 2001; Komarudin et al., 2013; Yusuf et al., 2013) and coral-reefs associated biota (Sudaryanto et al., 2004; Pet et al., 2005; Susilo et al., 2009; Ayodya et al., 2021; Mustagfirin et al., 2021), which happened to be commercially exploited as well.

In line with research on moon-phase-related spawning behavior, research on spawning aggregations was also focused on reef-associated fishes such as groupers and wrasse (Pet et al., 2005; Wilson et al., 2010; Mangubhai et al., 2011; Huffard et al., 2012). Especially groupers are known for certain spawning aggregation sites, where the months of aggregation were deduced to be the period when the spawning season takes place (Pet et al., 2005). These plausible reasons are related to the establishment of national marine protected areas within the boundary of territorial waters (< 12 nautical miles). Effort locating the spawning grounds of commercially exploited pelagic fish such as tuna has resulted in abundant studies. Although caught off Indonesian waters (Farley et al., 2015), spawning grounds for this species usually occurred offshore, i.e., the northeastern Indian Ocean (Farley and Davis, 1998; Evans et al., 2012). The information gap on the spawning grounds of Indonesia's marine species left a huge room for exploration since only a few species have been investigated. In addition to the reproductive biology, **Retnoningtyas et al. (2024)** also investigated the spawning behavior of the small pelagic species, *Decapterus macarellus*, which is still relatively unknown to date. The study found that *D. macarellus* in the Sulawesi Sea spawns all year round, and through investigation on the gonadosomatic index, specific spawning grounds were identified. The authors found that the spawning peak of *D. macarellus* occurred during the first quarter of the moon phase. Lunar-related reproductive patterns have been observed for reef fish, such as Acanthuridae, Apogonidae, Balistidae, Blenniidae, Carangidae, Chaetodontidae, Epinephelinae, Labridae, Lutjanidae, Mugilidae, Mullidae, Opistognathidae, Pomacentridae, Pseudochromoids, Pteroidae, Scaridae, Siganidae, Sphyraenidae and Sparidae (Thresher, 1984 *in* Takemura et al. 2010, Ikegami et al., 2014); however, a report on the mackerel scad was not found. Spawning behavior can give an idea about fecundity, or the number of eggs produced and the survival rate of offspring, which plays a significant role in determining the species' population dynamics. Unfortunately, once fishers can locate spawning aggregations, the fish often face intense exploitation. This can lead to such severe depletion that the aggregations sometimes cease to form altogether (Heyman et al., 2004). Therefore, protecting spawning grounds as critical habitats is strongly encouraged.

In conclusion, in-depth knowledge of the biological parameters of commercially exploited fish species, especially concerning their reproductive cycles and spawning behaviors, is a fundamental requirement. It serves as the bedrock upon which sustainable fisheries management can be built, ensuring that these species thrive for future generations while supporting the livelihoods and industries that depend on them. Ignoring these aspects may lead to overexploitation and potential depletion, thereby upsetting ecological balance and jeopardizing food security. Findings from **Retnoningtyas et al. (2024)** contribute to the understanding of the reproductive biology and spawning behaviour of the mackerel scad, one of the most prominent small pelagic catch in Indonesia’s fisheries, and hence support the **working hypothesis 1: the reproductive biology of mackerel scad *Decapterus macarellus* allows identification of spawning behavior and potential spawning areas around the Sulawesi Sea, Indonesia**.

6.2. Understanding the impact of fishing on the biology of the exploited species

The health of fish populations is affected by various factors, including direct human activities, such as fisheries, and indirect effects resulting from broader environmental changes. Fishing, both commercial and recreational, has profound effects on aquatic ecosystems. It potentially reduces fish populations, induces changes in species composition, and disrupts aquatic food webs’ balance. Overfishing, happens when stock abundance is fished to below the level that can produce maximum sustainable yield (FAO, 2022), has resulted in the widespread depletion of several fish populations on a global scale. Disruption of marine food webs occurs when overfishing of a critical species increases its prey population, potentially affecting the abundance of other species (Scheffer et al., 2005). Fishing also affects the genetic diversity of fish populations (Allendorf et al., 2008; Pinsky and Palumbi, 2014) as it mainly targets larger individuals, and when the larger fish with particular genetic traits are consistently removed, it may lead to a genetic shift in the population (Beverton, 1990). When larger individuals are absent, fish may reproduce at an earlier or younger age to survive their population. Over time, this can lead to genetic changes in the population, thereby influencing characteristics such as growth rate and maturity size (Trippel, 1995; De Roos et al., 2006; Kuparinen and Merilä, 2007). On the other hand, environmental changes, e.g., habitat destruction, pollution, or climate change, can also independently stress or reduce fish populations. Even if the effect of environmental changes on the physiology of an organism is known, assessing the implications of organism-level physiological responses on population or ecosystem dynamics remains challenging (MacKenzie and Köster, 2004).

Ranked as the second largest fisheries producer in the world, Indonesia is facing signs of overfishing in various types of fisheries, ranging from benthic (Nane and Paramata, 2020; Yanti et al., 2020), reef (Campbell and Pardede, 2006; Maynard et al., 2010; Pane et al., 2021), demersal (Blaber et al., 2009), and pelagic (Indra et al., 2022; Purwanto et al., 2022; Bintoro et al., 2023). Indonesia’s fisheries are unique for their multi-species and multi-gear characteristics (Sumiono, 1997; Fauzi, 1998), making the management much more challenging. Understanding interactions between several species is necessary in multi-species fisheries. Due to predation interactions, competition, or other ecological interactions, the loss of one species may impact the population dynamics of a different species. For multi-gear fisheries, non-target species may be unintentionally caught when non-selective fishing gear is used, which can lead to significant bycatch.

To the biology of an exploited fish, fishing reduces population size, alters population structure in age, size, and maturity status, and modifies sex ratio (Kendall and Quinn, 2013; Ohlberger et al., 2022). Reflecting the ever-growing pressure from fishing activities due to population growth, rising food demands, economic progress, and technological advancements (Muawanah et al., 2012), it is crucial to improve the understanding of the impact of fishing. Past studies have shown diverse topics on the impact of fishing, e.g., to the population structure of the fish (Pet-Soede et al., 2001; Madduppa et al., 2012), to the ecosystem (Pet-Soede and Erdmann, 1998; Tamarol et al., 2012; Kasim et al., 2014; Sari et al., 2017), and to the social-economy of coastal communities (Fauzi, 1998; Asri et al., 2019; Karisma et al., 2019). The number of studies investigating the impact of fishing on the biological aspects of the fish is, unfortunately, deficient compared to the diversity of exploited marine fish species in Indonesia. Examples of studies on reproductive biology of exploited fish have been mentioned in Chapter 6.1; however, those studies did not directly compare the changes in biological aspects due to fishing.

Significant evidence suggests that continuous fishing over the past century has led to notable changes in various phenotypic traits in many of the world's fish stocks. Fishing as an artificial selection that can affect the change of life history traits, where the most prominent impact of fishing is on the fish’s reproductive biology, becomes a central topic in the theory of fisheries-induced evolution (Enberg et al., 2010, 2012; Heino et al., 2015). This theory refers to the changes in fish populations’ genetic characteristics and life history traits resulting from selective pressures imposed by fishing activities. Research on fisheries-induced evolution began to gain attention in the late 1970s, particularly with studies on Canadian whitefish (Handford et al., 1977) and Pacific salmon (Ricker, 1981). Some observed changes, such as decreasing size-at-age and earlier maturity, align with predictions based on evolutionary life history theory (Law, 2000; Jørgensen et al., 2007; Mollet et al., 2007). These changes, however, can arise from two primary causes: 1) an adaptive response to environmental changes, known as phenotypic plasticity, or 2) changes brought about by fishing, termed fisheries-induced evolutionary change (Stokes et al., 1993).

Distinguishing between the effects of genetic selection and phenotypic plasticity in wild fish populations is complicated (Wright, 2007). Nevertheless, fisheries-induced evolution must be explored in Indonesia since many species are currently under overfishing and fully exploited conditions (MMAF, 2022a). Those conditions can shift fish biology and ecology, including habitat choice, diet choice, social behavior, maintenance, immune defense, neural development and cognition, morphology, migration, energy storage, somatic growth, reproduction, and phenology (Neuheimer and Taggart, 2010). The recent study by **Retnoningtyas et al. (2023a)** exposed the differences in maturity size of the mackerel scad *Decapterus macarellus* associated with different fishing pressures. The authors argued that the smaller size at maturity observed from the fish in the Maluku Sea was caused by higher fishing pressure, hence fishing-induced evolution. Size or age of maturity is indeed not solely affected by high fishing pressure (Jonsson et al., 2013; Amarasinghe and Pauly, 2021); however, stocks experiencing significant levels of fishing mortality may show evolutionary reactions through changes in life-history variables, such as earlier ages at maturity and smaller sizes at maturity (Wootton et al., 2014; Trippel, 1995). Therefore, age and size at maturity could be indicators of fishing pressure (Trippel, 1995; Lappalainen et al., 2016).

In conclusion, considering fisheries-induced changes within the stock-assessment frameworks (Hutchings and Kuparinen, 2020) to formulate better harvest strategies is encouraged to avoid overfishing and stock collapse. More data is certainly needed to confirm whether maturity size changes due to the long history of fishing or due to environmental factors (Wright, 2007). Therefore, undertaking evolutionary impact assessments and genetic monitoring is deemed important to detect genetic changes induced by fishing that might affect long-term sustainability for the management of valuable marine fisheries (Jørgensen et al., 2007; Schwartz et al., 2007; Allendorf et al., 2014). Findings from **Retnoningtyas et al. (2023a)** may contribute insights to the theory of fisheries-induced evolution and to this thesis, support **working hypothesis 2: pressure from fishing affects the maturity size of the mackerel scad *Decapterus macarellus* in tropical eastern Indonesia**.

6.3. Parasites as an indicator for stock delineation and connectivity

Fisheries contribute significantly to the global economy, providing livelihoods to millions of people. Along with the growing concern of declines in fish stock production as a direct impact of fishing (Worm et al., 2009; Branch et al., 2011; Pauly et al., 2013), understanding the dynamics of fish populations is essential to ensure that the fish are harvested at sustainable level. Therefore, proper assessment helps set catch limits that prevent overfishing while allowing for economic benefits. The process of estimating the abundance, health, and dynamics of fish populations, also known as stock assessment, involves the collection and analysis of various data, including the spatial structure of the selected stock, catch and effort data, biological characteristics of the fish (age, sex, mortality), genetic information, habitat, and environmental factors (Maunder and Watters, 2003; Brown et al., 2019; Maunder and Thorson, 2019; Punt, 2023). In managing fisheries, including assessing the fish stocks, we not only aim to determine changes in the abundance of fish stocks in response to fishing but also to predict future trends of stock abundance (Sparre and Venema, 1998).

The concept of stock and stock identification

The concept of stock was developed to categorize distinct groups of fish, allowing for a precise analysis of their population dynamics concerning fishing activities (Cadrin and Secor, 2009). The term “unit stocks” emphasized these groups’ unique reactions to fishing and other external factors. Early definitions of the unit stocks prioritized more pragmatic or practical descriptions that were based on characteristics observed during fisheries, such as where and when certain groups of fish were caught or their observable behaviors to fishing activities and on demographic attributes that were consistent or homogeneous within a group, i.e., similar age or size distributions among fish in a particular group (Russell, 1931; Waples et al., 2008; Cope and Punt, 2009). Operationally, a stock can be defined depending on its ecological, technical, recreational, economic, or fishery attributes, and an operational definition can be tailored for a specific function or situation without ignoring the underlying biological realities of a population or species (Secor, 2014). Booke (1981), for instance, due to practical consideration of the geographic extent of fishing, proposed that a stock is a group of fish that remains relatively stable and self-sustaining within a specific, identifiable area at a given time. Over time, the importance of understanding stocks as biologically distinct, self-reproducing groups emerged (Waldman, 2005). In managing fisheries, these definitions have remained useful; the FAO, for instance, views a stock as a subset of a species with consistent growth and mortality rates in a specific region (Sparre and Venema, 1998). Over the past century, the identification of stocks has primarily used methods assessing reproductive isolation, emphasizing the biological aspects of the stock concept.

However, determining the stock structure of fish might be challenging due to their variability and instability (Fréon et al., 2005), as the distribution might fluctuate at different spaces and times (Izzo et al., 2017). Several factors contribute to the identification of fish stocks, including life history traits, genetic diversity, migration patterns, and other environmental factors, and from there, the methods used in stock identification were developed (Cadrin et al., 2014). Various techniques for stock identification include the commonly available catch and effort data (Cope and Punt, 2009), life history characteristics (Haddon, 2011), morphology (Begg and Waldman, 1999), genetics (Arnaud et al., 1999; Abedi et al., 2012; Habib and Sulaiman, 2017), and tagging, both artificial and biological (Baker et al., 2007; Buckworth et al., 2012; Klapper et al., 2016). As biological tags, parasites also provide phylogenetic descriptions and clarify ancestral dispersal routes and feeding habits of their hosts (Moser, 1991). Certain advantages of parasite tags over artificial tags are that they are more appropriate for studies of species that are unlikely to survive capture, handling, and tagging. They can, therefore, eliminate doubts concerning possible abnormal behavior of artificially tagged hosts (MacKenzie, 2002). Every fish is already tagged with parasites, and artificially tagged fish are often, after all efforts, not recovered from the wild for subsequent analyses.

Stock delineation of pelagic fish: case studies of the mackerel scad and the narrow-barred Spanish mackerel by using fish parasites

Despite its applicability to study diverse groups of fish (Bower and Margolis, 1991; Arthur and Albert, 1993; Moore et al., 2003; Baker et al., 2007; Luque et al., 2010; Henriquez et al., 2011; Baldwin et al., 2012; Cantatore and Timi, 2015; Anglade and Randhawa, 2018), parasites are rarely used to delineate stock in Indonesia's fisheries, particularly small pelagic fisheries. In addition to the already applied methods, i.e., general morphometry (Ardi, 2018), otolith morphometry (Manginsela et al., 2020), and genetic (Suwarso and Zamroni, 2013; Zamroni and Suwarso, 2018), **Retnoningtyas et al. (2023b)** used metazoan parasites as indicators to delineate small pelagic fish stocks between adjacent fishing grounds in eastern Indonesian waters. The study revealed different stocks of mackerel scad *Decapterus macarellus* which were not only observed between fish from the Sulawesi Sea and Maluku Sea, but possibly with other areas such as Java Sea, Bali Sea, and Papua New Guinea, with regards to the nematode Anisakidae. As reported by Palm et al. (2017) and Theisen (2019), Anisakidae can be considered a common fish parasite of scads, however, **Retnoningtyas et al. (2023)** found no Anisakidae in their samples from both Sulawesi Sea and Maluku Sea. The presence or absence of certain parasites is associated with different preys in the respective habitats, thus indicating different origins of the host populations.

Using parasites as biological tags for migratory species distributed over long distances proves notably beneficial. Parasites have been used as biological tags, i.e., to examine the infestation between wild and domesticated salmon (Price et al., 2010; Bui et al., 2018), to investigate the swimming ability of European eel, *Anguilla anguilla* L. 1758, during their migration (Myrenås et al., 2023); to identify the nursery ground of Atlantic bluefin tuna *Thunnus thynnus* (Rodríguez-Llanos et al., 2015); and to track the movement of the narrow-barred Spanish mackerel *Scomberomorus commerson* (Lester et al., 2001; Moore et al., 2003). A similar study was undertaken by Latama (2006) in the Sulawesi Sea and the adjacent waters and revealed four distinct population groups of the narrow-barred Spanish mackerel within the respective region. Latama (2006) also compared their results to Lester et al. (2001) and concluded that the narrow-barred Spanish mackerel in Sulawesi belonged to different population from the Australian's as well as from Kupang. To investigate the stocks in western Indonesian waters, **Retnoningtyas et al. … (a)** compared the metazoan parasites composition of the narrow-barred Spanish mackerel caught off of the northern and southern Java coasts. The study, which revealed that both populations belonged to different groups as indicated by significant numbers of trypanorhynch cestode *Callitetrarhynchus gracilis* harbored by the fish from the northern Java coast, also compared the results to Latama's work in Sulawesi and concluded that the stocks from Java coasts were different with Sulawesi's stocks.

Findings from Lester et al. (2001), Moore et al. (2003), Latama (2006), and **Retnoningtyas et al. …(a)** were important to the Indonesian narrow-barred Spanish mackerel fisheries. Despite its continuous exploitation, no sufficient information on the distribution of the narrow-barred Spanish mackerel is available for Indonesian waters. This species is commonly found at almost every fishing port nationwide, and the landings were made throughout the year. Although known as a migratory species, their migratory route over the Indonesian archipelago remains undiscovered. The narrow-barred Spanish mackerel is a pelagic fish belonging to the Scombrid group known to move across large distances but also signals local stocks formation. Therefore, this species is likely to become a shared stock, typically where the distribution and migration patterns span across the waters of different regions or territories. Studies from the authors mentioned above demonstrate the helpful application of parasites as a stock indicator in investigating stock delineation of either locally-distributed pelagic species, such as the mackerel scad, or a wider-scale migrating species, such as the narrow-barred Spanish mackerel.

The parasites approach can provide background information to investigate the stock structure further or complement and confirm the results from other techniques. Findings from **Retnoningtyas et al. (2023b)** confirmed the stock separation of the mackerel scad based on a molecular approach by Zamroni et al. (2014), while **Retnoningtyas et al. …(a)** confirms a molecular study from Habib and Sulaiman (2016) which indicated a possible connection between the narrow-barred Spanish mackerel population of the Bali Sea, Java Sea, and the South China Sea. This assumption supports the theory that the narrow-barred Spanish mackerel migrates through this route and that the population between the South China Sea, Sumatra, and the Java Sea probably belongs to a single stock. Although research in parasites as biological tags for stock identification of Indonesia's fisheries resources is still limited, the above examples demonstrate the advantage of using parasites to undertake stock delineation and define stock boundaries for further developing appropriate management measures. In addition to understanding the reproductive biology and spawning behaviour (Chapter 6.1) and fishing mortality (Chapter 6.2) of the exploited pelagic fish species, undertaking stock delineation is an inseparable part of the stock assessment process. The study by **Retnoningtyas et al. (2023b)** supports **working hypothesis 3,** that **it is possible to discriminate different mackerel scad stocks in the two adjacent waters (Sulawesi Sea and Maluku Sea) based on the metazoan fish parasites**. By harnessing this approach and combining it with other approaches, we can achieve a more nuanced and precise understanding of fish populations, enabling better management tailored to the unique ecological dynamics of each region. This will support not only sustainable Indonesia's marine resources but also the countless communities and industries reliant on these pelagic fish stocks.

6.4. The development of parasite studies and its expanding implementation in Indonesia

Parasite research in Indonesia, which initially concentrating on taxonomical identification and zoonotic parasite species (e.g. Hadidjaja et al., 1978; Ilahude et al., 1978; Palm, 2000, 2004, 2008; Jakob and Palm, 2006; Palm et al., 2007, 2008; Bray and Palm, 2009; Dewi and Palm, 2013, 2017; H. Palm et al., 2017; Theisen et al., 2017, 2018; Bray et al., 2019), and has undergone significant development over the years. This early research laid a strong foundation for understanding the diversity of parasites that affect these fish populations and the effective methods to control and manage their impact on the industry. Over time, the knowledge garnered from studying parasites taxonomy has proven to be invaluable in exploring their potential as indicators for environment quality (Palm and Rückert, 2009; Rückert et al., 2009; Rueckert et al., 2009; Palm et al., 2011; Kleinertz et al., 2014, 2016; Kleinertz and Palm, 2015; Neubert et al., 2016; Kunzmann et al., 2022), mariculture (Rückert et al., 2009; Palm et al., 2015; Kleinertz et al., 2022b), as well as host biology and ecology (Palm et al., 2017; Koepper et al., 2021, 2022; Pambudi et al., 2021; Kleinertz et al., 2022a). Researchers have discovered that parasites are crucial in predator-prey interactions within ecosystems. By examining the presence and abundance of various parasite species, one can gain insights into the overall health and balance of the environment, which has far-reaching implications for management and conservation efforts. By recognizing broader applications of parasites, researchers have unlocked new possibilities for harnessing parasites as tools to monitor and assess the health and stability of aquatic ecosystems. This multidimensional approach enhances our understanding of the complex interconnections in nature and offers opportunities for developing sustainable use of resources.

Through extensive research, we can better understand the metazoan parasite communities associated with different fish populations. Parasites act as natural tags that can differentiate and identify distinct regional fish stocks. Parasites' affinity for specific host species and ability to form distinct communities in different habitats make them reliable indicators of stock boundaries. By studying the variations in parasite composition among different fish populations, researchers can delineate the geographical distribution of various stocks. The use of parasites in stock delineation offers several advantages over traditional methods, for instance, it provides a cost-effective and non-invasive means of gathering essential data on fish populations. Unlike invasive techniques like tagging or genetic sampling, parasite analysis can be conducted without harming the fish, making it a more sustainable approach. Moreover, parasites are a natural recorder of the fish's movement and migration patterns. As fish move between different habitats and regions, they acquire new parasites from their environment. By analyzing these parasites, researchers can trace the migratory routes of different fish stocks and understand their distribution. This knowledge provides significant implications for fisheries management in Indonesia. It allows for targeted and tailored management strategies for each stock, ensuring sustainable harvesting practices and reducing the risk of overexploitation. By conserving and managing each stock independently, fisheries can maintain healthy populations and promote the overall ecological balance of marine ecosystems. In addition, by leveraging this valuable information, policymakers and scientists can make informed decisions to protect the marine environment and ensure the long-term viability of fish populations in the region.

Latama (2006) was the first to reveal different populations of the narrow-barred Spanish mackerel (*Scomberomorus commerson*) through its metazoan parasite composition in Indonesian waters. The research identified four clusters of parasite populations in Sulawesi waters based on sampling localities. Furthermore, his study also compared the parasite composition of *S. commerson* in Sulawesi with parasites of *S. commerson* from Australia and found that the parasite composition from both locations was different. Therefore, the result concluded that the stock of *S. commerson* in Sulawesi is different and isolated from those in Australia. Previously, Lester et al. (2001) concluded that the stock of *S. commerson* from

Australian waters is separated from Kupang (East Nusa Tenggara) as it showed no fish movement from Australian waters to Kupang. This finding supports **working hypothesis 4: the metazoan fish parasites fauna allows identification of the population structure of the narrow-barred Spanish mackerel *Scomberomorus commerson* across the Indonesian archipelago**

The knowledge available on parasites from Indonesia's marine waters has opened up exciting opportunities for their application in fisheries stock delineation (Latama, 2006; Heirina et al., 2021; **Retnoningtyas et al., 2023b, Retnoningtyas et al. …(a)**), supporting the **working hypothesis 5: knowledge of marine fish parasites in Indonesia contributes to develop further methodological approaches in fisheries science in order to support a better sustainable fisheries management in future**. The study by **Retnoningtyas et al. (2023b) and Retnoningtyas et al. …(a)**, in particular, demonstrate promising potential for distinguishing between the stocks of mackerel scad and narrow-barred Spanish mackerel from their parasite fauna, respectively; however, the effectiveness of this method may be limited by the current lack of information on extensive migration routes, especially in the case of the narrow-barred Spanish mackerel. Therefore, a multi-disciplinary approach is strongly suggested to understand the stock structure and dynamics comprehensively. Looking ahead, it would be invaluable to expand this research to understand the stock distributions of other highly exploited fish species in Indonesia. Specifically, focus could be directed towards species with a broader regional presence than the mackerel scad but a less extensive distribution, such as those in the grouper (Epinephelidae), snapper (Lutjanidae), and fusilier (Caesionidae) families, as well as Bali sardinella (*Sardinella lemuru*).

6.5. Management and conservation of fisheries resources in Indonesia

Due to the expanding global population, food security has become a significant issue on the national and worldwide levels. This makes proper management of the available natural resources inevitable. In many coastal areas, typically situated in rural parts of the world, fishery resources contribute an essential source of nutrition; thus, the sustainable use of these resources invites significant attention as research subjects. Despite considerable advances, the challenges of preserving or restoring fishery's sustainability and stock numbers, minimizing environmental impact and degradation, and enhancing local and global food security remain enormous in unpredictable and changing ecosystems (Garcia and Rosenberg, 2010).

Appropriate management practices should be applied to help maintain the health and productivity of marine ecosystems, to prevent overfishing and depletion of fish stocks, and to ensure the availability of fish resources for present and future generations.

Resource management is closely intertwined with the primary goal of conservation, which is to protect against extinction. From the perspective of a fisheries manager, conservation encompasses both habitat and species preservation, as it plays a vital role in effective resource management. In addition, the ultimate aim of conservation is to maintain the ecosystem balance, including intricate food webs created through predator-prey relationships. Disturbing one component of the food web can have far-reaching consequences. For instance, the loss of one population can lead to the depletion of certain species due to food scarcity.

On the other hand, explosive growth occurs due to the predator's absence. In nature, the foundation of the food web, excluding humans, is built by various life forms ranging from tiny to gigantic, including free-living and non-free-living organisms such as parasites. Despite the common perception as sources of disease to be eliminated, parasites play a critical role in living systems on Earth. Without parasites to keep certain animal populations in check, some species would experience explosive growth, much like invasive species, when removed from their natural predators. In conclusion, conservation is an integral part of resource management, ensuring the preservation of ecosystems and their intricate interdependencies. Recognizing the importance of parasites in ecological balance challenges us to reconsider their significance. It emphasizes the need to protect them to maintain a thriving and healthy environment.

In addition to conducting a biological assessment of exploited fish species, this thesis also focuses on using a parasitic approach to distinguish pelagic fish stocks. Delving into the complexities of host-parasite interactions has revealed a profound connection between the parasite and its host. Events affecting the host also impact the parasite, and vice versa. Environmental conditions and the host's habitat play a crucial role in shaping both the host and the parasite's lives, creating a complex interdependence. Understanding parasites has shed light on a notable characteristic of natural pelagic fish: migration and movement. While it was previously understood that fish move in search of food, comprehending the life cycle of parasites has revealed another motive: the role of parasites in influencing their host's movement to find another host, essential for the parasite's life cycle and their survival on Earth. From a management standpoint, this natural cycle is of the utmost importance to preserve. Managing fish resources goes beyond maintaining human livelihoods reliant on the sea and ensuring food security. It also encompasses sustaining the critical roles of the main actors in nature: predators, prey, and parasites living in them. Parasites, often underestimated, hold significant power and influence in the ecosystem. In summary, the research in this thesis highlights the use of the parasitic approach to differentiate pelagic fish stocks. However, it also emphasizes the profound link between parasites and their hosts. Understanding this connection reveals the importance of preserving all species' natural cycles and roles, including parasites, in maintaining a balanced and thriving ecosystem.

In the last part of this chapter, I would like to reflect on the journey of this research, tracing back to its primary topic: stock delineation to support fisheries management. Fish, a vital resource supporting life and human livelihoods, requires careful measures to protect it from extinction. The aim is to ensure that future generations can benefit from this resource long-term. Human activities are crucial in shaping the Earth as we live in the Anthropocene era. To my understanding, managing resources represents a responsible approach to the extraction and exploitation actions we undertake to sustain ourselves, provide for our families, and drive economic growth. Effectively managing resources demands a comprehensive understanding of their fundamental characteristics. For instance, fish populations, particularly pelagic species, are highly dynamic and challenging to estimate within an area precisely. However, we can predict their growth patterns and reproductive behaviors to determine appropriate harvesting ages and sizes. This ensures sufficient time for the fish to mature and reproduce, promoting regeneration.

Moreover, monitoring and assessing the level of exploitation is vital to prevent overfishing and depletion. We have learned from past events where a certain amount of fish species significantly decreased from fishermen's catches, leading to fisheries collapse and the need to halt fishing activities (Rose et al., 2000; Toresen and Østvedt, 2000; Hylen, 2002; Bundy et al., 2009; Hutchings and Rangeley, 2011; Sguotti et al., 2019; Falsone et al., 2021). These experiences have instilled a sense of caution, driving us to take proactive measures to avoid such consequences in the future. In essence, managing resources not only secures their preservation but also involves establishing a sustainable use of these resources. This balance allows us to safeguard these valuable resources for the benefit of present and future generations.

7. Future outlook

To achieve sustainability, research which related to fisheries resources management should be focused on understanding the ecological, social, and economic implications of fishing practices. Evaluating the effectiveness of selective fishing techniques and mitigating the adverse impacts of fishing pressure on their reproductive biology, for instance, are examples of subjects related to the ecological aspects that help managers in formulating better management measures. Selective fishing techniques, designed to target specific size classes or non-reproductive individuals, can help reduce the pressure on the spawning stock and ensure a higher proportion of mature individuals are left to reproduce. For commercially valuable commodities, such as the mackerel scad *Decapterus macarellus* and the narrow-barred Spanish mackerel *Scomberomorus commerson*, monitoring the exploitation rate and fish reproduction is crucial. By minimizing the capture of the juveniles, these practices can facilitate the replenishment of the population and sustain its reproductive capacity.

Additionally, establishing marine protected areas (MPAs) tailored specifically to spawning grounds of commercially exploited fish can provide a sanctuary for the species to reproduce and grow with minimum human interference. MPAs act as safe havens, supporting the fish's natural reproductive behavior and fostering strong and healthy populations. Advanced technologies, such as acoustic and satellite tracking, can aid in monitoring the movement and behavior of fish populations within and outside the designated MPAs. This study, particularly for the mackerel scad, was partly conducted under the Pelagic MPA project, which was newly-developed in Indonesia. This project aimed to identify the target areas and focus species to be managed. Data and information collected through this study offer critical insights into their spatial distribution, migration patterns, and habitat preferences, and therefore, informing more targeted and effective conservation measures for future development.

In the future, exploring the influence of environmental factors (e.g., temperature and ocean acidification) on the reproductive biology of exploited fish species is of the utmost importance in facing climate change effects. With the Earth experiencing unprecedented shifts in climate patterns, understanding how these changes affect the reproductive processes of exploited fish species becomes crucial for their conservation and management. Temperature, for instance, plays a pivotal role in the reproductive success of fish, as it directly affects their metabolic rates, spawning behavior, and larval development. Research can investigate how rising sea temperatures impact the timing and location of spawning events, potentially leading to mismatches with optimal environmental conditions for egg and larval survival. Furthermore, changes in ocean currents and upwelling patterns driven by climate change can alter the distribution and abundance of plankton, a critical food source, especially for many fish larvae. Studying the relationship between food availability and the reproductive success of exploited fish species can help us understand the potential cascading effects throughout the food web. To conduct such studies, applying multidisciplinary approach is encouraged, as well as combining different techniques, such as field observations, laboratory experiments, and computational modelling. For pelagic fish species, in particular, long-term monitoring programs can track reproductive events in populations over time, while controlled experiments can simulate various environmental scenarios to assess their effects on reproductive biology.

In recent years, research on parasites has been poised to take a significant leap forward by applying molecular methods, yielding more precise and in-depth results regarding parasite identification and their relationship with their hosts. Traditional methods of parasite identification have limitations, but molecular techniques offer opportunities to unlock the genetic information embedded within parasites and their hosts. Advances in molecular techniques offer accuracy in identifying parasites which serve as biological tags for different fish populations. This will enable a finer resolution of parasite diversity within host populations and ecosystems, providing a more comprehensive understanding of parasite-host interactions. As these methods can identify even subtle genetic differences, researchers can uncover previously hidden parasite diversity, which is crucial for understanding the complexities of parasite-host relationships.

The field of parasite study present opportunities for the investigation of stocks of exploited fish species. Such markers can help researchers understand the migratory patterns, therefore allowing for more effective fisheries management. The present study recommends that research on reproductive biology, spawning behavior, and stock structures should be prioritized for fish species which are highly exploited and need strong management measures to prevent from overfishing, such as grouper (Epinephelidae), snapper (Lutjanidae), and fusilier (Caesionidae) families, as well as Bali sardinella (*Sardinella lemuru*). Applying different approaches to study stock structures and their dynamics will result in a more comprehensive conclusion, and therefore, enable managers in developing more effective management strategies.

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Eidesstattliche Erklärung

Hiermit erkläre ich durch eigenhändige Unterschrift, die vorliegende Dissertation selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet zu haben. Die aus den Quellen direkt oder indirekt übernommenen Gedanken sind als solche kenntlich gemacht. Die Dissertation ist in dieser Form noch keiner anderen Prüfungsbehörde vorgelegt worden.

Independence Declaration for the Dissertation

I hereby declare with my signature that I have written the dissertation on my own and that I have not used any sources other than those specified. The thoughts taken directly or indirectly from the sources are identified as such. The dissertation has not yet been submitted to any other examination authority in this form.

Rostock, 14 September 2023 Unterschrift der Doktorandin

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Appendix 1

Mean length (cm) and weight (g) of immature and mature individuals of *Decapterus macarellus* caught in northern Sulawesi based on its sex (male and female). Range of length and weight of the samples are presented in the bracket.

Year	Month	Female					
		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 (113.4-277.83)
2020	Jul	95	18.00 (13.40-23.40)	57.97 (2.26-130.4)	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 (152.8-312.98)
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)

Year	Month	Male					
		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)

Year	**Month**	**Male**					
		Immature			**Mature**		
		n	**Length**	**Weight**	**n**	**Length**	**Weight**
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)

Appendix 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
Sulawesi Sea, Indonesia	1.02:1	22.59 (M), 21.62 (F) TL	0.02-12.20	Jan, Mar, May, Sep	Present study
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

Sites	Sex ratio (M:F)	Lm (cm)	Range of Gonadosomatic Index (%)	Reproductive Season	Source
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

Appendix 3

Prevalence (P), mean intensity (I), and mean abundance (mA) of parasites found in *Decapterus macarellus* from North Sulawesi (Sitaro and Sangihe) and North Maluku (West Halmahera). Ranges are given in brackets. Site of infections were the body cavity (bc), gill cavity (gc), gills (gi), gut wash (gw), intestine (i), mouth cavity (mc), pyloric caeca (py). Kruskal-Wallis H test with p-value <0.05 (*) indicates parasite species with significantly different distribution between locations.

Parasite taxa	Site of infection	Sitaro			Sangihe			West Halmahera		
		Sample size: 35			Sample size: 35			Sample size: 35		
		P (%)	mA	mI	P (%)	mA	mI	P (%)	mA	mI
Monogenea										
*Allopseudodiclidophora opelu**	gi, gw, i	88.57	2.83	3.19 (1-13)	97.14	5.57	5.74 (1-24)	100	18.91	18.91 (1-53)
*Pseudodiclidophora decapteri**	gi, bc	100	62.89	62.89 (23-139)	100	57.17	57.17 (12-133)	62.86	13.43	21.36 (1-94)
Pseudaxine cf. *trachuri*	gi	14.29	0.17	1.2 (1-2)	28.57	0.51	1.80 (1-3)	17.14	0.26	1.5 (1-4)
Polyopisthocotylea indet.	gi	2.86	0.03	1.0 (1)	5.71	0.06	1.0 (1)	2.86	0.06	2.0 (2)
Digenea										
*Ectenurus selari**	gw, bc	68.57	1.26	1.83 (1-4)	37.14	0.46	1.23 (1-2)	22.86	0.46	2.0 (1-4)
*Neonotoporus trachuri**	gw	17.14	0.63	3.67 (1-16)	0.0	0	-	5.71	0.06	1.0 (1)
Pseudopecoeloides opelu	gw	5.71	0.06	1.0 (1)	0.0	0	-	2.86	0.03	1.0 (1)
Tergestiinae indet.	gw	0	0	-	5.71	0.14	2.50 (1-4)	0	0	-
Didymozoidea (larvae) indet.*	gw	5.71	0.06	1.0 (1)	51.43	1.14	2.22 (1-4)	14.29	0.14	1.0 (1)
Digenea indet. 1	gw, bc	0	0	-	2.86	0.03	1.0 (1)	5.71	0.06	1.0 (1)
Digenea indet. 2	gw	0	0	-	8.57	0.34	4.0 (1-9)	5.71	0.06	1.0 (1)
Digenea indet. 3	gw	0	0	-	5.71	0.09	1.5 (1-2)	0	0	-
Acanthocephala										
Rhadinorhynchus sp.	gw, i, bc, py	5.71	0.06	1.0 (1)	5.71	0.06	1.0 (1)	17.14	0.37	2.17 (1-7)
Crustacea										
Caligus sp.	gi	0	0	-	2.86	0.03	1.0 (1)	2.86	0.06	2.0 (2)
*Cerathotoa carinata**	mc, gc	0	0	-	2.86	0.06	2.0 (2)	14.29	0.2	1.4 (1-2)

Appendix 4

Statistical difference of parasites' mean abundance with *p*-value <0.05 (indicated by [*]). Mann-Whitney U test identifies which paired sites were significantly different. Sites are coded as SI (Sitaro/North Sulawesi), SA (Sangihe/North Sulawesi), and WH (West Halmahera (North Maluku).

Species	SI-SA		SA-WH		SI-WH	
	W	*p*	W	*p*	W	*p*
Allopseudodiclidophora opelu	337.5	<0.002*	161	<0.001*	68.5	<0.001*
Pseudodiclidophora decapteri	678.5	0.44	1126.5	<0.001*	1143	<0.001*
Ectenurus selari	844	0.003*	681.5	0.32	884.5	<0.001*
Neonotoporus trachuri	717.5	0.01*	577.5	0.16	684.5	0.13
Didymozoidea (larvae) indet.	319.5	<0.001*	872.5	<0.001*	560	0.24
Cerathotoa carinata	595	0.33	544	0.1	525	0.02*

Appendix 5

Statistical difference of parasites' prevalence with *p*-value <0.05 (indicated by [*]) as resulted from Two Proportion Z Test. Sites are coded as SI (Sitaro/North Sulawesi), SA (Sangihe/North Sulawesi), and WH (West Halmahera (North Maluku).

Species	SI-SA		SA-WH		SI-WH	
	z	*p*	z	*p*	z	*p*
Allopseudodiclidophora opelu	-1.31	0.1	-1.03	0.15	-2.02	0.022*
Pseudodiclidophora decapteri	NA	NA	3.99	<0.001*	3.99	<0.001*
Ectenurus selari	2.68	0.004*	1.28	0.10	3.86	<0.001*
Neonotoporus trachuri	2.55	0.005*	-1.47	0.07	1.44	0.08
Didymozoidea (larvae) indet.	-4.17	<0.001*	3.31	<0.001*	-1.12	0.13
Cerathotoa carinata	-1.03	0.15	-1.65	0.05	-2.3	0.01*