

Original Article

Population dynamics of three *Epinephelus* groupers in the Sulawesi Sea, Indonesia

Dewi Shinta Achmad^{*1}, Muh. Saleh Nurdin², Pipin Yunus³, Abigail Mary Moore⁴

¹Department of Aquaculture, Faculty of Science and Computer Science, Muhammadiyah University of Gorontalo, Jl. Prof. Dr. H. Mansoer Pateda, 96181 Gorontalo, Gorontalo, Indonesia.

²Department of Aquatic Resources, Faculty of Animal Husbandry and Fisheries, Tadulako University, Jl. Soekarno Hatta Km. 9, 94148 Palu, Central Sulawesi, Indonesia.

³Department of Nursing, Faculty of Health Education, Muhammadiyah University of Gorontalo, Jl. Prof. Dr. H. Mansoer Pateda, 96181 Gorontalo, Gorontalo, Indonesia.

⁴Graduate School, Hasanuddin University, Jl. Perintis Kemerdekaan km 10, Makassar 90245, South Sulawesi, Indonesia.

Abstract: Groupers of the genus *Epinephelus* play important roles in coastal ecosystems and small-scale fisheries. Market demand has driven intensive exploitation, threatening stock status and coastal community livelihoods if these valuable fisheries are poorly managed. This research on grouper population dynamics in Kwandang Bay, on the Sulawesi Sea coast of Gorontalo Province, Sulawesi, Indonesia, focused on three *Epinephelus* species: *E. fasciatus*, *E. faveatus*, and *E. ongus*. The mean length at first maturity (L_{m50}) was estimated using the Spearman-Kärber formula, and population dynamics parameters were estimated through Response Surface Analysis using the ELEFAN I suite in FISAT II. Catches of all three species were dominated by juveniles with total length $TL < L_{m50}$. The respective asymptotic lengths (TL_{∞}) for *E. fasciatus*, *E. faveatus*, and *E. ongus* were 47.52, 53.50, and 52 cm, with von Bertalanffy growth coefficient K values of 0.49, 0.54 and 0.53, respectively. Natural and fishing mortality estimates were $1.01/\text{year}^{-1}$ and $1.23/\text{year}^{-1}$ for *E. fasciatus*, $1.05/\text{year}^{-1}$ and $2.00/\text{year}^{-1}$ for *E. faveatus*, and $1.04/\text{year}^{-1}$ and $2.44/\text{year}^{-1}$ for *E. ongus*. The Beverton and Holt yield per recruit analysis indicates overexploitation with respective exploitation rates (E) of $0.55/\text{year}^{-1}$, $0.66/\text{year}^{-1}$, and $0.70/\text{year}^{-1}$, all exceeding $E_{\max} = 0.37/\text{year}^{-1}$. Recommendations include setting minimum legal size limits (above 25 cm for *E. fasciatus* and *E. faveatus*, 26 cm for *E. ongus*), as well as reductions in fishing effort of 31% for *E. fasciatus*, 42% for *E. faveatus*, and 46% for *E. ongus*.

Article history:

Received 3 March 2025

Accepted 31 July 2025

Available online 25 August 2025

Keywords:

Epinephelinae
Overexploitation
Length at first maturity
Minimum size limit
Fisheries management

Introduction

Groupers (Epinephelinae) are high-value fisheries commodities, typically caught in multi-species, multi-gear tropical fisheries (Dimarchopoulou et al., 2021; Khasanah et al., 2020). They are also high-trophic-level predators that play important ecological roles in marine ecosystems (Félix-Hackradt et al., 2022). Indonesia is a major grouper exporter, contributing to the live reef food fish trade (LRFFT) as well as to the global and domestic markets for fresh, frozen, and processed grouper commodities (Amorim et al., 2020; Kadir et al., 2023). High market demand is driven by consumer preference based on organoleptic (Hughes et al., 2020; Li et al., 2024) and cultural factors (Kindsvater et al., 2017), and groupers are considered

a prime commodity in Indonesian fisheries policy (Amorim et al., 2019; Sadovy de Mitcheson et al., 2020; Tapilatu et al., 2021). While groupers are served in high-class restaurants around the world, including in producer countries such as Indonesia, the main importers and top-end consumers are Hong Kong, China, and Singapore (Anjali et al., 2019; Andriyono et al., 2020). Top-end market demand for groupers has driven increasingly widespread and intensive exploitation (O'Neill et al., 2019; Rowan, 2023). Meanwhile, grouper fisheries are typically unselective in terms of species and size (Sadovy de Mitcheson et al., 2013; Nadiarti et al., 2021). The preference for “plate-sized” fish encourages the capture of immature individuals of many species (Kindsvater et al., 2017),

*Correspondence: Dewi Shinta Achmad
E-mail: dewishintaachmad@umgo.ac.id

and in Indonesia, there is also a ready market for groupers that do not meet export market size or quality standards (Nadiarti et al., 2021; Kadir et al., 2023).

In Indonesia, groupers are typically caught by small-scale fishers, supporting the economy and food security of impoverished coastal communities (Ochieng et al., 2015; Humphries et al., 2019; Achmad et al., 2023; Syukri et al., 2025). Despite their socio-economic and ecological importance, many grouper fisheries are in trouble, with widespread declines in the abundance of many grouper populations and/or the size of the fish caught (Sadovy de Mitcheson et al., 2020; Dimarchopoulou et al., 2021; Achmad et al., 2023). While several grouper species are listed in at-risk categories in the IUCN Red List (Khasanah et al., 2020; Sadovy de Mitcheson et al., 2020; Achmad et al., 2023), assessments of species listed as “least concern” (LC) also mostly note that some populations may be at risk, even if the species is not considered at high risk of global extinction (IUCN, 2024).

Epinephelus is the most speciose genus in the Epinephelinae (Ma and Craig, 2018), and often dominates grouper catches, in particular in Indonesia (Sadovy de Mitcheson et al., 2013; Achmad et al., 2023). The Sulawesi Sea in Indonesian Fisheries Management Area (FMA 716) is an important grouper fishing ground, and Kwandang Bay on the north coast of Gorontalo Province is a major grouper fishing hub (Achmad et al., 2022; Achmad et al., 2023). The grouper catches landed in Kwandang are typically dominated by the genus *Epinephelus*, in terms of volume as well as diversity, including 11 of the 26 grouper species identified in a survey in 2021 (Achmad et al., 2023). Population dynamics studies on four of the 26 species identified in Kwandang Bay grouper catches (*Epinephelus coioides*, *Plectropomus leopardus*, *Variola albimarginata*, and *V. louti*) concluded that all four were overfished, and that without appropriate interventions, these stocks would likely continue to decline (Achmad et al., 2022, 2024). In turn, this decline is likely to have adverse impacts on the marine ecosystem (Boelter et al., 2024), impacting grouper and other fisheries and related livelihoods (Liese and Crosson, 2023). Impacts could

include range collapse, with fishers having to go further afield and/or spend more time fishing to catch enough fish (Solarin et al., 2024), raising operational costs and reducing net fisher income (N’Souvi et al., 2023).

Heavy fishing pressure can lead to a reduction in the size of fish caught (Osman et al., 2018; Mohammed-AbdAllah et al., 2022). If many individuals are caught before reaching first sexual maturity, and therefore are unable to reproduce (Artero et al., 2023), this will reduce the reproductive potential of the stock and disrupt the balance between exploitation and natural regeneration of the stock (Croll et al., 2023; Pham et al., 2023). Such a situation can also lead to early maturation, with a reduction in the size at first maturity due to fishing-driven selection, although such shifts are not always due to fishing pressure, as a similar effect can also be caused by elevated water temperatures (Chen and Liu, 2022). Furthermore, fishing pressure and fishing-driven selection can result in an altered gene pool (Sadler et al., 2023), potentially resulting in phenotypic shifts that are hard to reverse. If overfishing is not addressed through appropriate regulations and other effective mitigation measures, over time the economic impacts will be felt by fishers and their communities (Pontón-Cevallos et al., 2020) as well as fisheries-related industries, and businesses related to wild-caught grouper trade and consumption (Buchholz-Sørensen and Vella, 2016; Roca Florido and Padilla Rosa, 2024).

Population dynamics research is needed to identify stock status and prevent or address overexploitation (Burton et al., 2015; Mehanna and Samy-Kamal, 2024). Such studies evaluate fish population size structure, growth patterns, mortality, exploitation rates, and yield per recruit (Mudjirahayu et al., 2017; Sanchez and Rooker, 2021; Murie et al., 2023), providing estimates of key parameters to inform sustainable fisheries management strategies (Gebremedhin et al., 2021). Population dynamics parameters provide a scientific basis for interventions to conserve fish stocks, such as regulations on fishing vessels and fleets, setting minimum size limits, and

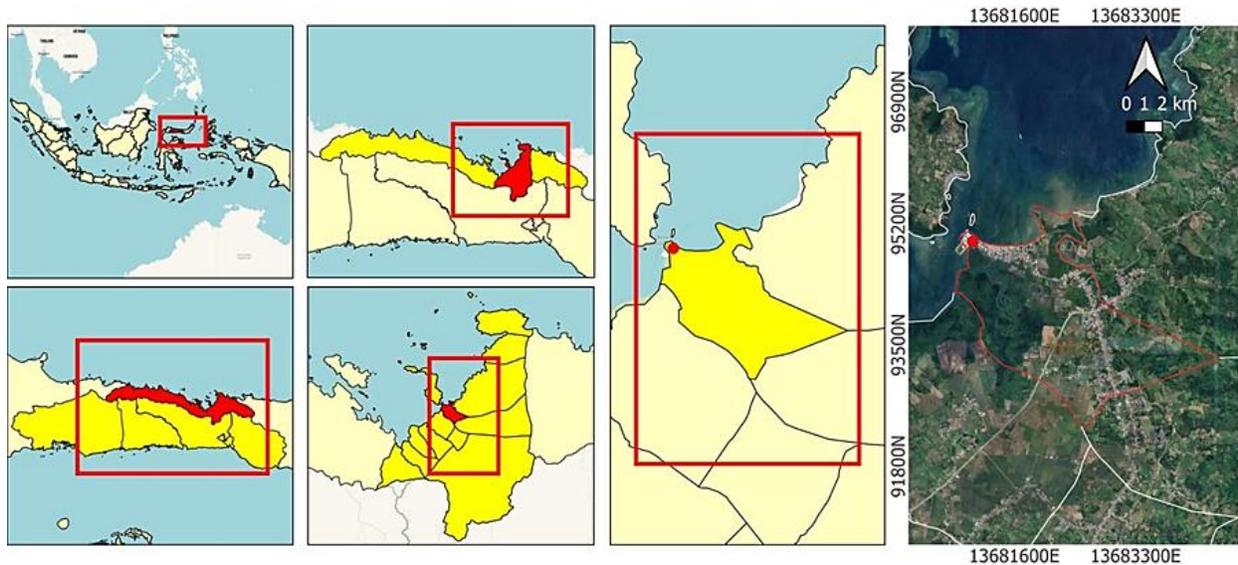


Figure 1. *Epinephelus* grouper fishing grounds in Kwandang Bay, Sulawesi Sea, Indonesia (Achmad et al., 2024).

total allowable catch volume (Richter et al., 2018; Yildiz and Ulman, 2020; Achmad et al., 2020; Meissa et al., 2025).

Studies on the population dynamics of Indonesian *Epinephelus* grouper populations are limited in terms of the species and locations covered, including *E. fuscoguttatus* in the Spermonde Archipelago (Ernaningsih et al., 2022), *E. fuscoguttatus* in the Takabonerate National Park (Fatma et al., 2022), *E. areolatus* in the Java Sea (Tirtadanu et al., 2023), and *E. coioides* in Kwandang Bay (Achmad et al., 2022). The purpose of this study was to estimate population dynamics parameters for three previously unstudied *Epinephelus* species caught in the Sulawesi Sea and landed in Kwandang Bay. Together with the four afore-mentioned grouper population dynamics studies, the results will contribute valuable data to inform the responsible management of fisheries resources in this important grouper fishing region.

Materials and Methods

Study site and time: Data were collected over a one-year period, from November 2023 to October 2024, in Kwandang Bay, on the Sulawesi Sea coast of Gorontalo Province, Sulawesi, Indonesia (Fig. 1). Many small-scale fishers live in and around Kwandang Bay. The biodiverse coastal and marine ecosystems in this area, including extensive coral reefs, provide feeding, nursery, and spawning habitat

for many fishes, in particular groupers (Achmad et al., 2019, 2023). However, these habitats are in a heavily used coastal area and have suffered noticeable degradation (Achmad et al., 2023). Most fishers operate one-day fishing trips, typically lasting around six hours, with fishing grounds generally around 30 minutes from their fishing base (Achmad et al., 2024). **Data collection:** Length-frequency data were collected by sampling groupers belonging to the genus *Epinephelus*. Samples were taken twice a month from the fish caught and landed by Kwandang Bay fishers. Three species known to be fished in Kwandang Bay (Achmad et al., 2023) were included in this study: *E. fasciatus*, *E. faveatus*, and *E. ongus*. Over the study period, data were collected on 1094 specimens: 319 *E. fasciatus*, 360 *E. faveatus*, and 415 *E. ongus*. The total length (TL) of each specimen was measured using a Cadwell fish ruler.

Data on gonad maturity were obtained through dissection and observation of the gonads of each specimen. The maturity stage was determined based on the methods described in Achmad et al. (2019, 2023), and divided the sampled fish into the following categories: (1) Immature: oogonia present; (2) Developing/resting: previtellogenic oocytes present; (3) Maturing: yolk precursor stage, some non-staining yolk; (4) Ripe: non-staining yolk, chorion developed; (5) Running ripe: homogeneous red-staining yolk, oocytes hydrated, development complete; and (6)

Spent: atresia of ripe oocytes plus previtellogenic oocytes, presence of post-vitellogenic follicles.

Data Analysis: The parameters estimated in this study included the mean length at first maturity (L_{m50}), defined as the length at which 50% of individuals in the population had mature gonads and were ready to spawn. The L_{m50} can be used to determine a minimum legal size (MLS) that should enable sufficient individuals to reach maturity to maintain fish stocks (Udupa, 1986). The L_{m50} (based on total length TL measurements) was estimated with a 95% confidence interval (CI_{95}) using the Spearman-Kärber formula (Udupa, 1986) as follows: $m = xk + X/2 - (X \sum p_i)$, and $L_{m50} \pm CI_{95} = \text{anti log} [m \pm 1.96 \sqrt{(X^2 \sum (p_i \times q_i) / (n_i - 1))}]$, where $xk = \ln$ of the first size at which 100% of individuals are fully mature, $X = \ln$ of the size increment, $r_i =$ number of fully mature individuals in the i^{th} class, $n_i =$ number of individuals in the i^{th} class, $p_i = r_i/n_i$, and $q_i = 1 - p_i$.

Population dynamics and life history parameters of three *Epinephelus* species were estimated through Response Surface Analysis using ELEFAN I (Electronic Length Frequency Analysis) in the FISAT II (Fish Stock Assessment Tools) program (Gayanilo et al., 2005). These included asymptotic length (L_{∞}), growth parameter (K), mortality, exploitation rate, and yield per recruit (Y/R). The asymptotic length (L_{∞}) is an estimate of the maximum length that could be reached by an individual fish within the population, while the growth equation indicates the average rate at which individuals within the population increase in length over time. The growth parameters for *E. fasciatus*, *E. faveatus*, and *E. ongus* were estimated using the von Bertalanffy Growth Function (VBGF) model (Beverton and Holt, 1957) based on the length-frequency data collected using the following equations: $L_t = L_{\infty} \{1 - e^{-K(t-t_0)}\}$, and $\text{Log}(-t_0) = -0.3922 - 0.2752 \log L_{\infty} - 1.038 \log K$, where: $L_t =$ total length at time t , $L_{\infty} =$ maximum (asymptotic) total length, $K =$ growth coefficient, and $t_0 =$ theoretical age at zero length calculated using the formula in Pauly (1980).

Total mortality (Z) comprises natural mortality (M) and fishing mortality (F). Mortality estimates enable

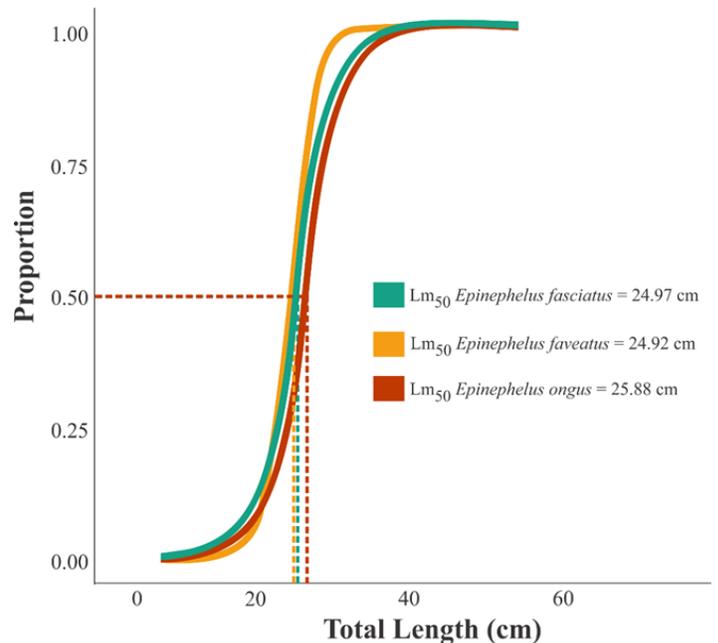


Figure 2. Mean lengths at first maturity (L_{m50}) for three *Epinephelus* grouper species in Kwandang Bay, Sulawesi Sea, Indonesia.

the estimation of the exploitation rate (E). Total mortality (Z) was estimated using the method in Ricker (1975) using the length converted catch curve as follows: $Z = K ((L_{\infty} - L) / (L - L'))$, where: $Z =$ total mortality (per year), $K =$ growth coefficient, $L_{\infty} =$ asymptotic total length (cm), $L =$ mean total length of the fish caught (cm), and $L' =$ length of the smallest fish caught (cm).

Natural mortality (M) was calculated using the following equation (Pauly, 1980): $\text{Log } M = -0.0066 - 0.279 \log TL_{\infty} + 0.6543 \log K + 0.4634 \log T$, where: $L_{\infty} =$ asymptotic length, $K =$ growth coefficient, and $T =$ annual temperature average ($^{\circ}\text{C}$). Fishing mortality (F) was calculated using the following equation (Sparre and Venema, 1998): $F = Z - M$, where: $F =$ fishing mortality, $Z =$ total mortality, and $M =$ natural mortality. The exploitation rate (E) was calculated using the following equation (Pauly, 1980): $E = F / Z$, where $E =$ exploitation rate, $F =$ fishing mortality, and $Z =$ total mortality. The yield per recruit (Y/R) is used to estimate the expected lifetime yield from a given cohort entering the population. Yield per recruit (Y/R) was calculated using the following equation (Beverton and Holt, 1964):

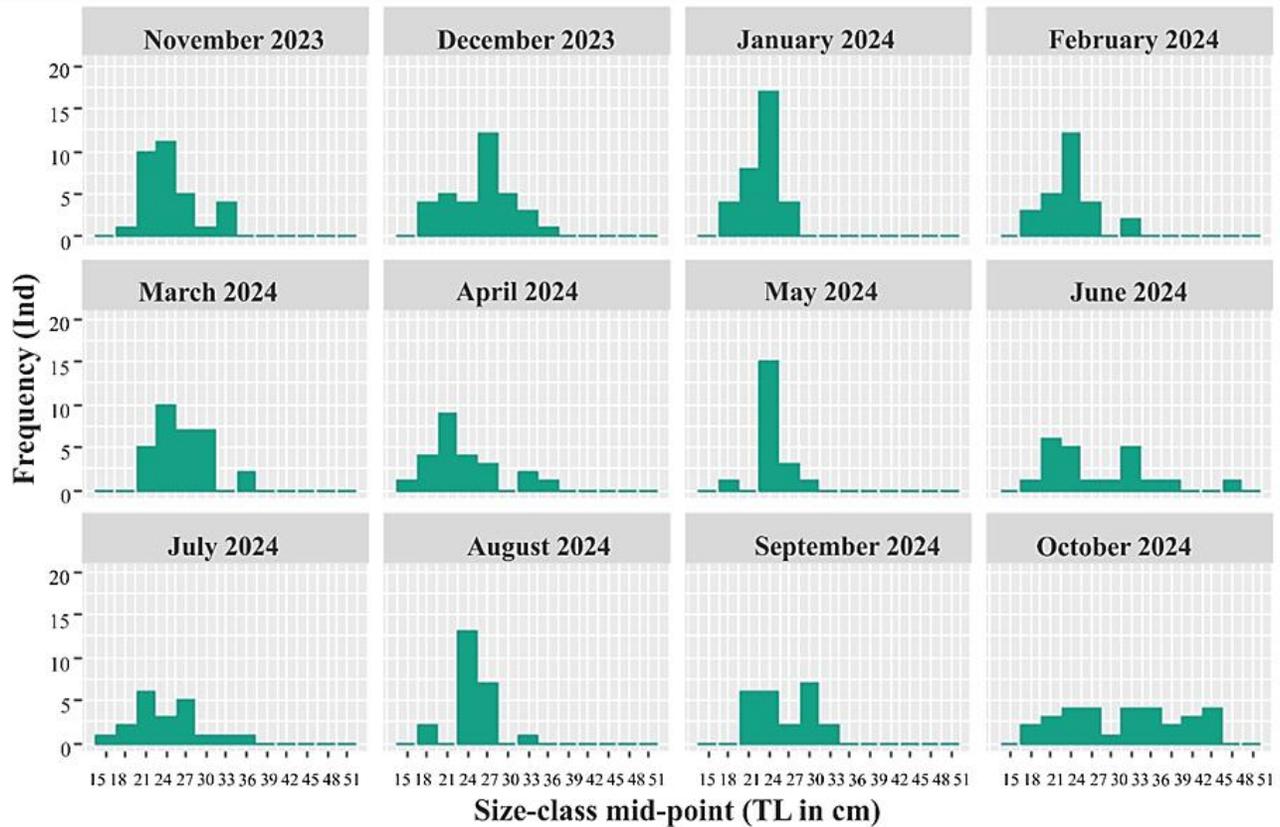


Figure 3. Monthly length-frequency histograms for *Epinephelus fasciatus* from Kwandang Bay, Sulawesi Sea, Indonesia.

$$\frac{Y'}{R} = E(1-c)^{\frac{M}{K}} \cdot 1 - \frac{3(1-c)}{1 + \frac{1-E}{\frac{M}{K}}} + \frac{3(1-c)^2}{1 + \frac{2(1-E)}{\frac{M}{K}}} + \frac{(1-c)^3}{1 + \frac{3(1-E)}{\frac{M}{K}}}$$

Where: E = exploitation rate, M = natural mortality, c = 0.05, and K = growth coefficient.

Results

Length at first maturity: The mean lengths at first maturity were similar for the three grouper species (Fig. 2). The estimated values of L_{m50} for *E. fasciatus*, *E. faveatus*, and *E. ongus* in Kwandang Bay were 24.97 cm, 24.92 cm, and 25.88 cm TL, respectively.

Size structure and Growth: The total length (TL) of the *E. fasciatus*, *E. faveatus*, and *E. ongus* samples collected from Kwandang Bay fishermen's catches over one year were expressed as range and mean \pm standard deviation (SD) and presented as histograms. The values were: 15.65–48.90 cm (25.39 \pm 5.48 cm) for *E. fasciatus* (Fig. 3); 14.35–46.10 cm (23.22 \pm 5.20 cm) for *E. faveatus* (Fig. 4), and 14.60–49.50 cm

(26.11 \pm 8.00 cm) for *E. ongus* (Fig. 5). The most abundant size class was 23–25 cm for all three species, contributing 104 *E. fasciatus* (32.60%), 123 *E. faveatus* (34.16%), and 101 *E. ongus* (24.33%). Based on the estimates for length at first maturity, the sampled Kwandang Bay catch was dominated by immature fish for all three *Epinephelus* species: *E. fasciatus* 52.66%, *E. faveatus* 75%, and *E. ongus* 60.24%.

The asymptotic length (L_{∞}) and growth coefficients (K) were similar for the three Kwandang Bay grouper species populations: 47.52 cm and 0.49 for *E. fasciatus*; 53.50 cm and 0.54 for *E. faveatus*; and 52 cm and 0.53 for *E. ongus* (Fig. 6). The growth equations for the three species were: $L_t = 47.52 \{1 - e^{-0.49(t+0.2937)}\}$ for *E. fasciatus*; $L_t = 53.50 \{1 - e^{-0.54(t+0.2570)}\}$ for *E. faveatus*; and $L_t = 52 \{1 - e^{-0.53(t+0.2641)}\}$ for *E. ongus*.

Mortality and yield per recruit: The estimated total mortality (Z), natural mortality (M), and fishing

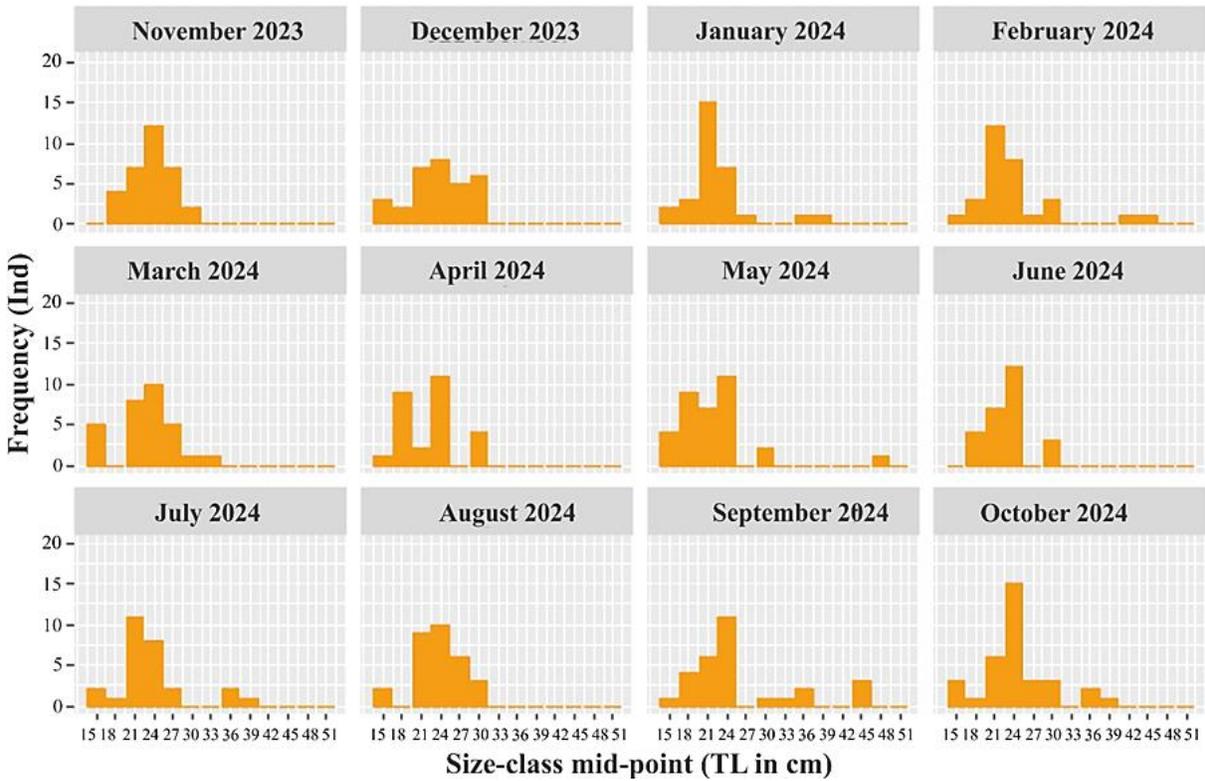


Figure 4. Monthly length-frequency histograms for *Epinephelus faveatus* from Kwandang Bay, Sulawesi Sea, Indonesia.

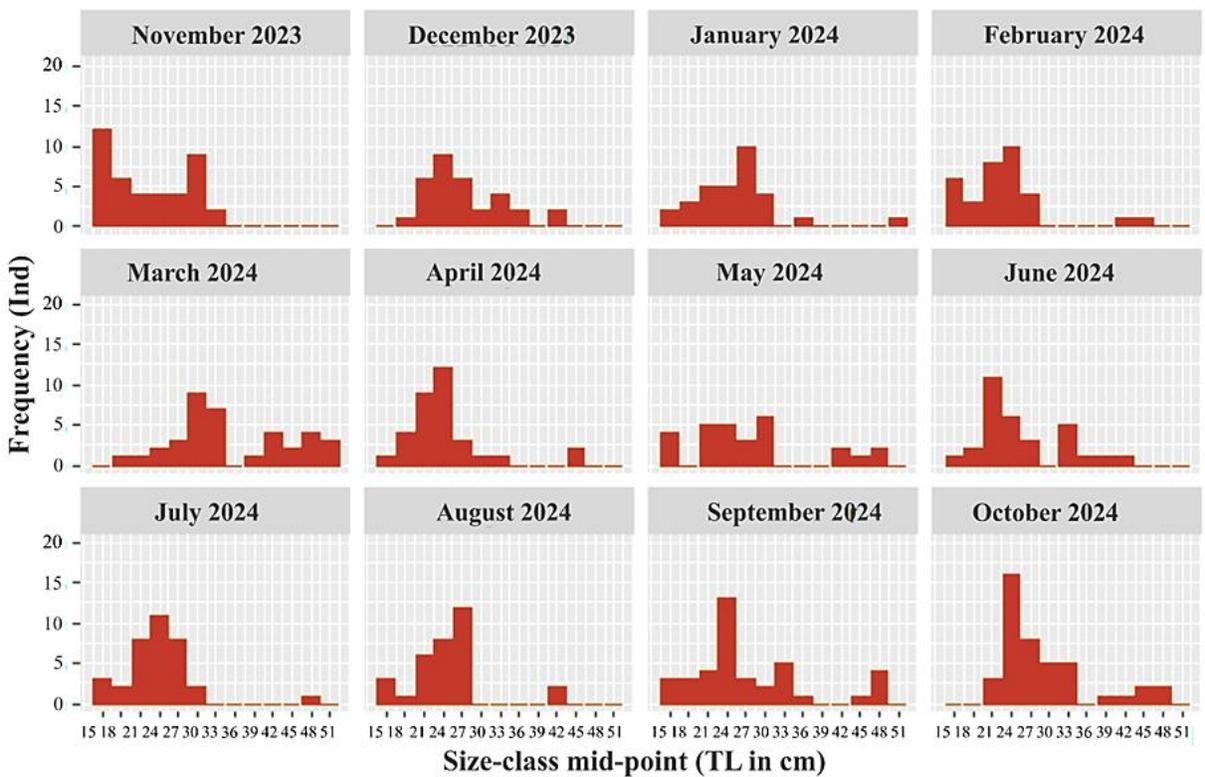


Figure 5. Monthly length-frequency histograms for *Epinephelus ongus* from Kwandang Bay, Sulawesi Sea, Indonesia.

mortality (F) for the three grouper species populations in Kwandang Bay were: $Z = 2.24/\text{year}^{-1}$, $M =$

$1.01/\text{year}^{-1}$, $F = 1.23/\text{year}^{-1}$ for *E. fasciatus* (Fig. 7); $Z = 3.05/\text{year}^{-1}$, $M = 1.05/\text{year}^{-1}$, $F = 2.00/\text{year}^{-1}$ for

Table 1. Mean length at first maturity (L_{m50}) reported for Indonesian *Epinephelus* populations.

Region of Indonesia	Species	L_{m50} (TL in cm)	Reference
Takabonerate National Park	<i>E. fuscoguttatus</i> (F)	45.43	Fatma et al. (2022)
Takabonerate National Park	<i>E. fuscoguttatus</i> (M)	66.34	Fatma et al. (2022)
Takalar, South Sulawesi	<i>E. areolatus</i> (F)	23	Sitepu (2014)
Takalar, South Sulawesi	<i>E. areolatus</i> (M)	29	Sitepu (2014)
Karimunjawa National Park	<i>E. areolatus</i>	33	Simbolon et al. (2020)
North Maluku	<i>E. ongus</i>	21.07	Ernawati et al. (2021)
Kwandang Bay, Sulawesi Sea	<i>E. coioides</i>	40	Achmad et al. (2020)
Takabonerate National Park	<i>E. polyphkadion</i>	37.48	Khasanah et al. (2019)
Wakatobi National Park	<i>E. polyphkadion</i>	40.90	Khasanah et al. (2019)
Kwandang Bay	<i>E. ongus</i>	25.88	This study
Kwandang Bay	<i>E. fasciatus</i>	24.97	This study
Kwandang Bay	<i>E. faveatus</i>	24.92	This study

Note: M = Male; F = Female

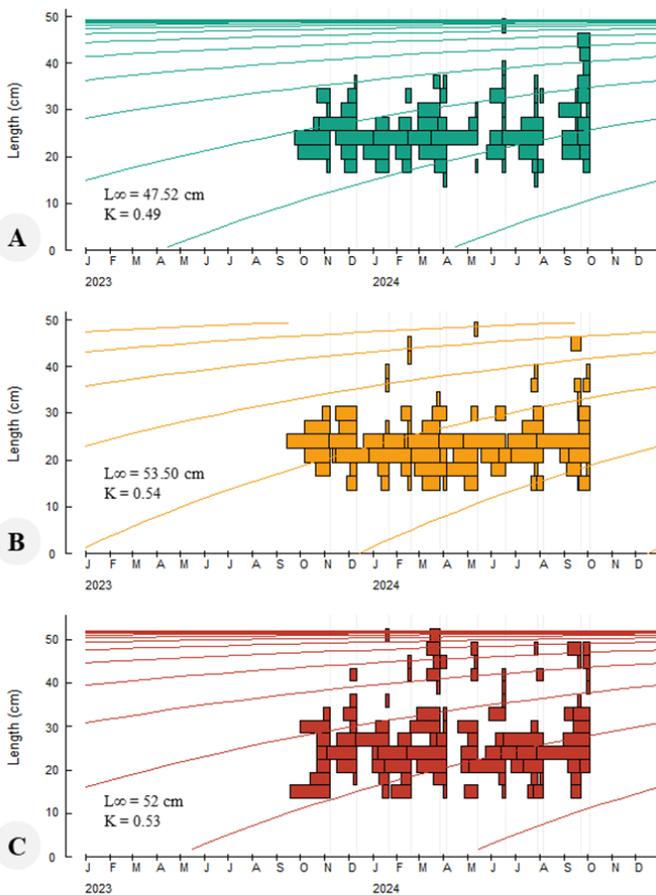


Figure 6. Length-frequency based growth curves for three *Epinephelus* groupers from Kwandang Bay, Sulawesi Sea: *Epinephelus fasciatus* (A), *E. faveatus* (B), and *E. ongus* (C).

E. faveatus (Fig. 8); and $Z = 3.48/\text{year}^{-1}$, $M = 1.04/\text{year}^{-1}$, $F = 2.44/\text{year}^{-1}$ for *E. ongus* (Fig. 9). The Beverton and Holt yield per recruit analysis indicates that all three species are overexploited, with

exploitation rates exceeding the maximum sustainable rate $E_{\max} = 0.37/\text{year}^{-1}$. The values were $E = 0.55/\text{year}^{-1}$ for *E. fasciatus*, $E = 0.66/\text{year}^{-1}$ for *E. faveatus*, and $E = 0.70/\text{year}^{-1}$ for *E. ongus*. For all three species, the exploitation rate that would result in a 50% reduction in biomass was $E_{50} = 0.24$.

Discussions

Groupers of the genus *Epinephelus* are mostly reef-associated demersal fishes (Amorim et al., 2019; Kadir et al., 2022; Mahé et al., 2022). However, post-larvae and juveniles are also found in mangrove and seagrass ecosystems, which function as nursery grounds (Jaxion-Harm et al., 2012; Utama et al., 2022). The genus *Epinephelus* comprises around 110 currently recognized species with distributions across the Indo-Pacific region (Heemstra and Randall, 1993). At least 41 species have been reported from Indonesia (Froese and Pauly, 2023). Of these, 23 have been reported from South Sulawesi (Kadir et al., 2023), 21 from Aceh (Fadli et al., 2022; Razi et al., 2022), 11 from Kwandang Bay (Achmad et al., 2023), and seven each from Papua and Madura (Basith et al., 2021; Dwifajri et al., 2022).

Biological characters, including reproductive parameters such as the mean length at first maturity (L_{m50}), vary between species and can also vary between populations within a given species, as illustrated by the examples from Indonesian

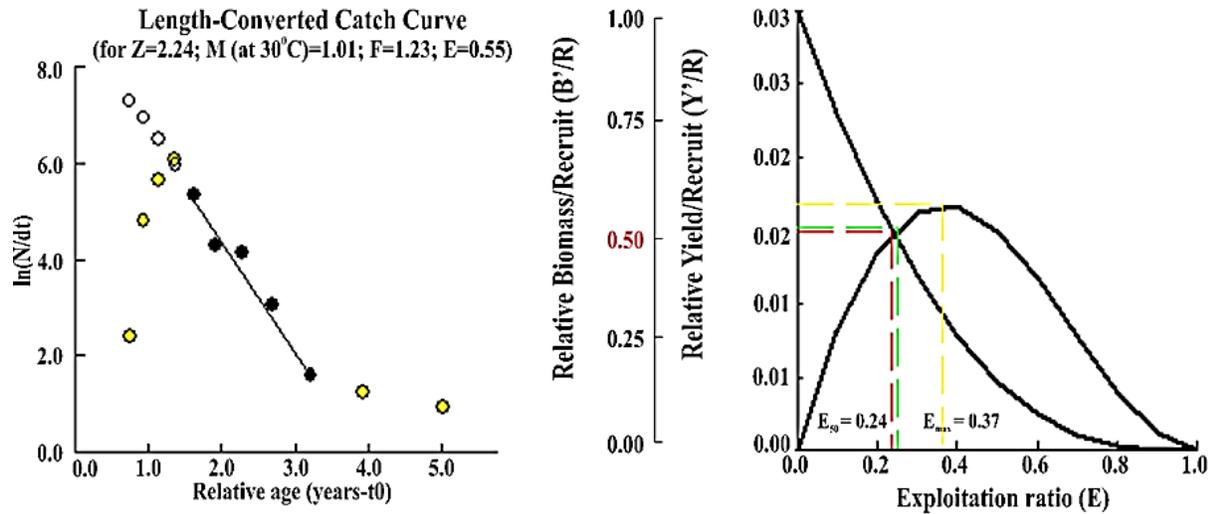


Figure 7. Length-converted catch curve and mortality estimates for *Epinephelus fasciatus* from Kwandang Bay, Sulawesi Sea (left); Beverton and Holt yield per recruit analysis (right).

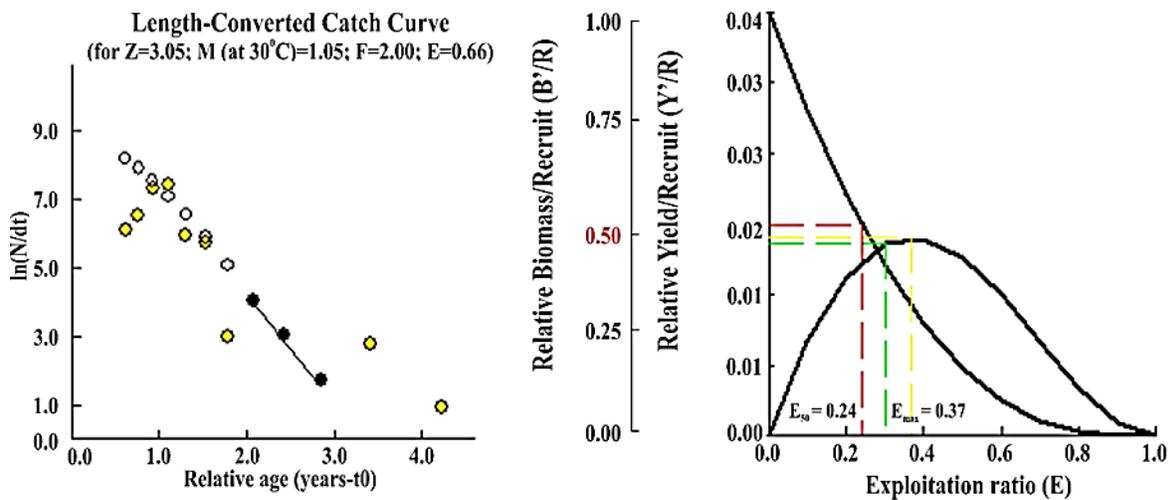


Figure 8. Length-converted catch curve and mortality estimates for *Epinephelus faveatus* from Kwandang Bay, Sulawesi Sea (left); Beverton and Holt yield per recruit analysis (right)

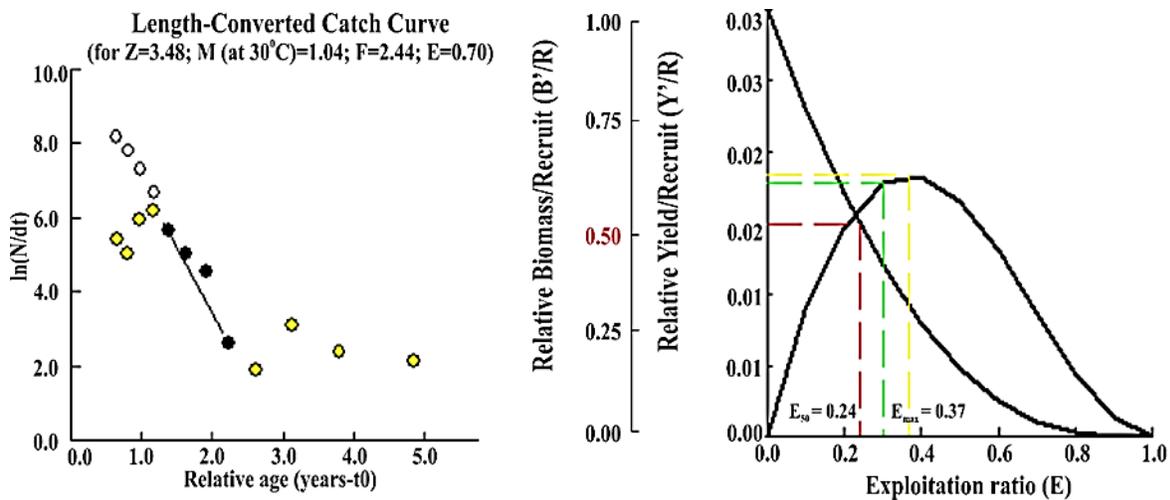
Epinephelus populations in Table 1. For example, the L_{m50} for Kwandang Bay *E. ongus* (25.88 cm TL) is higher than that reported for this species in North Maluku (Ernawati et al., 2021). Similarly, the L_{m50} of *E. polyphkadion* from Takabonerate National Park is lower than that reported for the same species in Karimunjawa National Park (Khasanah et al., 2019). The L_{m50} of *E. areolatus* from Karimunjawa National Park (Simbolon et al., 2020) was higher than that of both males and females of the same species in Takalar, South Sulawesi (Sitepu, 2014). Furthermore, as most epinephelids are protogynous hermaphrodites (Félix-Hackradt et al., 2022), the L_{m50} for females tends to be considerably lower than that for males, all or most of which are likely terminal males that have completed

the transition from female to male. This difference is more marked for *E. fuscoguttatus* from the Takabonerate National Park in South Sulawesi (Fatma et al., 2022) than for *E. areolatus* from Takalar, South Sulawesi (Sitepu, 2014). Some *Epinephelus* species can grow quite large, with correspondingly large L_{m50} values, for example, *E. coioides* (Achmad et al., 2020). However, in Kwandang Bay, the *Epinephelus* species in this study have relatively low L_{m50} values compared to the genus *Variola*, and catches of both genera tend to be dominated by immature individuals (Achmad et al., 2020, 2023).

The high exploitation rate for the three *Epinephelus* species in this study indicates overfishing, while the predominance of juveniles in the catch indicates

Table 2. Reported size ranges of *Epinephelus* groupers caught in Indonesia.

Region of Indonesia	Species	Length range TL (cm)	Reference
Spermonde Archipelago	<i>E. fuscoguttatus</i>	19-40	Ernaningsih et al. (2022)
Takabonerate National Park	<i>E. fuscoguttatus</i>	23-97	Fatma et al. (2021)
Aceh, Sumatra	<i>E. fuscoguttatus</i>	14.20-20.39	Ramadhani et al. (2017)
Misool, Raja Ampat, Papua	<i>E. fuscoguttatus</i>	53-58	Sala et al. (2022)
Wakatobi National Park	<i>E. fuscoguttatus</i>	24-97	Setiawan et al. (2019)
Padang, Sumatra	<i>E. coeruleopunctatus</i>	20.50-50	Bulanin et al. (2017)
Aceh, Sumatra	<i>E. coioides</i>	19.41-23.76	Fadli et al. (2021)
Kwandang Bay	<i>E. coioides</i>	16.50-101	Achmad et al. (2022)
Karimunjawa National Park	<i>E. areolatus</i>	18-51	Simbolon et al. (2020)
Misool, Raja Ampat, Papua	<i>E. areolatus</i>	25-30	Sala et al. (2022)
Aceh, Sumatra	<i>E. bleekeri</i>	15.30-20.79	Ramadhani et al. (2017)
Misool, Raja Ampat, Papua	<i>E. fasciatus</i>	20-27	Sala et al. (2022)
Kwandang Bay	<i>E. fasciatus</i>	15.65-48.90	This study
Kwandang Bay	<i>E. faveatus</i>	14.35-46.10	This study
Kwandang Bay	<i>E. ongus</i>	14.60-49.50	This study

Figure 9. Length-converted catch curve and mortality estimates for *Epinephelus ongus* from Kwandang Bay, Sulawesi Sea (left); Beverton and Holt yield per recruit analysis (right).

selective harvesting of larger, mature individuals, likely related to market preferences. The sustained removal of larger size classes can lead to a reduction in the mean and maximum sizes, both directly and indirectly through selection for early maturation, as observed in poorly managed fisheries elsewhere (Jennings et al., 1998; Sadovy and Domeier, 2005). The results indicate that the multi-species grouper fishery in Kwandang Bay is likely unsustainable and poses a threat to the stocks of the three species in this study.

The number of size classes recorded during this

study was similar for all three species (12 for *E. fasciatus* and *E. faveatus*, 13 for *E. ongus*). The size range and maximum size of *E. fasciatus* from Kwandang Bay in this study were greater than those of *E. fasciatus* from Misool, Raja Ampat, Papua (Sala et al., 2022) (Table 2). No comparative data were found for the other two species studied. However, the between-site differences in size range for other species such as *E. fuscoguttatus*, *E. coioides*, and *E. areolatus* (Table 2), in particular the large difference between *E. fuscoguttatus* from Raja Ampat and all other sites for this species, demonstrate the need to evaluate grouper

Table 3. Growth parameter values reported from Indonesian *Epinephelus* populations.

Species	TL ∞ (cm)	K	Region of Indonesia	Reference
<i>E. ongus</i>	36.17	0.37	Maluku	Ernawati et al. (2021)
<i>E. fuscoguttatus</i>	109	0.46	Takabonerate National Park	Fatma et al. (2021)
<i>E. fuscoguttatus</i>	45.40	0.45	Spermonde Archipelago	Ernaningsih et al. (2022)
<i>E. coioides</i>	110.21	0.10	Saleh Bay, West Nusa Tenggara	Efendi et al. (2020)
<i>E. coioides</i>	105.10	0.38	Kwandang Bay	Achmad et al. (2022)
<i>E. fasciatus</i>	47.52	0.49	Kwandang Bay	This study
<i>E. faveatus</i>	53.50	0.54	Kwandang Bay	This study
<i>E. ongus</i>	52	0.53	Kwandang Bay	This study

Table 4. Mortality and exploitation rates of grouper populations in Indonesia and elsewhere.

Species	Z	M	F	E	Location	Reference
<i>V. louti</i>	2.21	1.04	1.17	0.53	Kwandang Bay	Achmad et al. (2024)
<i>V. albimarginata</i>	3.61	1.05	2.56	0.71	Kwandang Bay	Achmad et al. (2024)
<i>E. coioides</i>	1.56	0.69	0.87	0.56	Kwandang Bay	Achmad et al. (2022)
<i>P. leopardus</i>	2.67	1.16	1.47	0.56	Kwandang Bay	Achmad et al. (2022)
<i>E. fuscoguttatus</i>	2.44	0.96	1.48	0.61	Spermonde Archipelago	Ernaningsih et al. (2022)
<i>E. fuscoguttatus</i>	2.19	0.77	1.42	0.65	Takabonerate National Park	Fatma et al. (2021)
<i>E. summana</i>	0.82	0.33	0.49	0.60	Egyptian Red Sea	Mehanna et al. (2019)
<i>E. ongus</i>	0.93	0.40	0.53	0.57	Maluku	Ernawati et al. (2021)
<i>E. ongus</i>	3.48	1.04	2.44	0.70	Kwandang Bay	This Study
<i>E. fasciatus</i>	2.24	1.01	1.23	0.55	Kwandang Bay	This Study
<i>E. faveatus</i>	3.05	1.05	2.00	0.66	Kwandang Bay	This Study

life history parameters for each stock rather than relying on estimates for the same species from another site.

The values of the growth coefficient K indicate that the three Kwandang Bay *Epinephelus* populations in this study have relatively fast growth rates and, on average, are likely to reach first maturity in a shorter time than most other Indonesian grouper populations for which similar data are available (Table 3). In particular, the growth coefficient of *E. ongus* from Kwandang Bay in this study was higher than that of the same species in Maluku (Ernawati et al., 2021). Similarly, in a previous study of *E. coioides* (Achmad et al., 2022), the growth coefficient for the Kwandang Bay population was higher than that for a population in Saleh Bay, West Nusa Tenggara Province (Efendi et al., 2020). This comparatively fast growth rate could be a response to a favorable environment and/or a response to fishing pressure (Félix-Hackradt et al., 2022).

The proportion of total mortality (Z) from natural mortality (M) and fishing mortality (F) of the three Kwandang Bay *Epinephelus* species in this study was similar to that of other grouper populations in Kwandang Bay, including species of the genera

Epinephelus, *Variola* and *Plectropomus* (Achmad et al., 2022, 2024), as well as groupers from other regions of Indonesia and the Red Sea (Table 4). These mortality rates reflect the widespread pressure on groupers, even in marine protected areas (Boelter et al., 2024). For example, in the Takabonerate National Park, the estimated fishing mortality of *E. fuscoguttatus* was nearly twice the natural mortality (Fatma et al., 2021). Such high mortality rates are likely to cause an imbalance in population dynamics, with mortality exceeding recruitment, posing a significant risk to the sustainability of the grouper stocks and the fisheries that depend on them (Ault et al., 2019; Sanchez and Rooker, 2021).

Studies on groupers in Kwandang Bay from 2021 to 2024 reveal heavy fishing pressure and indicate that all the stocks studied to date are overexploited. This situation has likely already reduced grouper biomass and threatens the long-term viability of the grouper stocks and the fisheries that depend on them. As high-value fisheries commodities, groupers are primarily (though not exclusively) targeted for economic gain to meet market demand rather than for subsistence or food security in source regions (Sadovy de Mitcheson et al., 2013; Khasanah et al., 2020; Achmad et al.,

2023). This paradigm is evident in Kwandang Bay, where the high proportion of fishing mortality is reflected in the generally high exploitation rates (E) in Table 4, both for the three species in this study and the four species (*V. louti*, *V. albimarginata*, *E. coioides*, and *P. leopardus*) studied previously (Achmad et al., 2024). The maximum sustainable exploitation rate has been estimated as $E_{\max} = 0.37/\text{year}^{-1}$, while the optimum exploitation rate to enable sustainable replenishment through reproduction and avoid reducing biomass below 50% of virgin stock biomass was estimated as $E_{50} = 0.24/\text{year}^{-1}$. The exploitation rates for all Kwandang Bay grouper stocks studied to date exceed both E_{50} and E_{\max} by a considerable margin. This study reinforces previous indications that grouper fisheries in Kwandang Bay are exerting heavy fishing pressure (Achmad et al., 2022, 2024), demonstrating that fishing mortality has already exceeded sustainable biological limits for multiple species from at least three genera (*Epinephelus*, *Plectropomus*, and *Variola*).

In addition to overexploitation in general, there are strong indications of specific forms of overexploitation, in particular growth overfishing, which can result in gradual reduction in size at first maturity, while the removal over time of large, fecund individuals can reduce reproductive potential to a no-return state, even after fishing pressure is reduced or removed (Félix-Hackradt et al., 2022). The predominance of small, immature individuals ($TL < L_{m50}$) in fisheries catch is a typical sign of growth overfishing, and was observed in the three *Epinephelus* species in this study, as well as in other Kwandang Bay grouper stocks (Achmad et al., 2020, 2023). Over the longer term, growth overfishing will reduce the biomass that can be sustainably harvested, and the effects can be particularly severe on protogynous hermaphrodites such as many groupers (Félix-Hackradt et al., 2022), including species caught in Kwandang Bay (Achmad et al., 2019, 2021). Excessive catch of young fish in the female phase can affect spawning success through reducing the number and quality of female and male spawners (Sadovy and Domeier, 2005). In turn, this will tend to reduce the

number and quality of fertilized eggs, leading to a decline in population fitness as well as slow recovery even if measures to stop or reduce overexploitation are successful (Molloy et al., 2009; Sadovy de Mitcheson, 2016; Chong-Montenegro and Kindsvater, 2022).

The important role of groupers as high-level or apex predators in tropical coastal ecosystems means that overexploitation can have consequences beyond the immediately apparent economic impacts (Howlett et al., 2016; Boelter et al., 2024). The ecological impacts can be widespread and complex, destabilizing and altering food chains in ways that are hard to predict (Fortuna et al., 2024; Lemrabott et al., 2024). One intensively studied phenomenon, first reported in 1960 and now thought to have been caused or greatly enhanced by such destabilization, is the massive *Acanthaster planci* outbreaks on the Great Barrier Reef (Jackson et al., 2001; Babcock et al., 2016). The crown of thorns starfish (COTS) *A. planci* is a voracious coral predator that extends its stomach to cover coral colonies, digesting the polyps in place and sucking up the dissolved nutrients, and outbreaks can cause mass coral mortality (Hall et al., 2017). In a balanced ecosystem, COTS outbreaks are rare, as COTS population density is regulated by predation, mostly on juvenile COTS, by a range of predators including the gastropod *Charonia tritonis*, the Napoleon wrasse *Cheilinus undulatus*, and many other carnivorous fish, including groupers (Babcock et al., 2016; Cowan et al., 2017; Kroon et al., 2021). However, many known COTS predators are heavily exploited across all or most of their range, including groupers such as those fished in Kwandang Bay. Direct observations of groupers feeding on COTS introduced into live reef fish holding cages confirm the potential of Indo-Pacific groupers as COTS predators (Abigail Mary Moore, unpublished data, 2004). Maintaining healthy and resilient grouper populations should reduce the risk of COTS outbreaks and other phenomena due to ecological imbalance.

From an economic perspective, an increase in the proportion of smaller, less valuable fish means fewer larger adult fish with a high market value. It will have a negative impact on fishers' livelihoods and

businesses involved in the market chain, with knock-on impacts on the economy at local and regional levels. The study by Costello et al. (2016) showed that, at the global level, overfishing results in the loss of billions of dollars per year in potential revenue. There is widespread recognition of an urgent need to address grouper overfishing, especially in the small-scale multi-species fisheries that are common in many tropical regions (Jentoft et al., 2017). However, overfishing is not easy to address and has been considered a “wicked problem” (Chuenpagdee and Jentoft, 2019), particularly in regions such as Kwandang Bay, where fishing is vital for the local economy.

Fisheries management approaches that could be applied to maintain and rebuild grouper stocks include setting minimum legal sizes (MLS) and reducing fishing effort (King, 2007; Ben-Hasan et al., 2021). Ideally these should be applied for each stock; however, in a multi-species fishery this can be challenging and possibly unworkable, especially as gears are generally unselective in terms of species and sometimes also in terms of size, and it may be difficult or impossible to return non-target (e.g., based on species or size) individuals alive and in good condition. These complexities can be addressed through compromise policies that aim to protect a majority or a priority subset of the stocks (species) caught in the fishery (Khasanah et al., 2019, 2020). However, both individual stock-based and compromise interventions aiming to cover many species and/or stocks rely on data at the stock/species level. In Kwandang Bay, this study brings the number of grouper stocks with population dynamics data to seven (27%) of the 26 species identified by Achmad et al. (2023).

Furthermore, MLS limits, reductions in effort, or other direct fisheries management interventions may be ineffective if the fish habitat is degraded (King, 2007). In this context, ecological perspectives and tools can be valuable in fisheries stock management, as total mortality is comprised of both fishing and natural mortality. If natural mortality is reduced, then there should be more fish, and the volume that can be

fished sustainably should increase. Measures to increase the number of individuals entering the population can be enhanced through measures to promote reproduction, settlement, and early survival (Geist and Hawkins, 2016; Taylor et al., 2017). Identifying and protecting spawning aggregations, for example, through spatio-temporal measures, can maximize the reproductive potential of the remaining mature individuals in the population, enhancing the number of fertilized eggs and larvae (Sadovy de Mitcheson, 2016; Sadovy de Mitcheson et al., 2020). Measures to protect and restore grouper habitat, including nursery habitat used for settlement and juvenile growth as well as adult habitat, should increase the number of post-larvae that are attracted to and survive in coastal ecosystems, including coral reefs, seagrass beds, and mangroves (King, 2007; Félix-Hackradt et al., 2022; Lamont et al., 2022). Both passive and active restoration could be considered in Kwandang Bay, where grouper habitat has been degraded, primarily due to destructive fishing practices and coastal development (Achmad et al., 2023).

With respect to size limits, in the case of Kwandang Bay *Epinephelus* groupers, the MLS limit should be at least 25 cm for *E. fasciatus* and *E. faveatus*, and 26 cm for *E. ongus*. These MLS limits should enable a reasonable proportion of individuals to reproduce before they are caught. Several groupers are in a similar size class to the three *Epinephelus* groupers, and a MLS of around 26 cm could be applied to these as a group. This group should be treated separately from groupers that can grow to much larger sizes and require larger MLS limits. These include *E. coioides*, which can reach over 1 m TL in Kwandang Bay (Achmad et al., 2022), with a recommended MLS of 64 cm (Achmad et al., 2020), while the recommended MLS for the genera *Plectropomus* and *Variola* in Kwandang Bay is 34 cm (Achmad et al., 2023).

To rebuild the grouper stocks in Kwandang Bay, a reduction in fishing effort is strongly recommended, at least in the short term. Based on current exploitation rates, the recommended reductions in fishing effort to reach the optimal rate ($E_{50} = 0.24$) are 31% for

E. fasciatus, 42% for *E. faveatus*, and 46% for *E. ongus*. With regards to fishing effort, studies on two other grouper species caught in the Kwandang Bay multi-species grouper fishery recommend a fishing effort reduction of 25% (Achmad et al., 2022). A compromise solution for the multi-species fishery would therefore involve an overall fishing effort reduction of around 30-40%, resulting in fishing effort levels above the optimal level for two of the three species in this study. This would present severe challenges to fisheries managers and the fishing communities in this area, and require innovative and multi-disciplinary socio-ecological approaches. In addition to setting MLS limits and/or limiting fishing effort, approaches aiming to increase grouper reproductive success and habitat-based approaches to enhance settlement and survival could be adopted to increase recruitment and reduce natural mortality. Such an integrated approach should promote stock recovery and maintain or increase the sustainable yield of grouper fisheries in Kwandang Bay.

Acknowledgements

The authors gratefully acknowledge support for this research from the Ministry of Education, Culture, Research and Technology of the Republic of Indonesia through the Fundamental Research grant scheme under contract number 1048/LL16/AL/2024 and 001/PK-Pen/LPPM-UMGO/VI/2024.

References

- Achmad D.S., Ali S.A., Sudirman., Indar Y.N. (2019). The gonad maturity development and spawning season of orange-spotted grouper (*Epinephelus coioides*) at Kwandang Bay, Gorontalo Province, Indonesia. *AACL Bioflux*, 12(2): 642-649.
- Achmad D.S., Sudirman., Jompa J., Nurdin M.S. (2020). Estimating the catchable size of orange-spotted grouper (*Epinephelus coioides*) in Kwandang Bay, Gorontalo Utara District, Indonesia. *IOP Conference Series: Earth and Environmental Science*, 473: 012133.
- Achmad D.S., Nurdin M.S., Yasin I.A., Indrianti M.A., Mokoginta M.M., Fahrullah, Suparwata D.O., Gobel., Atika Y., Djibran M.M., Mokoolang S. (2021). A preliminary study on the size structure and sex ratio of orange-spotted grouper (*Epinephelus coioides* Hamilton, 1822) harvested from Kwandang Bay, Sulawesi Sea, Indonesia. *Aceh Journal of Animal Science*, 6(2): 34-38.
- Achmad D.S., Gani S., Ardiansyah W., Mokoginta M.M., Nurdin M.S., Jompa J., Indrianti M.A., Achmad N. (2022). Population dynamics of reef fish in the Kwandang Bay, Sulawesi Sea, Indonesia. *Biodiversitas*, 23(10): 5217-5226.
- Achmad D.S., Nurdin M.S., Azmi F., Indrianti M.A., Hulukati E., Jompa J., Haser T.F., Achmad N. (2023). Species composition and growth pattern of a multi-species grouper in Kwandang Bay, Sulawesi Sea, Indonesia. *Jurnal Ilmiah Perikanan Dan Kelautan*, 15(1): 31-43.
- Achmad D.S., Nurdin M.S., Jompa J., Taslim I., Sari N. (2023). Minimum legal size of commercially important groupers in the Coral Triangle Sulawesi Sea, Indonesia. *IOP Conference Series: Earth and Environmental Science*, 1272: 012019.
- Achmad D.S., Nurdin M.S., Taslim I., Moore A.M. (2023). Population structure of commercially important groupers in the coral triangle Gorontalo, Indonesia to support conservation. *Biodiversitas*, 24(12): 6592-6601.
- Achmad D.S., Nurdin M.S., Tilome A.A., Moore A.M. (2024). Population dynamics of *Variola albimarginata* Baissac, 1953 and *Variola louti* Fabricius, 1775 (Perciformes : Serranidae) in Sulawesi Sea, Indonesia. *Biodiversitas*, 25(3): 978-989.
- Amorim P., Sousa P., Jardim E., Menezes G.M. (2019). Sustainability Status of Data-Limited Fisheries: Global Challenges for Snapper and Grouper. *Frontiers in Marine Science*, 6(654): 1-17.
- Amorim P., Sousa P., Jardim E., Azevedo M., Menezes G.M. (2020). Length-frequency data approaches to evaluate snapper and grouper fisheries in the Java Sea, Indonesia. *Fisheries Research*, 229(March): 105576.
- Andriyono S., Damora A., Hidayani A.A. (2020). Genetic diversity and phylogenetic reconstruction of grouper (Serranidae) from Sunda Land, Indonesia. *Egyptian Journal of Aquatic Biology and Fisheries*, 24(3): 403-415.
- Anjali K.M., Mandal A., Gunalan B., Ruban L., Anandajothi E., Thineshsanthar D., Manojkumar T.G., Kandan S. (2019). Identification of six grouper species under the genus *Epinephelus* (Bloch, 1793) from Indian waters using PCR-RFLP of cytochrome c oxidase I (COI) gene fragment. *Food Control*, 101(February), 39-

- 44.
- Artero C., Koenig C.C., Marsh J.E. (2023). Are the coastal waters of French Guiana a source or sink habitat for Atlantic Goliath grouper *Epinephelus itajara*? *Fishes*, 8(5): 274.
- Ault J.S., Smith S.G., Bohnsack J.A., Luo J., Stevens M.H., DiNardo G.T., Johnson M.W., Bryan D.R. (2019). Length-based risk analysis for assessing sustainability of data-limited tropical reef fisheries. *ICES Journal of Marine Science*, 76(1): 165-180.
- Babcock R.C., Dambacher J.M., Morello E.B., Plagányi É.E., Hayes K.R., Sweatman H.P.A., Pratchett M.S. (2016). Assessing different causes of Crown-of-Thorns starfish outbreaks and appropriate responses for management on the great barrier reef. *PLoS ONE*, 11(12): 1-20.
- Basith A., Abinawanto A., Kusriani E., Yasman Y. (2021). Genetic diversity analysis and phylogenetic reconstruction of groupers *Epinephelus* spp. from Madura Island, Indonesia based on partial sequence of CO1 gene. *Biodiversitas Journal of Biological Diversity*, 22(10): 4282-4290.
- Ben-Hasan A., Walters C., Hordyk A., Christensen V., Al-Husaini M. (2021). Alleviating Growth and Recruitment Overfishing through Simple Management Changes: Insights from an Overexploited Long-Lived Fish. *Marine and Coastal Fisheries*, 13(2): 87-98.
- Beverton R.J.H., Holt S.J. (1957). *On the Dynamics of Exploited Fish Populations (Facsimile)*. Springer Science+Business Media. <https://doi.org/10.1007/978-94-011-2106-4>
- Beverton R.J.H., Holt S.J. (1964). *Manual of methods for fish stock assessment. Part 2. Tables of yield functions*, FAO Fisheries Technical Paper 38. Food and Agriculture Organization of the United Nations.
- Boelter J.P., Silva F.C., Quimbayo J.P., Floeter S.R. (2024). Broken expectations: Population decline of a key grouper species within a 30-year-old no-take MPA in the Southwestern Atlantic. *Ocean and Coastal Management*, 257: 107318.
- Buchholz-Sørensen M., Vella A. (2016). Population structure, genetic diversity, effective population size, demographic history and regional connectivity patterns of the endangered Dusky Grouper, *Epinephelus marginatus* (Teleostei: Serranidae), within Malta's fisheries management zone. *PLOS ONE*, 11(7): e0159864.
- Bulanin U., Masrizal M., Muchlisin Z.A. (2017). Length-weight relationships and condition factors of the whitespotted grouper *Epinephelus coeruleopunctatus* in the coastal waters of Padang City, Indonesia. *Aceh Journal of Animal Science*, 2(1): 23-27.
- Burton M.L., Potts J.C., Carr D.R. (2015). Age, growth, and natural mortality of yellowfin grouper (*Mycteroperca venenosa*) from the southeastern United States. *PeerJ*, 3(7): e1099.
- Chen X., Liu B. (2022). Biology of fishery resources. In: X. Chen, B. Liu (Eds.), *Biology of Fishery Resources*. Springer Nature Singapore. <https://doi.org/10.1007/978-981-16-6948-4>
- Chong-Montenegro C., Kindsvater H.K. (2022). Demographic Consequences of small-scale fisheries for two sex-changing groupers of the tropical Eastern Pacific. *Frontiers in Ecology and Evolution*, 10(March): 850006.
- Chuenpagdee R., Jentoft S. (2019). Transdisciplinarity for Small-Scale Fisheries Governance. In: R. Chuenpagdee, S. Jentoft (Eds.), *MARE Publication Series (Vol. 21, Issue December 2018)*. Springer International Publishing. <https://doi.org/10.1007/978-3-319-94938-3>
- Costello C., Ovando D., Clavelle T., Kent Strauss C., Hilborn R., Melnychuk M.C., Branch T.A., Gaines S.D., Szuwalski C.S., Cabral R.B., Rader D.N., Leland A. (2016). Global fishery prospects under contrasting management regimes. *Proceedings of the National Academy of Sciences of the United States of America*, 113(18): 5125-5129.
- Cowan Z.L., Pratchett M., Messmer V., Ling S. (2017). Known predators of crown-of-thorns starfish (*Acanthaster* spp.) and their role in mitigating, if not preventing, population outbreaks. *Diversity*, 9(1): 1-19.
- Croll J.C., van Kooten T., de Roos A.M. (2023). The consequences of density-dependent individual growth for sustainable harvesting and management of fish stocks. *Fish and Fisheries*, 24(3): 427-438.
- Dimarchopoulou D., Mous P.J., Firmana E., Wibisono E., Coro G., Humphries A.T. (2021). Exploring the status of the Indonesian deep demersal fishery using length-based stock assessments. *Fisheries Research*, 243(April): 106089.
- Dwifajri S., Tapilatu R.F., Pranata B., Kusuma A.B. (2022). Molecular phylogeny of grouper of *Epinephelus* genus in Jayapura, Papua, Indonesia inferred from Cytochrome Oxidase I (COI) gene. *Biodiversitas*, 23(3): 1449-1456.
- Efendi D.S., Adrianto L., Yonvitner Wardiatno Y.,

- Agustina S. (2020). The performance of stock indicators of grouper (Serranidae) and snapper (Lutjanidae) fisheries in Saleh Bay, Indonesia. *AACL Bioflux*, 13(5): 2431-2444.
- Ernaningsih., Jamal M., Hasnidar., Hadijah S. (2022). Population parameters and eksploitation rate of tiger grouper (*Epinephelus fuscoguttatus*) in the Spermonde Islands of South Sulawesi. *BAWAL Widya Riset Perikanan Tangkap*, 14(1): 1-9.
- Ernawati T., Agustina S., Kembaren D.D., Yulianto I., Satria F. (2021). Life history parameters and spawning potential ratio of some reef fish species in fisheries management area 715 of Indonesia. *AACL Bioflux*, 14(5): 3092-3103.
- Fadli N., Damora A., Muchlisin Z.A., Dewiyanti I., Ramadhaniaty M., Nur F.M., Batubara A.S., Razi N.M., Macusi E.D., Siti-Azizah M.N. (2022). Biodiversity of commercially important groupers (Epinephelidae) in Aceh, Indonesia: A checklist. *IOP Conference Series: Earth and Environmental Science*, 956: 012015.
- Fadli N., Damora A., Muchlisin Z.A., Dewiyanti I., Ramadhaniaty M., Zhelfi Z., Roka N.F., Fitriani F., Rusdi M., Nur F.M., Batubara A.S., Siti-Azizah M.N. (2021). A preliminary study on biological aspects of the orange-spotted grouper (*Epinephelus coioides*) harvested in the northern coast of Aceh, Indonesia. *IOP Conference Series: Earth and Environmental Science*, 674: 012085.
- Fatma F., Mallawa A., Najamuddin N., Zainuddin M., Ayyub F.R. (2021). A study of brown-marbled grouper (*Epinephelus fuscoguttatus*) population dynamics in Takabonerate National Park Waters, South Sulawesi, Indonesia. *Biodiversitas Journal of Biological Diversity*, 22(10): 4298-4307.
- Fatma F., Mallawa A., Najamuddin., Zainuddin M., Ayyub F.R. (2022). Biological aspects of brown-marbled grouper (*Epinephelus fuscoguttatus*) from Taka Bonerate National Park, District of Selayar Islands, South Sulawesi, Indonesia. *Biodiversitas*, 23(2): 1140-1153.
- Félix-Hackradt F.C., Hackradt C.W., García-Charton J.A. (2022). Biology and ecology of groupers. In: *Biology and Ecology of Groupers*. CRC Press. <https://doi.org/10.1201/b20814>
- Fortuna C.M., Fortibuoni T., Bueno-Pardo J., Coll M., Franco A., Giménez J., Stranga Y., Peck M.A., Claver C., Brasseur S., Fernández-Corredor E., Frascchetti S., Garcia-Garin O., van Leeuwen A., Louzao M., Pedrajas A., Raicevich S., Ramírez F., Ransijn J., ... Katsanevakis S. (2024). Top predator status and trends: ecological implications, monitoring and mitigation strategies to promote ecosystem-based management. *Frontiers in Marine Science*, 11: 1282091.
- Froese R., Pauly D. (2023). FishBase, The global database of fishes.
- Gayanilo F.C.J., Sparre P., Pauly D. (2005). FAO-ICLARM stock assessment tools II (FiSAT II). Revised version. User's guide. FAO Computerized Information Series (Fisheries). No. 8, Revised version 2. Food and Agriculture Organization of the United Nations (FAO). 168 p.
- Gebremedhin S., Bruneel S., Getahun A., Anteneh W., Goethals P. (2021). Scientific methods to understand fish population dynamics and support sustainable fisheries management. *Water*, 13(4): 574.
- Geist J., Hawkins S.J. (2016). Habitat recovery and restoration in aquatic ecosystems: current progress and future challenges. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26(5): 942-962.
- Hall M.R., Kocot K.M., Baughman K.W., Fernandez-Valverde S.L., Gauthier M.E.A., Hatleberg W.L., Krishnan A., McDougall C., Motti C.A., Shoguchi E., Wang T., Xiang X., Zhao M., Bose U., Shinzato C., Hisata K., Fujie M., Kanda M., Cummins S.F., ... Degnan B.M. (2017). The crown-of-thorns starfish genome as a guide for biocontrol of this coral reef pest. *Nature*, 544(7649): 231-234.
- Heemstra P., Randall J. (1993). FAO Species Catalogue. Vol. 16. Groupers of the world (family Serranidae, subfamily Epinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date. Food and Agriculture Organization of the United Nations.
- Howlett S.J., Stafford R., Waller M., Antha S., Mason-Parker C. (2016). Linking protection with the distribution of grouper and habitat quality in Seychelles. *Journal of Marine Biology*, 7851425.
- Hughes A.T., Hamilton R.J., Choat J.H., Rhodes K.L. (2020). Declining grouper spawning aggregations in Western Province, Solomon Islands, signal the need for a modified management approach. *PLOS ONE*, 15(3): e0230485.
- Humphries A.T., Gorospe K.D., Carvalho P.G., Yulianto I., Kartawijaya T., Campbell S.J. (2019). Catch composition and selectivity of fishing gears in a multi-species Indonesian coral reef fishery. *Frontiers in*

- Marine Science, 6: 00378.
- IUCN. (2024). The IUCN Red List of Threatened Species. Version 2024-2.
- Jackson J.B.C., Kirby M.X., Berger W.H., Bjorndal K.A., Botsford L.W., Bourque B.J., Bradbury R.H., Cooke R., Erlandson J., Estes J.A., Hughes T.P., Kidwell S., Lange C.B., Lenihan H.S., Pandolfi J.M., Peterson C.H., Steneck R.S., Tegner M.J., Warner R.R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293: 629-637.
- Jaxion-Harm J., Saunders J., Speight M.R. (2012). Distribution of fish in seagrass, mangroves and coral reefs: Life-stage dependent habitat use in Honduras. *Revista de Biología Tropical*, 60(2): 683-698.
- Jennings S., Reynolds J.D., Mills S.C. (1998). Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society B: Biological Sciences*, 265: 333-339.
- Jentoft S., Chuenpagdee R., Barragán-Paladines M.J., Franz N. (2017). The Small-Scale Fisheries Guidelines. Vol. 14. Springer International Publishing. <https://doi.org/10.1007/978-3-319-55074-9>
- Kadir N.N., Ala Husain A.A., Priosambodo D., Jamal M., Irmawati., Indrabayu., Moore A.M. (2023). Diverse and predominantly sub-adult *Epinephelus* sp. groupers from small-scale fisheries in South Sulawesi, Indonesia. *Fisheries and Aquatic Sciences*, 26(6): 380-392.
- Kadir N.N., Ambo Ala Husain A., Irmawati I., Priosambodo D., Jamal M., Ilyas M., Malkab A.N.I., Fasirah E., Moore A.M. (2022). Short Communication: Rare grouper *Epinephelus miliaris* from market surveys in South Sulawesi, Indonesia. *Biodiversitas Journal of Biological Diversity*, 23(11): 6070-6074.
- Khasanah M., Kadir N.N., Jompa J. (2019). Reproductive biology of three important threatened/near-threatened groupers (*Plectropomus leopardus*, *Epinephelus polyphekadion* and *Plectropomus areolatus*) in eastern Indonesia and implications for management. *Animals*, 9: 643.
- Khasanah M., Nurdin N., Sadovy de Mitcheson Y., Jompa J. (2020). Management of the grouper export trade in Indonesia. *Reviews in Fisheries Science and Aquaculture*, 28(1): 1-15.
- Kindsvater H.K., Reynolds J.D., Sadovy de Mitcheson Y., Mangel M. (2017). Selectivity matters: Rules of thumb for management of plate-sized, sex-changing fish in the live reef food fish trade. *Fish and Fisheries*, 18(5): 821-836.
- King M. (2007). Fisheries biology assessment and management (2nd Editio). Blackwell Publishing Ltd.
- Kroon F.J., Barneche D.R., Emslie M.J. (2021). Fish predators control outbreaks of Crown-of-Thorns Starfish. *Nature Communications*, 12: 6986.
- Lamont T.A.C., Williams B., Chapuis L., Prasetya M.E., Seraphim M.J., Harding H.R., May E.B., Janetski N., Jompa J., Smith D.J., Radford A.N., Simpson S.D. (2022). The sound of recovery: Coral reef restoration success is detectable in the soundscape. *Journal of Applied Ecology*, 59(3): 742-756.
- Lemrabott S.Y.C., van Leeuwen A., Piersma T., Braham C.B., Ball A.C., Araujo A., Olf H., El-Hacen E.H.M. (2024). The chronology of overfishing in a remote West-African coastal ecosystem. *Ecology and Society*, 29(1): 9.
- Li T., Ding, R., Zhan, J., Zho Y., Liu C., Cao Z., Sun Y. (2024). The establishment of the multi-visual loop-mediated isothermal amplification method for the rapid detection of *Vibrio harveyi*, *Vibrio parahaemolyticus*, and Singapore grouper iridovirus. *Fishes*, 9(6): 225.
- Liese C., Crosson S. (2023). Quantifying the economic effects of different fishery management regimes in two otherwise similar fisheries. *PLoS ONE*, 18(6), e0287250.
- Ma K.Y., Craig M.T. (2018). An inconvenient monophyly: An update on the taxonomy of the groupers (Epinephelidae). *Copeia*, 106(3): 443-456.
- Mahé K., Gentil C., Brisset B., Evano H., Lepetit C., Boymond-Morales R., Telliez S., Dussuel A., Rungassamy T., Elleboode R., MacKenzie K., Roos D. (2022). Biology of exploited groupers (Epinephelidae family) around La Réunion Island (Indian Ocean). *Frontiers in Marine Science*, 9: 935285.
- Mehanna S.F., Osman Y.A.A., Khalil M.T., Hassan A. (2019). Age and growth, mortality and exploitation ratio of *Epinephelus summana* (Forsskål, 1775) and *Cephalopholis argus* (Schneider, 1801) from the Egyptian Red Sea coast, Hurghada fishing area. *Egyptian Journal of Aquatic Biology and Fisheries*, 23(4): 65-75.
- Mehanna S.F., Samy-Kamal M. (2024). Population dynamics parameters and exploitation status of 55 commercial species in Egyptian Red Sea fisheries: A key to sustainable fisheries. *Fishes*, 9(7): 255.
- Meissa B., Quemper F., Thiaw M., Ba K., Tfeil B.M., Jallow M.S., Guitton J., Sharma R., Gascuel D. (2025). Assessment of over Four Decades the Status of White

- Grouper *Epinephelus aeneus* (Geoffroy Saint-Hilaire, 1817) Population in the Eastern Central Atlantic. *Fishes*, 10(3): 98.
- Mohammed-AbdAllah E., El-Ganainy A., Farrag M.M., Moustafa M.A., Osman A.G. (2022). Reproductive biology of greasy grouper, *Epinephelus tauvina* and coral hind grouper *Cephalopholis miniata* (Family: Serranidae) in the southern Red Sea, Shalatién, Egypt. *International Journal of Aquatic Biology*, 10(6): 524-536.
- Molloy P., Reynolds J., Gage M., Côté I. (2009). Effects of an artisanal fishery on non-spawning grouper populations. *Marine Ecology Progress Series*, 392: 253-262.
- Mudjirahayu., Bawole R., Rembet U.N.W.J., Ananta A.S., Runtuboi F., Sala, R. (2017). Growth, mortality and exploitation rate of *Plectropomus maculatus* and *P. oligocanthus* (Groupers, Serranidae) on Cenderawasih Bay National Park, Indonesia. *Egyptian Journal of Aquatic Research*, 43(3): 213-218.
- Murie D.J., Parkyn D.C., Koenig C.C., Coleman F.C., Malinowski C.R., Cusick J.A., Ellis R.D. (2023). Age, growth, and functional gonochorism with a twist of diandric protogyny in goliath grouper from the Atlantic Coast of Florida. *Fishes*, 8(8): 412.
- N'Souvi K., Sun C., Rivero Rivero Y.M. (2023). Development of marine small-scale fisheries in Togo: An examination of the efficiency of fishermen at the new fishing port of Lomé and the necessity of fisheries co-management. *Aquaculture and Fisheries*. <https://doi.org/10.1016/j.aaf.2023.07.009>
- Nadiarti N., Moore A., Abu N., Rahim S.W., Chasanah M. (2021). Ecosystems Approach to Fisheries Management (EAFM) assessment for grouper and snapper fisheries in Bontang, East Kalimantan, Indonesia. *IOP Conference Series: Earth and Environmental Science*, 763(1): 012031.
- O'Neill E.D.D., Lindahl T., Daw T., Crona B.I., Ferrer A.J., Pomeroy R. (2019). An experimental approach to exploring market responses in small-scale fishing communities. *Frontiers in Marine Science*, 6: 491.
- Ochieng O.B., Chenje M.E., Mulwa F.B. (2015). Distribution and reproductive patterns of the *Epinephelus* genus groupers off Kenyan south coast marine waters. *Journal of Fisheries and Aquatic Science*, 10(3): 159-170.
- Osman A.G.M., El-Ganainy A., Abd-Allah E. (2018). Some reproductive aspects of the areolate grouper, *Epinephelus areolatus* from the Gulf of Suez. *Egyptian Journal of Aquatic Research*, 44(1): 51-56.
- Pauly D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science*, 39(2): 175-192.
- Pham C.-V., Wang H.-C., Chen S.-H., Lee J.-M. (2023). The Threshold Effect of Overfishing on Global Fishery Outputs: International Evidence from a Sustainable Fishery Perspective. *Fishes*, 8(2): 71.
- Pontón-Cevallos J.F., Bruneel S., Marín Jarrín J.R., Ramírez-González J., Bermúdez-Monsalve J.R., Goethals P.L.M. (2020). vulnerability and decision-making in multispecies fisheries: a risk assessment of Bacalao (*Mycteroperca olfax*) and Related Species in the Galapagos' Handline Fishery. *Sustainability*, 12(17): 6931.
- Ramadhani A., Muchlisin Z. A., Sarong M.A., Batubara A.S. (2017). Hubungan panjang berat dan faktor kondisi ikan kerapu Famili Serranidae yang tertangkap di Perairan Pulo Aceh Kabupaten Aceh Besar, Provinsi Aceh. *Depik Jurnal Ilmu-Ilmu Perairan, Pesisir Dan Perikanan*, 6(2): 112-121.
- Razi N.M., Muchlisin Z.A., Ramadhaniaty M., Damora A., Nur F.M., Siti-Azizah M.N., Fadli N. (2022). Diversity of commercially important grouper (Family: Epinephelidae) in Simeulue and Banyak Islands, Aceh, Indonesia. *Depik Jurnal Ilmu-Ilmu Perairan, Pesisir Dan Perikanan*, 11(1): 29-33.
- Richter A., Eikeset A.M., van Soest D., Diekert F.K., Stenseth N.C. (2018). Optimal management under institutional constraints: Determining a total allowable catch for different fleet segments in the Northeast Arctic Cod Fishery. *Environmental and Resource Economics*, 69(4): 811-835.
- Ricker W. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*. <https://doi.org/10.1038/108070b0>
- Roca Florido A., Padilla Rosa E. (2024). Analysing the impacts of a reform on harmful fishery subsidies in Spain using a social accounting matrix. *Journal of Economic Structures*, 13(1): 9.
- Rowan N.J. (2023). The role of digital technologies in supporting and improving fishery and aquaculture across the supply chain – Quo Vadis? *Aquaculture and Fisheries*, 8(4): 365-374.
- Sadler D.E., Watts P.C., Uusi-Heikkilä S. (2023). The

- Riddle of How Fisheries Influence Genetic Diversity. *Fishes*, 8(10): 510.
- Sadovy de Mitcheson Y. (2016). Mainstreaming fish spawning aggregations into fishery management calls for a precautionary approach. *BioScience*, 66(4): 295-306.
- Sadovy de Mitcheson Y., Colin P.L., Lindfield S.J., Bukurrou A. (2020). A Decade of Monitoring an Indo-Pacific Grouper Spawning Aggregation: Benefits of Protection and Importance of Survey Design. *Frontiers in Marine Science*, 7(November): 1-23.
- Sadovy de Mitcheson Y., Craig M.T., Bertoni A.A., Carpenter K.E., Cheung W.W.L., Choat J.H., Cornish A.S., Fennessy S.T., Ferreira B.P., Heemstra P.C., Liu M., Myers, R.F., Pollard D.A., Rhodes K.L., Rocha L.A., Russell B.C., Samoily M.A., Sanciangco J. (2013). Fishing groupers towards extinction: A global assessment of threats and extinction risks in a billion dollar fishery. *Fish and Fisheries*, 14(2): 119-136.
- Sadovy de Mitcheson Y., Linardich C., Barreiros J.P., Ralph G.M., Aguilar-Perera A., Afonso P., Erisman B.E., Pollard D.A., Fennessy S.T., Bertoni A.A., Nair R.J., Rhodes K.L., Francour P., Brulé T., Samoily M.A., Ferreira B.P., Craig M.T. (2020). Valuable but vulnerable: Over-fishing and under-management continue to threaten groupers so what now? *Marine Policy*, 116: 103909.
- Sadovy Y., Domeier M. (2005). Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs*, 24(2): 254-262.
- Sala R., Tarigan R.B., Dasmase H.Y., Parenden D., Tururaja T., Manan J., Marsaoly D.N.R., Matulesy M., Bawole R. (2022). Catch structures, growth patterns and condition factor of grouper fish (Serranidae) caught in the waters near Wayaban, Misool, Raja Ampat. *AACL Bioflux*, 15(1): 240-250.
- Sanchez P.J., Rooker J.R. (2021). Age, growth, and mortality of threatened Warsaw grouper, *Hyporhamphus nigritus*, in the Gulf of Mexico. *Fisheries Research*, 243: 106097.
- Setiawan H., Fahrudin A., Kamal M.M. (2019). Analisis hubungan panjang berat pada ikan hermaphrodit: kerapu sunu (*Plectropomus leopardus*) dan Kerapu Macan (*Epinephelus fuscoguttatus*). *Jurnal Biologi Tropis*, 19(2): 124130.
- Simbolon D., Tarigan D.J., Yolanda D.F., Antika M.R. (2020). Determination of potential fishing zones of areolate grouper (*Epinephelus areolatus*) based on analysis of productivity, gonad maturity, and fish length in Karimunjawa National Park, Indonesia. *AACL Bioflux*, 13(2): 833-848.
- Sitepu G.F. (2014). Biological aspect of areolate grouper (*Epinephelus areolatus* Forsskal, 1775) in waters of Galesong Kota Village, District Takalar. *Torani (Jurnal Ilmu Kelautan dan Perikanan)*, 24(2): 9-19.
- Solarin S.A., Kundu P., Sahu P.K., Law J.Y. (2024). The impact of aggregated and disaggregated fisheries production and licensed fishermen on fishing grounds footprint: A time series analysis. *Marine Pollution Bulletin*, 203: 116423.
- Sparre P., Venema S.C. (1998). Introduction to tropical fish stock assessment - Part 1: Manual. In FAO.
- Syukri M., Idrus M.R., Husain A.A.A., Moore A.M., Tresnati J. (2025). Analysis of maximum sustainable yield of the small-scale grouper (Serranidae) in Banggai Laut Waters to Promote Indonesian Marine Conservation. *Egyptian Journal of Aquatic Biology and Fisheries*, 29(1): 695-706.
- Tapilatu R.F., Tururaja T.S., Sipriyadi., Kusuma A.B. (2021). Molecular phylogeny reconstruction of grouper (Serranidae: Epinephelinae) at northern part of bird's head seascape-Papua inferred from COI gene. *Fisheries and Aquatic Sciences*, 24(5): 181-190.
- Taylor M.D., Chick R.C., Lorenzen K., Agnalt A., Leberm K.M., Blankenship H.L., Haegen G., Vander, Loneragan N.R. (2017). Fisheries enhancement and restoration in a changing world. *Fisheries Research*, 186: 407-412.
- Tirtadanu., Prihatiningsih., Yusuf H.N., Zamroni A., Amri K., Chodrijah U. (2023). Assessing the stock status of areolate grouper (*Epinephelus areolatus*) in Java Sea, Indonesia. *Regional Studies in Marine Science*, 66: 103116.
- Udupa K.S. (1986). Statistical method of estimating the size at first maturity in fishes. *Fishbyte*, 4(2): 8-10.
- Utama R.S., Renyaan J., Nurdiansah D., Makatipu P.C., Suyadi, Hapsari B.W., Rahayu E.M., Della, Sugiharto A., Akbar N. (2022). Diversity of reef fish species in presence of mangrove habitat in Ternate, North Maluku, Indonesia. *Biodiversitas*, 23(10): 5184-5193.
- Yildiz T., Ulman A. (2020). Analyzing gaps in policy: Evaluation of the effectiveness of minimum landing size (MLS) regulations in Turkey. *Marine Policy*, 115: 103829.