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Population dynamics of *Variola albimarginata* Baissac, 1953 and *Variola louti* Fabricius, 1775 (Perciformes: Serranidae) in Sulawesi Sea, Indonesia

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Abstract. *Achmad DS, Nurdin MS, Tilome AA, Moore AM. 2024. Population dynamics of* Variola albimarginata *Baissac, 1953 and* Variola louti *Fabricius, 1775 (Perciformes: Serranidae) in Sulawesi Sea, Indonesia. Biodiversitas 25: 978-989.* The lyretail groupers *Variola louti* Fabricius, 1775 and *Variola albimarginata* Baissac, 1953 (Epinephelinae) are valuable foodfishes. IUCN Red List assessments classified both species as Least Concern, while noting that some stocks are overfished. The purpose of this study on the population dynamics of *Variola* groupers in Kwandang Bay was to evaluate the exploitation level for both species in this important grouper fishing area of the Sulawesi Sea, Indonesia. Population dynamics parameters were calculated based on length-frequency data collected from October 2022 to September 2023 using the ELEFAN I response surface analysis option in FISAT II. The asymptotic length at infinity TL_∞ was 54.90 cm for *V. louti* and 54.40 cm for *V. albimarginata* with von Bertalanffy growth function K values 0.54 and 0.55, respectively. Recruitment occurred throughout the year, with monthly percentages of 1.08-13.52 % and 1.61-14.99%, respectively. Natural and fishing mortality were M = 1.04/year^{-1} and F = 1.17/year^{-1} for *V. louti* and M = 1.05/year^{-1} and F= 2.56/year^{-1} for *V. albimarginata* giving F/M ratios of 1.13:1 and 2.44:1. Beverton and Holt yield per recruit analysis gave exploitation rates (E = 0.53/year^{-1} and E = 0.71/year^{-1}) exceeding the maximum sustainable value E_{max} = 0.37/year^{-1}, indicating overexploitation of both species. To achieve the optimum exploitation rate of E_{50} = 0.24, fishing effort needs to be reduced by 29% for *V. louti* and 47% for *V. albimarginata*. Management options include setting a minimum legal size with recommended values of 32-33 cm and temporary closures during the peak reproductive season in May-June.

Keywords: Epinephelinae, fisheries management, overexploitation, *Variola*

INTRODUCTION

Coral reef fish are prone to overexploitation worldwide, with around 51% of stocks overfished and 19% fully exploited globally (Amorim et al. 2019). The overexploitation of key predators such as groupers has serious implications for ecosystem integrity, especially for coral reefs ecosystems (Dirhamsyah 2012), in addition to the socio-economic impacts such as reduced income and profits for fishers and fisheries sector businesses (Amorim et al. 2018a; Squalli 2020). Groupers (subfamily Epinephelinae, family Serranidae) are a premium commodity traded on international markets and support the livelihoods of millions of people around the world (Ferse et al. 2014; Dimarchopoulou et al. 2021); they are also important for the tourism sector, the restaurant trade, and contribute to global food security (Sadovy et al. 2013; Shideler et al. 2015; Frisch et al. 2016; Condini et al. 2018).

Declining grouper population abundance has become a major global and local fisheries issue (Sadovy et al. 2013; Yulianto et al. 2015; Waterhouse et al. 2020). The overexploitation of grouper stocks has been driven by strong demand and *de jure* or *de facto* open access regimes, exacerbated by destructive fishing practices and policies leading to over-capitalization that have had significant and worrying impacts on many grouper and other fish stocks (Babcock et al. 2013; Khasanah et al. 2020; Mavruk 2020; Sadovy et al. 2020; Echazabal-Salazar et al. 2021). Consequences for grouper populations include reductions in reproductive output (Chong-Montenegro and Kindsvater 2022; Mahé et al. 2022), reduced population size (Anderson et al. 2014; Giglio et al. 2017), and reduction in intra-species genetic diversity (Sherman et al. 2016).

Maintaining fish stocks at an optimum level is a primary principle and main goal of fisheries management worldwide (Fujita et al. 2014; Harford et al. 2019; Hilborn et al. 2020; Hasan et al. 2023). In the context of groupers, which tend to have a low reproductive capacity and life-history traits making them intrinsically vulnerable to overexploitation (Sadovy et al. 2020; Stock et al. 2021), in-depth and comprehensive understanding of population dynamics parameters such as growth, mortality, exploitation rate and recruitment patterns is particularly crucial (Vo et al. 2014; Mehanna et al. 2019). A good understanding of population dynamics can lead to more effective and precisely targeted fisheries management, including population monitoring programs and tools such as setting minimum legal sizes, fishing quotas, maximum limits for fishing gears, fishing vessels, and fishing capacity (Mudjirahayu et al. 2017; Osman et al. 2018; Efendi et al. 2020; Bravo-Calderon et al. 2021). Such science-based approaches are urgently needed to maintain grouper stocks, prevent overexploitation in order to maintain the ecological integrity of marine ecosystems and support sustained economic benefits to fishing communities and the fisheries sector.

Indonesia is consistently one of the top 10 global producers of reef fish groupers (Amorim et al. 2020), with around 10,000 fishing units or vessels operating in Indonesian archipelagic waters (Wibisono et al. 2022). Kwandang Bay on the Sulawesi Sea (north) coast of Gorontalo Province is one of many Indonesian grouper fishing grounds (Achmad et al. 2020; Achmad et al. 2021). At least 26 groupers are caught in and traded from Kwandang Bay (Achmad et al. 2023a), including two assessed as vulnerable (VU), two as data deficient (DD), and 24 as least concern (LC) in the International Union for Conservation of Nature (IUCN) Red List (IUCN 2022; Achmad et al. 2023a). At least two of the groupers classified as LC globally, *Epinephelus coioides* Hamilton, 1822 (Amorim et al. 2018b) and *Plectropomus leopardus* Lacepède, 1802 (Choat and Samoilys 2018), are overexploited in Kwandang Bay (Achmad et al. 2022). This points towards the need for research on the population dynamics of other groupers in Kwandang Bay that have been classified globally as LC in order to better understand their status and identify species currently or potentially at risk of overexploitation in this important grouper fishing ground.

The two recognized species in the genus *Variola*, both assessed as least concern (LC) in the IUCN Red List, are the white-edged lyretail *Variola albimarginata* Baissac, 1953 and the yellow-edged lyretail *Variola louti* Fabricius, 1775, although both assessments note that some populations are likely overexploited (Nair et al. 2018; Sadovy et al. 2018). Research on the population dynamics of Indonesian *Variola* populations has been limited, although there have been studies on *V. albimarginata* in the Indonesian Fisheries Management Area (FMA) 715 (Ernawati et al. 2021), *V. louti* in Sibolga (Hargiyatno and Faizah 2021), *V. albimarginata* and *V. louti* in Sumbawa (Hilyana et al. 2021), and *V. albimarginata* in Labuan Bajo (Rachmawati and Puspasari 2021). The purpose of this research was to estimate population dynamics parameters for the *V. louti* and *V. albimarginata* populations in Kwandang Bay, on the Sulawesi Sea coast of Sulawesi in Indonesian FMA 716. These data can inform efforts to improve grouper stock management in this region.

MATERIALS AND METHODS

Study area

Data were collected from October 2022 to September 2023 in Kwandang Bay (Sulawesi Sea), Moluo Village, Kwandang Sub-district, North Gorontalo District, Gorontalo Province, Indonesia. This site is in the Indonesian FMA 716, which includes reaches of the Sulawesi Sea north of Sulawesi Island and the border with the Philippines. The approximate site coordinates are 00°54'15" N and 122°52'79" E (Figure 1).

Groupers of the genus *Variola* are generally caught around the small islands close to the offshore boundary of Kwandang Bay, where coral reefs are the predominant substrate type (Achmad et al. 2022). The main fishing gears used are handlines and spearguns; both gears are effective as they are well adapted to the behavior of groupers, which tend to hide in nooks and crannies in the reef or in coral caves (Rahim et al. 2021). Fishing trips mostly last around 6 hours (one day fishing), with a travel time from the fishing base to the fishing ground of around 30 min.

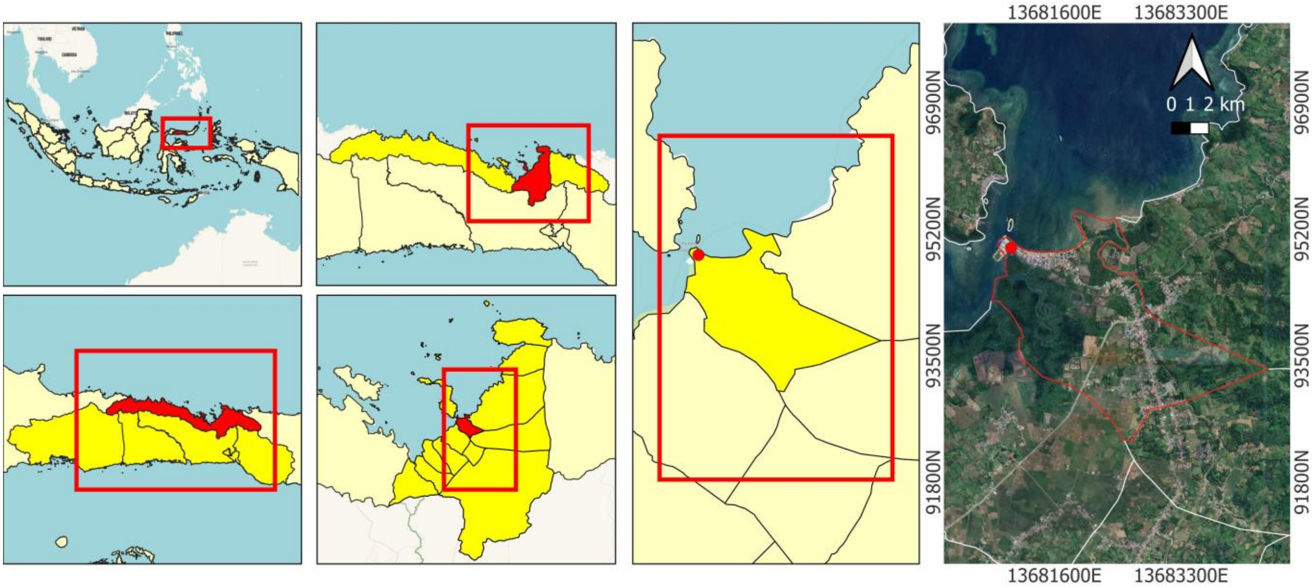

Figure 1. Grouper fishing grounds in Kwandang Bay (Sulawesi Sea), Gorontalo Province, Indonesia

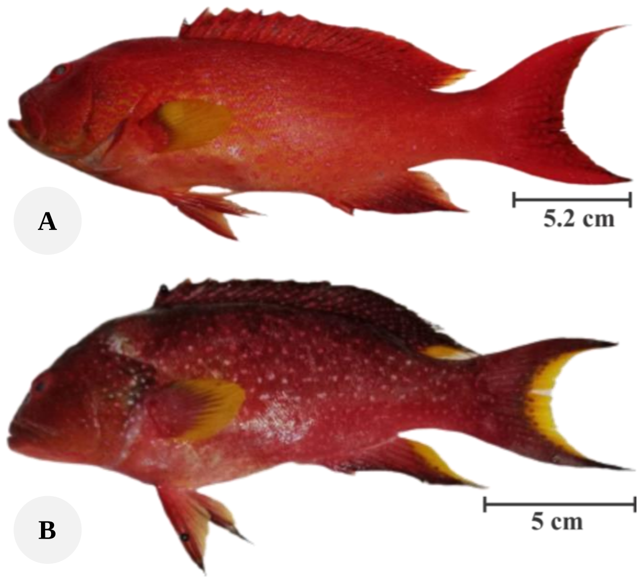

Figure 2. The specimen of lyretail groupers from Kwandang Bay, Gorontalo Province, Indonesia. A. *V. albimarginata* and B. *V. louti*

Procedures

Sampling was conducted twice a month (24 times). Samples of the *Variola* genus (n = 903) comprised white-edged lyretail *V. albimarginata* (n = 529) and the yellow-edged lyretail *V. louti* (n = 374) (Figure 2), both of which are commonly caught in Kwandang Bay (Achmad et al. 2023a) and globally assessed as least concern (Nair et al. 2018; Sadovy et al. 2018). The species of each *Variola* specimen was determined with reference to the FAO guide to groupers of the world (Heemstra and Randall 1993) and other references (ADB 2017; Michailidis et al. 2020). The total length of each specimen was measured using a Cadwell fish ruler (precision 1 mm). When the catch volume was low, all available specimens were sampled (census); when the catch volume was high, a simple random sampling method was used.

The population dynamics parameters estimated included asymptotic length (length at infinity), growth, mortality, exploitation rate, recruitment pattern, and relative yield per recruit (Y'/R). These parameters were estimated from the length-frequency data using the ELEFAN I (Electronic Length Frequency Analysis) suite in FISAT II (Fish Stock Assessment Tools) (Gayanilo et al. 2005).

Data analysis

The growth coefficient K for each species (*V. albimarginata* and *V. louti*) can be estimated based on the length-frequency based von Bertalanffy Growth Function (VBGF) (Beverton and Holt 1957):

$$Lt = TL\infty\left\{1 - e^{-K(t-t0)}\right\}$$

Where:
Lt : fish length at time t;
TL∞ : the asymptotic length; K is the growth coefficient;
t0 : the theoretical age at which length is zero.

To solve this equation, the various parameters need to be calculated or estimated. The theoretical age at which length is zero (t0) can be estimated using the empirical equation developed by (Pauly 1980):

$$\text{Log}\,(-t_0) = -0.3922 - 0.2752 \log TL\infty - 1.038 \log K$$

Where:
TL∞ : the asymptotic length (cm)
K : the growth coefficient.

The ELEFAN I functions were applied to solve these equations using length-frequency data to provide values for K, TL∞, and t0.

Total mortality (Z) was estimated using the equation developed by Ricker (1975) as implemented in ELEFAN I (Gayanilo et al. 2005) using a length-converted catch curve as:

$$Z = K\,\frac{(TL\infty - L)}{L - L'}$$

Where:
Z : total mortality (annual rate),
K : the growth coefficient, TL∞ is the asymptotic length (cm),
L : the mean length of the catch (cm),
L' : the length at first capture (length of the smallest fish caught) (cm).

Natural mortality (M) was calculated based on the empirical formula in (Pauly 1980):

$$\text{Log}\,M = -0.0066 - 0.279 \log TL\infty + 0.6543 \log K + 0.4634 \log T$$

Where:
TL∞ : the asymptotic length (cm)
K : the growth coefficient
T : the mean annual temperature (°C). T was set at 30°C based on recent data for Kwandang Bay.

Fishing mortality (F) was calculated using the formula in (Sparre and Venema 1998) as implemented in ELEFAN I (Gayanilo et al. 2005) as:

$$F = Z - M$$

Where:
F : fishing mortality
Z : total mortality
M : natural mortality

Exploitation rate (E) was calculated using the formula in (Pauly 1980) as:

$$E = \frac{F}{Z}$$

Where: E is exploitation rate, F is fishing mortality, and Z is total mortality. In general, the optimum exploitation rate range is ≤0.5 (Beverton and Holt 1964), although the upper limit can vary depending on species or population characteristics.

Using the estimated values obtained for parameters E, M, and K, the yield per recruit (Y'/R) was calculated (Beverton and Holt 1964) as:

$$\frac{Y'}{R} = E(1-c)^{\frac{M}{k}}\, x \left[1 - \frac{3(1-c)}{1+\frac{1-E}{\frac{M}{k}}} + \frac{3(1-c)^2}{1+\frac{2(1-E)}{\frac{M}{k}}} + \frac{(1-c)^2}{1+\frac{3(1-E)}{\frac{M}{k}}}\right]$$

Where the value of c was set at c = 0.050 for both *V. albimarginata* and *V. louti*.

RESULTS AND DISCUSSION

Growth parameters

The length-frequency data show similar ranges for both lyretail species. The total length (TL) range and mean TL were 19-50 cm (mean ± SD = 30.73±5.44 cm) for *V louti* (Figure 3) and 19-49 cm (mean ± SD = 31.16±4.80 cm) for *V albimarginata* (Figure 4). The most frequently caught size class for *V. louti* (25-27 cm, 110 individuals representing 29.41% of the sampled catch) was slightly smaller than for *V. albimarginata* (28-30 cm, 133 individuals representing 25.14% of the sampled catch).

The growth parameters for Kwandang Bay *V. louti* and *V. albimarginata* populations were relatively similar. The respective lengths at infinity (TL∞) were 54.90 cm and 54.40 cm, with growth coefficients (K) of 0.54 and 0.55 (Figure 5). These results yielded the growth equations $Lt = 54.90\left\{1 - e^{-0.54(t+0.2552)}\right\}$ for *V\ louti* and $Lt = 54.40\left\{1 - e^{-0.55(t+0.2510)}\right\}$ for *V. albimarginata*. Based on these equations, for both *V. louti* and *V. albimarginata* the smallest size at capture (TL =19 cm) corresponds to an estimated age of 6-8 months, while the estimated age at asymptotic length TL∞ was 9-10 years (Figure 5).

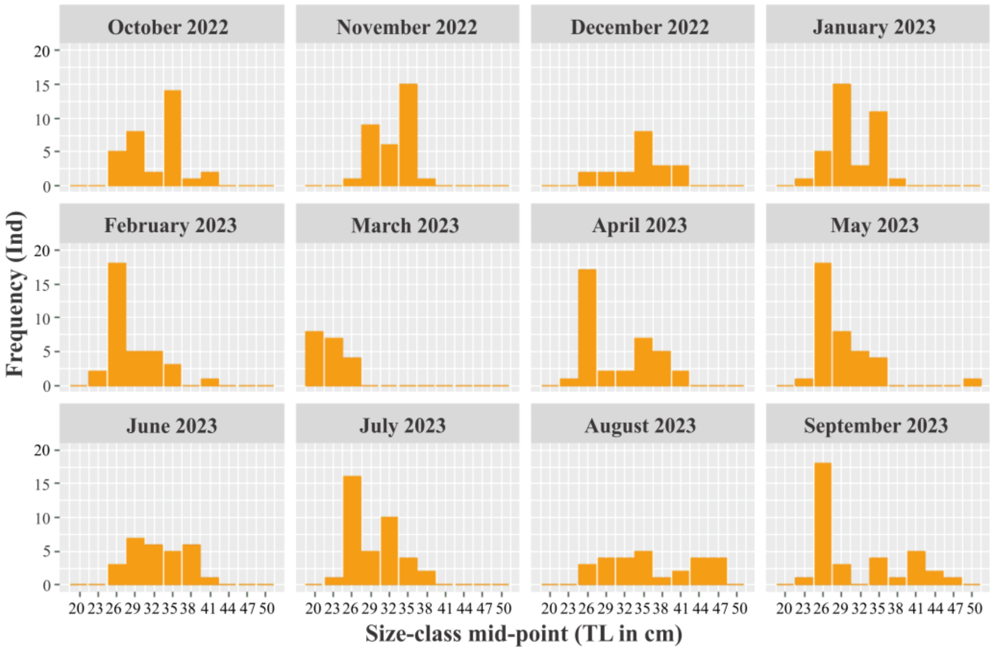

Figure 3. Monthly length-frequency for *Variola louti*

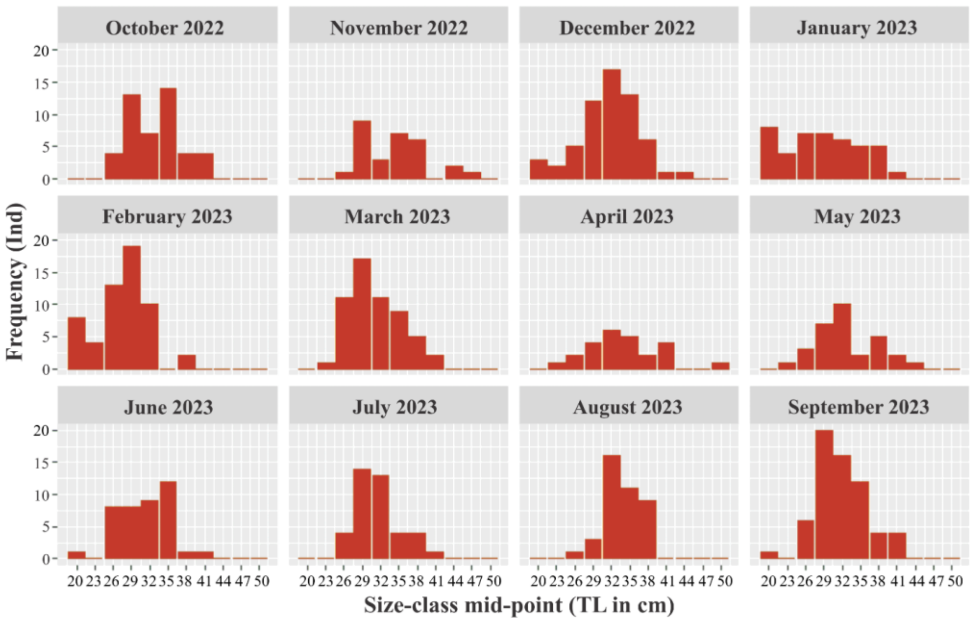

Figure 4. Monthly length-frequency for *Variola albimarginata*

Recruitment

The recruitment analyses for the lyretail groupers *V. louti* and *V. albimarginata* in Kwandang Bay indicate that these groupers recruit to the area throughout most of the year, with the onset of recruitment each year around June (Figure 6). Monthly recruitment percentages varied from 1.08-13.52 % for *V. louti* and 1.61-14.99% for *V. albimarginata*. The recruitment peak for *V. louti* occurred in May, one month earlier than the peak for *V. albimarginata* in June (Figure 7), indicating spawning peaks for *V. louti* and *V. albimarginata* around May-June.

Mortality and yield per recruit

The mortality rates for *V. louti* were: total mortality Z = 2.21 $year^{-1}$; natural mortality M = 1.04/$year^{-1}$; and fishing mortality F = 1.17/$year^{-1}$ (Figure 8). For *V. albimarginata*, Z = 3.61/$year^{-1}$, M = 1.05/$year^{-1}$ and F= 2.56/$year^{-1}$ (Figure 9). An exploitation rate of 0.24 would reduce the biomass of both *V. louti* and *V. albimarginata* by 50% (E_{50}). For *V. louti* E = 0.53/$year^{-1}$ and for *V. albimarginata* E = 0.71/$year^{-1}$. The Beverton and Holt yield per recruit analysis indicates that both lyretail grouper populations are over-exploited, as the exploitation rates were in excess of the recommended maximum E_{max} = 0.37/$year^{-1}$.

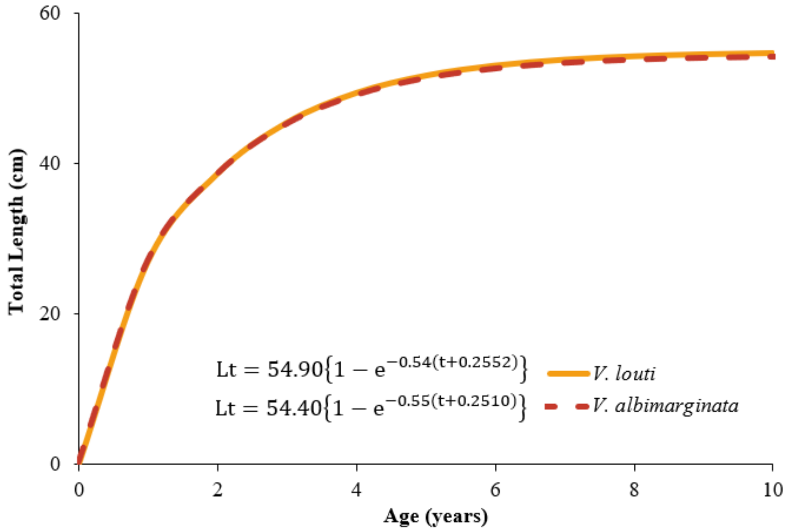

Figure 5. The von Bertalanffy growth equation for the lyretail groupers *Variola louti* and *V. albimarginata* based on length-frequency data

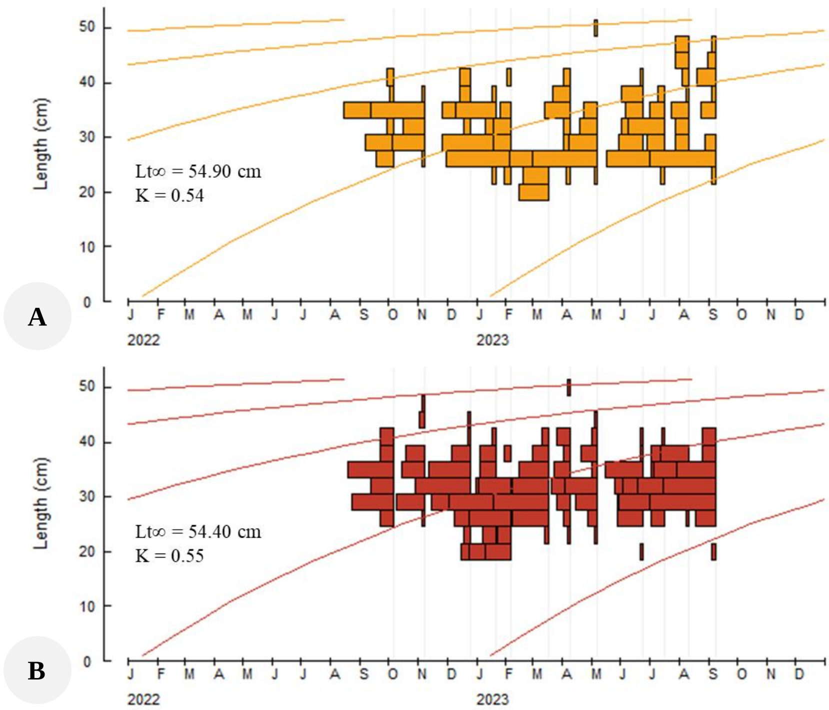

Figure 6. Length-frequency-based growth models for A. *Variola louti* and B. *V. albimarginata*

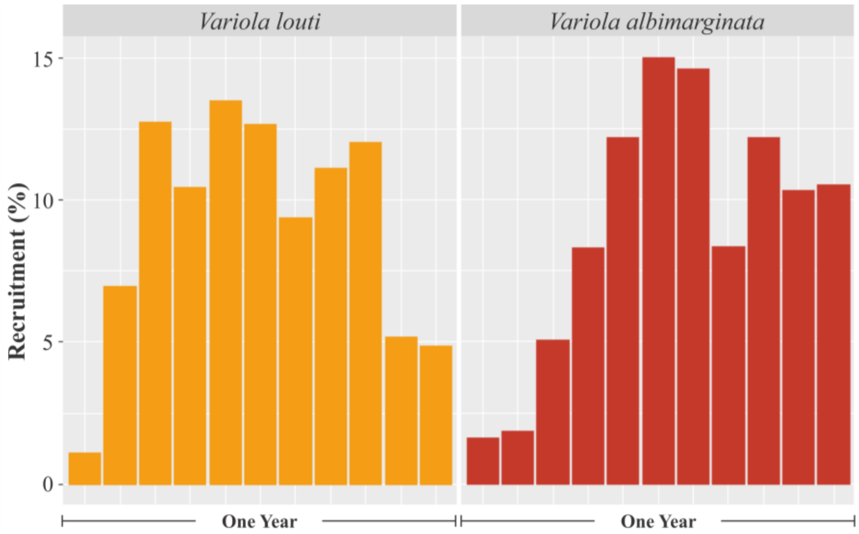

Figure 7. Monthly recruitment of the lyretail groupers *Variola louti* and *V. albimarginata* in Kwandang Bay, Gorontalo Province, Indonesia, over a one-year period

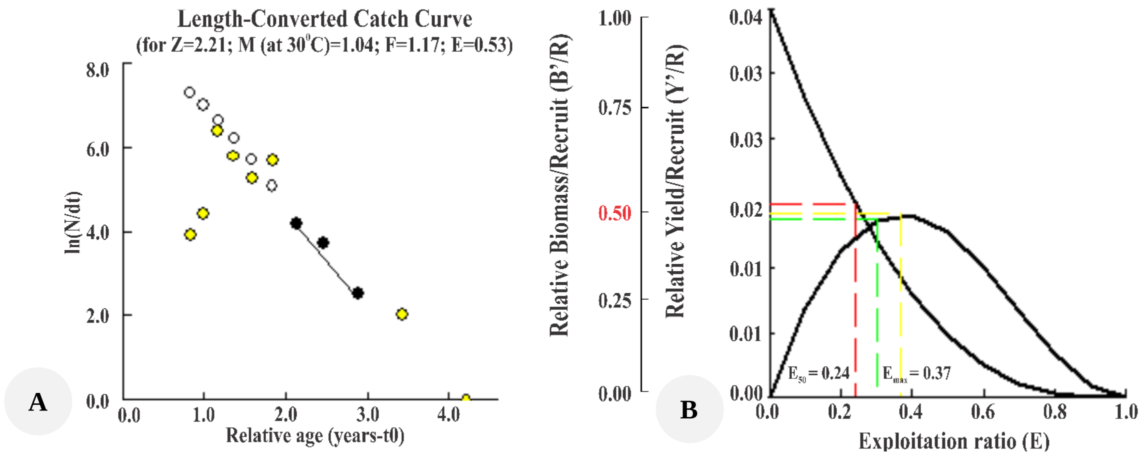

Figure 8. Mortality analysis based on A. Length-converted catch curve and B. Beverton and Holt yield per recruit analysis for *Variola louti* in Kwandang Bay, Gorontalo Province, Indonesia

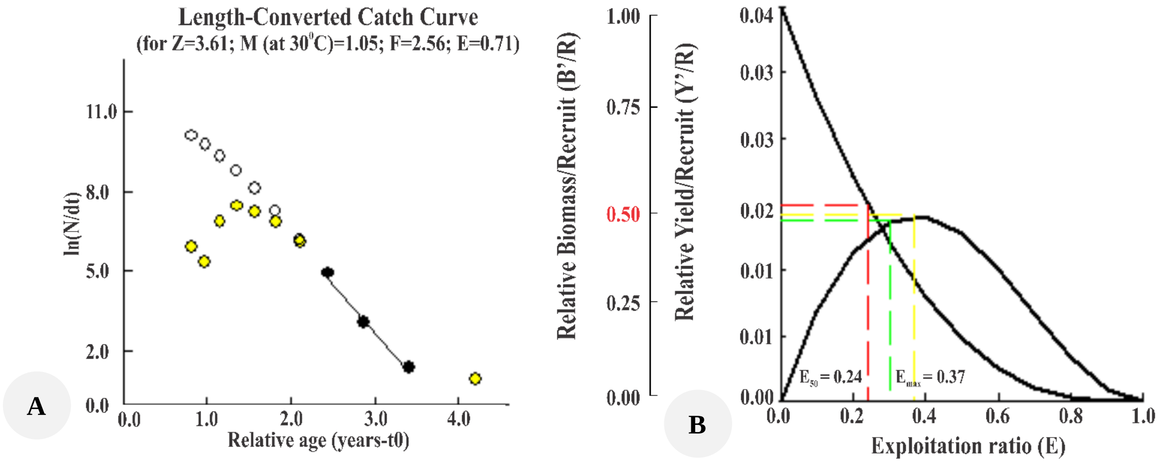

Figure 9. Mortality analysis based on A. Length-converted catch curve and B. Beverton and Holt yield per recruit analysis for *Variola albimarginata* in Kwandang Bay, Gorontalo Province, Indonesia

Discussion

Studies on Indonesian populations of lyretail groupers of the genus *Variola* are limited in terms of the aspects addressed and the geographic scope. Most such studies are recent and published since 2020 (Halim et al. 2020; Damora et al. 2021; Ernawati et al. 2021; Hargiyatno and Faizah 2021; Hilyana et al. 2021; Rachmawati and Puspasari 2021; Sala et al. 2022). The two species currently recognized in the genus *Variola* are both widespread, often occur in sympatry, and can be easily confused with each other (Abdullah and Rehbein 2016; Nair et al. 2018; Sadovy et al. 2018; Andriyono et al. 2020), although a molecular (DNA) study found two genetically distinct *V. louti* populations, raising the possibility of sub-species or cryptic species within this genus (Durand et al. 2020). This genus can be distinguished from other groupers by the lunate shape of the caudal fin, reflected in the common name lyretail. The two species can be distinguished by the color of the caudal fin margin, which is yellow in *V. louti* and white in *V. albimarginata* (Michailidis et al. 2020; Oshiro et al. 2023); this coloration is reflected in the common names for both species and the Latin name of *V. albimarginata*. The two lyretail groupers are similar in size (Achmad et al. 2023a,b), and classified as medium-sized groupers with TL in the range of 36-51 cm (Irigoyen-Arredondo et al. 2016).

The red coloration of the body makes these groupers especially desirable in many markets (Shimose and Kanaiwa 2022), and the exotic shape of the tail can further enhance their attractiveness. This popularity is reflected in the price; at the time of the study, grouper fishermen in Kwandang Bay were typically paid 65,000-85,000 IDR per kg (approximately US$ 4.2-5.5), which was quite high by local standards. Although the use of destructive fishing methods in grouper fisheries is not uncommon, especially for the live reef food fish trade (Halim et al. 2020), this does not appear to be the case for the Kwandang Bay grouper fishery, where the fish are generally sold fresh but dead. During the study, most of the lyretail groupers landed in Kwandang Bay and were caught using handlines or spearguns. However, in the absence of appropriate management, the use of gears widely considered non-destructive or relatively environmentally friendly does not necessarily prevent overfishing (Latuconsina et al. 2020; Efendi et al. 2020).

The total length (TL) of *Variola* groupers caught in Kwandang Bay during this research was similar to that reported in 2021 (Achmad et al. 2023a,b). The value of the asymptotic length $TL\infty$ estimated for the Kwandang Bay Variola populations in the Sulawesi Sea is smaller than for populations in Sumbawa (Hilyana et al. 2021) but larger than in North Maluku (Ernawati et al. 2021) and Labuan Bajo (Rachmawati and Puspasari 2021), and within the range reported for Variola populations from other countries (Table 1). The high growth coefficient K values for both Kwandang Bay Variola groupers indicate that Kwandang Bay provides a suitable habitat for lyretail groupers. Reef-associated groupers such as *V. louti* and *V. albimarginata* are high trophic level predators and rely on healthy coral reef ecosystems to provide prey and refuges or places to rest (Frisch et al. 2016). While data are limited, Kwandang Bay has extensive coral reefs, some at least in good condition, despite degradation due to destructive fishing and other human impacts (Achmad et al. 2023a). The relatively high mean temperature (30 ºC) observed at the site likely influenced fish growth and, therefore, the length-frequency data obtained. Temperature influences fish metabolism and therefore has a direct effect on fish growth, accelerating growth initially until the optimum range is exceeded (Speers-Roesch and Norin 2016; Neubauer and Andersen 2019). As temperature increases above this range, growth will decrease until the thermal niche limit is reached, resulting in mortality. Temperature can also have an indirect effect on fish growth through the influence of temperature on primary productivity, with knock-on effects at higher levels in the food chain (Moloney et al. 2011; Neubauer and Andersen 2019). Furthermore, temperature is a key factor influencing growth and natural mortality (Pauly 1980) and is one of the parameters in the empirical equations used for the analyses in FISAT II.

The growth coefficient K is related to the time required to approach the asymptotic length $TL\infty$. Higher values of K reflect a shorter time to reach $TL\infty$. Values of $K > 0.5$, as estimated for the lyretail groupers *V. louti* and *V. albimarginata* in Kwandang Bay, correspond to relatively rapid growth (Sparre and Venema 1998). These results for Sulawesi Sea lyretail groupers are consonant with findings of relatively fast growth and relatively short time to maturity of *V. louti* and *V. albimarginata* compared to other groupers in the waters around La Réunion Island, despite lower values of K in this region of the Indian Ocean (Mahé et al. 2022). In general, faster fish growth equates to a shorter lifespan (Pauly 1980). Bomb and otolith radiocarbon dating has shown that some groupers, at least, can live for 56-61 years (Sanchez et al. 2019; Barnett et al. 2020). The maximum lifespan of *V. louti* has been estimated at 17 years (Schemmel and Dahl 2023), and FishBase gives estimates of 11 years for *V. louti* and 12 years for *V. albimarginata* (Froese and Pauly 2023). However, grouper growth and life-history patterns are complex, and there does not seem to be any validation of the longevity of lyretail groupers.

The recruitment patterns of *V. louti* and *V. albimarginata* in Kwandang Bay indicate a long spawning season for both species, with a temporal shift between the two species in the extended spawning peaks. A similar pattern is reported for both lyretail groupers from La Réunion Island in the Indian Ocean (Mahé et al. 2022) as well as for two other groupers (*E. coioides* and *P. leopardus*) in Kwandang Bay (Achmad et al. 2022). Although the *V. louti* recruitment season in Kwandang Bay began earlier than for *V. albimarginata*, both overlap with the peak recruitment of *E. coioides* and *P. leopardus* in the bay (Achmad et al. 2019; Achmad et al. 2022). Although further research on reproductive biology is needed to validate this hypothesis, it seems likely that May-June is an important reproductive peak for at least four and possibly more grouper species in Kwandang Bay. The peaks for *E. coioides* and *P. leopardus* appear more marked than for the lyretail groupers, with monthly percentages peaking at 17.11% and 19.22%, respectively (Achmad et al. 2022).

Several studies on Indonesian grouper populations have found two annual recruitment peaks, for example in *Plectropomus maculatus* Bloch, 1790 (Adibrata et al. 2018), *Anyperodon leucogrammicus* Valenciennes, 1828) (Pane et al. 2021), *P. leopardus* and *E. coioides* (Tapilatu et al. 2021), although the spread and intensity of the peaks varies between species. Such dual recruitment peaks indicate partial spawning patterns (Hargiyatno and Faizah 2021), which are common in tropical regions (Abesamis et al. 2015), such as Indonesia. Partial spawning as a reproductive strategy enables fish to spawn several times over an extended period (Araújo et al. 2012; Condini et al. 2013). This can enable groupers to maximize the chances of successful reproduction and thereby increase the number of recruits joining the population (Harrison et al. 2023), although groupers can also recruit to a given population through migration from nearby waters (Bodilis et al. 2003; Waldie et al. 2016; Stock et al. 2021).

Reported mortality figures vary between lyretail grouper populations (Table 2). In Kwandang Bay, the natural mortality of both *V. louti* and *V. albimarginata* was less than the fishing mortality, similar to most other Indonesian Variola populations, with the exception of *V. louti* in Sumbawa (Hilyana et al. 2021). The ratios of fishing mortality to natural mortality for *V. louti* (F:M 1.13:1) and *V. albimarginata* (2.44:1) in Kwandang Bay can be considered high enough to cause a decline in population abundance (Mehanna et al. 2019; Barnett et al. 2020), especially as the exploitation rates can also be considered as high (E >0.5) (Beverton and Holt 1964). Similarly high values of F:M and E were also found for *E. coioides* and *P. leopardus* in Kwandang Bay (Achmad et al. 2022); together with the results of this study, this indicates a pattern of heavy fishing pressure on commercially valuable groupers in this area of the Sulawesi Sea.

While the F/M ratio and exploitation rate in Kwandang Bay are high, they are similar to those for some other Indonesian lyretail grouper populations in Table 2. However, the values of total, natural and fishing mortality (Z, M, F) are all higher than for any of the other populations in Table 2, with the closest being a recent study in Labuan Bajo (Rachmawati and Puspasari 2021). Reasons for this could include the high mean temperature, as discussed above, as well as the intensity of exploitation. The heavy fishing pressure on *V. louti* and *V. albimarginata* populations in Kwandang Bay is reflected in the exploitation rates, with $E > E_{50}$ and $E > E_{max}$. Over the 14 years from 2009 to 2022, there was a substantial increase in fishing efforts in terms of both vessels and fishing gear (Achmad et al. 2022). The situation has been further exacerbated by the high proportion of immature fish caught, with the size classes comprising the majority of the catch below Lm_{50}, the mean length at first maturity (Achmad et al. 2020). The data strongly suggest growth overfishing of both *V. louti* and *V. albimarginata* populations; this will not only have a negative impact on stock biomass but will also reduce recruitment (Bailey 2013; Mohamed et al. 2014; Ben-Hasan et al. 2021). Although the analysis indicates ongoing recruitment of *V. louti* and *V. albimarginata* during most months of the year, sooner or later, the abundance of spawners will decline if fishing effort is not controlled and kept to a sustainable level (Siepker and Michaletz 2013; Shaw and Allen 2016). Indeed, given the current high levels of overexploitation, stocks are likely to continue to decline, at least in the short term, irrespective of management interventions to improve the long-term status of the stocks due to the past and current loss of reproductive capacity (Echazabal-Salazar et al. 2021).

Table 1. Growth parameters for several lyretail grouper (genus *Variola*) populations

Species	TL∞ (cm)	K	Location	Source
V. albimarginata	60.44	0.17	Sumbawa	Hilyana et al. (2021)
V. louti	70.87	0.16		
V. albimarginata	44.42	0.38	North Maluku	Ernawati et al. (2021)
V. louti	48.55	0.13	Sibolga	Hargiyatno and Faizah (2021)
V. albimarginata	45	0.51	Labuan Bajo	Rachmawati and Puspasari (2021)
V. albimarginata	63.30	0.16	La Réunion	Mahé et al. (2022)
V. louti	76.57	0.21	Island, Indian ocean	
V. louti	43.70 (FL∞)	0.28	Guam	Schemmel and Dahl (2023)
V. louti	54.90	0.54	Kwandang Bay	*This study*
V. albimarginata	54.40	0.55		

Table 2. Mortality data for several lyretail grouper (genus *Variola*) populations

Species	Z	M	F	E	Location	Source
V. albimarginata	1.01	0.23	0.78	0.76	Sumbawa	Hilyana et al. (2021)
V. louti	0.42	0.23	0.19	0.44		
V. albimarginata	1.09	0.54	0.55	0.51	North Maluku	Ernawati et al. (2021)
V. albimarginata	2.92	0.89	2.03	0.70	Labuan Bajo	Rachmawati and Puspasari (2021)
V. louti	0.92	0.42	0.50	0.55	Sibolga	Hargiyatno and Faizah (2021)
V. louti	2.21	1.04	1.17	0.53	Kwandang Bay	*This study*
V. albimarginata	3.61	1.05	2.56	0.71		

Fisheries management interventions to address the growth overfishing of *V. louti* and *V. albimarginata* are urgently needed not only to maintain the stocks of these two valuable fish, but also because growth overfishing of key predators such as groupers can lead to a decline in coral reef ecosystem health with negative socio-economic impacts on fishing communities (Frisch et al. 2016; Usseglio et al. 2016). Management tools recommended for addressing the overfishing of groupers include designing marine protected areas (MPAs) to specifically protect spawning aggregation sites, often referred to by the acronym SPAGS (Yulianto et al. 2015; Osman et al. 2018; Stock et al. 2021), spatio-temporal closure of fishing grounds (Waterhouse et al. 2020), setting minimum legal sizes, and limitations on fishing gear (Babcock et al. 2013; Mudjirahayu et al. 2017; Bawole et al. 2018; Khasanah et al. 2019; Khasanah et al. 2020). Monitoring grouper stocks, including biological parameters and population dynamics, is also very important (Schemmel and Dahl 2023), in particular through the collection of catch data disaggregated by species, especially at fishing ports and fish landing sites (Condini et al. 2018; Khasanah et al. 2020; Kadir et al. 2023).

Fisheries and conservation management measures that could be applied to rebuild and maintain the *V. louti* and *V. albimarginata* populations in Kwandang Bay include setting size limits and spatio-temporal closures. Based on life-history data, setting minimum legal sizes at or above 33 cm for *V. louti* and 32 cm for *V. albimarginata* would enable most fish to reproduce (as protogynous females) before capture (Achmad et al. 2023b). In practice, this could require gear restrictions or modifications, for example, hook size, as well as monitoring of fish landed or traded. Temporary or permanent spatial fishery closures are another option. This could involve temporary closure of the fishery in Kwandang Bay, as life history data indicate that restricting or closing the fishery for one month in May or June should substantially increase the natural recruitment of several grouper species, including the lyretail groupers *V. louti* and *V. albimarginata* (Achmad et al. 2022, 2023b). If the required data were available, a more finely targeted approach would be possible; areas known or suspected as spawning aggregation sites could be closed to fishing, either temporarily during the peak spawning season or permanently (Sadovy 2016). This could be achieved through zonation as part of the current drive towards reaching Indonesian spatial targets for marine protection, through classic marine protected area (MPA) and/or other effective area-based conservation measure (OECM) approaches (Estradivari et al. 2022). Fishermen are likely to oppose such measures on economic grounds, so they will need to be persuaded of the benefits, as these regulations could increase annual and longer-term income and profits from grouper fishing. Furthermore, the data indicate a need to reduce fishing pressure by 29% for *V. louti* and 47% for *V. albimarginata* from current levels (E = 0.53 and 0.71, respectively) to reach the optimum exploitation rate of E_{50} = 0.24.

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