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Abstract: The present study aims to determine whether the rate of exploitation for grouper stocks is in accordance with their biological attributes (growth and mortality). The results showed that Plectropomus maculatus and P. oligocanthus taken from Cenderawasih Bay National Park (CBNP) were in the size category of actively productive spawning phase. P. maculatus could reach a maximum length ($L\infty$) of 484.05 mm and growth rate (K) of 0.34 per year. P. oligocanthus) was capable of reaching $L\infty$ of 481.95 mm and K of 0.66 per year. Estimation of total mortality (Z) for P. maculatus was 0.988 and P. oligocanthus was 2.056. In addition, fishing mortality (F) for P. maculatus and P. oligocanthus were 0.564 and 0.399 respectively. Based on the estimated mortality values, it was estimated that the exploitation rate (E) of P. maculatus was 0.570, and P. oligocanthus was 0.681. Management settings for P. maculatus and P. oligocanthus can be separately based on the species so that the fishing can be sustainable. The introduction of minimum size limits for fish caught can be applied as a protection from hook and hand line fishing activities in CBNP.

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Hereby I would like to submit the manuscript entitled "Growth, Mortality and Exploitation Rate of *Plectropomus maculatus* and *P. oligocanthus* (Groupers, Serranidae) on Cenderawasih Bay National Park, Indonesia" to Egyptian Journal of Aquatic Research.

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Growth, Mortality and Exploitation Rate of *Plectropomus maculatus* and *P. oligocanthus* (Groupers, Serranidae) on Cenderawasih Bay National Park, Indonesia

Abstract

The present study aims to determine whether the rate of exploitation for grouper stocks is in accordance with their biological attributes (growth and mortality). The results showed that *Plectropomus maculatus* and *P. oligocanthus* taken from Cenderawasih Bay National Park (CBNP) were in the size category of actively productive spawning phase. *P. maculatus* could reach a maximum length ($L\infty$) of 484.05 mm and growth rate (K) of 0.34 per year. *P.* o*ligocanthus*) was capable of reaching $L\infty$ of 481.95 mm and K of 0.66 per year. Estimation of total mortality (Z) for *P. maculatus* was 0.988 and *P. oligocanthus* was 2.056. In addition, fishing mortality (F) for *P. maculatus* and *P. oligocanthus* were 0.564 and 0.399 respectively. Based on the estimated mortality values, it was estimated that the exploitation rate (E) of *P. maculatus* was 0.570, and *P. oligocanthus* was 0.681. Management settings for *P. maculatus* and *P. oligocanthus* can be separately based on the species so that the fishing can be sustainable. The introduction of minimum size limits for fish caught can be applied as a protection from hook and hand line fishing activities in CBNP.

Keywords: reef fish, Cenderawasih Bay, growth, mortality, exploitation rate.

1 Introduction

The high demand for groupers has led to an increase in the sale value of the fish and has brought about substantially high profits for trading business of this commodities. As consequently, this has been pushing an increase in fishing intensity for groupers and become primary fishing target of fishery in coral reef areas. Groupers are caught in the wild by traditional fishermen using hook and lines, and fish traps. High fishing intensity brings consequences to grouper sustainability. That is, grouper population experiences high fishing pressure. In some regions of Indonesia, it has been reported that total catch of groupers has decreased and the stock has been overexploited (Sadovy, 2005).

Fishing continuously on large sizes of fish or spawning fish stock could reduce the genetic characteristics and could change fish shape and behavior. The genetic diversity of the population would be likely affected thereby reducing its resilience in confronting with environmental change and variability (Vrijenhoek, 1998). Hurtado et al. (2005) and Nelson (2007) note that populations experiencing high exploitation is characterized by a change in the fish size composition, which is dominated by smaller sizes. This would significantly affect reproductive outcome since small fish size has less production potential than the large fish size. Large-scale of exploitation could cause structural changes in the fish. Sanchez (2000) suggests that in overfishing state of fish stock, the fish population are dominated by small sizes or young fish since fishermen tend to catch large size of fish.

Aside from fishing activities, the production of groupers in nature is strongly influenced by geomorphology and hydrographic characteristics of water; these affect the overall productivity and spawning aggregation (Coleman et al., 2011). Fish spawning areas of groupers, nowadays, become the target fishing areas by fishermen in order to increase their catch per unit effort. Although fisheries production increases in short term, such fishing practices in long term are likely to lessen fishery production as a result of the damage of spawning habitat, the decrease in reproductive output and the changes in sex ratio (Heyman et al., 2005; Koenig et al., 2000; Koenig et al., 2005; Sadovy & Domeier, 2005). To protect grouper from overfishing and extinction, the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species 2015 declared several species of groupers such as *Plectropomus leopardus*, *P. maculatus*) and *P. oligocanthus* as endangered species.

Groupers known as reef fish are the main component of reef fisheries in Cenderawasih Bay National Park (CBNP) (Bawole et al., 2014). There are three species in CBNP, *P. leopardus*, *P. maculatus* and *P. oligocanthus,* that are marketed commercially and are purchased by a commercial company. *P. leopardus* is the main target species for commercial fishermen (Bawole et al., 2017). However, other reef fish species known to be the fishing target are of *P. maculatus* and *P. oligocanthus*. These species are managed as a single species because there is no specific-biological information available for the species in the fishing areas that could be used in assessing whether different species have the same response to fishing pressure. Therefore, this study aimed to determine whether the rate of exploitation is in accordance with the biological attributes (growth and mortality) of groupers in CBNP. The research is needed for the management of reef fish as a single species group and necessary management actions for the species in the fishing areas.

2 Material and Method

The research location is situated in waters around Napan Yaur, a grouper fishing areas. Fishing area is inside CBNP. Geographically the study site is located at position of

02°54'43.00 S and 134°49'57.00 E (Figure 1). In the area is also found coral reef ecosystem which is in good condition, in particularly in the west, north and east of Yaur Napan water. Because of the good condition of coral, this area is designated as one of core zone in CBNP area. As a core zone, Napan Yaur water functions as protection area for a variety of organisms that lives in association with coral reef.

This study was conducted in April and May 2016. Fish samples were collected from local traders, who buy living groupers from local fishermen. The groupers were recorded by species and number of individuals. Each individual was measured its total length and standard length by using a caliper with an accuracy of 1.0 mm. Then, it was weighed using hanging scales with accuracy of 5 grams.

Analysis of growth models used von Bertalanffy growth model where fish length is a function of age (Pilling et al., 1999; Jennings et al., 2001). This growth model has become one of the bases in fisheries biology since it uses as a sub model in a number of more complicated models to explain various fish population dynamics (Sparre and Venema, 1998). The mathematical model of von Bertallanffy equation is:

$$L(t) = L\infty\ (1-e^{-k(t-to)})$$

Where: $L(t)$ = Length at time t

$L\infty$ = Asymptotic length

K = Growth coefficient

t_o = Theoretical age at length equals to zero.

The values of $L\infty$ and K were calculated using ELEFAN in FiSAT II package program. The value of t_O was calculated using empirical equation of Pauly (1982) as follows:

$$\text{Log}(-t_o) = -0{,}3922 - 0{,}2752\ \text{Log}\ L\infty - 1{,}038\ \text{Log}\ K$$

The relative age at a variety of lengths was estimated by using derivative of von Bertalanffy formula (Sparre and Venema, 1998), as follows:

$$t = t_0 \frac{1}{K}.\ \text{Ln}\frac{(1-Lt)}{L\infty}$$

The estimation of total mortality rate used length frequency distribution data which was applied to Beverton-Holt method in which shows the functional relationship between Z and L (Sparre and Venema, 1998). The formula is as follows:

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

Where: Z = Rate of total mortality

L_∞ = Asymptotic length

$K =$ Growth coefficient

$L =$ Average length of the fish (mm)

$L_c =$ The smallest length of fish caught (mm)

Natural mortality of fish could occur due to predation, disease, age and environmental factors. Pauly (1982) suggests relationship between the natural mortality and water temperatures. An increase in water temperature will lead to the increase in natural mortality of fish. The natural mortality (M) can be estimated by using Pauly empirical equation (Pauly, 1982) as follows:

$$\text{Log } M = -0.0066 - 0.279 \log (L_\infty) + 0.6543 \log (K) + 0.4634 \log (T)$$

Where $M =$ Natural mortality

$L_\infty =$ Asymptotic length

$K =$ Growth coefficient

$T =$ Average surface temperature of the water (°C)

Pauly (1980) and King (1995) state that the total mortality rate is summation of natural mortality and fishing mortality (F) or written as:

$$F = Z - M$$

Rate of exploitation (E) is ratio of fishing mortality (F) and total mortality (Z) (Pauly, 1982), and written as follows:

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

Gulland (1971) states that the optimal exploitation for a fish stock occurs when fishing mortality (F) is proportional to the natural mortality:

$$F_{\text{optimum}} = M$$

Thus, the optimal rate of exploitation (E_{optimum}) is 0.5. Resource is said to suffer from overexploitation (overfishing) if the rate of exploitation is greater than 0.5.

3 Results and Discussion

3.1 Length and weight

P. maculatus had length range between 230 and 485 mm, and weight between 180 and 615 grams. *P. oligocanthus* had length range between 235 and 485 mm, and weight between 200 and 775 grams (Table 1).

Table 1. Length and weight of groupers taken from Napan Yaur waters, Cenderawasih Bay National Park

Species	Number	Length (mm)		Weight (g)	
		Min	Max	Min	Max
P. maculatus	98	230	485	180	615
P. oligocanthus	104	235	485	200	775

The results of measurements in Table 1 when compared to the data of biological characteristics of the two species published in FishBase.org (Table 2), the groupers caught by fishermen in Napan Yaur water were in the category of actively spawning phase. The average length of *P. maculatus* was 278 mm and *P. oligochantus* was 275 mm which were within the range of spawning size of the two species. This means that the fish caught in the study had been spawning even though still in the early stages of spawning ages. Thus, the management efforts should be made to ensure the spawning process can take place better (i.e. fish spawn more than once). Settings minimum legal size of larger than 350 mm, as applied in the Coastal Waters of Africa in controlling catches of groupers (Burtos et al., 2009), can be adopted for management of grouper fishery the CBNP. Thus, it would allow fish to spawn effectively and guarantee the successful reproduction of fish in generating new fish generation (recruitment).

Table 2. Size of length at first maturity, length range at active spawning, and mean length of catches

species	First Mature gonads (mm) *	Length range at active spawning (mm) *	The mean length of catches (mm)
P. maculatus	210	250- 410	278
P. oligocanthus	200	210 - 420	275

* Source: Fasebase.org (2014)

3.2 Growth model

Results of analysis of growth parameters for *P. maculatus* and *P.*oligocanthus are presented in Table 3. *P. maculatus* could reach a maximum length (L_∞) of 484.05 mm with the average growth rate (K) of 0.34 per year and age t_0 at -0.27 mm. *P.*oligocanthus was capable of reaching a maximum length of 481.95 mm, with the average growth rate of 0.66 per year and age t_0 equal to 0,11 mm. Although asymptote length tended to be smaller than that of Seranids group found at various research sites in the world (Table 3), *P. maculatus* and *P. oligochantus* in this study had a faster growth. Food availability and favorable oceanographic environmental conditions in CBNP supported the rapid growth of grouper fish (Bawole et al., 2014) since fish growth influences by physiological and environmental conditions such as temperature, pH, salinity and water geography (Jenning *et al*., 2001).

Table 3. Growth parameters some grouper

Species	Parameters			Specification
	L_∞ (mm)	K (year^{-1})	t_0	
P. maculatus	484.05	0.34	-0.27	Current Research
P. oligocanthus	481.95	0.66	-0.11	Current Research
P. maculatus	600	0.21	-0.95	Great Barrier Reef (Ferrera & Russ, 1992)
Epinephelus marginatus	955	0.09	-1.12	Mediterranean Sea (Renones et al. 2007)
Mycteroperca venenosa	860	0.17	0.00	Ehrhardt & Ault,1992
Epinephelus niveatus	1320	0.09	-1.02	
Serranus atricauda	495	0.11	-0.76	Canary Islands, eastern-central Atlantic (Tuset et al. 2004)
Mycteroperca fusca	908	0.06	-3.38	Northwest coast of Africa (Bustos et al. 2009
Epinephelus labriformis	309.77	0.21	-0.17	Galápagos (Graig et al. 1999)
	256.16	0.32	-2.33	Puerto Vallarta (Graig et al. 1999)
Cephalopholis panamensis	249.05	to 4.15	0.30	Eastern Pacific (Graig et al., 1999)
Epinephelus coioides	979	to 1.50	0.14	Arabian Gulf (Grandcourt et al., 2005)

By knowing the parameter values of K, L∞, and t_0, then Lt can be estimated. The growth curves for the two grouper species followed the relationship of $Lt = 484.05\ [\ 1 - e^{-0.34(t-(-0.27)}]$ for *P. maculatus* and $Lt = 481.95\ [1 - e^{-0.66\ (t\ -\ (-\ 0.11))}]$ for *P. oligocanthus*. These growth curves can be plotted as shown in Figure 2 and Figure 3. The growth curves show that the grouper lengths increase exponentially at young ages and get slower with age until it reaches the asymptote length. This is a general phenomenon for fish growth where the rapid growth occurs at young ages (Effendie, 1997). On other hand, old fish grow slower because most the energy obtained from food are used for maintenance of the body and movement.

3.3 Mortality and exploitation rates

Total mortality rate (Z) was estimated by using Beverton-Holt method (Sparre and Venema, 1998), which found Z of 0.988 for P. *maculatus* and Z of 2.056 for *P oligocanthus*. The value of natural mortality rate (M) obtained using empirical equation of Pauly (1982), by applying the estimated value of K = 0.34, L∞ = 484.05 mm for *P.*

maculatus and value of K = 0.66, L ∞ = 481.95 mm for *P. oligocanthus.* The average water temperature (T) in the CBNP was 31°C (Bawole, 2012). Then, it was obtained the estimated Z of 0.988 and M of 0.425 for *P. maculatus,* and estimated Z of 2.056 and M of 0.656 for *P. oligocanthus*).

The value of fishing mortality rate (F) is obtained by subtracting Z by M. It was obtained that F values for *P. maculatus* and *P. oligocanthus* were 0.564 and 0.399 respectively. The value of the exploitation rate (E) is obtained by dividing F by Z. The estimated of E was 0.570 for *P. maculatus* and 0.681 for *P. oligocanthus*. The comparison of the estimated values of the fourth parameters with other studies are presented in Table 4.

Table 4. Total mortality rate (Z), natural mortality rate (M), fishing mortality rate (F), and optimal exploitation rate (E) of *P. maculatus* and *P. oligocanthus*

Species	Parameters ($year^{-1}$)				Description
	Total mortality rate (Z)	Natural mortality rate (M)	Fishing mortality rate (F)	The rate of exploitation (E)	
P. maculatus	0.988	0.425	0.564	0.570	Current Research
P. oligocanthus	2.056	0,656	1,399	0.681	Current Reserach
P. maculatus	0.569				Great Barrier Reef (Ferrera & Russ, 1992)
Mycteroperca venenosa	0.29				Ehrhardt & Ault, 1992
Epinephelus niveatus	0.18				
P. leopardus	1.01	0.49	0.52	0.52	Lasongko, Indonesia Prasetya 2010
	1.90	0.60	1:30	0.70	Kolaka, Buton , Indonesia Landu, 2013
	1.60	0.75	0.86	0:52	Cenderawasih Bay National Park. Indonesia (Bawole et al (in press)
E. coioides	0.97	0.19	0.79	0.80	Southern Arabian Gulf (Grandcourt et al., 2005)

Fishing mortality rates for *P. maculatus* and *P. oligocanthus* were significantly larger than the rates of natural mortality. This indicated that the mortality of the groupers in CBNP largely was caused by fishing activities. This was the same as the mortality of *P. leopardus* as reported by several studies research in some places in Indonesua, for example in Southeast Sulawesih (Landu, 2013 and Prasetya, 2010) and CBNP (Bawole, et al., 2017). Furthermore, low natural mortality rate and high fishing mortality may indicate the occurrence of growth overfishing, in which more young fish were caught than old fish (Sparre and Venema, 1998).

The rate of exploitation of 0.57 for *P. maculatus* and E of 0,68 for *P. oligocanthus* indicated that the exploitation for the groupers was higher than the optimum exploitation level. Gulland (1983) suggests the optimum rate of exploitation of a resource is 0.5. Therefore, precautionary management approaches are necessary by controlling and restricting the number of fishing fleets targeting groupers to maintain the sustainability of the fish stock in CBNP.

3.4 Concern and Management Directions

High demand on the target fish species and the particular interval fish size has contributed to the increase in fishing pressure on the species. This causes the symptom to capture more fish. Biologically, most groupers grow slowly and are known to be very vulnerable to fishing. Most of catch consists of young fish and high market value. As such type of fish is very popular with consumers. Furthermore, several species of groupers with high market values are often found in low densities in reef waters. Unfortunately, the species are now being fishing targeted by fishermen. Species such as *P. maculatus* and *P. oligocanthus* have been included in the IUCN Red List due to the potential harmful impact of trafficking of live groupers (Hudson and Mace, 1996). The decline in grouper stocks in the wild as consequence of trade live groupers has been reported, such as in Palau and Papua New Guinea (Johannes and Reipen, 1995) and in some other spawning areas (Heymanet al., 2005; Sadovy & Domeier 2005). In many cases, the spawning areas (where many of grouper individuals aggregate for spawning), become specific targets of fishing activities and has resulted in degradation number of reproductive individuals.

In anticipation of ongoing development changes and the dynamics of reef fish utilization, especially grouper species, management efforts are needed to achieve sustainable fisheries. Management activities can be done by applying management of entry (input and output controls. Control on fishing inputs can be done by regulating fishing efforts (i.e. number of fishing boats, type of fishing auxiliary, number and specification of fishing gears, number of fishing days, and fishing boat propulsion). In addition, output control can be performed by setting the maximum quota for sustainable fishing and the minimum legal size of fish caught).

Another thing that can be done is to encourage people to experience transformation from the "common-property" economic system to economic forms based on sustainable capture quota or the right of resource utilization. Furthermore, high dependence on marine resources can be reduced by creating commercial agricultural economic activities because agricultural land is available near residential areas. That is, fishermen not only conduct fisheries activities, but also in the agricultural sector of food crops. Thus, the economic multiplier effect will occur at the fishermen's level because fisherman's income can come from fishery and agriculture activities.

Control of grouper fish demand can also be applied to the granting of business permits to local collectors since there is tendency of increase in fishing pressure to meet the demand of grouper fish market. Stakeholders in CBNP can form a community economic development path that begins with an environmental conservation approach. This serves as an effective buffer for extractive economic shifts to conservation economies.

4 Conclusion

P. muculatus was substantially different from *P. oligocanthus* in aspects of growth, mortality and exploitation (fishing). Although it was difficult to predict fish response to fishing activities, *P. oligocanthus* was more vulnerable to being caught by fishermen than *P. maculatus*. The size of the captured *P. oligocanthus* was smaller and but it was larger in quantities. Management setting of *P. maculatus* and *P. oligocanthus* may be separate or species by species so that the fishery can be sustainable. The introduction of the minimum legal size of captured fish can be applied as a protective measure for the highly dominant hook and hand lining activities in CBNP.

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Figure

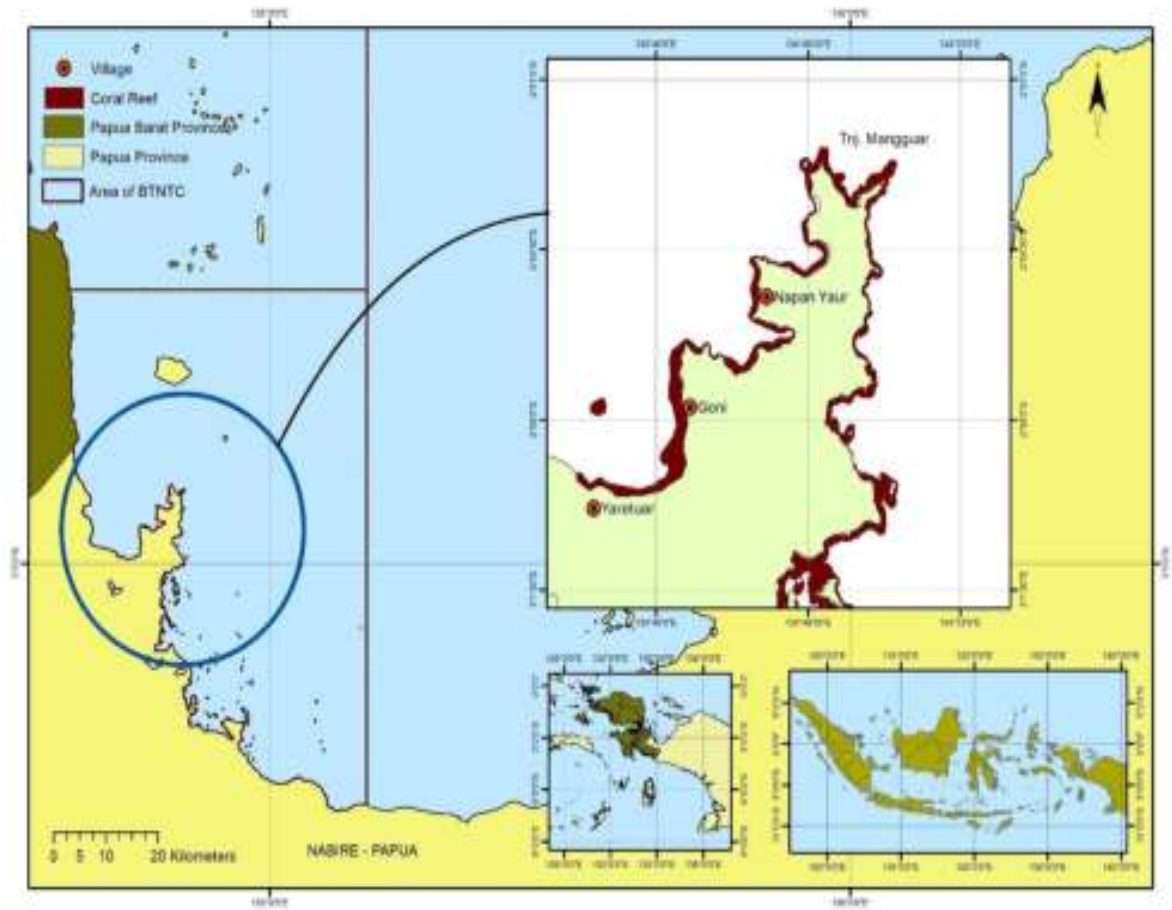


Figure 1. Map of the study area in the Napan Yaur waters, Cenderawasih Bay National Park, Papua, Indonesia

Figure

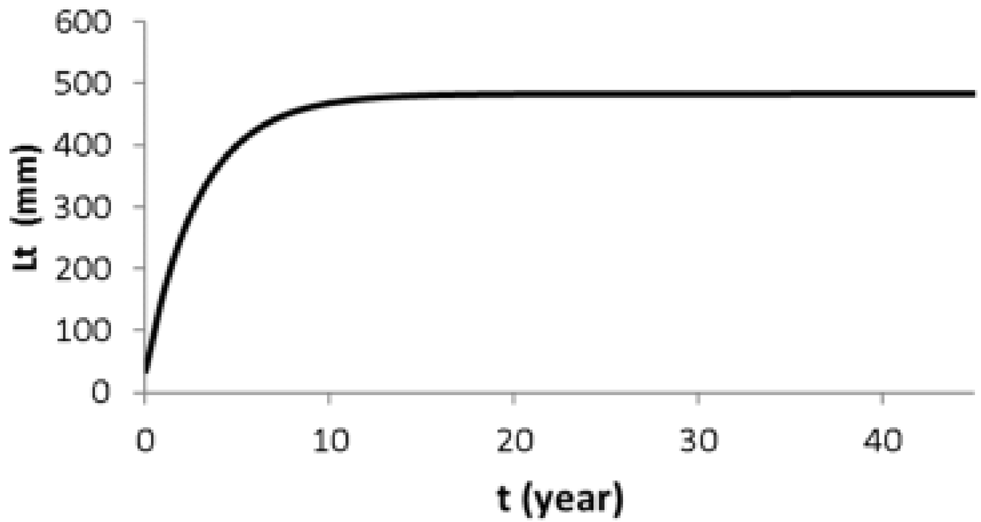
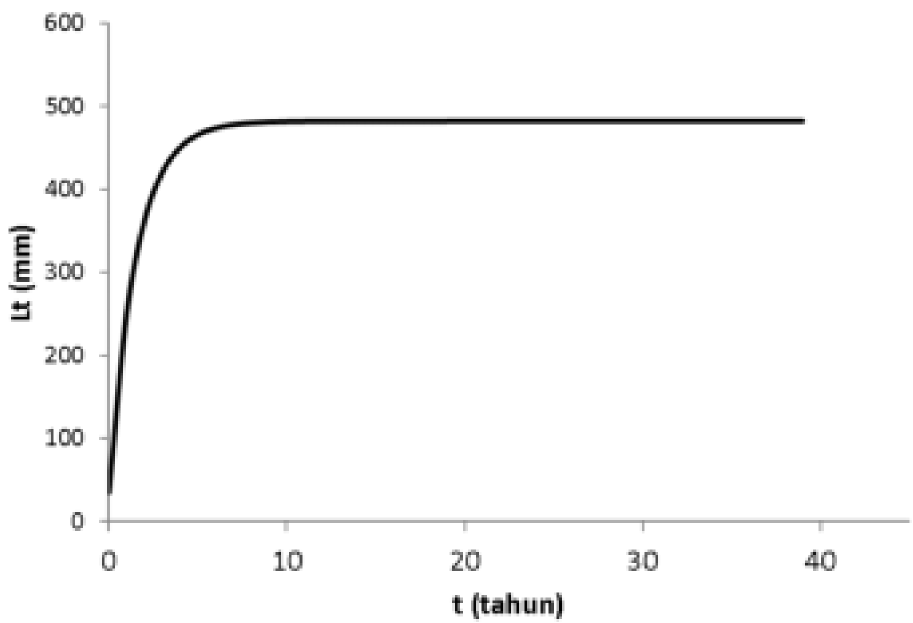


Figure 2. The growth curve of *Plectropomus maculatus* taken from Napan Yaur water, Cenderawasih National Marine Park



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Manuscript Draft

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Title: Growth, Mortality and Exploitation Rate of Plectropomus maculatus and P. oligocanthus (Groupers, Serranidae) on Cenderawasih Bay National Park, Indonesia

Article Type: Full length article

Section/Category: Fisheries

Keywords: reef fish; Cenderawasih Bay; growth; mortality; exploitation rate

Corresponding Author: Mr. Ridwan Sala,

Corresponding Author's Institution: University of Papua

First Author: Mudji Rahayu

Order of Authors: Mudji Rahayu; Roni Bawole, Doctoral; Unstain N Rembet; Arnold S Ananta; Ferawati Runtuboi; Ridwan Sala

Abstract: The present study aims to determine whether the rate of exploitation for grouper stocks is in accordance with their biological attributes (growth and mortality). The results showed that Plectropomus maculatus and P. oligocanthus taken from Cenderawasih Bay National Park (CBNP) were in the size category of actively productive spawning phase. P. maculatus could reach a maximum length ($L\infty$) of 484.05 mm and growth rate (K) of 0.34 per year. P. oligocanthus) was capable of reaching $L\infty$ of 481.95 mm and K of 0.66 per year. Estimation of total mortality (Z) for P. maculatus was 0.988 and P. oligocanthus was 2.056. In addition, fishing mortality (F) for P. maculatus and P. oligocanthus were 0.564 and 0.399 respectively. Based on the estimated mortality values, it was estimated that the exploitation rate (E) of P. maculatus was 0.570, and P. oligocanthus was 0.681. Management settings for P. maculatus and P. oligocanthus can be separately based on the species so that the fishing can be sustainable. The introduction of minimum size limits for fish caught can be applied as a protection from hook and hand line fishing activities in CBNP.

Suggested Reviewers: Myriam Lteif
National Center for Marine Sciences (CNRS-L/CNSM), Batroun, Lebanon
myriamlteif@hotmail.com

Andre Batista Nobile
Laboratorio de Biologia e Ecologia de Peixes, Departamento de Morfologia, Instituto de Biociencias (IBB), Universidade Estadual Paulista “Julio de Mesquita Filho” (UNESP), Campus de Botucatu, 18.618-970, Botucatu, SP, Brasil
andrenobile@hotmail.com

Opposed Reviewers:

Response to Reviewers: Responses to Reviewers' comments:

Reviewer #2: dear editor,
The specified data must be included in the article". To include the actual length-frequency distributions for each species as graphs".
"Response to reviewer #2: We have included the the actual length-frequency distributions for each species as graphs (see Figure 2 in the manuscript)."

Reviewer #3: Please answer the following comments:
1- The authors calculate the parameters of the von Bertalanffy formula as only the length or length frequency at age and use the FISAT II software program ?
"Response to reviewer #3: Yes, we calculated the parameters of the von Bertalanffy formula as only the length frequency and use the FISAT II software program."

2- If it is only a length frequency, it need many of individuals for days / weeks (from 4 April 2016 to 2 May 2016). In this paper, only 98 individuals (P. maculatus) and 104 individuals (P. oligocanthus) were obtained and frequency histograms as Fig 2 is not normal distribution, so if the age of fish was not determined at length, the results of the values of L_∞ and K were not confidentially calculated
"Response to reviewer #3: We tested the normality of the length frequency distributions of the two species by using Kolmogorov-Smirnov Test. We obtained $P = 0.157$ for P. muculatus and $P = 0.200$ for P. oligocanthus, which explain that frequencies are normally distributed."

3- The authors have been provided weekly detailed frequency histograms or a diagram of FISAT II calculating screen.
"Response to reviewer #3: We provide weekly frequency distributions for the two species on the histograms (see attachment)."

4- Based on the frequency of the length of the fish and reference to the length of the first maturity, How does the authors commented on their exploitation status?
"Response to reviewer #3: We used the Fishbase data to compare the maturity levels obtained from this study. This is already clearly stated in our manuscript (Section 3.1 Length and weight). In terms of the length of the first maturity, the fishers mostly caught the groupers which were length sizes larger than the length first maturity. Nevertheless, we recommend setting the minimum size allowed to be caught at 400 mm (see the second paragraph of section 3.4 Concern and Management Directions)."

Reviewer #4: Accept with revisions:

- Fix spelling errors (e.g. P. muculatus instead of P. maculatus)

"Response to reviewer #4: the correct name is P. maculatus (see http://www.fishbase.org/summary/4886)"

- Fix consistency in decimal point vs comma notation (see, for example, Table 4)

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- Graphs should indicate what kind of length was measured (I assume it was Total Length)
"Response to reviewer #4: We have indicated the measured length as total length in the graphs."

- Revise the following sentence "The growth curves show that the grouper lengths increase exponentially at young ages and get slower with age until it reaches the asymptote length." as follows "The growth curves show that length increases linearly with time at young ages, whereas growth slows down as the fish approach their asymptotic length".
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- The first paragraph of section 3.2 needs editing for English grammar, it is not acceptable in this form
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- The first paragraph of section 3.2 compares data of P leopardus to P maculatus and P oligocanthus, suggesting that the high L-inf of P leopardus may be related to fishing in deeper waters. This is incorrect argumentation. The authors should compare data from other studies on the *same* species. In addition, the authors may want to tabulate data from other Plectropomus species as well, esp. the values of F may be interesting since one could compare fishing mortality rates between study areas.
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- The authors should highlight that fishing mortality of these two species appears to be quite high, despite the fact that Cenderawasih is a National Park! The international audience would expect that protected area status should help to keep fishing mortality within acceptable limits, and apparently this is not the case for CNP. The authors should discuss why this national part fails to protect these two species. I think CNP has a zoning system that prohibits fishing in certain areas, but the zoning system is probably not enforced. If this is true, then the authors should elaborate on this in the paper.
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- Remove or shorten the paragraph starting with "Another thing that can be done..". This elaboration is not supported by the data, and the suggestions presented here are not related to the data or to the direct findings.
"Response to reviewer #4: We have removed the paragraph"

Cover Letter

Article title: **Growth, Mortality and Exploitation Rate of *Plectropomus maculatus* and *P. oligocanthus* (Groupers, Serranidae) on Cenderawasih Bay National Park, Indonesia**

Name of the authors: Mudjirahayu, Roni Bawole, Unstain NWJ Rembet, Arnold S. Ananta, Ferawati Runtuboi, Ridwan Sala

Hereby I would like to submit the manuscript entitled "Growth, Mortality and Exploitation Rate of *Plectropomus maculatus* and *P. oligocanthus* (Groupers, Serranidae) on Cenderawasih Bay National Park, Indonesia" to Egyptian Journal of Aquatic Research.

This manuscript was not submitted or published to any other journal. The authors declare that the manuscript is an original paper and contain no plagiarised text. All authors declare that they are not currently affiliated or sponsored by any organization with a direct economic interest in subject of the article. My co-authors have all contributed to this manuscript and approve of this submission.

Corresponding author

Ridwan Sala

Date: 26 May 2017

*Detailed Response to Reviewers

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		P. muculatus	P. oligocanthus
N		5	6
Normal Parameters[a,b]	Mean	19.6000	17.3333
	Std. Deviation	21.98409	23.65305
Most Extreme Differences	Absolute	.301	.245
	Positive	.301	.239
	Negative	-.256	-.245
Test Statistic		.301	.245
Asymp. Sig. (2-tailed)		.157[c]	.200[c,d]

a. Test distribution is Normal.

b. Calculated from data.

c. Lilliefors Significance Correction.

d. This is a lower bound of the true significance.

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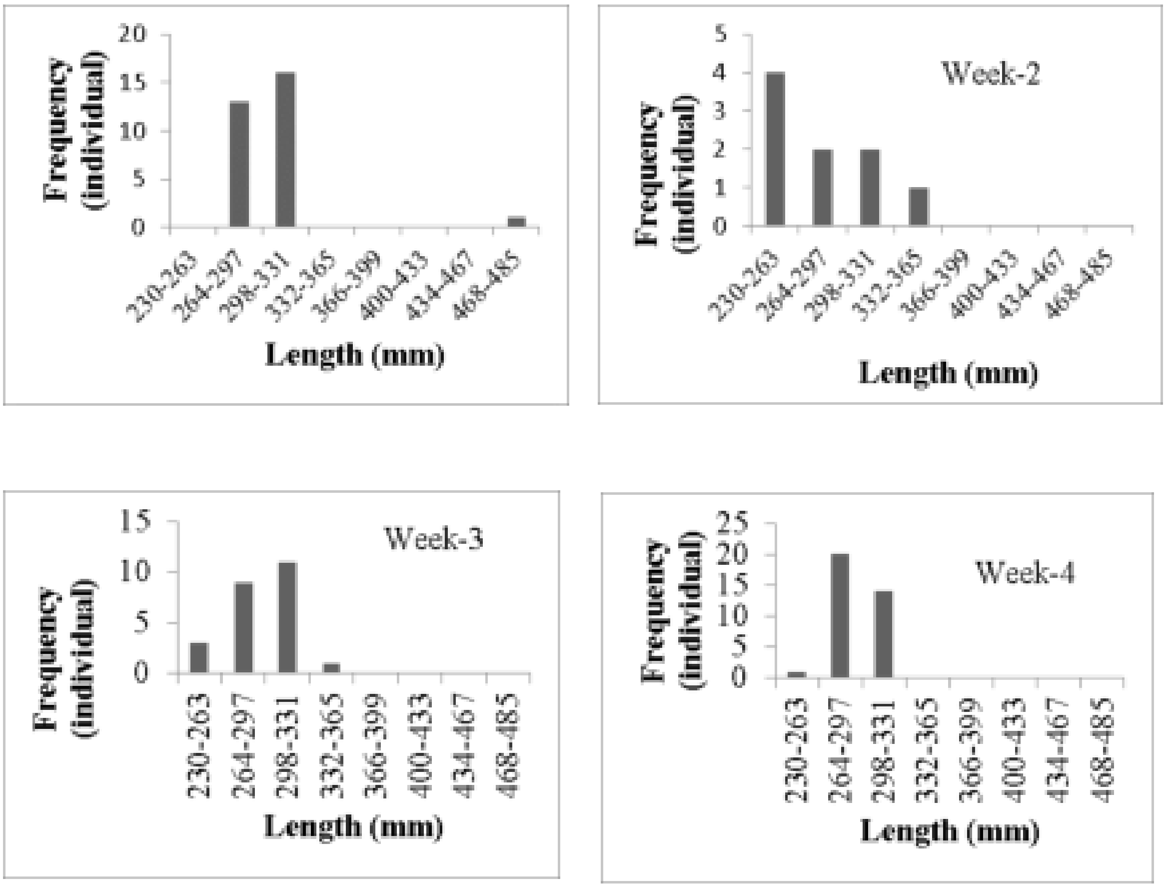
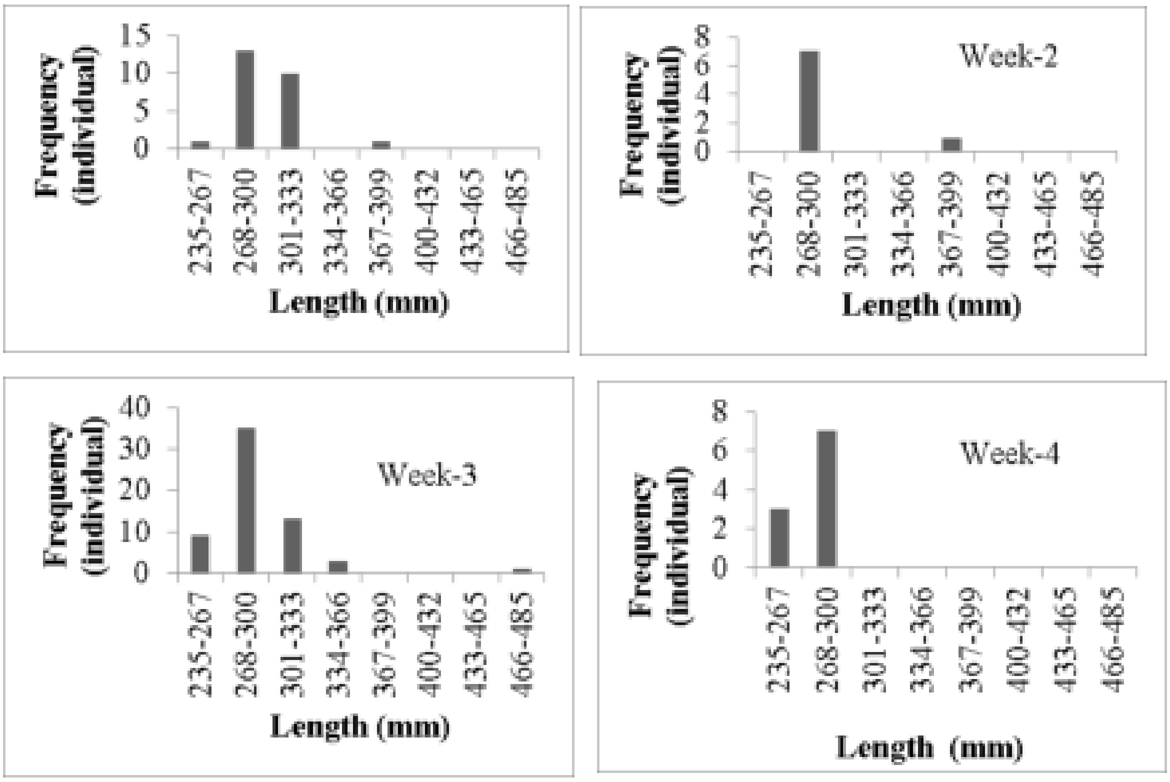


Figures of weekly length distributions of *P. Maculatus*



Figures of weekly length distributions of *P. oligocanthus* taken from Napan Yaur water, Cenderawasih National Marine Park.

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*Manuscript

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Keywords: reef fish, Cenderawasih Bay, growth, mortality, exploitation rate.

1 Introduction

The high demand for groupers has led to an increase in the sale value of the fish and has brought about substantially high profits for trading business of this commodities. As consequently, this has been pushing an increase in fishing intensity for groupers and become primary fishing target of fishery in coral reef areas. Groupers are caught in the wild by traditional fishermen using hook and lines, and fish traps. High fishing intensity brings consequences to grouper sustainability. That is, grouper population experiences high fishing pressure. In some regions of Indonesia, it has been reported that total catch of groupers has decreased and the stock has been overexploited (Sadovy, 2005).

Fishing continuously on large sizes of fish or spawning fish stock could reduce the genetic characteristics and could change fish shape and behavior. The genetic diversity of the population would be likely affected thereby reducing its resilience in confronting with environmental change and variability (Vrijenhoek, 1998). Hurtado *et al.* (2005) and Nelson (2007) note that populations experiencing high exploitation is characterized by a change in the fish size composition, which is dominated by smaller sizes. This would significantly affect reproductive outcome since small fish size has less production potential than the large fish size. Large-scale of exploitation could cause structural changes in the fish. Sanchez (2000) suggests that in overfishing state of fish stock, the fish population are dominated by small sizes or young fish since fishermen tend to catch large size of fish.

Aside from fishing activities, the production of groupers in nature is strongly influenced by geomorphology and hydrographic characteristics of water; these affect the overall productivity and spawning aggregation (Coleman et al., 2011). Fish spawning areas of groupers, nowadays, become the target fishing areas by fishermen in order to increase their catch per unit effort. Although fisheries production increases in short term, such fishing practices in long term are likely to lessen fishery production as a result of the damage of spawning habitat, the decrease in reproductive output and the changes in sex ratio (Heyman et al., 2005; Koenig et al., 2000; Koenig et al., 2005; Sadovy and Domeier, 2005). To protect grouper from overfishing and extinction, the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species 2015 declared several species of groupers such as *Plectropomus leopardus*, *P. maculatus*) and *P. oligocanthus* as endangered species.

Groupers known as reef fish are the main component of reef fisheries in Cenderawasih Bay National Park (CBNP) (Bawole et al., 2014). There are three species in CBNP, *P. leopardus*, *P. maculatus* and *P. oligocanthus,* that are marketed commercially and are purchased by a commercial company. *P. leopardus* is the main target species for commercial fishermen (Bawole et al., 2017). However, other reef fish species known to be the fishing target are of *P. maculatus* and *P. oligocanthus*. These species are managed as a single species. Although as a group of high-economic species, little information is known about the two species. Numerous studies conducted on several places concerning the parameter of grouper growth, e.g. nortwest coast of Africa (Burtos et al., 2009), west coast of Florida (Carlason et al., 2008), western Mediterranean Sea (Renones et al., 2001) and eastern Pacific (Craig et al., 1999), but no studies of *P. maculatus* and *P. oligocanthus* in the CBNP region. Information on the growth parameters of *P. maculatus* in the Great Barrier Reef was provided by Ferreira and Russ (1992) but there is no information about the mortality and exploitation aspects. The CBNP area has been a potential commercial fishing area of the grouper species since 2010. Yet, there is no specific-biological information available for the species in the fishing areas that could be used in assessing whether different species have the same response to fishing pressure. Therefore, this study aimed to determine whether the rate of exploitation is in accordance with the biological attributes (growth and mortality) of groupers in CBNP. The research is needed for the management of reef fish as a single species group and necessary management actions for the species in the fishing areas.

2 Material and Method

The research location is situated in waters around Napan Yaur, a grouper fishing areas. Fishing area is inside CBNP. Geographically the study site is located at position of 02°54'43.00 S and 134°49'57.00 E (Figure 1). In the area is also found coral reef ecosystem which is in good condition, in particularly in the west, north and east of Yaur Napan water. Because of the good condition of coral, this area is designated as one of core zone in CBNP area. As a core zone, Napan Yaur water functions as protection area for a variety of organisms that lives in association with coral reef.

This study was conducted in April and May 2016. Fish samples were collected from fishermen and local traders, who buy living groupers from local fishermen every day started from 4 April 2016 to 2 May 2016. Fishermen fished by using small boats (canoe, outboard engine) and handlining. The presence of local traders made fishing activities for the grouper become more intensive. There were 10 fishing fleets with the frequency of fishing 3-4 times per week during the study period. The groupers were recorded by species and number of individuals. Each individual was measured its total length by using a caliper with an accuracy of 1.0 mm. Then, it was weighed using hanging scales with accuracy of 5 grams.

Analysis of growth models used von Bertalanffy growth model where fish length is a function of age (Pilling et al., 1999; Jennings et al., 2001). This growth model has become one of the bases in fisheries biology since it uses as a sub model in a number of more complicated models to explain various fish population dynamics (Sparre and Venema, 1998). The mathematical model of von Bertallanffy equation is:

$$L(t) = L\infty (1-e^{-k(t-to)})$$

Where: L(t) = Length at time t

$L\infty$ = Asymptotic length

K = Growth coefficient

t_o = Theoretical age at length equals to zero.

The values of L∞ and K were calculated using ELEFAN in FiSAT II package program. The value of t_O was calculated using empirical equation of Pauly (1984) as follows:

$$\text{Log}(-t_o) = -0{,}3922 - 0{,}2752\ \text{Log}\ L\infty - 1{,}038\ \text{Log}\ K$$

The relative age at a variety of lengths was estimated by using derivative of von Bertalanffy formula (Sparre and Venema, 1998), as follows:

$$t = t_0 \frac{1}{K} . \text{Ln} \frac{(1-Lt)}{L\infty}$$

The estimation of total mortality rate used length frequency distribution data which was applied to Beverton-Holt method in which shows the functional relationship between Z and L (Sparre and Venema, 1998). The formula is as follows:

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

Where: Z = Rate of total mortality

L_∞ = Asymptotic length

K = Growth coefficient

L = Average length of the fish (mm)

L_c = The smallest length of fish caught (mm)

Natural mortality of fish could occur due to predation, disease, age and environmental factors. Pauly (1984) suggests relationship between the natural mortality and water temperatures. An increase in water temperature will lead to the increase in natural mortality of fish. The natural mortality (M) can be estimated by using Pauly empirical equation (Pauly, 1984) as follows:

$$\text{Log}\ M = -0.0066 - 0.279 \log (L_\infty) + 0.6543 \log (K) + 0.4634 \log (T)$$

Where M = Natural mortality

L_∞ = Asymptotic length

K = Growth coefficient

T = Average surface temperature of the water (°C)

Pauly (1984) state that the total mortality rate is summation of natural mortality and fishing mortality (F) or written as:

$$F = Z - M$$

Rate of exploitation (E) is ratio of fishing mortality (F) and total mortality (Z) (Pauly, 1984), and written as follows:

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

Gulland (1983) states that the optimal exploitation for a fish stock occurs when fishing mortality (F) is proportional to the natural mortality:

$$F_{optimum} = M$$

Thus, the optimal rate of exploitation ($E_{optimum}$) is 0.5. Resource is said to suffer from overexploitation (overfishing) if the rate of exploitation is greater than 0.5.

3 Results and Discussion

3.1 Length and weight

P. maculatus had total length range between 230 and 485 mm, and weight between 180 and 615 grams. *P. oligocanthus* had total length range between 235 and 485 mm, and weight between 200 and 775 grams (Table 1). The highest frequency distribution of *P. maculatus* was in length range of the 298-331 mm (44 individuals) and the 264-297 mm (43 individuals) (Figure 2, upper). For *P. oligocanthus*, the highest frequency distribution (62 individuals) was in length range of 268-300 mm with (Fig. 2, lower).

Table 1. Length and weight of groupers taken from Napan Yaur waters, Cenderawasih Bay National Park

Species	Number	Total length (mm)		Weight (g)	
		Min	Max	Min	Max
P. maculatus	98	230	485	180	615
P. oligocanthus	104	235	485	200	775

The results of measurements in Table 1 dan Figure 2 when compared to the data of biological characteristics of the two species published in FishBase.org (Table 2), the groupers caught by fishermen in Napan Yaur water were in the category of actively spawning phase. The average length of *P. maculatus* was 278 mm and *P. oligochantus* was 275 mm which were within the range of spawning size of the two species. This means that the fish caught in the study had been spawning even though still in the early stages of spawning ages. Thus, the management efforts should be made to ensure the spawning process can take place better (i.e. fish spawn more than once). Settings minimum legal size of larger than 350 mm, as applied in the Coastal Waters of Africa in controlling catches of groupers (Burtos et al., 2009), can be adopted for management of grouper fishery the CBNP. Thus, it would allow fish to spawn effectively and guarantee the successful reproduction of fish in generating new fish generation (recruitment).

Table 2. Size of length at first maturity, length range at active spawning, and mean length of catches

Species	First Mature gonads (mm) *	Length range at active spawning (mm) *	The mean length of catches (mm)
P. maculatus	210	250 - 410	278
P. oligocanthus	200	210 - 420	275

* Source: Fasebase.org (2014)

3.2 Growth model

The results of growth parameter analysis of *P. maculatus* and *P.oligocanthus* are presented in Table 3. *P. maculatus* could reach an asymptotic length ($L\infty$) of 484.05 mm, with an average growth rate (K) of 0.34 per year and the age of t_0 at -0.27 years. *P.oligocanthus* could reach an asymptotic length of 481.95 mm, with an average growth rate of 0.66 per year and the age of t_0 at 0.11 years. The asymptotic length of the two species is smaller than that of the Seranide group found in several other research sites in the world (Table 3). This may because most the fishermen in CBNP used small hook sizes (fishing lines with hook numbers of 9 - 15). Handling with the hook sizes is likely to catch groupers of sizes less than 400 mm.

P. maculatus and *P. oligochantus* in this study had a faster growth. Food availability and favorable oceanographic environmental conditions in CBNP supported the rapid growth of grouper fish (Bawole et al., 2014) since fish growth influences by physiological and environmental conditions such as temperature, pH, salinity and water geography (Jennings *et al*., 2001).

Table 3. Growth parameters some *Plectropomus*

Species	Parameters			References
	L_∞ (mm)	K ($year^{-1}$)	t_0	
P. maculatus	484.05	0.34	-0.27	Current Research
P. oligocanthus	481.95	0.66	-0.11	Current Research
P. maculatus	600	0.21	-0.95	Great Barrier Reef (Ferreira and Russ, 1992)
P. leopardus	75.70	0.21	-0.24	Indonesia (Prasetya 2010)
P. leopardus	92.40	0.75	-0.15	Indonesia (Landu 2013)

By knowing the parameter values of K, L∞, and t_0, then Lt can be estimated. The growth curves for the two grouper species followed the relationship of $Lt = 484.05 [1 – e^{-0.34(t-(-0.27)}]$ for *P. maculatus* and $Lt = 481.95 [1 - e^{-0.66 (t - (-0.11)}]$ for *P. oligocanthus*. These growth curves can be plotted as shown in Figure 3 and Figure 4. The growth curves show that length increases linearly with time at young ages, whereas growth slows down as the fish approach their asymptotic length. This is a general phenomenon for fish growth where the rapid growth occurs at young ages. On other hand, old fish grow slower because most the energy obtained from food are used for maintenance of the body and movement.

3.3 Mortality and exploitation rates

Total mortality rate (Z) was estimated by using Beverton-Holt method (Sparre and Venema, 1998), which found Z of 0.988 for P. *maculatus* and Z of 2.056 for *P oligocanthus*. The value of natural mortality rate (M) obtained using empirical equation of Pauly (1984), by applying the estimated value of K = 0.34, L∞ = 484.05 mm for *P. maculatus* and value of K = 0.66, L ∞ = 481.95 mm for *P. oligocanthus.* The average water temperature (T) in the CBNP was 31^{o}C (Bawole, 2012). Then, it was obtained the estimated Z of 0.988 and M of 0.425 for *P. maculatus,* and estimated Z of 2.056 and M of 0.656 for *P. oligocanthus*). The value of fishing mortality rate (F) is obtained by subtracting Z by M. It was obtained that F values for *P. maculatus* and *P. oligocanthus* were 0.564 and 0.399 respectively. The value of the exploitation rate (E) is obtained by dividing F by Z. The estimated of E was 0.570 for *P. maculatus* and 0.681 for *P. oligocanthus*. The comparison of the estimated values of the fourth parameters with other studies are presented in Table 4.

Table 4. Total mortality rate (Z), natural mortality rate (M), fishing mortality rate (F), and optimal exploitation rate (E) of *P. maculatus* and *P. oligocanthus*

Species	Parameters (year-1)				References
	Total mortality rate (Z)	Natural mortality rate (M)	Fishing mortality rate (F)	The rate of exploitation (E)	
P. maculatus	0.988	0.425	0.564	0.570	Current Research
P. oligocanthus	2.056	0.656	1.399	0.681	Current Reserach
P. maculatus	0.569	-	-	-	Great Barrier Reef (Ferreira and Russ, 1992)
P. leopardus	1.01	0.49	0.52	0.52	Lasongko, Indonesia Prasetya, 2010
	1.90	0.60	1.30	0.70	Kolaka, Buton , Indonesia Landu, 2013
	1.60	0.75	0.86	0.52	Cenderawasih Bay National Park. Indonesia (Bawole et al., 2017

Fishing mortality rates for *P. maculatus* and *P. oligocanthus* were significantly larger than the rates of natural mortality. This indicated that the mortality of the groupers in CBNP largely was caused by fishing activities. This was the same as the mortality of *P. leopardus* as reported by several studies research in some places in Indonesua, for example in Southeast Sulawesih (Landu, 2013; Prasetya, 2010) and CBNP (Bawole et al., 2017). Furthermore, low natural mortality rate and high fishing mortality may indicate the occurrence of growth overfishing, in which more young fish were caught than old fish (Sparre and Venema, 1998). The high fishing mortality of the two species might be related to the increase in fishing activities in the traditional fishing zones. In addition, there were still fishing activities in the protected zones (core zones) as a result of ineffective monitoring and surveillance by the CBNP authority. Therefore, controlling and surveillance on fishing activities including restriction on the minimum fish size of the groupers by taken fishermen in the traditional fishing zones as well as in the protected zones should be improved.

The rate of exploitation of 0.57 for *P. maculatus* and E of 0.68 for *P. oligocanthus* indicated that the exploitation for the groupers was higher than the optimum exploitation level. Gulland (1983) suggests the optimum rate of exploitation of a resource is 0.5.

Therefore, precautionary management approaches are necessary by controlling and restricting the number of fishing fleets targeting groupers to maintain the sustainability of the fish stock in CBNP.

3.4 Concern and Management Directions

High demand on the target fish species and the particular interval fish size has contributed to the increase in fishing pressure on the species. This causes the symptom to capture more fish. Biologically, most groupers grow slowly and are known to be very vulnerable to fishing. Most of catch consists of young fish and high market value. As such type of fish is very popular with consumers. Furthermore, several species of groupers with high market values are often found in low densities in reef waters. Unfortunately, the species are now being fishing targeted by fishermen. Species such as *P. maculatus* and *P. oligocanthus* have been included in the IUCN Red List due to the potential harmful impact of trafficking of live groupers (Hudson and Mace, 1996). The decline in grouper stocks in the wild as consequence of trade live groupers has been reported, such as in Palau and Papua New Guinea (Johannes and Reipen, 1995) and in some other spawning areas (Heyman et al., 2005; Sadovy and Domeier, 2005). In many cases, the spawning areas (where many of grouper individuals aggregate for spawning), become specific targets of fishing activities and has resulted in degradation number of reproductive individuals.

In anticipation of ongoing development changes and the dynamics of reef fish utilization, especially grouper species, management efforts are needed to achieve sustainable reef fisheries (Bawole et al., 2013). Management activities can be done by applying management of entry (input and output controls). Control on fishing inputs can be done by regulating fishing efforts (i.e. number of fishing boats, type of fishing auxiliary, number and specification of fishing gears, number of fishing days, and fishing boat propulsion). In addition, output control can be performed by setting the maximum quota for sustainable fishing and the minimum legal size of fish caught. Also, it is suggested to set minimum legal size of fish groupers taken from CBNP to be larger than 400 mm or larger than 700 grams (Ananta et al., 2016). This can be achieved when the handlining fishermen who targeting groupers use hook size of number 6 or 7.

Control of grouper fish demand can also be applied to the granting of business permits to local collectors since there is tendency of increase in fishing pressure to meet the demand of grouper fish market. Stakeholders in CBNP (Bawole et al., 2011; Bawole, 2011) can form a community economic development path that begins with an environmental conservation approach. This serves as an effective buffer for extractive economic shifts to conservation economies.

4 Conclusion

P. maculatus was substantially different from *P. oligocanthus* in aspects of growth, mortality and exploitation (fishing). Although it was difficult to predict fish response to fishing activities, *P. oligocanthus* was more vulnerable to being caught by fishermen than *P. maculatus*. The size of the captured *P. oligocanthus* was smaller and but it was larger in quantities. Management setting of *P. maculatus* and *P. oligocanthus* may be separate or species by species so that the fishery can be sustainable. The introduction of the minimum legal size of captured fish can be applied as a protective measure for the highly dominant hook and hand lining activities in CBNP.

Acknowledgements

Our gratitude is addressed to Ministry of Research and Higher Education of Republic Indonesia for funding this research. We thank WWF Indonesia, Site Project Cenderawasih Bay National Park, for helping with accommodation and local transportation, Management Body of Cenderawasih Bay National Park for issuing a letter of the permit, and fishers who assisted in collecting a field data.

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Figure

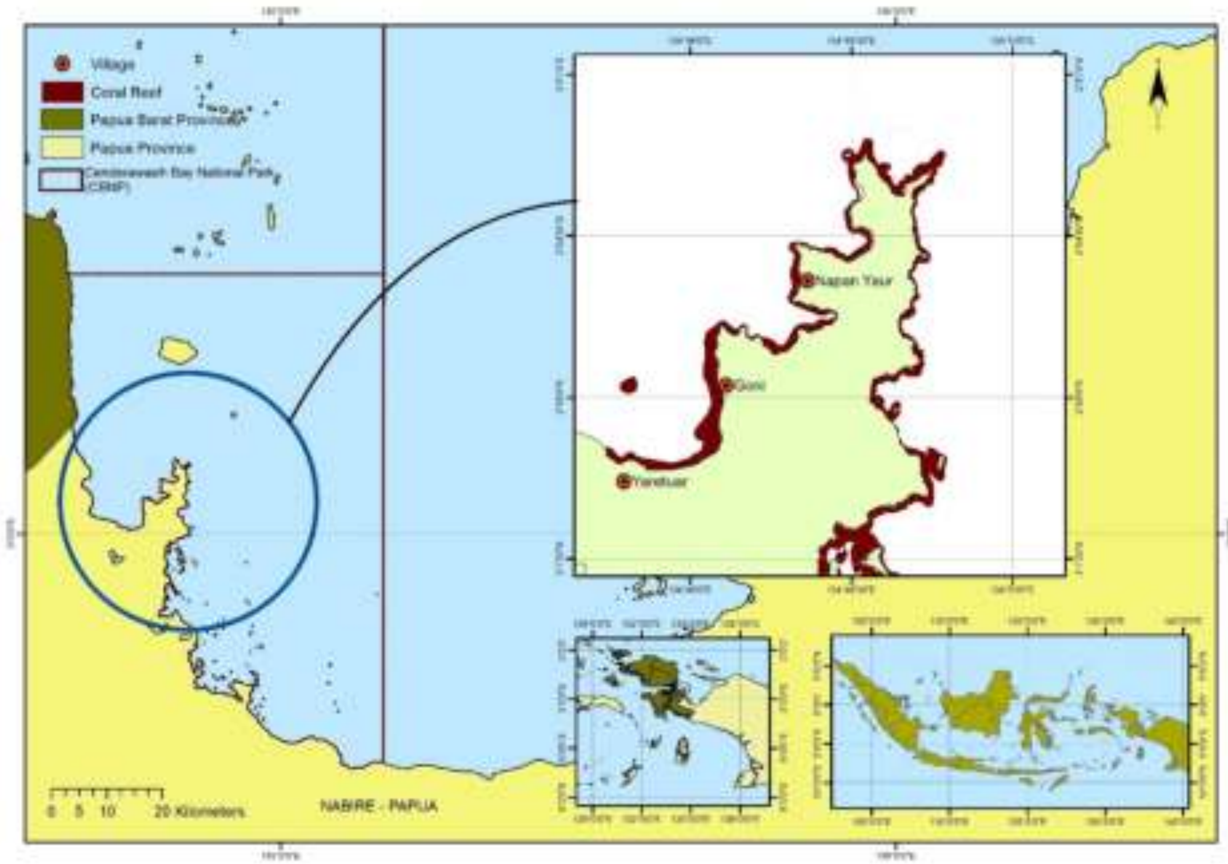

Figure 1. Map of the study area in the Napan Yaur water, Cenderawasih Bay National Park, Papua, Indonesia

Figure

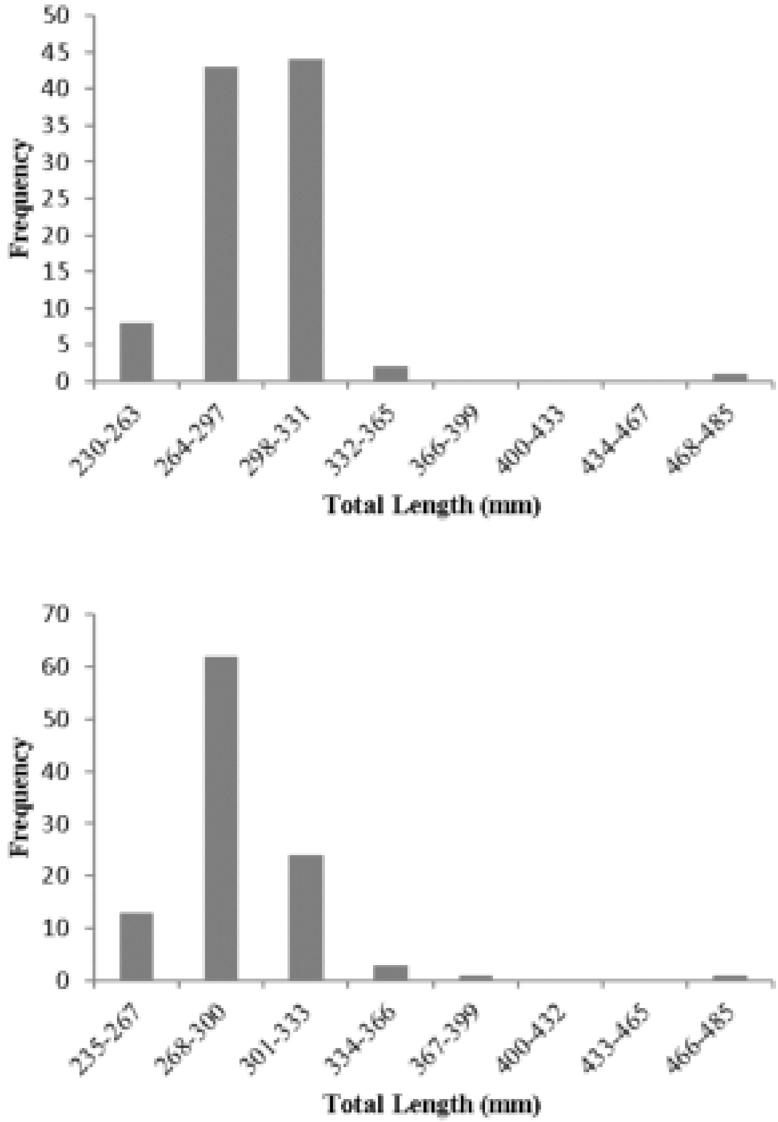

Figure 2. Total length distribution frequency of *P. maculatus* (upper) and *P. oligocanthus* (lower) taken from Napan Yaur water, Cenderawasih National Marine Park.

Figure

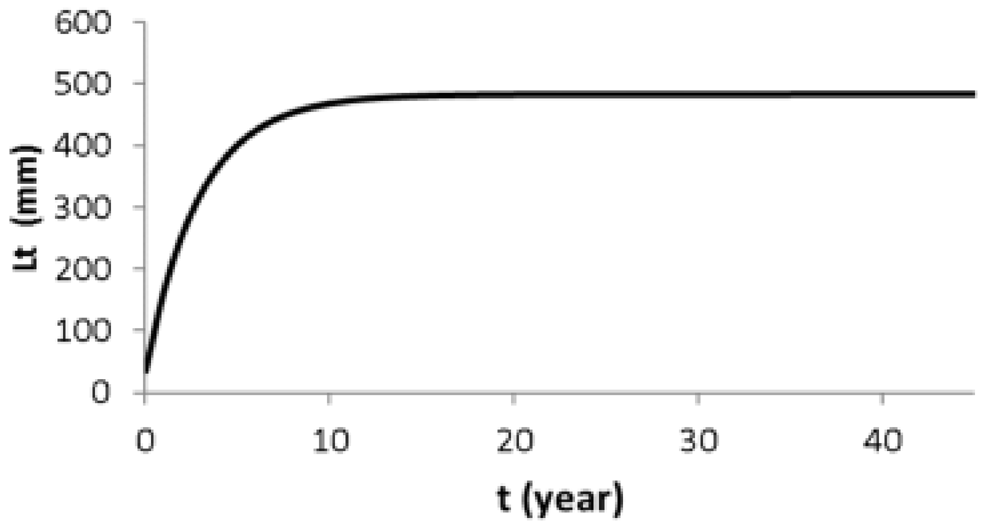

Figure 3. The growth curve of *Plectropomus maculatus* taken from Napan Yaur water, Cenderawasih National Marine Park

Figure

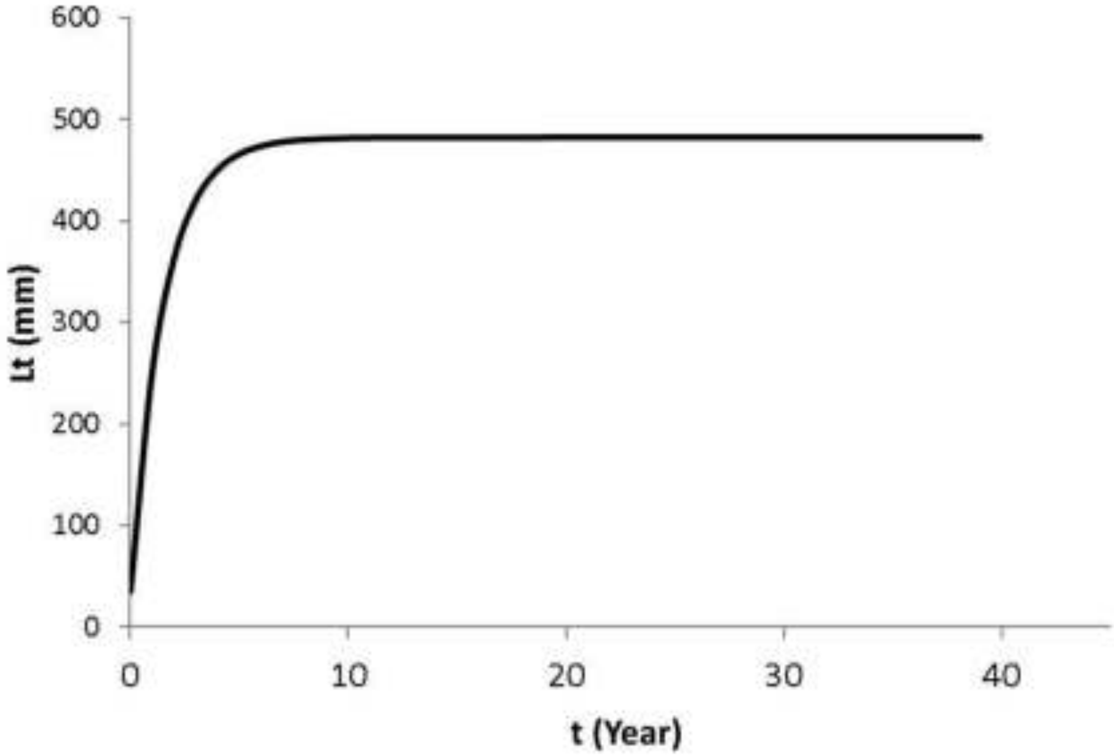

Figure 4. Growth curve of *Plectropomus oligocanthus* taken from Napan Yaur water, Cenderawasih National Marine Park

Responses to reviewer comments:

Reviewer #2: Mentioned corrections and omissions should be completed
Figure 3. Growth curve of Plectropomus oligocanthus taken from Napan Yaur water, Cenderawasih National Marine Park
T (tahun) (Year)
"Response to reviewer #2 comment no 1: Revised"

(Heymanet al., 2005) (Heyman et al., 2005)
Coleman et al., 2011). Not referans

Pauly (1982) not referens
Pauly (1980) not referens
King (1995 not referens
Hudson and Mace, 1996
Johannes and Reipen, 1995
(Renones et al. 2007)
Pauly (1984) not manuscript

"Response to reviewer #2 comment no 2: Revised"

art of the debate in the study should be enriched.

"Response to reviewer #2 comment no 3: Added some arguments in the fourth paragraph of the introductory section"

Some of the resources available in the text are not referenced. should be added
There is a reference but there are resources out of the text etc.

"Response to reviewer #2 comment no 4: Revised"

Error correction in Figure 3
"Response to reviewer #2 comment no 5: Revised"

Reviewer #3: The study only collects samples in 2 months from April to May 2016, so how many times have the authors collected samples ?

"Response to reviewer #3 comment no 1: Fish samples were collected from local traders collecting living groupers from local fishermen every day started from 4 April 2016 to 2 May 2016"

It is important to provide a distribution chart of the length of the specimen of the species in order to see how the size of the specimen was collected.

“Response to reviewer #3 comment no 2: Length distribution charts are added (Figure 2)”

How fish age and fish reproduction are conducted ?

“Response to reviewer #3 comment no 3: we estimated age at particular length base on derivative of von Bertalanffy formula (Sparre and Venema, 1998) as stated in the material and methods. We did not conduct study on the fish reproduction. We took reference of length of first maturity of the grouper from Fishbase.org and compared it with the grouper fish length taken from Napan Yaur in order to understand whether the fish catches were mature or not.”

There is a need to provide an insight into the minimum size allowed for exploitation in this sea and how to propose control and restriction of fishing.

“Response to reviewer #3 comment no 4 : We added insight into minimum size allowed at the second paragraph of section 3.4 of the manuscript.”

Reviewer #4:
I had a quick look at the manuscript, and I think it should not be too difficult to improve it for publication. The research presented is rather conventional: It is really just an elefan analysis on two length-frequency distributions. Though the paper is based on rather basic data analyzed in a standard way, not much has been published about the fisheries in Cenderawasih, and therefore I would still accept it after revision.

The three major points I would ask the authors to consider are:

- To include the actual length-frequency distributions for each species as graphs. This gives the reader the opportunity to get a better idea of the data that are the basis of the paper.

“Response to reviewer #4 comment no 1: We added length distribution frequencies of the two species (Table 2).”

- To discuss the implications of selectivity for the findings. The trade in life food fish is very selective, and it is likely that the length-frequency distribution are influenced by the preference of the owner of the live fish facility from where the fish were sampled, as well as the tendency of fishers to only bring fish caught in shallow waters to the holding cages (fish caught in deeper waters usually die). For example, P. maculatus is also caught in deeper water by dropliners and longliners in Indonesia. The maximum length found in this fishery is 80 cm, with an L-infinity of 72 cm, which is much higher than the 50cm found in this study---I think this is because the authors measured fish from a fishery that focuses on shallow waters, whereas the larger individuals migrate to deeper water (> 50 m depth).

“Response to reviewer #4 comment no 2 : We agree that most of the catches taken by handline fishermen from shallower water (<50 m). Also, large proportions of small size groupers might

be related to the use of small hook sizes. (added some discussion about this at the end of first paragraph of section 3.2).”

- To compare findings in this study to studies on the same species elsewhere---There is some comparison in Table 3, but the authors do not really discuss the differences. The authors could consider to only show data on closely related (Plectropomus) species from other studies.

“Response to reviewer #4 comment no 3 : We revised Table 3 and Table 4 by only including closely related species. ”