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Population dynamics of reef fish in the Kwandang Bay, Sulawesi Sea, Indonesia

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Abstract. *Achmad DS, Gani S, Ardiansyah W, Mokoginta MM, Nurdin MS, Jompa J, Indrianti MA, Achmad N. 2022. Population dynamics of reef fish in the Kwandang Bay, Sulawesi Sea, Indonesia. Biodiversitas 23: 5217-5226.* The grouper stocks in Kwandang Bay, Sulawesi Sea, Indonesia, are dominated by orange-spotted grouper (*Epinephelus coioides*) and coral trout (*Plectropomus leopardus*). However, the Kwandang Bay grouper fishery is currently experiencing serious challenges due to population decline resulting in a decline in both the average size of fish caught and the production volume. This study was conducted in Kwandang Bay, Sulawesi Sea, from January to December 2021. The population dynamics parameters estimated were growth, recruitment, mortality, exploitation rate and yield per recruit. The results showed that the total length (TL) of *E. coioides* and *P. leopardus* ranged from 16.50-101 cm and 17.90-60 cm, respectively, with Von Bertalanffy K-coefficients of 0.38 and 0.69, respectively. Recruitment occurred during most of the year, with respective recruitment value ranges of 0.99-17.11% and 0.08-19.22%. Natural and fishing mortality was 0.69/year^{-1} and 0.87/year^{-1} for *E. coioides*, 1.16/year^{-1} and 1.47/year^{-1} for *P. leopardus*. Beverton and Holt yield per recruit analysis indicated recruitment overfishing of both *E. coioides* and *P. leopardus*. Fishing regulations are needed to maintain a sustainable grouper fishery, including a 25% reduction in fishing vessels and gear, to enable the groupers of Kwandang Bay to spawn at least once during their life cycle.

Keywords: Grouper, recruitment overfishing, stock

INTRODUCTION

Groupers are arguably the most intensively exploited group of coral reef-associated fish, especially in the Live Reef Fish Food Trade (LRFFT); they are a highly-priced commodity much in demand in both domestic and export markets (Jefri et al. 2015; Damora et al. 2021; Dwifajri et al. 2022). With the rising global demand for reef fish, the LRFFT in general and the grouper export trade, in particular, have made significant contributions to the Indonesian economy, both financially and in terms of employment, with annual export values reaching 571 billion IDR (MMAF 2020). While with groupers are also exported frozen and fresh, live groupers comprise over 50% of Indonesian grouper exports and also fetch the highest price. The main destination for live reef fish from Indonesia is Hongkong, which is both a major consumer and a hub for the Asian LRFFT, including markets in mainland China (Khasanah et al. 2020).

Kwandang Bay, facing the Sulawesi Sea on the north coast of Gorontalo Province, is situated in the Coral Triangle, which is also the center of reef fish diversity (Allen 2008). According to official statistics, there are 21 islands in the Kwandang Bay area. These islands are surrounded by coral reefs, with many also having seagrass and/or mangrove ecosystems (Olii et al. 2015; Kasim et al. 2018; Yusuf and Indrawan 2019). Several have been or are being developed as tourist attractions, including Saronde, Ponelo, Bogisa, Hulawa and Lampu Island (Yusuf and Indrawan 2019; Manyoe et al. 2022). The tropical coastal ecosystems and plankton-rich waters of Kwandang Bay combined with natural harbor features have made Kwandang Bay in North Gorontalo District the main center for both pelagic and reef fisheries in Gorontalo Province (Sahami et al. 2017; Chodrijah et al 2020; Achmad et al. 2021). The Kwandang Bay grouper fishery is dominated by small-scale fishers and community fisheries operated at the household scale, using simple fishing gear and fishing methods (Achmad et al. 2020; Achmad et al. 2021). It is

estimated that around 3700 people depend on the Kwandang Bay grouper fisheries for their livelihoods, and the area is the site of a pilot project for implementing the Ecosystems Approach to Fisheries Management (EAFM) (Achmad et al. 2020).

The high price of groupers in the international marketplace has increased the demand for this commodity (Ogongo et al. 2015). In Kwandang Bay, fishermen can be paid around IDR 300,000/kg for live coral trout (*Plectropomus leopardus*) and IDR 65,000/kg for live orange-spotted grouper (*Epinephelus coioides*). The market demand for fresh and frozen grouper commodities has also increased (Sadovy et al. 2013). The high price and market demand have driven fishers to catch groupers in large quantities in an uncontrolled manner (Khasanah et al. 2020). These efforts have included the use of destructive gears, including explosives, poisons, and trawls, further exacerbating the risk of overfishing (Bulanin et al. 2017; Sadovy et al. 2020).

According to Giménez-Hurtado et al. (2005) signs of high levels of exploitation include changes in the size composition of fish populations with a higher proportion of small-sized fish, which in turn has a significant negative impact on reproductive capacity. This phenomenon has been reported in Kwandang Bay. Achmad et al. (2019) found that the grouper catch was dominated by small-sized groupers. Furthermore, a positive (increasing) trend in the fishing effort has been accompanied by a negative trend in grouper production volume (Achmad et al. 2017; Achmad et al. 2018). The uncontrolled increase in fishing efforts can be considered a threat to the grouper stocks (Cheung et al. 2013; Kandula et al. 2015) in Kwandang Bay.

Rational and appropriate fisheries management approaches are required to maintain the grouper stocks of Kwandang Bay. Formulating such measures requires up-to-date and valid data on the population dynamics of the target stocks (Suradi et al. 2017; Sabrah et al. 2018; AbouelFadl and Farrag 2021). Key population dynamics parameters include growth, mortality, exploitation rate, and recruitment (Kirubasankar et al. 2013; Mehanna et al. 2013; Sabrah et al. 2015; Ramachandran and Ramalingam 2020). Data on grouper population dynamics in Indonesia are still limited, although studies have been carried out in Taka Bonerate National Park Waters (Fatma et al. 2021), Spermonde Archipelago in South Sulawesi (Ernaningsih et al. 2014; Ernaningsih et al. 2019), Cendrawasih Bay National Park Waters in Papua (Bawole et al. 2017; Mudjirahayu et al. 2017; Bawole et al. 2018), Saleh Bay in West Nusa Tenggara and East Nusa Tenggara (Halim et al. 2020; Efendi et al. 2022), Wangi-wangi Island in Southeast Sulawesi (Patanda et al. 2017), and in Bangka Regency (Adibrata et al. 2018).

The Kwandang Bay grouper fishery is a multispecies fishery involving at least 26 species from eight genera. The goal of this research was to estimate key population dynamics parameters for the stocks of two grouper species (*Epinephelus coioides* and *Plectropomus leopardus*), which comprise the largest proportion of the groupers fished in Kwandang Bay, Sulawesi Sea (Achmad et al. 2019). The results will inform the formulation of fisheries management measures to improve the management of grouper stocks in the Bay.

MATERIALS AND METHODS

Study area

This study was conducted in Kwandang Bay, North Kwandang District, Gorontalo Province, Indonesia (Figure 1), from January to December 2021. The Bay faces the Sulawesi Sea and is within the Coral Triangle at approximate coordinates 00º52'12" N and 122º57'23" E. There are several grouper fishing grounds in Kwandang Bay, mainly grouped around islands such as Mohinggito, Malambe, and Saronde, with Lampu Island being the furthest offshore. The fishing boats are mostly small with 5.5-15 HP engines and typically operate in waters around 20-50 m in depth. Fishing gears used include woven fish traps (locally called bubu, around 30 cm diameter), spearguns (50-60 cm spears), and handlines typically around 30 m long and baited with live mackerel scad (*Decapterus* sp.). One-day fishing is the norm, with fishing trips generally lasting around 12 hours (Achmad et al. 2019).

Procedures

The grouper specimens sampled in this study represent the two dominant fishery species in Kwandang Bay, i.e., the orange-spotted grouper (*E. coioides*) and the coral trout (*P. leopardus*) (Achmad et al. 2019). Primary data were collected by measuring the total length (TL) of groupers caught in the Bay by local fishermen using a fish ruler with a precision of 0.1 cm. Grouper sampling data were collected once a month over a 12-month period. When a few target groupers were caught, all the groupers of the two target species were included in the sample for the month. When the catch volume was high, specimens were selected through simple random sampling. Seawater temperature data using satellite data and obtained the average seawater temperature was 30ºC.

Data analysis

Total length (TL) data were tabulated and presented as range and mean ± standard deviation (SD). The growth coefficient of each grouper species was estimated based on length-frequency data using the von Bertalanffy equation (Sparre and Venema 1998) shown below:

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

Where: Lt is the length of the fish at time t (cm); L∞ is the asymptotic length (TL, in cm); K is the growth coefficient; t0 is the theoretical age of the fish at zero length. The theoretical age of the fish at zero length (t0) was estimated using the following formula from Pauly (1980):

$$\text{Log}\,(-t0) = -0.3922 - 0.2752 \log\, L\infty - 1.038 \log K$$

Where: L∞ is the asymptotic length (cm) and K is the growth coefficient.

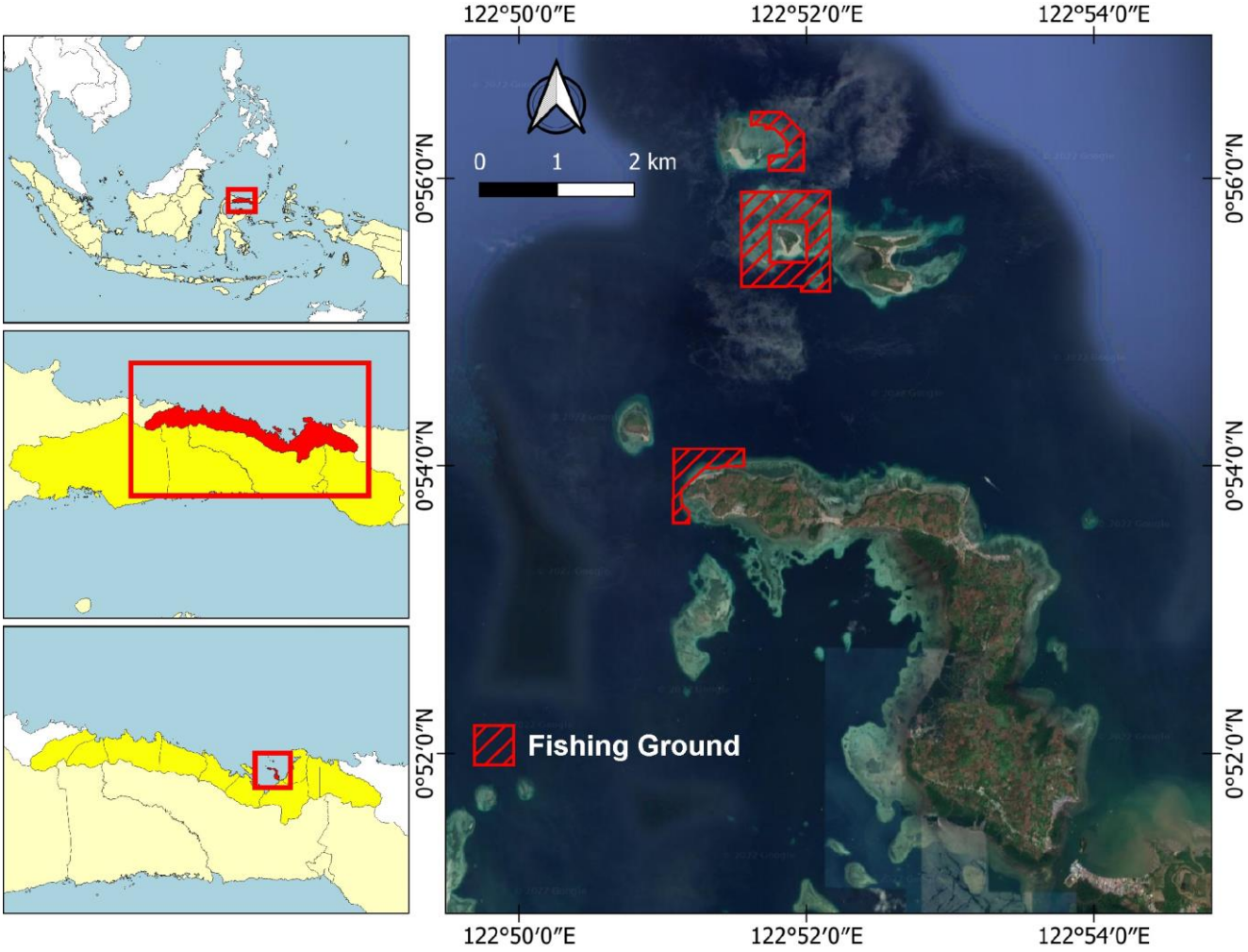


Figure 1. Grouper fishing grounds in Kwandang Bay, North Gorontalo District, Gorontalo Province, Indonesia

Recruitment was estimated using the recruitment patterns sub-program in FISAT II (Azmi et al. 2022). The yield per recruit was presented as a percentage (%) and estimated in FISAT II based on the length-frequency data and the values obtained for L∞, K and t0. After entering the input parameters, such as L∞, K, and t0, a peak recruitment graphic was produced in FISAT II.

Total mortality (Z) was estimated from the length converted catch curve in FISAT II (Sparre and Venema 1998) as:

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

Where: Z is total mortality (per year); K is the growth coefficient; L∞ is the asymptotic length (cm); L is the mean length at capture (cm); L' is the smallest length at capture (cm).

Natural mortality (M) was estimated using the empirical equation in Pauly (1980) as follows:

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T$$

Where: L∞ is the asymptotic length (cm); K is the intrinsic growth coefficient; and T is the mean annual water temperature (◦c).

Fishing mortality (F) was estimated using the following equation from Sparre and Venema (1998):

$$F = Z - M$$

Where: F is fishing mortality; Z is total mortality; and M is natural mortality.

Exploitation rate (E) was estimated using the following equation (Pauly 1980):

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

Where: E is exploitation rate; F is fishing mortality; and Z is total mortality.

The relative yield per recruit (Y/R) was estimated using the following analytic equation from Beverton and Holt (1964):

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

Where: c: 0.33 for *Epinephelus coioides* and c: 0.37 for *Plectropomus leopardus*.

RESULTS AND DISCUSSION

Size structure

The total length ranges of *Epinephelus coioides* (n: 379) and *Plectropomus leopardus* (n: 289) samples from fishermen's catches in Kwandang Bay during the study period were, respectively, 16.50-101 cm (mean ± SD = 44.70 ± 18.27 cm) and 17.90-60 cm (mean ± SD = 37.23 ± 11.92 cm). The size classes comprising the most individuals were 31-35 cm for *E. coioides* with 49 specimens representing 13% of the total sampled population, and 21-25 cm for *P. leopardus*, with 66 specimens representing 23% of the total sampled population (Figure 2).

Growth rate

The von Bertalanffy growth patterns modelled in FISAT II based on the length-frequency data gave growth parameter values L∞: 105.10 cm and K: 0.38 for *E. coioides* (Figure 3A); L∞: 65.90 cm and K: 0.69 for *P. leopardus* (Figure 3B). The length-frequency data indicate that both *E. coioides* and *P. leopardus* populations in Kwandang Bay grow at a relatively fast rate from 0.01-4 years old, after which growth rate declines, slowly approaching the asymptotic value (L∞).

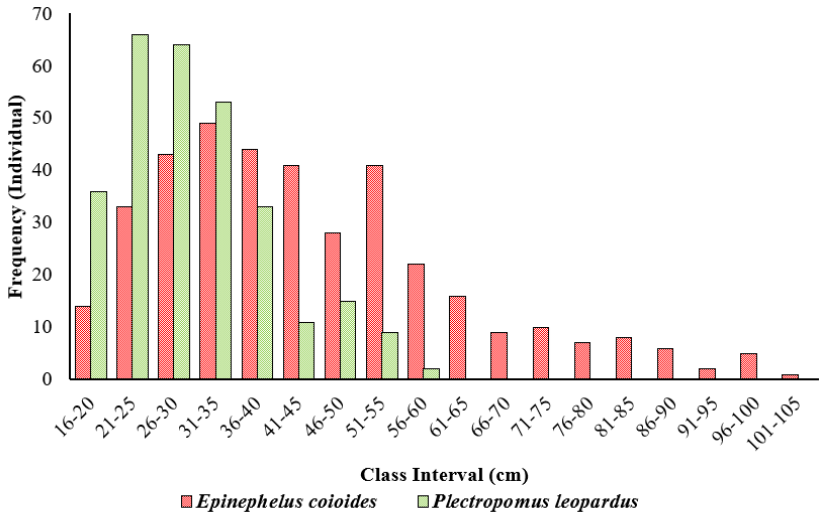


Figure 2. Size structure of *Epinephelus coioides* and *Plectropomus leopardus* in Kwandang Bay, North Gorontalo District, Indonesia

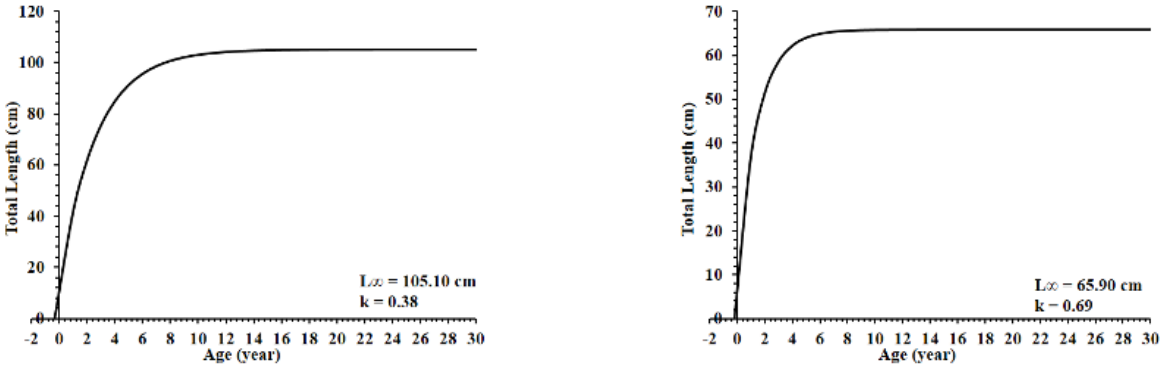


Figure 3. Length-frequency based growth curves for (A) *Epinephelus coioides*; (B) *Plectropomus leopardus* generated in FISAT II

Recruitment patterns

The recruitment patterns based on length-frequency data for *Epinephelus coioides* and *Plectropomus leopardus* populations in Kwandang Bay indicate recruitment occurring almost throughout the year with monthly recruitment ranges of 0.99-17.11% for *E. coioides* and 0.08-19.22% for *P. leopardus*. *Epinephelus coioides* had the main peak in June with a secondary peak in August, while the main *P. leopardus* recruitment peak was in July, with an earlier secondary peak in April (Figure 4).

Mortality and yield per recruit

The total mortality (Z), natural mortality (M), fishing mortality (F), and exploitation rate (E) for *E. coioides* and *P. leopardus* populations in Kwandang Bay were estimated based on the length-converted catch curves produced by the routines in FISAT II using the estimated values of L∞ and K as inputs. For *E. coioides* the estimated mortality values were Z: 1.56/year^{-1}, M: 0.69/year^{-1}, and F: 0.87/year^{-1} (Figure 5), while for *P. leopardus* the values were Z: 2.63/year^{-1}, M: 1.16/year^{-1} and F: 1.47/year^{-1} (Figure 6). These results show that fishing mortality was higher than natural mortality for both *E. coioides* and *P. leopardus*. The Beverton and Holt yield per recruit analysis indicated over-exploitation of both grouper species, with current exploitation rates of E: 0.56/year^{-1}, very close to the maximum exploitation rates, which were, respectively, E_{max}: 0.57 and 0.58. The exploitation rate, which would reduce the virgin stock biomass by 50% (E_{50}) was estimated as E_{50}: 0.31 for *E. coioides* and E_{50}: 0.32 for *P. leopardus*.

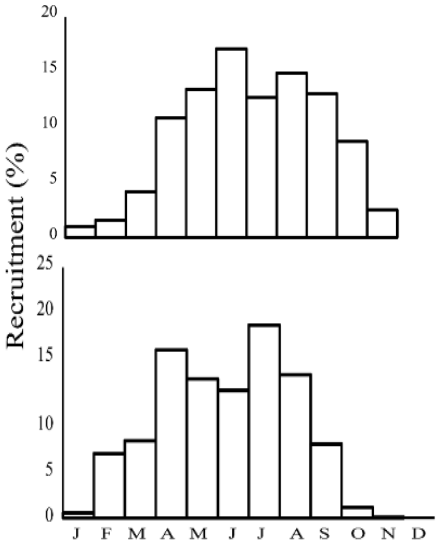
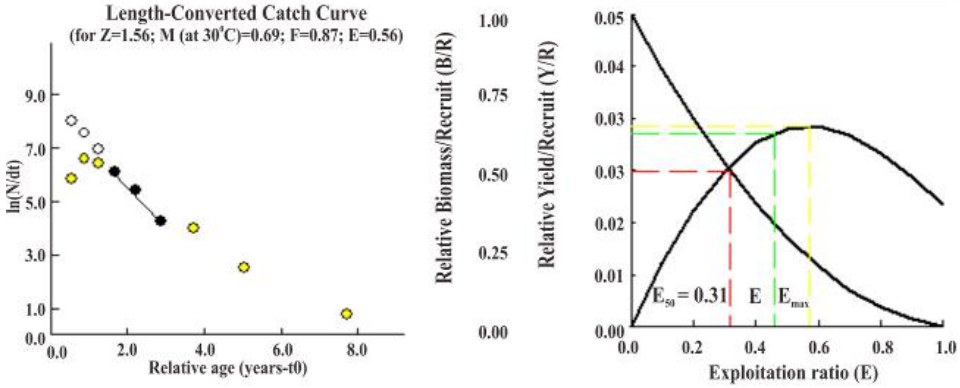
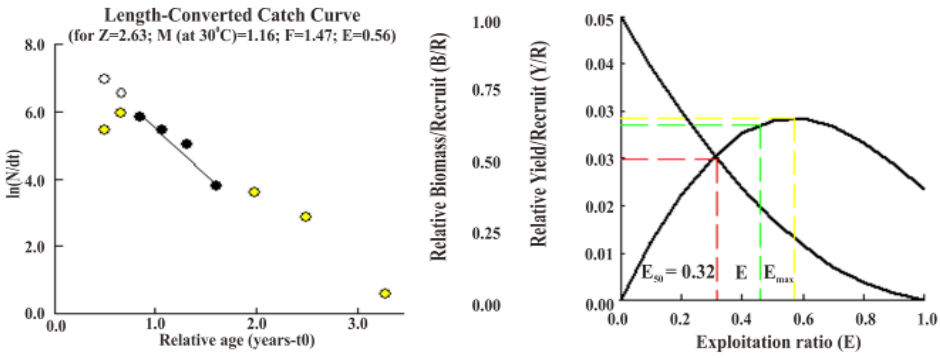


Figure 4. Recruitment patterns of *Epinephelus coioides* (above) and *Plectropomus leopardus* (below) in Kwandang Bay, North Gorontalo District, Indonesia (January-December 2021)



A **B**

Figure 5. Length-converted catch curve (A) and yield per recruit versus exploitation rate (B) for *Epinephelus coioides* in Kwandang Bay, North Gorontalo District, Indonesia



A **B**

Figure 6. Length-converted catch curve (A) and yield per recruit versus exploitation rate (B) for *Plectropomus leopardus* in Kwandang Bay, North Gorontalo District, Indonesia

Discussion

Groupers are top predators in coral reef ecosystems, playing key roles in the formation of coral reef biotic communities (Anderson et al. 2014; Ranjeet et al. 2015). Groupers are a major target of the reef fisheries operating in almost all Indonesian coral reef areas due to their high market value and rising market demand (Khasanah et al. 2019). In recent years there has been a shift in market demand patterns from frozen fish to fresh and live fish products (Khasanah et al. 2020), prompting an increase in the use of destructive fishing methods, in particular the use of poisons, to satisfy the demand for live reef fish (Setiawan et al. 2019; Dwifajri et al. 2022).

The fish sampled during this study fell into 18 size classes for *Epinephelus coioides* but only nine size classes for *Plectropomus leopardus*. The total length of *E. coioides* caught in Kwandang Bay, Sulawesi Sea, was mostly larger than the range reported from a study in Aceh, western Indonesia (Fadli et al. 2021), where all 30 fish sampled were immature females of 19.4-23.8 cm. The mean size at first maturity for the Kwandang Bay population has been estimated as 40 cm (Achmad et al. 2020), meaning that around half of the *E. coioides* landed in Kwandang Bay during this study were likely mature, mostly as females with some (in the largest size classes) likely to mature males. In heavily exploited stock in Oman (McIlwain et al. 2016), the mean size at first maturity for females was 58 cm, substantially larger than for Kwandang Bay, although the overall size range was familiar. Unlike the Aceh study (Fadli et al. 2021), in which relatively limited data indicates a juvenile fishery, in Kwandang Bay the fishery appears to target all size classes of *E. coioides*. While a non-negligible proportion of individuals should have reached sexual maturity and spawned as females prior to being caught, it is possible that, as in Oman (McIlwain et al. 2016), few individuals in Kwandang Bay may be reaching maturity as males.

In this study, the minimum size was smaller (17.9 cm) and the mean and maximum size of *P. leopardus* (37.23 and 60 cm) were larger than for the same species in Cendrawasih Bay National Park, eastern Indonesia, where the range was 24.5-48 cm with a mean size of 32.34 cm (Bawole et al. 2018). One reason for the greater range in our study could be the larger sample size (289 compared to 123), especially as very few individuals over 50 cm TL. Importantly, the size distribution in both this study and in Cendrawasih National Park (Bawole et al. 2018) indicated that a majority of groupers harvested at both sites had likely not reached sexual maturity (Kasanah et al. 2019).

In general, groupers take a long time to reach their maximum length (Condini et al. 2013; Ranjeet et al. 2015). Table 1 shows that the growth coefficient values for *E. coioides* and *P. leopardus* populations in Kwandang Bay are within the range of growth coefficients reported for grouper populations worldwide. Furthermore, in general, the growth of fish belonging to the genus *Epinephelus* tends to be slower than that of those in the genus *Plectropomus*.

Based on fish productivity criteria (Musick 1999), fish with a growth coefficient higher than 0.3 tend to have a relatively high reproduction rate. Based on this criterion, *E. coioides* and *P. leopardus* in Kwandang Bay could be categorized as having a fast rate of reproduction. Fast reproduction rates are thought to be one-factor enabling grouper populations to survive despite levels of fishing that are high enough to reduce production volume (Cheung et al. 2013; Baso et al. 2016).

The recruitment pattern for *E. coioides* and *P. leopardus* in Kwandang Bay, with recruitment throughout most of the year, is also consonant with a high reproduction rate, and a similar pattern has also been reported from the Andaman Islands (Kirubasankar et al. 2013). However, the recruitment patterns in Kwandang Bay showed two recruitment peaks for each species, while in the Andaman Islands, there was only one peak. Recruitment is vital to maintain the quality of the grouper catch in Kwandang Bay, as well as to ensure the ongoing survival of the stocks. *Epinephelus coioides* recruitment peak in June (Figure 4) is consonant with reports of a spawning peak during this month (Achmad et al. 2019), as well as the statement by Sparre and Venema (1998) that recruitment can only happen if there are individual fish surviving to adulthood that are able to reach gonad maturity. Spawn, and produce fertilized eggs that can then hatch and grow to produce new individuals. The peak in June may be related to the monsoonal pattern. Several studies indicated that tropical reef-associated fishes tend to have spawning peaks during the local calm season, which is generally also accompanied by higher seawater temperatures which can promote gonad development (Abesamis and Russ 2010; Nurdin et al. 2021), which in Kwandang Bay corresponds to the east monsoon from around May to August. Although there is no information on the spawning period(s) of the *P. leopardus* population in Kwandang Bay, the recruitment pattern (Figure 4) indicates a similar spawning peak during the east monsoon.

Reported mortality values vary between grouper populations from different sites within Indonesia and in other countries (Table 2). Fishing mortality exceeded natural mortality for both *E. coioides* and *P. leopardus* populations in Kwandang Bay and for several other grouper populations around the world (Table 2).

The high fishing mortality relative to natural mortality for groupers in Kwandang Bay is thought to be mostly due to the high levels of fishing effort by local fishermen. According to Achmad et al. (2017), the number of fishing boats operating in the Kwandang Bay area has increased every year since 2009, with around ten additional grouper fishing boats per year. They also found that the annual increases in the fishing effort were not accompanied by an increase in fisheries production volume (Kandula et al. 2015). A decline in the annual grouper production volume in Kwandang Bay was accompanied by an increase in the number of grouper fishing boats in 2009, 2010, 2012, 2015, 2016, and 2017, i.e., in six out of nine or two-thirds of the years studied by Achmad et al. (2017).

In addition to the increase in fishing boats, the gear type used has also become more diverse. Initially, the grouper fishermen only used fish traps, but more recently, they have also begun to use handlines and spearguns as well as

traps. These conditions have increased the pressure on grouper populations in Kwandang Bay. Without management interventions by the government, the future of grouper stocks in the Bay can be considered under threat, especially as groupers, in general, are considered to have relatively low resistance and resilience to high levels of fishing pressure (Brunel and Piet 2013; Osman et al. 2018).

The heavy fishing pressure experienced by the groupers in Kwandang Bay is reflected in the exploitation rates, which were very close to Emax for both species, indicating that *Epinephelus coioides* and *Plectropomus leopardus* stocks are overfished. Exploitation rates above E_{max} will result in reduced recruitment to the population (Sabrah et al. 2015). According to Achmad et al. (2019), the majority of groupers who landed in the Kwandang Bay fishery are in the mature gonad or spawning phase. This indicates that over-exploitation of adult groupers is already leading to recruitment overfishing due to the loss of potential spawners, as described by Hartati and Kasim (2016). Exploitation rates indicative of overfishing are also reported from other areas (Table 3). The current exploitation rates are a warning that needs to be taken seriously by Kwandang Bay grouper fishery stakeholders, as management measures are urgently needed to maintain the grouper stocks in the Bay.

Overexploitation of groupers in the mature gonad and spawning phases will, eventually, lead to a drop in or lack of recruitment to the stock and a decline in stock abundance (Fatma et al. 2022). However, the grouper fishermen in the Bay belong to an economically weak class; they go fishing to fulfill their basic everyday needs (for subsistence). This makes regulations in the form of fishing bans or limits difficult to implement. Therefore, in order to maintain grouper stocks and enable sustainable grouper fisheries in the Bay, there is a need for measures to manage and conserve grouper stocks by regulating the level of fishing effort in Kwandang Bay, including the number of fishing boats and the fishing gears used. Based on the results of the Beverton and Holt yield per recruit analysis, in order to retain 50% of the original grouper stocks, fishing effort needs to be reduced by 25% from the current exploitation rate (E: 0.56) to around the values of E_{50} for the two species studied, (0.31 and 0.32). Other measures that could be taken include spatio-temporal closures, specifically closing some fishing grounds during the spawning season(s), and creating spawning reserve zones where groupers could spawn without being caught.

Table 1. Growth coefficient of several grouper populations from around the world

Species	Growth coefficient	Location	Source
Plectropomus leopardus	0.69	Kwandang Bay, Indonesia	*This study*
Epinephelus coioides	0.38	Kwandang Bay, Indonesia	*This study*
Plectropomus leopardus	1.20	Cendrawasih Bay National Park	Bawole et al. (2018)
Plectropomus maculatus	0.52	Bangka District, Indonesia	Adibrata et al. (2018)
Epinephelus coioides	0.13	Northern Oman	McIlwain et al. (2016)
Epinephelus coioides	0.14	Southern Arabian Gulf	Grandcourt et al. (2005)
Epinephelus areolatus	0.15	Gulf of Suez	Abd-Allah et al. (2015)
Epinephelus diacanthus	0.22	Arabian Sea, Oman	Mehanna et al. (2013)
Epinephelus fuscoguttatus	0.46	Takabonerate National Park	Fatma et al. (2021)
Plectropomus leopardus	0.12	Saleh Bay, Indonesia	Efendi et al. (2020)
Plectropomus maculatus	0.10	Saleh Bay, Indonesia	Efendi et al. (2020)
Epinephelus coioides	0.10	Saleh Bay, Indonesia	Efendi et al. (2020)
Plectropomus oligacanthus	0.40	Southeast Sulawesi, Indonesia	Patanda et al. (2017)
Plectropomus areolatus	0.40	Southeast Sulawesi, Indonesia	Patanda et al. (2017)

Table 2. Mortality data for various grouper populations

Species	Location	Mortality			Source
		Z	M	F	
Epinephelus coioides	Kwandang Bay, Indonesia	1.56	0.69	0.87	*This study*
Plectropomus leopardus	Kwandang Bay, Indonesia	2.67	1.16	1.47	*This study*
Plectropomus leopardus	Cendrawasih Bay National Park	1.61	0.75	0.86	Bawole et al. (2017)
Plectropomus leopardus	Cendrawasih Bay National Park	4.85	0.99	3.86	Bawole et al. (2018)
Epinephelus malabaricus	Andaman Islands, India	2.53	1.05	1.48	Kirubasankar et al. (2013)
Epinephelus diacanthus	Arabian Sea, Oman	0.86	0.37	0.49	Mehanna et al. (2013)
Plectropomus maculatus	Bangka District, Indonesia	2.58	0.50	2.08	Adibrata et al. (2018)
Plectropomus maculatus	Cendrawasih Bay National Park	0.98	0.42	0.56	Mudjirahayu et al. (2017)
Plectropomus oligocanthus	Cendrawasih Bay National Park	2.05	0.65	1.39	Mudjirahayu et al. (2017)
Epinephelus coioides	Southern Arabian Gulf	-	0.19	0.78	Grandcourt et al. (2005)
Anyperodon leucogrammicus	Arafura Sea, Indonesia	-	0.51	0.55	Pane et al. (2021)
Epinephelus fuscoguttatus	Taka Bonerate National Park	2.19	0.77	1.42	Fatma et al. (2021)

Table 3. Exploitation rates for groupers in various locations

Species	Location	Exploitation rate	Source
Epinephelus coioides	Kwandang Bay, Indonesia	0.56	*This study*
Plectropomus leopardus	Kwandang Bay, Indonesia	0.56	*This study*
Plectropomus leopardus	Cendrawasih Bay National Park	0.53	Bawole et al. (2017)
Plectropomus leopardus	Cendrawasih Bay National Park	0.79	Bawole et al. (2018)
Epinephelus malabaricus	Andaman Islands, India	0.58	Kirubasankar et al. (2013)
Epinephelus diacanthus	Arabian Sea, Oman	0.57	Mehanna et al. (2013)
Plectropomus maculatus	Bangka District, Indonesia	0.81	Adibrata et al. (2018)
Plectropomus oligocanthus	Cendrawasih Bay National Park	0.58	Mudjirahayu et al. (2017)
Epinephelus coioides	Southern Arabian Gulf	0.80	Grandcourt et al. (2005)
Anyperodon leucogrammicus	Arafura Sea, Indonesia	0.52	Pane et al. (2021)
Epinephelus fuscoguttatus	Taka Bonerate National Park	0.65	Fatma et al. (2021)

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