Population Status of Two Wedgefish Species in Western Indonesian Inner Waters, Inferred from Demographic Models with Limited Data

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Abstract—Wedgefish (family Rhinidae) is a group of elasmobranchs that experience a global threat due to its highly valued fins. Similar condition happens to most species of wedgefish inhabiting Indonesian waters where fishing activities are intense without sufficient management controls and lack of supporting studies on their sustainabilities. In order to get a picture of wedgefish populations in Indonesia, the current study employing demographic analysis was performed to know the population status of two wedgefish species (*Rhynchobatus australiae* and *Rhina ancylostoma*) from western Indonesian waters (including the Java Sea, Karimata and southern Makassar Straits). Age-based matrix models were used involving two scenarios of populations with and without fishing. Monte carlo simulation was applied to incorporate uncertainties in life-history parameters. The results show contrasting productivities for *R. australiae* and *R. ancylostoma*. *R. australiae* is sufficiently productive, indicated by high population growth rates in both with and without fishing scenarios. In contrast, the population of *R. ancylostoma* grows positively only in the unfished scenario, but the growth is negative in the with-fishing scenario. This finding indicates that the current level of exploitation caused the depletion in the population of *R. ancylostoma*. The current level of fishing can be maintained for *R. australiae* to give optimum benefits to fishery communities, while for *R. ancylostoma*, substantial reduction in fishing is required. Protection of young fish (juveniles up to age at first reproduction) is recommended in both fish since population growths are very sensitive to the changes in these stages.

Keyword: demographic analysis, Indonesian waters, matrix model, population growth, wedgefish

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INTRODUCTION

Elasmobranchs (sharks, rays and skates) are considered one among the most endangered marine biota (Campana et al., 2017). Their intrinsic biological traits make them vulnerable to exploitation compared to teleost fishes (Hoenig and Gruber, 1990; Stobutzki et al., 2002; Blaber et al., 2009). Consequently, the sustainability of elasmobranchs has become a global concern in recent years (Garcia et al., 2008, Kynoch et al., 2015; Ward-Paige, 2017, Braccini et al., 2020).

Order Rhinopristiformes (including wedgefish) is arguably the most threatened elasmobranch globally (Dulvy et al., 2014; Jabado, 2018). This group is claimed to be experiencing global declines due to over-exploitation (Jabado, 2018; D'Alberto et al., 2019).

Moore (2017) noted local extinctions had been reported for some species of guitarfish (probably including wedgefish). The very high-value fins of sawfish and guitarfish become the driver of this threat (Moore, 2017; Kyne et al., 2020). All species in wedgefish (family Rhinidae) except for *Rhynchobatus palpebratus*, are currently listed as Critically Endangered in IUCN Red List (The IUCN Red List of Threatened Species: https://www.iucnredlist.org. Version 03/2020). Furthermore, at the CoP 18, CITES also decided to list all species of wedgefish in Appendix II.

Among all wedgefish species, *Rhynchobatus australiae* and *Rhina ancylostoma* are commonly caught in Indonesian waters. Both species are demersal and inhabit coastal areas to a depth of about 60 m (Last

et al., 2016). Almost all body parts of wedgefish are utilized, particularly their fins that have the highest price in international market (Djunaidi, PESIHIP-INDO, Surabaya, Indonesia, personal communication, 2020).

As the largest elasmobranch-exploiting country (Dharmadi et al., 2009; Fahmi et al., 2013; Tull, 2014) and is located in Indo-West Pacific which is the center of wedgefish diversity (Kyne et al., 2020), Indonesia is required to implement sustainable management strategy towards the wedgefish. Unfortunately, the population status of these wedgefish in Indonesia remains unknown. This situation makes the research on the population status of wedgefish in Indonesian waters urgent.

Despite the global concern about these fish, to the best of our knowledge, so far, no stock assessment research has been conducted for these two wedgefish species both in Indonesia and other regions. D'Alberto et al. (2019) did a demographic analysis on Rhinopristiformes which includes *R. australiae*, while Kyne et al. (2020) did extinction risk study on wedgefish and giant guitarfish including both *R. australiae* and *R. ancylostoma*. However, their works were aimed to evaluate "the biological nature of populations" rather than to assess particular stocks which are subject to fishing. We conducted the present study to assess the population status of *R. australiae* and *R. ancylostoma* in western Indonesian inner waters. A demographic model using Leslie projection matrix was applied to achieve this goal. Two scenarios of populations with and without fishing were incorporated, hence, complementing the analysis done by D'Alberto et al. (2019) for *R. australiae*.

The demographic model was chosen for the following reasons. Firstly, this is a standard method applied to elasmobranch (Hoenig and Gruber, 1990; Simpfendorfer, 2005; Gedamke et al., 2007). Secondly, this method does not require extensive data as a full age-structured stock assessment does (Tsai et al., 2010; Hisano et al., 2011). Therefore, this method is suitable for fisheries in Indonesia which are mostly data-poor, in particular elasmobranch fisheries. This study is expected to generate scientific information which can be used as input to design suitable management strategies in attempts to achieve fisheries sustainability of these wedgefish in Indonesia.

MATERIALS AND METHODS

The current study applied demographic analysis to assess the population status of *R. australiae* and *R. ancylostoma* in western Indonesian waters which includes Karimata Strait (Fisheries Management Area; FMA 711), Java Sea (FMA 712) and southern Makassar Strait (FMA 713) as shown in Fig. 1. Leslie projection (age-based) matrix model was chosen, rather than the stage-based model, since the former is

more suitable for long-lived species like elasmobranch (Mollet and Cailliet, 2002). We applied scenarios of population with and without fishing to find the effect of current fishing mortalities to the sustainabilities of both wedgefish species. All analyses were done in R Language and Environment for Statistical Computing (R Core Team, 2019).

The basic equation of the matrix model was described by Simpfendorfer (2005) and Geng and Zhu (2017):

$$N_{t+1} = AN_t, \qquad (1)$$

where N_t the vector representing age structure of the fish population at time t and A the Leslie projection matrix such that:

$$N_t = \begin{pmatrix} N_{0,t} \\ N_{1,t} \\ \cdots \\ N_{a_{max},t} \end{pmatrix} \text{ and } A = \begin{pmatrix} f_0 & f_1 & f_2 & \cdots & f_{a_{max}} \\ S_0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & S_{a_{max}-1} & 0 \end{pmatrix},$$

$N_{a,t}$ represents the number of individuals of age a at year t, f_a fecundity (female pups) at age a, S_a survival rate from age a to $a+1$. To apply this model, information on life-history parameters of fish of interest are required. These include parameters of the von Bertalanffy growth model (L_∞, k, L_0), age at first reproduction (a_p), fecundity at age a (f_a), longevity or maximum age (a_{max}), and frequency of reproduction or reproductive cycle (RC). Information on natural and fishing mortality rates at age (M_a and F_a) are also needed to know survival rates for each age (S_a).

N_t and N_{t+1} were assumed to be stable which could be represented by eigenvectors of the matrix A with the associated leading eigenvalue λ representing the finite rate of population increase. From this, the associated intrinsic rate of population increase (r) could also be obtained by equality $r = \ln\lambda$. Also, other parameters borrowed from life table analysis i.e. net reproductive rates (R_0) and doubling time ($t_{\times 2}$) for cases $\lambda > 1$ were also derived ($R_0 = \sum_{a=0}^{a_{max}} S_a f_a$ and $t_{\times 2} = \dfrac{\ln 2}{r}$). In addition, for cases where $\lambda < 1$, collapse time (t_{coll}) defined as the time by which population decrease to less than 1% of the initial abundance, was also computed $\left(t_{coll} = \dfrac{\ln 0.01}{r} \right)$.

The primary data we had in this study was length frequency data of *R. australiae* and *R. ancylostoma* from sampling programs in 2017−2019 at several fish landing ports i.e Tegalsari Coastal Fishing Port—Tegal, Bajomulyo Coastal Fishing Port—Pati, Tasik Agung Coastal Fishing Port—Rembang, Brondong Archipelagic Fishing Port—Lamongan and and Sungai Kakap Fish Landing Port—Pontianak (Fig. 1)
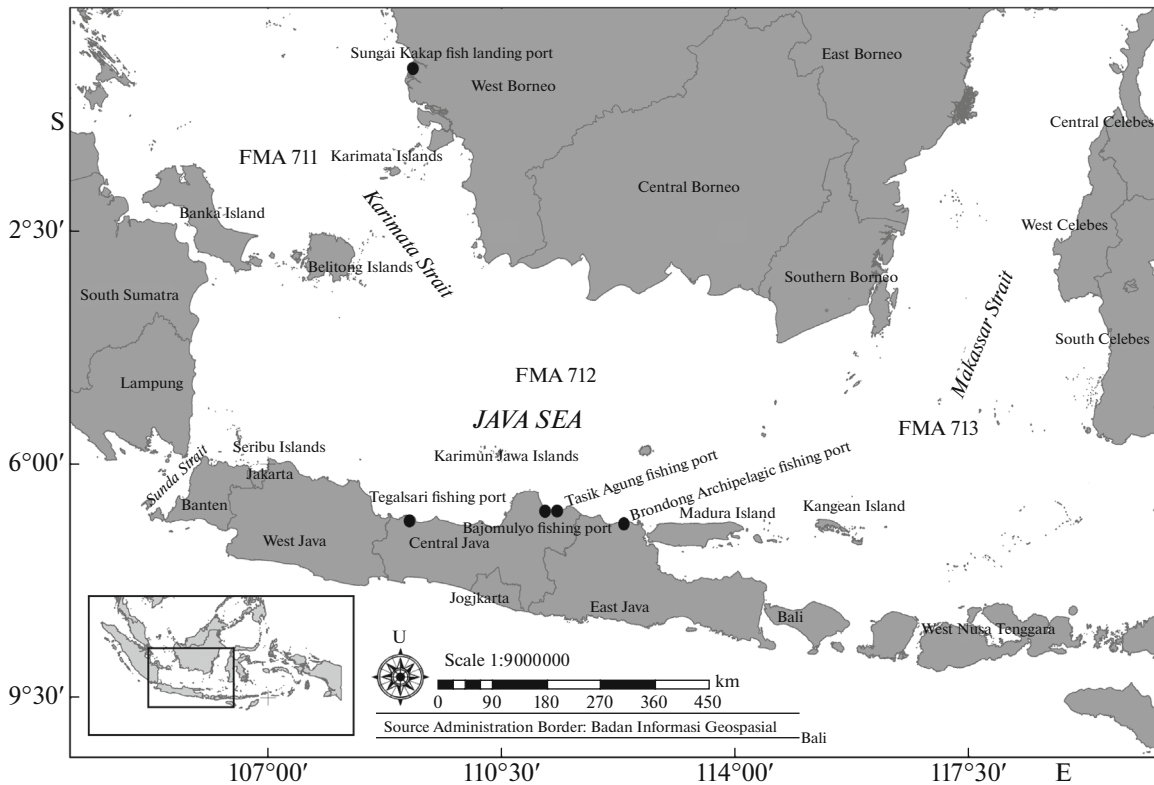
Fig. 1. Coverage of *R. australiae* and *R. ancylostoma* populations in western Indonesian inner waters along with sampling sites (●).

from which fishermen operate in Java Sea, Karimata and southern Makassar Strait. This data was used to estimate total mortality rates (Z) of each species. We also had length-frequency data from the eastern Indian Ocean (southern waters of Java Island, FMA 573), which, despite not being used in estimating Z, was also useful in this study. The rest of life history data was obtained directly or indirectly from existing literature all around the world.

Having length-frequency data, usually, von Bertalanffy growth parameters can be obtained from length-based methods like Electronic Length Frequency Analysis/ELEFAN (Pauly and David, 1981; Taylor and Mildenberger, 2017; Wang et al., 2020). The trials to implement ELEFAN method for both *R. australiae* and *R. ancylostoma* were really attempted, making use of package TropFishR (Mildenberger et al., 2017). Unfortunately, too few fish individuals caught daily hindered the ELEFAN method to work reliably. So, other methods including citing literature were attempted to obtain growth parameters.

Rhynchobatus australiae

White et al. (2014) have done age and growth study for species complex *Rhynchobatus* spp. which included *R. australiae*, *R. laevis* and *R. palpebratus* in eastern Australia. D'Alberto et al. (2019) re-examined their

data and suggested that they comprised primarily *R. australiae*. Ideally, this study could directly use the growth parameters generated by White et al. (2014). However, further examination showed that their result did not match our length-frequency data (see Results and Discussions). So, we re-analyzed the von Bertalanffy growth model ourselves, partly by reconstructing age-length keys from White et al. (2014). Two parameters, asymptotic length (L_∞) and length at birth (L_0) were predetermined without age−length data. L_∞ was estimated through Froese and Binohlan (2000) formula using maximum total length (TL) observed in our data (323 cm). For L_0, Weigmann (2011) suggested between 46−50 cm TL. White et al. (2014) used $L_0 =$ 50 cm in their analysis. However, our data showed the minimum size of fish caught to be 39 cm, lower than those suggested lengths at birth. So, in this work L_0 was taken as the midpoint of 39 and 50 cm TL. After that, the parameter of somatic growth rate (k) was estimated by fitting nonlinear regression to age-length data from White et al. (2014) using the package minpack.lm (Elzhov et al., 2016).

Age at first reproduction was set to be the age at first pupping (a_p); a_p was derived from age at maturity (a_m), which, in turn, was derived from the length at maturity (L_m). Weigmann (2011) suggested L_m for females to be 155 cm TL. While D'Alberto et al.

(2019), in their analysis, took $L_m = 150$ cm, borrowing from *Rhynchobatus djiddensis*. We did not take into account the estimated $L_m = 280$ cm from White and Dharmadi (2007) since it was unreasonably too close to L_∞. Using the inverse von Bertalanffy function, the two L_m from Weigmann (2011) and D'Alberto et al. (2019) were converted to $t_m = 5.4$ and 5.7 years. For the analysis of the matrix model, 1 year lag for gestation was assumed. So, a_p was estimated to be between 6.4–6.7. Since the resulting a_p was fractional, while the matrix model required round numbers, a_p was set to be 6–7 years. This agrees with the assumed age at reproduction used by White et al. (2014) i.e 6 years.

White and Dharmadi (2007) identified the litter size/fecundity (f_{tot}) for this species ranging between 7–19 pups per individual mother with mode 14 pups. No information about the relationship between mother's age and litter size, so constant fecundity across age ($f_a = f$) was assumed. Furthermore, since no information on sex ratio of litter was found, it was set to be 1:1, agreeing with D'Alberto et al. (2019). So, the number of female offspring (f) equals half the total fecundity (f_{tot}).

Rhina Ancylostoma

Similar to *R. australiae*, L_∞ parameter for *R. ancylostoma* was estimated using Froese and Binohlan (2000) formula, and L_0 was obtained from combining the minimum size in our data and information from the literature. Our data showed the minimum size observed to be 43 cm *TL*. Meanwhile, Last et al. (2016) suggested the size at birth to be 46–48 cm. Given these, we set L_0 as the midpoint of 43 and 48 cm. One more growth parameter k could not be determined since no relevant information was found. However, considering the usual range of k in elasmobranch (Cortés, 2000; Frisk et al., 2001) and the k value for *R. australiae* found in this study, it was reasonable to suggest the true k value for *R. ancylostoma* is in the interval (0.08, 0.20). Therefore, four equidistant points of k (0.08, 0.12, 0.16 and 0.20) were chosen from this interval, and further analysis was attempted for each of these k values.

No much information is available regarding age at first pupping (a_p) for *R. ancylostoma*. The only information is the estimate of L_m by Last et al. (2016) i.e. 180 cm, which is ambiguous between length at first maturity or length at first pupping. However, this value is still useful to estimate age at first pupping (a_p). Given multiple k, then multiple estimates of a_m and accordingly a_p were obtained. Each k has one a_m which was then converted to a_p ($a_p = a_m + 1$). From the lowest to highest k, we got $a_p = 11.4, 7.9, 6.2,$ and 5.2 years. To round up these numbers, at the same time incorporating ambiguity of L_m from Last et al. (2016), then a_p was set to be 10–12, 6–8, 5–7 and 5–6 years, in which

the last a_p (5–6 instead of 4–6 years) was chosen because $a_p = 4$ years was considered to be too early.

Several authors studied fecundity of *R. ancylostoma*. Masuda et al. (1975) suggested total fecundity (f_{tot}) to be four pups per mother, Last and Stevens (2009) suggested nine pups and Devadoss and Batcha (1995) 7–9 pups. However, the broadest range of f_{tot} is identified by Raje (2006) i.e., between 2–11 pups. Also, there does not seem to be a relationship between mother's age and litter sizes. So, f_{tot} was determined to be 2–11 with mode 8 pups. Again, litter sex ratio 1:1 was assumed.

For both *R. australiae* and *R. ancylostoma*, there is no information about longevity. So, longevities/maximum ages (a_{max}) were determined theoretically by means of Taylor's (1958) equation and Fabens' equation (used by: Goldman et al., 2006; Kadri et al., 2014). The two methods generated different estimates. Moreover, in *R. ancylostoma*, multiple k values resulted in multiple a_{max}. So, in total there were 8 a_{max} estimates for *R. ancylostoma*, two for each scenario of k.

Total mortality rates (Z) of both species were estimated using length-based linearized catch curve, making use of length-frequency data available. The formula used in the regression follows Sparre and Venema (1998):

$$\ln \frac{C(L_1, L_2)}{\Delta a} = c - Za\left(\frac{L_1 + L_2}{2}\right), \qquad (2)$$

where $C(L_1, L_2)$ is the number of individuals caught with the length between L_1 and L_2, Δa is age increment for fish from length L_1 to reach L_2, a $\left(\frac{L_1 + L_2}{2}\right)$ is the age at length $\frac{L_1 + L_2}{2}$. This method assumes constant Z with respect to time (resulting in $Z_a = Z$), which is unfortunate given fluctuating fishing efforts toward both fish. However, this is the best we can do in the face of limited data. Data shortages also pushed to pool both sexes (male and female) in generating single estimates of Z. Which points were included in the regression were assessed visually considering whether or not particular ages had been fully selected by fishing gear. From the linearized catch curve, selectivity at age (S_a) was also derived. In this study, gear selectivity was assumed to be logistic, which is reasonable considering that sharks and rays in this region were mostly caught by *cantrang* (seine net). Total mortality and selectivity analyses were implemented using the TropFishR package (Mildenberger et al., 2017).

As constant Z were used, constant natural mortality rates ($M_a = M$) were also assumed in this study. Several methods were applied to estimate these constant M, i.e. Alverson and Carney's (1975) method, two methods of Hoenig's (1983) i.e for fish and for a combination of mollusks, fish and cetaceans, Pauly's (1980)

Table 1. Life history parameters as input for matrix models of *R. australiae*

Parameter	Value
L_0	44.5
L_∞	307.9
k	0.095
a_p	$U_d (6, 7)$
f_tot	$Tr (7, 19, 14)$
Litter sex ratio	1:1
a_max	$U_d (29, 37)$
M	$Tr (0.10, 0.22, 0.15)$
Z	$N (0.34, 0.03)$

Here and in Table 2: U_d—discrete uniform distribution, Tr—triangular distribution, N—normal distribution.

method and two methods by Then et al. (2015), i.e third and sixth methods which use a_max and k. All computations of M were automated in package TropFishR (Mildenberger et al., 2017).

No study has documented the RC for either *R. australiae* or *R. ancylostoma*. D'Alberto et al. (2019) simply assumed 1 year RC for *R. australiae* without justification. To extend the generality of RC, this study accounted for one year and two years RC for both *R. australiae* and *R. ancylostoma*, following Geng and Zhu (2017) for the case of blue shark (*Prionace glauca*).

After all life-history parameters were readily available, matrix models were computed for each species, for each RC, for each scenario of fished and unfished populations and additionally for each k in *R. ancylostoma*. As some parameters have multiple (uncertain) values, these uncertainties were accounted for by means of Monte Carlo simulation. Matrices were generated 10000 times, with each time single random values of each life history parameter were used (Cortés, 2002; Geng and Zhu, 2017). For this purpose, probability distribution for parameters $a_p, f_\mathrm{tot}, a_\mathrm{max}, M$ and Z were constructed based on the ranges and modes

found; a_p and a_max were set to be discrete-uniformly distributed with parameters the lower and upper bounds of each; f_tot was set to be triangularly distributed with parameters the lowest, highest, and mode of total fecundity. M also followed triangular distribution with parameters the lowest, highest, and average of natural mortality estimates. Z was assumed to be normally distributed with parameters the estimate of Z itself and standard error from regression in the linearized catch curve. The complete list of parameters used in matrix models is summarized in Tables 1, 2.

Each iteration generates one matrix A along with the corresponding λ, r, $t_{\times 2}$, (or t_coll) parameters. So, each parameter has 10000 samples in each scenario. From these, the median and 95% confidence interval (CI) of each output parameter were calculated.

After that, 10000 R_0 was computed separately, also making use of random samples of life-history parameters. Accordingly, the median and 95% CI for R_0 were derived.

To demonstrate more clearly the long term trajectories of populations in each scenario, ten years projections were constructed. For this, the normal distribution for λ were assumed with the parameters the mean and standard deviation of λ samples from the matrix model. Each year, one random λ was drawn, and using this, 5000 samples of the female population at time t (N_t) were generated. From every 5000 N_t samples, the mean and 95% CI were computed.

To find the relative contribution of age, survival, and fecundity to the population growth rate (λ or r), then elasticity analysis was conducted. One matrix A was generated by drawing one random value for each of $a_p, f_\mathrm{tot}, a_\mathrm{max}, M$ and Z from their distributions. Leading eigenvalue and the associated eigenvector of matrix A were then computed. Elasticities were calculated using the formula (Simpfendorfer, 2005):

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{v_i w_j}{\langle v, w \rangle}, \qquad (3)$$

where a_{ij} elements of projection matrix A, v and w are left and right eigenvectors of A, and $\langle v, w \rangle$ is the dot

Table 2. Life history parameters as input for matrix models of *R. ancylostoma*

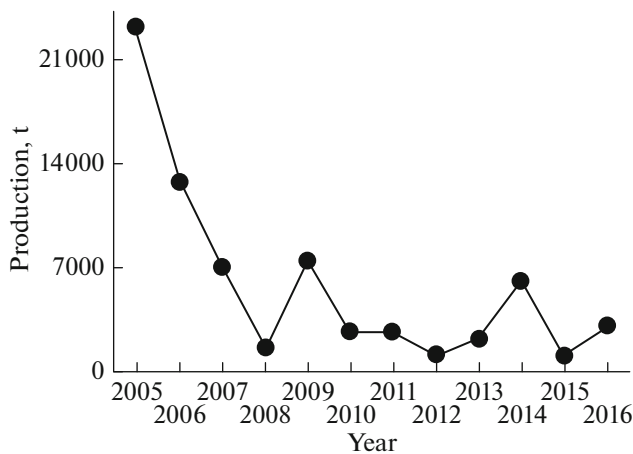| Parameter	$k = 0.08$	$k = 0.12$	$k = 0.16$	$k = 0.20$
L_0	45.5	45.5	45.5	45.5
L_∞	283.5	283.5	283.5	283.5
a_p	$U_d (10, 12)$	$U_d (6, 8)$	$U_d (5, 7)$	$U_d (5, 6)$
f_tot	$Tr (2, 11, 8)$	$Tr (2, 11, 8)$	$Tr (2, 11, 8)$	$Tr (2, 11, 8)$
Litter sex ratio	1 : 1	1 : 1	1 : 1	1 : 1
a_max	$U_d (35, 43)$	$U_d (23, 29)$	$U_d (17, 22)$	$U_d (14, 17)$
M	$Tr (0.09, 0.19, 0.13)$	$Tr (0.13, 0.27, 0.19)$	$Tr (0.17, 0.35, 0.24)$	$Tr (0.20, 0.43, 0.30)$
Z	$N (0.31, 0.01)$	$N (0.47, 0.02)$	$N (0.63, 0.03)$	$N (0.78, 0.03)$

Fig. 2. Annual production of wedgefish from FMA 711–713 during 2005–2016 according to official data of Ministry of Marine Affairs and Fisheries.

product of both eigenvectors. The elasticity of each age, the elasticity of survival and fecundity were simply derived from summing the relevant elements e_{ij}.

RESULTS AND DISCUSSIONS

Wedgefish Fisheries in Western Indonesian Inner Waters

In the western Indonesian inner waters, four species of wedgefish i.e *Rhynchobatus australiae*, *R. springeri*, *R. laevis* and *Rhina ancylostoma*, are commonly caught. These fish are caught both as target and bycatch. Fishers targetting wedgefish usually use tangle net as fishing gear, which is locally known as *jaring liongbun* or *jaring kemejan* (Sadri and Yuneni, 2019). As bycatch, wedgefish are caught by *cantrang* (kind of seine net), bottom longline, bottom gillnet and hand line (Sadri and Yuneni, 2019; Yuwandana et al., 2020). The latter four gears target demersal teleost fishes, but wedgefish are also caught. Most of wedgefish caught in these waters are bycatch from *cantrang*.

In Indonesia, there is no official data on species-specific catch/production of wedgefish. Until 2016, data on annual production of mixed wedgefish per FMA was documented by Ministry of Marine Affairs and Fisheries (MMAF). However, in 2016 MMAF changed its data collection system to *one data*. Since then, wedgefish and other rays have been reported as just "rays". DGCF-MMAF (2017) reported the annual production of wedgefish for each FMA in Indonesia. Despite the category "whitespotted wedgefish" used by DGCF-MMAF, it is actually a mixture of all different wedgefish species. Figure 2 shows the annual production of wedgefish in western Indonesian inner waters during 2005–2016, pooled from FMA 711–713 according to DGCF-MMAF (2017). Figure 2 indicates that the catch of wedgefish has been declining, particularly from 2005 to 2008. However, the offi-

cial data is usually considered not to represent the actual production. This is because of several problems in catch recording, i.e insufficient number of officers collecting the data, double-counting issues between subnational and national level, misidentification and other errors. Notwithstanding, Simeon et al. (2019) suggested the decrease in the number of vessels catching wedgefish, has contributed to the decline in wedgefish catch.

Length Frequency Distribution

Sampling programs in 2017–2019 around western Indonesian inner waters recorded a total of 2064 individuals of *R. australiae* and 334 of *R. ancylostoma*. The sizes of fish ranged between 39–300 cm *TL* for *R. australiae* and 43–297 cm *TL* for *R. ancylostoma*. It was this length-frequency data which was then used in the estimation of total mortality rates (Z). The length-frequency distributions for both wedgefish are displayed in histograms in Fig. 3.

The raw data contained one individual of *R. australiae* with *TL* 19 cm. However, this value is doubtful. There was no other fish with a length close to this both from the western Indonesian inner waters and from the eastern Indian Ocean. The second smallest individual was 39 cm, which was too far from 19 cm. Moreover, Weigmann (2011) found size at birth for *R. australiae* is between 46–50 cm. So, in this study 39 cm was chosen as the minimum length of *R. australiae* caught which was confirmed by the existence of individuals with similar sizes.

The maximum length observed from the eastern Indian Ocean was 323 cm, higher than the one from western Indonesian inner waters (300 cm). Considering the proximity of the two regions, the maximum size from the eastern Indian Ocean was used in generating asymptotic length. Actually, our data recorded an individual with *TL* 401 cm from the eastern Indian Ocean. However, with the similar reason as the minimum length, we set the second largest *TL*, 323 cm, as the maximum length naturally occurring for *R. australiae*. Those extreme small and large values (19 and 401 cm) were likely technical mistakes in the recording by enumerators. Fish of size 19 cm, if it really existed, was likely to be an embryo that was accidentally accounted for in the measurement.

For *R. ancylostoma*, the minimum and maximum sizes observed from western Indonesian inner waters were 43 and 297 cm *TL*. These values were used solely in the analysis because these were the smallest and largest lengths observed in the whole data. Furthermore, there were other lengths at the proximity of these values, confirming their validity.

Currently, the maximum size of 323 cm *TL* for *R. australiae* may be the highest ever recorded. White and Dharmadi (2007) reported the maximum size of 300 cm *TL* in eastern Indonesia, and White et al.
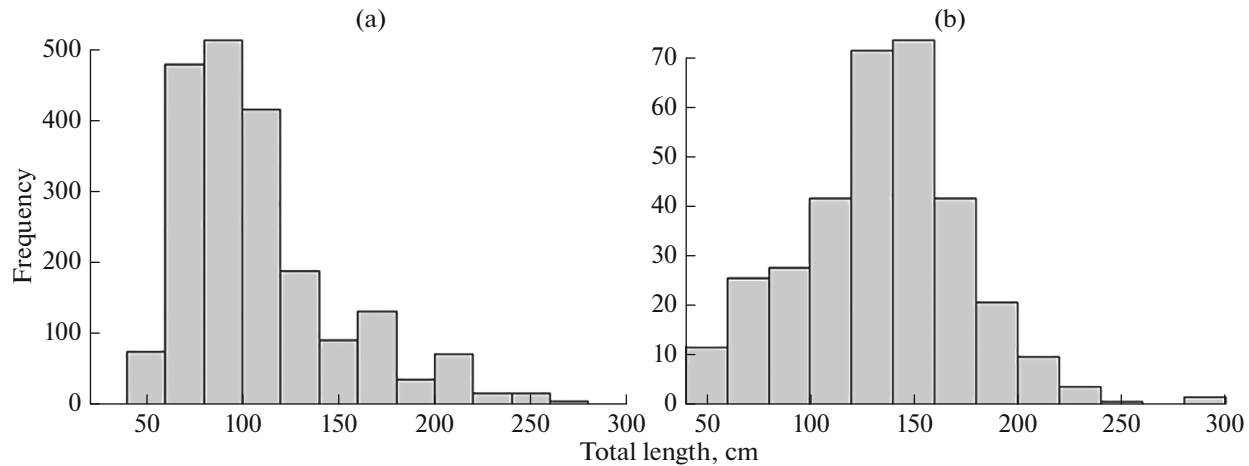
Fig. 3. Length frequency distribution of (a) *R. australiae*, (b) *R. ancylostoma* in western Indonesian inner waters.

(2014) observed only 263 cm *TL* in Australia. Meanwhile, for *R. ancylostoma* Vidthayanon (2005) *in* Borrell et al. (2011) suggested it attains as long as 300 cm in Thailand, higher than recorded in this study. However, in Indonesia, the *TL* of 297 cm might be the highest. Other studies in Indonesia reported the maximum size of only 270 cm *TL* (White et al., 2006; Last et al., 2016) and 250 cm *TL* (White and Dharmadi, 2007).

The length-frequency distribution for *R. australiae* is right-skewed (left-truncated), while that of *R. ancylostoma* is more symmetric (Fig. 3). From the perspective of conservation, catch with left-truncated size distribution is bad, since this is an indication of non-selective fishing gears. Young fish of *R. australiae* are as susceptible as adult fish to fishing, and this is generally not desired. On the other hand, more symmetric length-frequency means young *R. ancylostoma* is not fully selected, so it has higher probabilities to survive the fishing than adult fish.

From the perspective of analysis, however, samples with right-skewed length distribution are preferred. This gives more confidence about the larger part of size frequency in the catch proportionately resembling the frequency in nature. The decreasing frequency to the right of the highest-frequency length class seems to be solely made by mortality. It is what is assumed by logistic selectivity as used in ELEFAN method (Mildenberger et al., 2017). Symmetric length frequency distribution, on the other hand, raises suspicion of selectivity playing a role in shaping the right tail of length-frequency as it does to the left tail. This, in turn, raises doubt about the validity of the logistic-selectivity assumption. Another thing to notice is the small number of catches of *R. ancylostoma*. The fish is six times more rarely caught than *R. australiae*. The poor sample size of *R. ancylostoma* might also cause bias in its length frequency distribution (Fig. 3b). Whether it is selectivity assumption not met or insufficient samples,

all can lead to biased conclusions of this study. However, currently, this is the best available data, hence, further analysis relies on this data.

Growth Models

Re-analysis of von Bertalanffy growth model for *R. australiae* produced $L_\infty = 307.9$ cm, $k = 0.095$/year as displayed in Table 1 and plotted in Fig. 4a. These values are quite different from the ones estimated by White et al. (2014) i.e $L_\infty = 256.630$ cm *TL* and $k = 0.40$/year for two parameters von Bertalanffy model and L_∞ between $204.547-257.132$ cm *TL* for all growth models they attempted. Those L_∞ are suspicious because our data shows maximum length observed is 323 cm *TL* and there are a number of fish larger than 260 cm *TL*. While L_∞ can be lower than the maximum observed length, in this case, the one estimated by White et al. (2014) is too low in contrast with our data. Furthermore, based on data on 230 shark stocks, Cortés (2000) identified most sharks to have $k \leq 0.2$. Also, Frisk et al. (2001) found that large elasmobranchs ($TL > 200$ cm, excluding requiem sharks) have k averaging to 0.11. So, the k value generated by White et al. (2014) seems to be too high. Meanwhile, our results ($k = 0.095$) seem to be more realistic. There are some issues with White et al. (2014) results. Firstly, their data only cover a small range of total length, and the maximum length observed is too small. Secondly, the data is of small sample size as also admitted by White et al. (2014) themselves.

For *R. ancylostoma*, the estimated L_∞ is 283.5 cm. However, no definite growth model can be established due to the inability to generate growth rate parameter (k). To anticipate this, multiple k values (0.08, 0.12, 0.16 and 0.20) have been used. The range of $0.08-0.20$ was resulted from accounting for the metadata of Cortés (2000) and the average of k by Frisk et al.
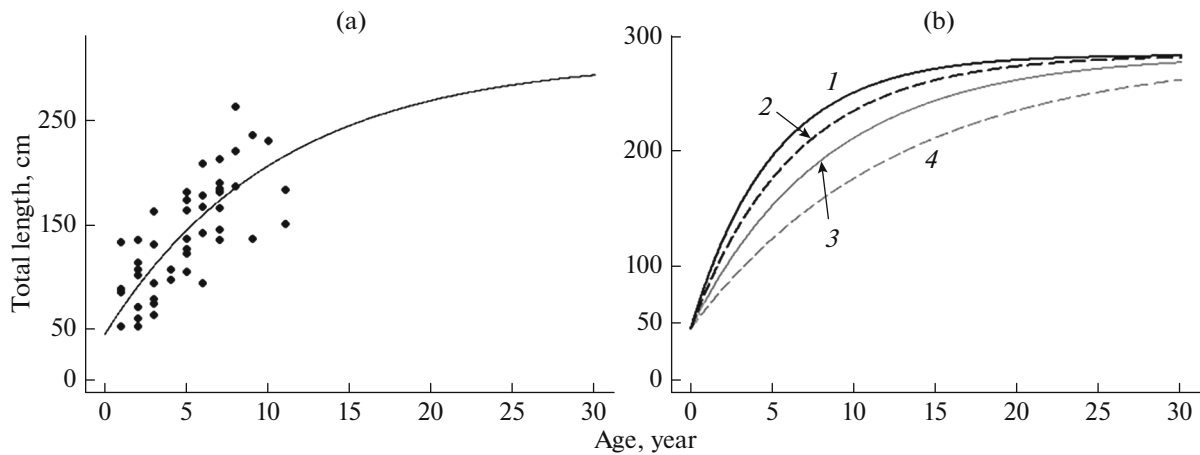
Fig. 4. Growth curve and age-length points for *R. australiae* (a) and possible growth curves of various *k* values for *R. ancylostoma* (b): *1—k* = 0.20, *2—k* = 0.16, *3—k* = 0.12, *4—k* = 0.08.

(2001). Also, Frisk et al. (2001) and Cortés (2000) argue that larger elasmobranch tends to have lower *k*. Asymptotic length (L_∞) of *R. australiae* appears to be higher than *R. ancylostoma*. So, expecting the *k* value for *R. anclylostoma* to be higher than 0.095 is reasonable, again, justifying the *k* range we made. In addition, this range of *k* is appropriate in terms of the plausibility of a_{max} and *M* estimates derived from *k*. If k is set too low (<0.08), the resulting a_{max} becomes too high, which is unrealistic. Similarly, if *k* is too high (>0.20), the resulting *M* becomes unreasonably too high (see subsection "Survivorship"). The growth curve for *R. australiae* along with age—length pairs from White et al. (2014) is presented in Fig. 4a, while the growth curve for *R. ancylostoma* for various *k* values is displayed in Fig. 4b.

The L_∞ estimate for *R. australiae* is a bit higher than that of *R. ancylostoma*. This is because the maximum observed *TL* for *R. australiae* is also higher (323 vs 297 cm) and the estimations of L_∞ in this study was entirely based on maximum length.

Survivorship

Six methods for estimating natural mortality rates (*M*) generated survivorship values in scenario without fishing, as displayed in Tables 3, 4. Estimates of survival rates for *R. australiae* are broadly consistent with each other (Table 3). The differences across different methods were small, the survivorship ranges between 0.804—0.901, indicating the robustness of the estimates. These values told us that each year, as many as 9.9—19.6% of individuals in a cohort die of natural causes. In scenario with fishing, survivorship is still high (0.715), indicating that the fishing mortality rate (*F*) is still low. Coupled with survivorship in the unfished population, in the fished population of *R. australiae*, only as many as 8.9—18.6% of individu-

als die of fishing after the cohort is fully selected by fishing gears. So, if at particular time a fully selected cohort consist of 1000 individuals, then one year later the cohort will leave 715 individuals surviving, with 99—196 individuals die of natural causes and 89—186 individuals of fishing. Of course, it is just a crude estimate, particularly because constant *M* and *Z* across different ages and years have been assumed which should be given cautions given fluctuations both in ecosystem dynamics and fishing intensities over time Secondly, the example above takes one fixed *Z*, when, in fact, the estimate is random with positive variance.

Noticeable is that difference in *k* leads to different survivorship estimate for *R. ancylostoma* in unfished and fished populations (Table 4). All methods for estimating natural mortality rates (accordingly survival rates in unfished population) depend on *k*. They are the functions of *k* either directly or indirectly. Pauly's method and one of Then et al.'s method are functions in *k*, while the rest are functions in a_{max}, which in turn depend on k as well (due to the absence of empirical a_{max}). There is a trend of monotonically increasing natural mortality rate (*M*) as *k* increases, accordingly survivorships in unfished populations decrease. The case for the fished population is no different. Total mortality rate (*Z*) was estimated from a length—based linearized catch curve involving inverse von Bertalanffy function, which definitely uses *k* in the calculation. The trend is similar i.e as *k* increases, *Z* increases, so survivorship in fished populations decreases.

However, it can be seen for the same *k* value, the estimates of survivorship for *R. ancylostoma* cohort in scenarios without fishing agree among different methods, similar to the case for *R. australiae*. As *k* gets bigger, the survivorship estimate gets lower. In the fished population the decrease in survivorship is more apparent. For *k* = 0.2, the survivorship is only 0.456, which means each year less than half of the cohort survives.

Table 3. Annual survivorship for *R. australiae* cohort in unfished and fished population

Population	Methods	e^{-Z}
Unfished	Alverson and Carney, 1975	0.864 (a_{max} = 29.9), 0.901 (a_{max} =3 6.5)
	Hoenig, 1983—joint equation	0.861 (a_{max} = 29.9), 0.884 (a_{max} = 36.5)
	Hoenig, 1983—fish equation	0.870 (a_{max} = 29.9), 0.892 (a_{max} = 36.5)
	Pauly, 1980	0.819
	Then et al., 2015—a_{max}	0.804 (a_{max} = 29.9), 0.834 (a_{max} = 36.5)
	Then et al., 2015—k	0.895
Fished	Length−based linearized catch curve	0.715

Table 4. Annual survivorship for *R. ancylostoma* cohort in unfished and fished population for various scenarios of *k*

Population	Methods	e^{-Z}
	$k = 0.08$	
Unfished	Alverson and Carney, 1975	0.882 (a_{max} = 35.3), 0.916 (a_{max} = 43.3)
	Hoenig, 1983—joint equation	0.880 (a_{max} = 35.3), 0.901 (a_{max} = 43.3)
	Hoenig, 1983—fish equation	0.889 (a_{max} = 35.3), 0.908 (a_{max} = 43.3)
	Pauly, 1980	0.833
	Then et al., 2015—a_{max}	0.829 (a_{max} = 35.3), 0.856 (a_{max}= 43.3)
	Then et al., 2015—k	0.904
Fished	Length−based linearized catch curve	0.731
	$k = 0.12$	
Unfished	Alverson and Carney, 1975	0.829 (a_{max} = 23.5), 0.876 (a_{max} = 28.9)
	Hoenig, 1983—joint equation	0.827 (a_{max} = 23.5), 0.856 (a_{max} = 28.9)
	Hoenig, 1983—fish equation	0.838 (a_{max} = 23.5), 0.866 (a_{max} = 28.9)
	Pauly, 1980	0.788
	Then et al., 2015—a_{max}	0.762 (a_{max} = 23.5), 0.799 (a_{max} = 28.9)
	Then et al., 2015—k	0.873
Fished	Length−based linearized catch curve	0.624
	$k = 0.16$	
Unfished	Alverson and Carney, 1975	0.779 (a_{max} = 17.6), 0.839 (a_{max} = 21.7)
	Hoenig, 1983—joint equation	0.777 (a_{max} = 17.6), 0.814 (a_{max} = 21.7)
	Hoenig, 1983—fish equation	0.789 (a_{max} = 17.6), 0.824 (a_{max} = 21.7)
	Pauly, 1980	0.750
	Then et al., 2015—a_{max}	0.702 (a_{max} = 17.6), 0.746 (a_{max} = 21.7)
	Then et al., 2015—k	0.845
Fished	Length−based linearized catch curve	0.534
	$k = 0.20$	
Unfished	Alverson and Carney, 1975	0.732 (a_{max} = 14.1), 0.803 (a_{max} = 17.3)
	Hoenig, 1983—joint equation	0.731 (a_{max} = 14.1), 0.774 (a_{max} = 17.3)
	Hoenig, 1983—fish equation	0.743 (a_{max} =1 4.1), 0.786 (a_{max} = 17.3)
	Pauly, 1980	0.717
	Then et al., 2015—a_{max}	0.648 (a_{max} = 14.1), 0.698 (a_{max} = 17.3)
	Then et al., 2015—k	0.821
Fished	Length−based linearized catch curve	0.456

Table 5. Output of matrix models for *R. australiae* (median, 95% confidence interval)

Parameter	1 Year RC		2 Years RC	
	unfished	fished	unfished	fished
λ	1.30 (1.24, 1.36)	1.11 (1.06, 1.17)	1.23 (1.17, 1.29)	1.05 (1.00, 1.10)
r	0.26 (0.22, 0.30)	0.11 (0.06, 0.16)	0.21 (0.16, 0.25)	0.05 (0, 0.10)
R_0	16.50 (9.34, 23.39)	2.78 (1.64, 3.91)	8.92 (5.13, 12.56)	1.62 (0.96, 2.30)
$t_{\times 2}$, years	2.6	6.5	3.4	13.4

Here and in Tables 6−8: RC—reproductive cycle.

The survival rate of *R. ancylostoma* is lower than that of *R. australiae* in most k values, except for $k = 0.08$. The difference gets bigger for higher k. This holds for both unfished and fished scenarios.

The survival rates for fished populations in the two species were based on catch-curve analysis, which assumes fish recruitments as relatively constant over time (Hilborn and Walters, 1992; Sparre and Venema, 1998; Hisano et al., 2011). This assumption is unlikely because low fecundities in elasmobranch (moreover in these two wedgefishes) makes the stock-recruitment relationship more direct (Hoenig and Gruber, 1990; Smith et al., 1998; Cortés, 2011). So, the number of offsprings should be highly dependent on the number of mothers. However, currently, linearized catch-curve is the best method for estimating total mortality rates given the limitation in data. Similar to this work, Hisano et al. (2011) also used catch-curve analysis to derive mortality rates for their demographic model in the absence of complete data.

Demographic Analysis

The results of the matrix model for *R. australiae* (Table 5) show $\lambda > 1$ (95% CI lies to the right of 1) or $r > 0$ (95% CI lies the right of 0) for both both with- and without-fishing scenarios, indicating that populations positively grow. Based on λ values, the unfished population increased at a rate of 30% per year (1 year RC) or 23% per year (2 years RC), revealing the relatively high productivity of this species. Despite using different k values, D'Alberto et al. (2019) also found the equally high productivity for unfished population of *R. australiae*, with instantaneous growth rate (r) between 0.22−0.49, consistent with this present study. This work also shows fished population increases at a rate of 11 or 5% per year for 1 or 2 years RC, respectively.

Based on R_0 values, an individual female in the unfished population on average produces 16.5 offsprings (1 year RC) or 8.92 offsprings (2 years RC) during its lifetime. Meanwhile, a female in the fished population produces only 2.78 or 1.62 offsprings during its lifetime (with 1 or 2 years RC). In all scenarios, $R_0 > 1$, showing that each single mother is being replaced by more than 1 offspring. This explains why

the population grows both in with- and without-fishing scenarios.

Ignoring the density-dependence mechanism, the population will double every certain period. Unfished population will double every 2.6 years (1 year RC) or 3.4 years (2 years RC), which is very fast. Meanwhile, the fished population takes 6.5 or 13.4 years to double in 1 or 2 years RC, which is still fast.

Positive growth in the fished population indicates that current exploitation has not endangered the stock of *R. australiae* in western Indonesian inner waters. In addition, the population of *R. australiae* increases quickly, indicating this species as productive. In all scenarios, the doubling time is less than 20 years (Table 5) which is quite short. Ten years projections as displayed in Fig. 5 confirm this high increase of *R. australiae*'s population. Within ten years, the populations will have grown to a very high level. In without-fishing scenarios the population will grow to nearly 1400% of initial abundance for 1 year RC and nearly 800% for 2 years RC which are exceptionally high. In fished scenarios, the population will grow to nearly 300 and 170% for 1 and 2 years RC respectively. Within 10 years the populations' increase is more than 100% in almost all scenarios, except the fished population with 2 years RC, 70%. This high increase will work only for a low initial population. For population size near carrying capacity, the density dependent mechanism due to limited food and space will hinder this high long-term growth rate. However, how big the actual long-term population is, is not very important. This is just to show that *R. australiae* has high productivity, hence, helps explain why it can withstand the current level of exploitation.

The analysis of matrix models for *R. ancylostoma* (Table 6) shows only population without fishing is positively growing, indicated from $\lambda > 1$ (95% CI lies to the right of 1 except for $k = 0.20$ with two years RC) and the corresponding r values. This unfished population only increases slightly, in contrast to *R. australiae*, which grows significantly. The annual increases vary according to k values, ranging 11−15% per year with 1 year RC or 4−9% per year with 2 years RC. While natural mortality rates increases, λ or r does not show a clear trend by the increase of k.
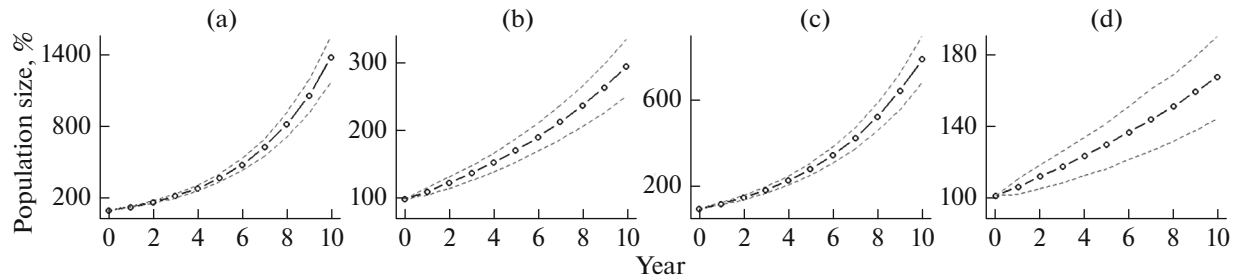
Fig. 5. Ten years projection of female population of *Rhynchobatus australiae* with the associated 95% confidence interval (CI) in (a) unfished population with 1 year reproductive cycle (RC), (b) fished population with 1 year RC, (c) unfished population with 2 years RC, (d) fished population with 2 years RC.

On the other hand, the fished populations reveal decline in most cases as represented by $\lambda < 1$ or $r < 0$. The exception is the case $k = 0.08$ with 1 year RC showing almost stagnant population. However, even for this case, the wide 95% CI of λ or r indicate the probability of population declining is high. For other k values, the decrease of the fish population is as many as 1−21 or 4−26% per year with 1 and 2 years RC respectively. There seem to be decreasing trends of λ or r with the increasing k. This is likely to be related to significantly increased total mortality rate Z.

According to Table 4, it is clear that the decrease in the survival rate of the fished population (driven by the increase in Z) is more significant. Bradshaw et al.

Table 6. Output of matrix models for *R. ancylostoma* with various scenarios of k (median and 95% confidence interval)

Parameter	1 Year RC		2 Years RC	
	unfished	fished	unfished	fished
		$k = 0.08$		
λ	1.12 (1.08, 1.15)	1.00 (0.97, 1.04)	1.08 (1.04, 1.11)	0.96 (0.93, 0.99)
r	0.11 (0.08, 0.14)	0.00 (−0.03, 0.03)	0.07 (0.04, 0.11)	−0.04 (−0.07, 0.00)
R_0	6.27 (2.91, 9.51)	1.03 (0.58, 1.51)	3.35 (1.61, 5.11)	0.58 (0.31, 0.88)
$t_{\times 2}$, years	6.3	402	9.6	−
t_{coll}, years	−	−	−	125
		$k = 0.12$		
λ	1.15 (1.09, 1.22)	0.99 (0.93, 1.06)	1.09 (1.04, 1.15)	0.94 (0.88, 1.01)
r	0.14 (0.08, 0.20)	−0.01 (−0.07, 0.06)	0.09 (0.04, 0.15)	−0.06 (−0.12, 0.01)
R_0	4.96 (2.35, 7.50)	0.92 (0.39, 1.57)	2.72 (1.30, 4.11)	0.55 (0.23, 0.99)
$t_{\times 2}$, years	4.9	−	7.7	−
t_{coll}, years	−	488	−	75
		$k = 0.16$		
λ	1.13 (1.05, 1.22)	0.92 (0.84, 1.01)	1.07 (1.00, 1.15)	0.87 (0.80, 0.96)
r	0.13 (0.05, 0.20)	−0.09 (−0.17, 0.01)	0.07 (0.00, 0.14)	−0.14 (−0.22, −0.04)
R_0	3.38 (1.44, 5.30)	0.50 (0.16, 0.99)	1.90 (0.80, 2.97)	0.33 (0.09, 0.65)
$t_{\times 2}$, years	5.5	−	10.2	−
t_{coll}, years	−	53	−	33
		$k = 0.20$		
λ	1.11 (1.02, 1.19)	0.79 (0.73, 0.84)	1.04 (0.96, 1.12)	0.74 (0.69, 0.79)
r	0.10 (0.02, 0.18)	−0.24 (−0.31, −0.17)	0.04 (−0.04, 0.11)	−0.30 (−0.37, −0.23)
R_0	2.35 (0.94, 3.71)	0.16 (0.07, 0.28)	1.36 (0.57, 2.16)	0.10 (0.04, 0.19)
$t_{\times 2}$, years	6.9	−	18.8	−
t_{coll}, years	−	19.1	−	15.2

(2018) reported that survival rate has a big effect on population growth in copper shark (*Carcharhinus brachyurus*). Meanwhile, while in unfished populations survival rate also decreases, the decrease is not significant. Other vital rates might have compensated the effect of increasing M in unfished populations of *R. ancylostoma*. Age at maturity (a_m) is likely to be the compensator.

According to Cortés (2002) and Pardo et al. (2018), age at maturity is negatively correlated with population growth. This is particularly sensible because in this study a_m are derived from L_m making use of k in the processes. As k increases, this quantity decreases (Table 2), making *R. ancylostoma* reproduce earlier. Early reproduction schedule provides significant additions to offspring because the abundance of younger mothers is significantly higher than older ones due to progressive mortality to a cohort. Even though at the same time longevity (a_{max}) decreases as well which consequently reduces the reproductive lifespan, variation in longevity has only little effect on population growth (Smith et al., 1998; Hisano et al., 2011). This is because older mature fish have been significantly reduced. So they do not produce significantly more offspring.

For each scenario of unfished and fished population with two different RC, the precision of λ (or r) estimate as represented by the 95% CI tend to be negatively correlated with k values. This seems to be related to change in age at maturity (a_m). Cortés (2002) also found that precision of λ estimates across various shark species decreases with decreasing a_m, which agree with this study on *R. ancylostoma*.

The net reproductive output (R_0) of *R. ancylostoma* in the unfished population also varies by k values, ranging from 2.35 to 6.27 offsprings (1 year RC) or 1.36 −3.35 offsprings (2 years RC) per female. While the corresponding fished population produces 0.16−1.03 offsprings or 0.10−0.58 offsprings per female with 1 or 2 years RC respectively, which is very small. $R_0 \leq 1$ in the with-fishing scenario means that every single mother in the population is replaced by less than one offspring, explaining why the population in this scenario decays. Different from λ, in both unfished and fished populations R_0 shows a clear pattern of decrease with the increase of k. This should be clear from its formula. R_0 is the function of only survival rate (S_a) and fecundity (f_a). While fecundity is constant across all k, survival rates (both in with- and without-fishing scenarios) decreases as k increases.

Due to the low rate of population increase, the unfished population of *R. ancylostoma* takes longer time to double. Across all k values, the doubling time is between 5−7 years with 1 year RC or 8−19 years with 2 years RC, significantly longer than their counterparts in *R. australiae*. Since $t_{\times 2}$ is derived from r values in unfished populations, then similar with r, it

does not show a trend as k increases. Meanwhile, for the with-fishing scenario, the population is undergoing a decline. With the current exploitation level (and ignoring the compensation mechanism), the population will be collapsed after a certain period. Similar to $t_{\times 2}$, this collapse time (t_{coll}) varies according to k values, i.e 19−488 years with 1 year RC or 15−125 years with 2 years RC. Furthermore, t_{coll} is also derived from r values in fished populations. So, t_{coll} shows a trend of decrease as k increases.

R. ancylostoma's population only shows an increase when fishing does not occur. However, this increase is significantly lower than that of *R. australiae*. Ten years projections (Fig. 6) shows that within 10 years the population of *R. ancylostoma* grows to less than 400% of initial population in 1 year RC and no more than 250% in 2 years RC, depending on k value. These are much lower than *R. australiae*, more than 1300 and 700% (Fig. 5). Similar to λ, the projected population size in the next 10 years fluctuates but does not show any trend with the increase of k. This is sensible because projections were entirely based on λ.

Theoretically, unfished population should always increase or at least stationary ($\lambda \geq 1$, $r \geq 0$) in order for the population to ever exist. Otherwise, the population will have been collapsed a long time ago. However, using a similar matrix model, Cortés (2002) really found $\lambda < 1$ in unfished populations for some species of *Carcharhinus*, *Squalus*, and *Alopias*. Particular care should be taken toward this. Cortés (2002) suggested that this unrealistic growth rate is partly due to violations in assumptions of demographic analysis. Biased life-history parameters used may also lead to this negative growth of unfished populations.

When current level of fishing is introduced, the population of *R. ancylostoma* generally declines. Ten years projection of female population (Fig. 6) confirms this. In almost all scenarios of fished population, the trajectories are going downward, showing the population gets lower and lower over time. Similar to λ, the projected population decreases more steeply as k increases. For $k = 0.2$, the population drops to very low levels, less than 10% for 1 year RC and less than 5% for 2 years RC. This corroborates the result in Table 6 that if $k = 0.20$ holds, the collapse of *R. ancylostoma* may occur within 20 years. This result is alarming. Even though this collapse is not mathematically equivalent to extinction due to the definition of t_{coll} (as time by which the population is depleted to less than 1% of initial abundance), but when this very low level of population is achieved, the risk for local extinction is high ecologically due to factors such as environmental stochasticity or Allee effect (Berec et al., 2007; Holden and McDonald-Madden, 2017).

Several things are suspected of leading to a difference in the productivity of *R. australiae* and *R. ancylostoma*. The first possible factor is the difference in survival rates. Tables 1 and 4 show that *R. australiae*
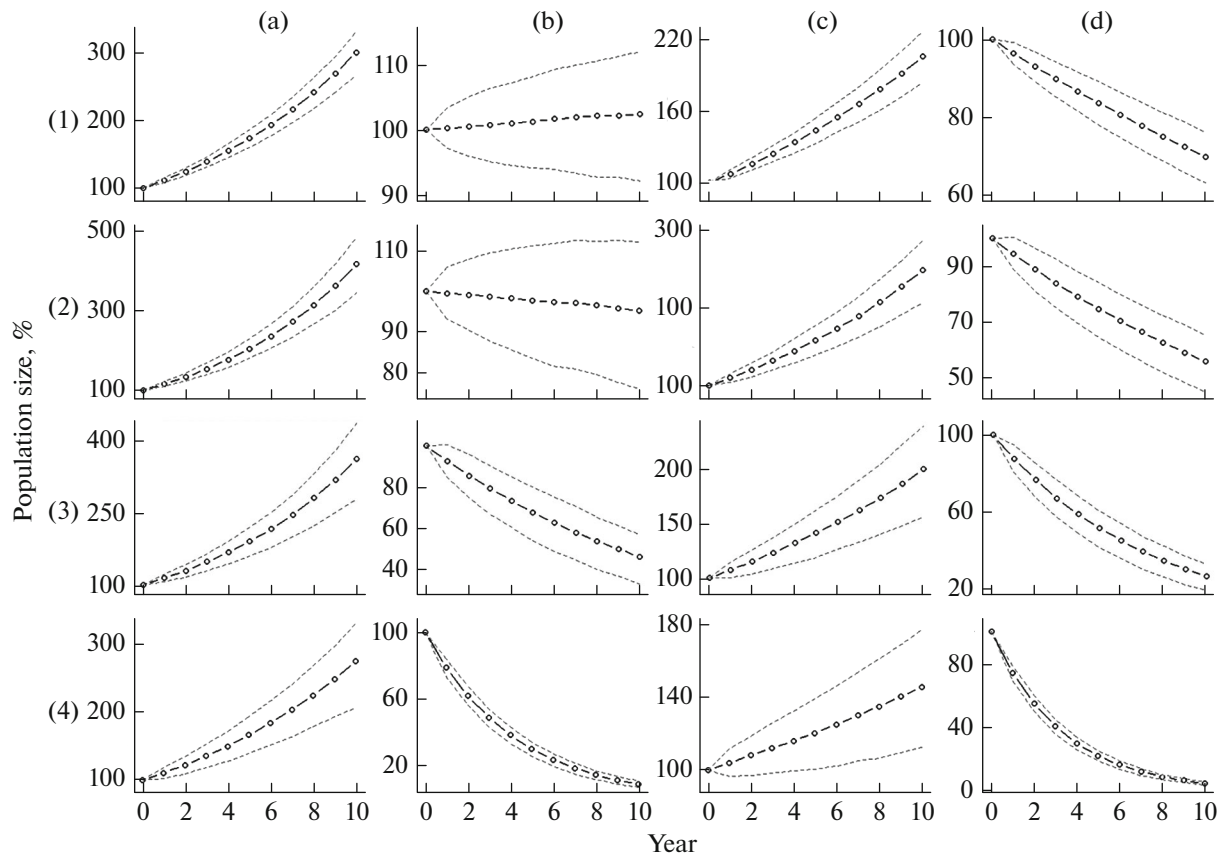
Fig. 6. Ten years projection of female population of *Rhina ancylostoma* with the associated 95% confidence interval (CI) for scenarios (1) $k = 0.08$, (2) $k = 0.12$, (3) $k = 0.16$, (4) $k = 0.20$ and (a) unfished population with 1 year reproductive cycle (RC), (b) fished population with 1 year RC, (c) unfished population with 2 years RC, (d) fished population with 2 years RC.

tend to have a higher survival rate than *R. ancylostoma* both in unfished and fished populations. This has been exemplified by *R. ancylostoma* (under various *k* values), in which higher survival rate leads to higher population growth, which was also supported by Bradshaw et al. (2018). Second and especially noticeable is the difference in fecundity in the two species. *R. australiae* is significantly more fecund than the latter species. It is easily understandable as fecundity is a very important factor influencing the number of offsprings produced, which ultimately determines how fast the population grows. Tsai et al. (2014) also found that survival rate and fecundity contribute significantly to population growth in shortfin mako shark (*Isurus oxyrinchus*). So, it is likely to be the case that higher fecundity and relatively higher survival rate leads to higher population growth in *R. australiae* compared to *R. ancylostoma*. This significant influence of fecundity was also confirmed by Pardo et al. (2018) and Cortés (2002). However, other than fecundity, Pardo et al. (2018) and Cortés (2002) also found age at maturity to be another important factor determining population growth and in Cortés, even more dominant than a fecundity. Generally, age at maturity is negatively cor-

related with the population growth rate. Unfortunately, the comparison of age at maturity in these two species is hindered by its uncertainty in *R. ancylostoma* resulted from uncertainty in growth parameter *k*. On the other hand, *R. ancylostoma* clearly has larger size at maturity than *R. australiae* (180 vs. 155 cm *TL*). This might be another factor leading to a lower population increase in *R. ancylostoma*. According to Smith et al. (1998), the instantaneous rate of population increase is closely related to age and size at maturity.

Following the categorization by Frisk et al. (2001), both *R. australiae* and *R. ancylostoma* belong to large elasmobranch (>2 m *TL*). It was hypothesized that large elasmobranch tend to have low productivity, making them more prone to population depletion (Smith et al., 1998; Fisk et al., 2001; Dulvy and Reynolds, 2002). The case of *R. ancylostoma* seems to follow this general theory. In contrast, Cortés (2002) found no correlation between body size and population growth rate based on 38 shark species. In addition, Garcia et al. (2008) found only a weak influence of body size to extinction risk and suggested this is due to a correlation between body size and other more meaningful life-history traits. The case of *R. australiae*

Table 7. Elasticities of fecundities, juvenile survivals and adult survivals in *R. australia*e

Elasticity	Scenarios			
	1 year RC		2 years RC	
	unfished	fished	unfished	fished
Fecundity	0.116	0.117	0.118	0.120
Juvenile survival	0.697	0.707	0.707	0.718
Adult survival	0.187	0.175	0.175	0.162

seems to favor these two studies rather than the above general theory.

The result of matrix models infers that for *R. australiae*, the current level of fishing can be maintained to give maximum benefit for the fishermen. While for *R. ancylostoma*, a substantial reduction in catch/fishing effort are needed in order for the population to persist in the long run. Otherwise, exploitation is driving the population of *R. ancylostoma* to severe depletion, and several years later, local extinction may happen.

The status of *R. australiae* which this study inferred seems to contradict its status as Critically Endangered in IUCN Red List. For this, several things should be noted. Firstly, the IUCN Red List status measures the global status of *R. australiae* given the global fishing pressure. Individual stocks can have different conditions. Our study and that of D'Alberto et al. (2019) agree that naturally *R. australiae* is productive in term of unfished population growth. Fish with high productivity can still be endangered if massive exploitation is imposed. However, closer look to *R. australiae* stock in western Indonesian inner waters, shows that exploitation is not so high that it can still withstand the current exploitation level.

Secondly, in IUCN Red List assessment, Kyne et al. (2019) conclude the status of *R. australiae* as Critically Endangered based on the global population decline they claimed to be more than 80% during 3 generations. However, this magnitude of population decline is crude. This does not come from formal stock assessment, rather from historical catch records from several places, with the assumption that catch reflects population abundance. This assumption is controversial (e.g Pauly et al., 2013) which Kyne et al. (2019) are also aware of. As an example, the declining trend of wedgefish catch from Indonesia as shown in Fig. 2, if it really happened, is due to the decrease in the number of vessels operating (Simeon et al., 2019), instead of decline in abundance. For comparison, analyses on the data from southern Indonesian waters (eastern Indian Ocean) show that the catch per unit effort (CPUE) of *R. australiae* has been increasing during 2014−2020, not decreasing. Furthermore, even if we insist to use catch as the proxy for abundance, almost nowhere catch report for wedgefish are segregated per species. What Kyne et al. (2019) observed is,

at best, the declining catch of aggregated wedgefish, instead of *R. australiae* alone. Worsely, in Southeast Asia, the signal of decline in wedgefish catch usually comes from the observed declines of overall demersal fisheries (Stobutzki et al., 2006). With this, it is difficult to see the real picture of catch trajectory for *R. australiae* alone. It is probable that while the catch of other demersal fish are declining, the one for *R. australiae* is not or at least the decline is not as significant as other fish. The likelihood increases when it is revealed that different species of wedgefish have very different productivities. Also, Kyne et al. (2019) used simplistic formula to compute the generation length (*GL*, as explained in Kyne et al., 2020) and got *GL* 15 years for *R. australiae*. Using this value, they estimated the global decline during 3 generations to be >80%. Using a more formal formula borrowed from life table analysis (Simpfendorfer, 2005), we computed the *GL* to be 8−12 years. We do not have access to Kyne et al. (2019) data to be able to recalculate the global decline of *R. australiae*. However, with this updated *GL*, we believe the decline will be less than 80% even if historical catch data of Kyne et al. (2019) is used without cautions.

Elasticity Analysis

In order to better understand the influence of demographic uncertainties on population growth (λ or r), Tables 7, 8 and Figs. 7, 8 summarize the results of elasticity analysis. Based on elasticity per age, younger individuals of both *R. australiae* and *R. ancylostoma* have higher elasticities regardless of scenarios of population with or without fishing (Figs. 7, 8). This holds in *R. ancylostoma* in all *k* scenarios. In both species, the peaks occur at age 0 up to (including) age at first pupping a_p. After that, the elasticities start to decline. The older the fish, the lower the elasticities of each age to population growth.

Disentangling elasticities of fecundity and survival, it is revealed that the survival of juvenile (age 0 up to age before pupping) has the highest elasticity in both wedgefish (Tables 7, 8). The elasticity of juvenile's survival is significantly higher than those of adult's survival and fecundity. This result agrees with the finding of Cortés (2002) on various shark species and Heppel et al. (1999) on leopard shark (*Triakis semifasciata*) and angel shark (*Squatina californica*). In all cases, elasticity of survival of age at first pupping a_p has started to decline; a_p being still at the peak of elasticity (Figs. 7, 8) is resulted from the sum of elasticities of survival and fecundity at that age.

Population growth rates in both with- and without-fishing scenarios are very sensitive to the survival of young fish (age 0 up to age before pupping). Small variations in survival rates of these ages can alter population growth rates dramatically. Since the survival of *R. ancylostoma* is generally lower than *R. australiae*,

the same pattern certainly occurs for juveniles. So, juveniles (as well as adults) of *R. ancylostoma* tend to have lower survival rates compared to *R. australiae*. This justifies the previous claim that the lower population growth of *R. ancylostoma* (even negative growth in fished population) is partly caused by its lower survival rate compared to *R. australiae*.

We also suspected that the lower *R. ancylostoma*'s fecundity become another factor leading to its lower population growth. Despite being not as significant as survival rate, positive elasticities of fecundities (Tables 7, 8) indicates that fecundity really has an influence on the population growth.

That elasticity of juvenile fish is high is sensible considering the fact that abundant juveniles determine the availability of mature individuals. If young individuals are depleted, then only a few fish (if any) reach the reproduction stage, while reproduction is ultimately the reason why the population even exists. It's likely to be the reason why age at first pupping is still at the peak of elasticity.

However, while older fish are assumed to reproduce continuously, Figs. 7 and 8 clearly show they have a decreasingly lower effect on population growth both in terms of survival or fecundity. First, enough offsprings may have been produced by younger mothers. So, more offspring from older mothers are not really needed to sustain the population. Second, while it is true that older mothers continuously give birth, their abundance has been reduced significantly. So, not many offspring can be produced by older mothers. This is especially true when fecundity per capita stays constant over ages (which is the case for this two wedgefishes). This is different from the finding of Tsai et al. (2010) in which the highest elasticity in pelagic thresher shark (*Alopias pelagicus*) occurs at the adult stage instead of younger fish. However, they used the stage-based matrix, with only four stages (neonate, juvenile, subadult, and adult) assumed to represent up to 30 age classes. Mollet and Cailliet (2002) reminded to caution elasticities from stage-based models as they usually underestimate the elasticity of juvenile survival and overestimate the one of the adults. Using the age-based matrix, Cortés (2002) found that the case where

Table 8. Elasticities of fecundities, juvenile survivals and adult survivals in *R. ancylostoma* for various scenarios of k

Elasticity	Scenarios			
	1 year RC		2 years RC	
	unfished	fished	unfished	fished
k = 0.08				
Fecundity	0.072	0.076	0.071	0.077
Juvenile survival	0.716	0.758	0.713	0.773
Adult survival	0.212	0.166	0.216	0.149
k = 0.12				
Fecundity	0.113	0.120	0.113	0.123
Juvenile survival	0.677	0.719	0.679	0.737
Adult survival	0.210	0.162	0.208	0.140
k = 0.16				
Fecundity	0.133	0.143	0.134	0.148
Juvenile survival	0.664	0.716	0.670	0.740
Adult survival	0.204	0.141	0.196	0.112
k = 0.2				
Fecundity	0.133	0.141	0.136	0.145
Juvenile survival	0.666	0.706	0.681	0.727
Adult survival	0.201	0.153	0.183	0.128

adult stages have higher elasticity occurs for sharks with early age at maturity.

According to this study, the existence of juveniles and young mothers seems determinant to maintain the population level. In this regard, protection toward young fish (juvenile up to the age at first reproduction) will be the most suitable strategy. For *R. australiae*, protection up to age seven years old is recommended. However, for *R. ancylostoma*, uncertainty in age at maturity generated from uncertainty in somatic growth parameter (k) complicates the management recommendation. Being precautionary, protection up to age 13 for *Rhina ancylostoma* may be implemented with the risk of sacrificing potential benefits from fisheries. These protections towards younger fish can be
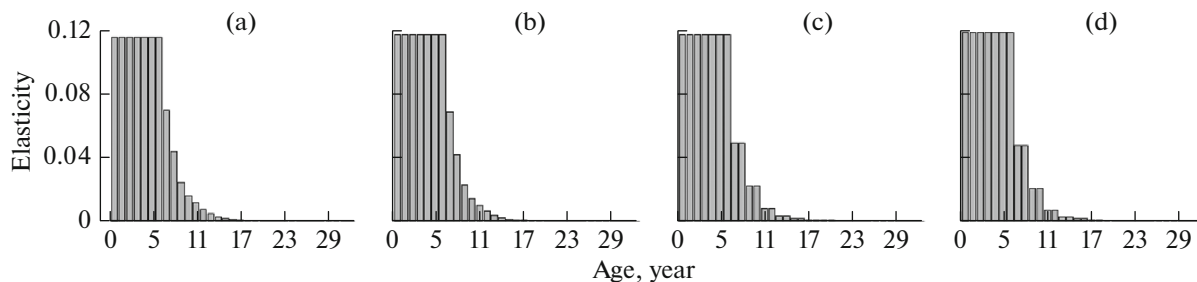

Fig. 7. Elasticity of each age to λ in *R. australiae* for (a) unfished population with 1 year reproductive cycle (RC), (b) fished population with 1 year RC, (c) unfished population with 2 years RC, (d) fished population with 2 years RC.
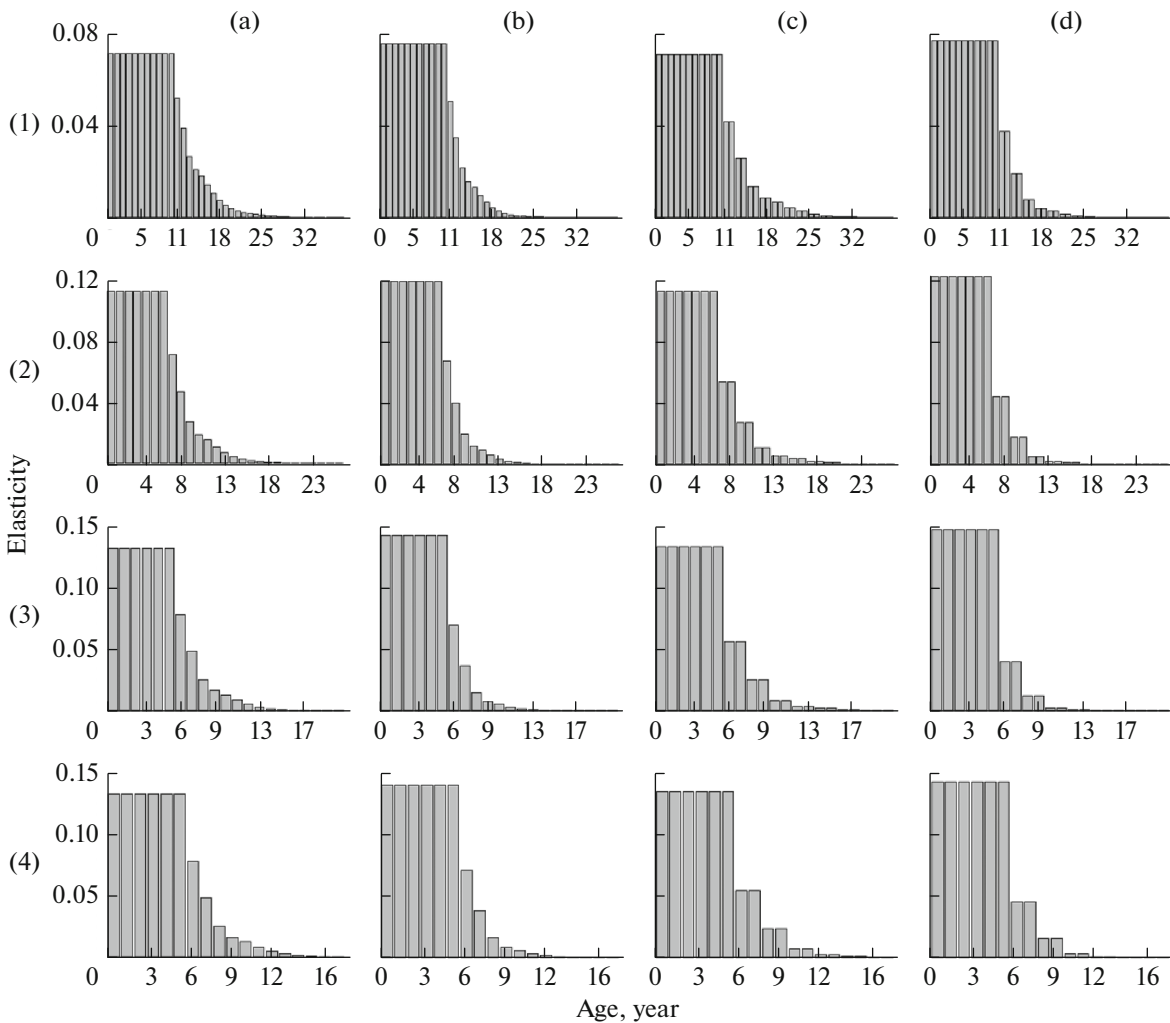
Fig. 8. Elasticity of each age to λ in *R. ancylostoma* for scenarios (1) *k* = 0.08, (2) *k* = 0.12, (3) *k* = 0.16, (4) *k* = 0.20 and (a) unfished population with 1 year reproductive cycle (RC), (b) fished population with 1 year RC, (c) unfished population with 2 years RC, (d) fished population with 2 years RC.

implemented by limiting or even prohibiting fishing activities in nursery areas.

Further Studies

Some aspects of the present work were based on simplistic assumptions and incomplete information on vital life-history parameters. Therefore, the result of this study should be regarded as preliminary, and further studies should be conducted both to provide more complete information on vital parameters and to improve stock assessments using this better information.

Throughout this study, uniform distributions have been used to represent uncertainties on some vital rates: age at first pupping, fecundity, and longevity driven by lack of information. A uniform distribution that has no mode is unlikely and contains greater uncertainties that are propagated to uncertainty in

population growth rate (λ and *r*). The lack of information on sex ratio and RC also forces to make simplistic assumptions, which may lead to inaccurate growth estimates. Finding empirical values and distribution of these vital parameters can lead to better and more accurate population growth estimates.

Age and growth studies for both *R. australiae* and *R. ancylostoma* are also still needed to generate more reliable growth parameters (L_∞ and *k*). In *R. australiae*, current growth parameters were based on incomplete data of White et al. (2014). The importance is twofold for *R. ancylostoma* in which age and growth study is not available at all.

For mortality, natural mortality rates seem to be the most difficult to estimate. However, this should not bother much because the population growth derived from demographic model is usually less sensitive to natural mortality (Pardo et al., 2018). Instead,

further study should focus on fishing mortality. Once a better catch recording system (by management authority) is achieved, more thorough mortality estimation methods such as virtual population analysis (VPA) should be attempted in place of the current linearized catch curve, which is less realistic.

In order to protect juveniles of both *R. australiae* and *R. ancylostoma* as recommended in this work, a study on nursery grounds for both species is important. Last but not least, throughout this study, *R. australiae* and *R. ancylostoma* in western Indonesian inner waters have been assumed to form unit stocks. To what extent this assumption holds remains uncertain. Tagging or genetic study can help find out the stock structure of both fish in these areas.

CONCLUSIONS

This study concludes that *R. australiae* is productive, while *R. ancylostoma* is not sufficiently productive in terms of population growth. The current level of fishing has not endangered the population of *R. australiae* in western Indonesian inner waters, so it can be maintained to give maximum benefit to fishermen and fisheries communities. Differently, the population of *R. ancylostoma* cannot withstand current levels of exploitation, so the substantial reduction in fishing is required to preserve its population in this region. Furthermore, protecting young fish (juveniles up to the age at first reproduction) is recommended for both wedgefish species in order for populations to sustain. For *R. australiae*, fish of age less than equal seven years should be protected, while for *R. ancylostoma* age-based restriction cannot be set yet due to lack of information on age at first reproduction.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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