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Stock Status of Whitespotted Bambooshark, *Chiloscyllium plagiosum* (Anonymous [Bennett], 1830) in Sabah, Malaysia, Using Yield-Per-Recruit and Spawning-Per-Recruit Analyses

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Abstract

Whitespotted bambooshark, *Chiloscyllium plagiosum* (Anonymous [Bennett], 1830), is a major shark species caught in waters off Sabah, Malaysia. Despite the massive landing amount, its biological and stock status information is limited. In 2015–2016, the elasmobranch data collection was conducted in Southeast Asia, including Sabah. A yield-per-recruit (YPR) and spawning-per-recruit (SPR) analyses were performed to assess this data-deficient species' stock status. The growth parameter, average maximum length, L_{∞} , and growth rate, *K*, for males and females were 81.13 cm and 0.21 year⁻¹, and 84.30 cm and 0.18 year⁻¹, respectively. Limit and target biological reference points, maximum fishing mortality and fishing mortality corresponding to 10 % of YPR slope (F_{max} and $F_{0.1}$, respectively) for YPR, and fishing mortality corresponding to 20 % and 30 % of spawning stock remained ($F_{20\%}$ and $F_{30\%}$, respectively) for SPR, were calculated. The results suggest neither growth nor recruit overfishing was occurring. Monitoring and surveillance of existing management measures are necessary to ensure sustainable utilisation of the stock.

Keywords: Southeast Asia, yield-per-recruit, spawning-per-recruit, stock assessment

Introduction

whitespotted bambooshark, The Chiloscyllium plagiosum (Anonymous [Bennett], 1830), is widely distributed throughout tropical and subtropical Indo-Pacific coastal waters to 50 m depth (Chen et al., 2007; Kyne et al., 2021). This coral reef-dwelling species attains a maximum length of 95 cm of total length (TL) and is one of the dominant shark species after brownbanded bambooshark (Chiloscyllium Punctatum Müller & Henle, 1838) in the southeast Asian waters, including Taiwan as bycatch species (Arai and Azri, 2019; Wanchana et al., 2020; Ebert et al., 2021; Kyne et al., 2021). The Southeast Asian Fisheries Development Center (SEAFDEC) project regarding data collection on sharks, rays, and skates reported landings of whitespotted bambooshark in Sabah, Malaysia, to represent about 23 % (1,017.15 kg) of total elasmobranch landings from this area. The data collection period was 12 months in total for each

landing site (Wanchana et al., 2020), similar to the report of Arai and Azri (2019), where the catch composition of whitespotted bambooshark was approximately 25 % of total sharks landed in Sabah.

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Shark catch has declined worldwide (Lam and Sadovy De Mitcheson, 2011), which is often thought to be related to the shark life cycle that cannot compensate for fishing pressure rather than effectiveness in implementing any fishing regulation (Davidson et al., 2015). For example, sharks' lower fecundity and late maturation may be vulnerable to fishing pressure. Accordingly, stock assessments for sharks are required. Yield-per-recruit (YPR) analysis has been implemented since the 1950s for various marine and freshwater fish and invertebrate species (Sun et al., 2005; Peixer et al., 2007; Preecha, 2012; Zischke and Griffiths, 2015). In the 1990s, per-recruit analysis was improved to cover spawning stock and thereafter became known as 'spawning-stock-per-recruit' or SPR (Prager et al., 1987; Goodyear, 1993; Mace and Sissenwine, 1993) analysis. These two analyses are often combined to assess yield- and spawning-stock biomasses (Sun et al., 2002).

Even though the YPR and SPR were originally designed from the biological information of teleost fish these models are also widely applied to the elasmobranch (Griffiths, 1997; Chang and Liu, 2009; Jutan et al., 2018). Therefore, when data of elasmobranch in Southeast Asian waters, such as catch, effort, and some age-based biological parameters, are limited, YPR and spawning-perrecruit (SPR) can be used to assess and provide the reference points related to yield and biomass. Since whitespotted bambooshark is also one of the elasmobranchs in Southeast Asia that lack stock status information. Thus, the objective of this study was to determine the stock status of this datadeficient shark species using YPR and SPR analyses.

Materials and Methods

Length-weight and length-frequency data (LFD) were collected from August 2015 to July 2016 in Southeast Asian countries by the SEAFDEC sharks, rays and skates data collection project, in cooperation with the Convention of International Trade in Endangered Species of Wild Fauna and Flora, and the Japanese Trust Fund. For whitespotted bambooshark, the catch data were derived from the landing site in Kota Kinabalu, Sabah (Fig. 1).



Fig. 1. Map of Southeast Asia, with Malaysia in blue. The Kota Kinabalu landing site where the data of whitespotted bambooshark *Chiloscyllium plagiosum* is shown in a white circle.

Data on whitespotted bambooshark fishing grounds were collected from Malaysian fisheries management zones B, C, C2, and C3 (Fig. 2), but 50 % of data were from zone C and 40 % from C2. A total of 1,017 kg of this species was landed during the survey period (Wanchana et al., 2020).

Zone A	Zone B	Zone C	Zone C2	Zone C3
<40 GRT	<40 GRT	40 - <70 GRT	≥70 GRT	≥70 GRT
0-5 nm Traditional fisherman and traditional anchovy purse seine	5-12 nm Owner operated trawlers and purse seiner	12-30 nm Owner and non-owner operated Trawlers and purse seiner	30 nm to EEZ Trawlers and purse seiner	High sea Tuna longliner and tuna purse seiner

Fig. 2. Malaysian fisheries management zonation scheme (Ramli, 2015). The fishing ground is divided into five zones based on the distance from the shoreline and gross tonnage of the vessel. The vessel from the inner zone can operate in the outer zone, but the vessel from the outer zone cannot operate in the inner zone.

Two to four trawl vessels ported at the Sabah landing site were randomly selected every 12 days.month⁻¹ to collect the data. Thus, there were 24 to 48 trawl vessels selected randomly every month. The species composition of elasmobranch, and the related catch statistics were collected simultaneously (Wanchana et al., 2020).

Definitions for parameters used in this study are provided in Table 1.

Length-weight relationship

The length-weight relationship provides information about a species' biological growth pattern. Parameters in equation (1) (Ricker, 1975) are estimated by linear regression after logarithmic conversion, following:

$$W = \alpha T L^{\beta} \tag{1}$$

Growth parameter estimation

The von Bertalanffy's growth curve is expressed as:

$$L_t = L_{\infty} \left(1 - e^{-k(t-t_0)} \right)$$
 (2)

Parameters L_{∞} , k, and t_0 are estimated by electronic length-frequency analysis, ELEFAN, provided in the package TropFishR (Taylor and Mildenberger, 2017). In this package, there are four ELEFAN functions: k-Scan, response surface analysis (RSA), ELEFAN combined with simulated annealing (ELEFAN_SA), and ELEFAN combined with genetic algorithm (ELEFAN_GA). For ELEFAN_SA, a run time was set at 5 min. For ELEFAN_GA, the calculation times of this function were set at 1000 times. The initial value for L_{∞} was set based on Powell and Wetherall's method (Powell, 1979; Wetherall, 1986).

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Symbol	Definition
Φ'	Growth performance index
α	Condition factor for length-weight relationship
a	The intercept of the linear regression for the observed probability of capture
a'	The intercept of the linear regression for the estimated probability of capture
β	Regression factor for length-weight relationship
b'	Regression factor for the estimated probability of capture
С	The intercept of the linear regression for total mortality estimation
C _{L1, L2}	Number of fish caught at length interval between L_1 and L_2
E	Exploitation ratio
Fcurr	Fishing mortality of the current situation (year-1)
F _{0.1}	Fishing mortality produced from the 10 % of the tangent of the YPR curve (year ⁻¹)
F _{max}	Fishing mortality produced from the peak of the YPR curve (year-1)
$F_{30\%}$ and $F_{20\%}$	Fishing mortality that spares 30 % and 20% of spawning stock (year-1)
k	growth coefficient of von Bertalanffy's growth function (vBGF)(year-1)
М	Natural mortality (year ⁻¹)
mL	Mid-length between length interval (cm)
L_1 and L_2	Lower and upper length interval of the length class (cm), respectively
L25, L50, and L50	The length at 25 %, 50 %, and 75 % of size selectivity (cm), respectively
$L_{\rm m}$, and $t_{\rm m}$	Length at first maturity (cm) and age at first maturity (year), respectively
L _r , and t _r	Length at recruitment (cm) and age at recruitment (year), respectively
L_t , and t_{\perp}	Length (cm) at age t (year) and age at length L (year), respectively
L∞	vBGF parameter (asymptotic length)(cm)
St, and S '	Observed and estimated size selectivity, respectively
TL	Total length (cm)
$\Delta t_{L1,L2}$	The difference in age between lengths L_1 and L_2 (years)
t_{λ}	Age endpoint (years)
t _{max}	Maximum age (years)
t _{mL}	Age at mid-length from length interval (years)
to	vBGF parameter (theoretical age at length 0)(years)
tc	Age at first capture (years)
W	Individual weight (kg)
W∞	Average maximum weight (kg)
Ζ	Total mortality (year-1)

The inverse von Bertalanffy's growth function (Mackay and Moreau, 1990) was used for age estimation as follows:

$$t = t_0 - \left(\frac{1}{k}\right) \ln\left(1 - \frac{L_t}{L_\infty}\right) \tag{3}$$

Using growth parameters from von Bertalanffy's growth equation, the growth performance index, Φ' , was calculated (Pauly and Munro, 1984) to compare growth curves between the same species or species with similar shapes using the following equation:

$$\Phi' = \log k + 2 \log L_{\infty} \tag{4}$$

Results from each function were scored by the

goodness of fit (R_n) based on Gayanilo et al. (2005) and Taylor and Mildenberger (2017), as follows:

$$R_n = \frac{10^{\text{ESP/ASP}}}{10} \tag{5}$$

This equation compares the number of peaks that pass by the growth curve in length-frequency data. Each peak in LFD is assumed to correspond to a different age group; the total number of peaks with the potential to be passed by the growth curve is denoted by the ASP (available sum of the peak). The number of peaks actually 'passed' by the growth curve denotes the ESP (explained sum of peaks). The result indicates the quality of the growth parameter estimation (Brey and Pauly, 1986).

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Estimation of mortality, gear selectivity, and maturation size by age

The length-converted catch curve, LCCV (Pauly, 1983, 1984), was applied to estimate mortality and gear selectivity. Total mortality (Z) was estimated from a linear regression between catch for each age class and the estimated age from mid-length of each size class using the following equation:

$$\ln \frac{c_{L1,L2}}{\Delta t_{L1,L2}} = c - Z * t_{mL}$$
(6)

where t_{mL} is estimated from the length between lengths L_1 and L_2 using equation (3).

The duration of age between the lower and upper limits of the length interval $L_1, L_2, \Delta t_{L_1,L_2}$, was calculated using equation (7):

$$\Delta t_{L_1,L_2} = \frac{1}{k} \ln \left(\frac{L_{\infty} - L_1}{L_{\infty} - L_2} \right)$$
(7)

Natural mortality is estimated using Tanaka's equation (Tanaka, 1960),

$$M = \frac{2.5}{t_{\rm max}} \tag{8}$$

We used the median value of four results when their values were ranked from highest to lowest from the following four methods to calculate t_{max} .

1) L_{max} was estimated from a parameter of von Bertalanffy's growth function (vBGF), L_{∞} . t_{max} was estimated using equation (3) and estimated L_{max} (Froese and Binohlan, 2000)

$$L_{\max} = \exp\left(\frac{\log L_{\infty} - 0.044}{0.9841}\right) \tag{9}$$

2) Taylor's method (Taylor, 1958)

$$t_{\max} = t_0 + \frac{2.996}{k} \tag{10}$$

3) Pauly's method (Pauly, 1983)

$$t_{\max} = \frac{3}{k} \tag{11}$$

4) t_{max} was estimated from equation (3) with the observed maximum body length.

Current fishing mortality F_{curr} was estimated as $F_{curr} = Z - M$. The exploitation ratio E was estimated from the ratio of F_{curr}/Z . The observed selection curve (known as selection ogive), S_{tr} , was estimated as follows:

$$S_t = \frac{C_{L_{1,L_2}}}{\Delta t_{L_{1,L_2}} e^{a - Z t_{mL}}}$$
(12)

and the estimated selection ogive S'_t was calculated. The regression parameter a' and b' were estimated from the regression between t_{mL} and $\ln\left(\frac{1}{s_t}-1\right)$ as follows:

$$S'_{t} = \frac{1}{1 + e^{a' + b'}}$$
(13)

Size selectivity for YPR and SPR analyses was assumed to be knife-edged at L_{50} and was converted to t_c using equation (3).

Age at first maturity (L_m) was assumed to be 4.5 years for both male and female bambooshark following Chen et al. (2007).

Per-recruit analysis

YPR was calculated as follows:

$$\frac{Y}{R} = FW_{\infty}e^{-M(t_{c}-t_{r})} \times \sum_{n=0}^{3} \frac{A_{n}e^{-nk(t_{c}-t_{0})}}{F+M+nk} \left\{ 1 - e^{-(F+M+nk)(t_{\lambda}-t_{c})} \right\}$$
(14)
$$\begin{cases} n = 0, 1, 2, 3\\ A_{n} = 1, -3, 3, -1 \end{cases}$$

The t_{λ} for YPR and SPR was assumed to be 20 years to include the possible range of the maximum age of the species. W_{∞} was calculated using L_{∞} from equation (1).

SPR analysis was conducted using the following equations:

For $t_c \leq t_m$,

$$\begin{split} & \text{SPR} = \\ & W_{\text{co}} e^{-M(t_{\text{c}} - t_{\text{r}}) - (F + M)(t_{\text{m}} - t_{\text{c}})} \sum_{n=0}^{3} A_{n} e^{-nk(t_{\text{m}} - t_{0})} \left\{ \frac{1 - e^{-(F + M + nk)((t_{\lambda} - t_{\text{m}})}}{F + M + nk} \right\}, \end{split}$$

For $t_c > t_m$,

$$SPR = W_{\infty}e^{-M(t_m-t_r)}\sum_{n=0}^{3}A_ne^{-nk(t_m-t_0)}\left\{\frac{1-e^{-(M+nk)(t_c-t_m)}}{M+nk}\right\} + W_{\infty}e^{-M(t_c-t_r)}\sum_{n=0}^{3}A_ne^{-nk(t_c-t_0)}\left\{\frac{1-e^{-(F+M+nk)(t_\lambda-t_m)}}{F+M+nk}\right\}$$
(15)

$$\begin{cases} n &= 0, 1, 2, 3 \\ A_n &= 1, -3, 3, -1 \end{cases}$$

The % SPR was estimated as follows:

% SPR = 100 %
$$\times \frac{SPR}{SPR_{F=0}}$$
 (16)

Biological reference points (BRPs)

For fishery management, two BRPs have been proposed: the limit reference point, which usually refers to the biological limit of fishing mortality; and the target reference point, which is set as the precautionary point of the limits (Caddy and McGarvey, 1996; Prager et al., 2003). For YPR, values for $F_{0.1}$, the fishing mortality with a 10 % tangent of the YPR curve from the origin, is used as a target BRP, and F_{max} , the fishing mortality that maximises the YPR at a given t_c , as a limit BRP (Beverton and Holt, 1957;

Goodyear, 1993; Grabowski and Chen, 2004; Zhou et al., 2020).

For SPR, it is the spawning unit available for each recruitment which the BRPs were set as $F_{X \ \% SPR}$, the fishing mortality produces X % of the expected spawning-stock biomass per recruit in the absence of fishing (Goodyear, 1993; Mace and Sissenwine, 1993; Katsukawa, 2005). The critical level is usually set between 20 % and 30 % because Zhou et al. (2020) noted that the $F_{\% \ SPR}$ for elasmobranchs should be higher than that for teleosts. Values for $F_{30 \ \%}$ and $F_{20 \ \%}$ were used as a target and limit BRPs, respectively (Zhou et al., 2020).

Results

A total of 356 male and 366 female whitespotted bamboosharks were caught by trawlers operated from fishing zone B to zone C2 and measured. Average \pm standard deviation, maximum, and minimum lengths were 69.61 \pm 7.09 cm, 87 cm, and 25 cm TL for males, and 67.33 \pm 9.02 cm, 96 cm, and 42 cm TL for females, respectively. Cumulative length-frequency data are shown in Figure 3.



Fig. 3. Length-frequency data for male and female whitespotted bamboosharks *Chiloscyllium plagiosum* in Sabah, Malaysia.

The length-weight relationship using equation (1) for males $W = 1.82 \times 10^{-6}L^{3.11}$, $R^2 = 0.82$, and females was $W = 2.97 \times 10^{-7}L^{3.55}$, $R^2 = 0.89$. Growth parameter estimation results and the R_n score is presented in Table 2.

ELEFAN_SA provided the maximum R_n and was selected as the best fitting curve growth parameter. The selected growth curve equation using equation (2) was $L_t = 81.13(1 - e^{-0.21(t-(-0.63))})$ for males, and $L_t = 84.30(1 - e^{-0.18(t-(-0.70))})$ for females. The fitting score is based on the ratio between the total available peak of the curve and the total peaks passed by the growth curve. The fitting of the growth curve to length-frequency data for male and female bamboosharks is shown in Figure 4.

Total mortality is estimated from the negative slope

Table 2. Growth parameter estimates for male and female whitespotted bamboosharks, *Chiloscyllium plagiosum*, caught in Sabah, Malaysia.

	k-Scan	RSA	ELEFAN Sa	_ ELEFAN_ GA
Male				
L_{∞} (cm TL)	77.68	77.90	81.13	77.82
k(year-1)	1.12	1.11	0.21	0.29
to (year)	-0.12	-0.12	-0.63	-0.47
Φ'	3.83	3.83	3.15	3.24
R _n	0.28	0.28	0.36*	0.33
Female				
L_{∞} (cm TL)	80.25	81.60	84.30	80.46
k(year-1-)	0.40	0.51	0.18	0.22
to(year)	-0.33	-0.26	-0.70	-0.60
Φ'	3.41	3.53	3.11	3.16
R _n	0.27	0.31	0.37*	0.35

*maximum R_n

**ELEFAN: electronic length-frequency analysis, GA: genetic algorithm, RSA: response surface analysis, SA: simulated annealing.

Fig. 4. Length-frequency data fitted with the selected growth curve of male and female whitespotted bambooshark, *Chiloscyllium plagiosum*, from electronic length-frequency analysis (ELEFAN_SA) using package TropFishR provided in R program.

of the catch (Fig. 5). The X-axis is the estimated age at mid-length, and Y-axis is the natural logarithm scale of cumulative catch at each length class.

From Figure 5, the catch curve of males and females provides different ages corresponding to the fully captured by fishing gear. The female bambooshark was entering fully captured at a younger age compared to the male bambooshark.

Maximum ages (t_{max}) for males and females estimated from four methods and summarised using the median of t_{max} from each model, and natural mortality based on the finalised t_{max} calculated using equation (8), are

Fig. 5. Length-converted catch curve for male and female whitespotted bambooshark, *Chiloscyllium plagiosum*, from Sabah, Malaysia.

presented in Table 3.

Table 3. Summary of maximum age (t_{max}) and natural mortality estimation of male and female whitespotted bambooshark, *Chiloscyllium plagiosum*.

	t _{max} (yea	_				
	VBGF	Taylor (1958)	Pauly (1983)	LCCV	Median	M (year-1)
Male	15.85	13.64	14.27	30.02	15.07	0.17
Female	18.63	15.94	16.67	22.48	17.65	0.14

*VBGF: von Bertalanffy, LCCV: length-converted catch curve.

Exploitation ratios (*E*), the ratio between current fishing mortality, F_{curr} , and total mortality, *Z*, for male and female bamboosharks, were 0.59 and 0.41, respectively (Table 4).

Table 4. Summary of total, natural, and current fishing mortality estimation, respectively, and exploitation ratios (*E*) of male and female whitespotted bambooshark, *Chiloscyllium plagiosum*.

	Z(year-1)	M(year ⁻¹)	F _{curr} (year ⁻¹)	E
Male	0.41	0.17	0.24	0.59
Female	0.24	0.14	0.10	0.41

Gear selectivity from age at first capture, L_c , age at 25 % captured, L_{25} , and age at 75 % captured, L_{75} , for trawlers using a length-converted catch curve are presented in Table 5. Regarding the model, the age at

Table 5. Gear selectivity for whitespotted bambooshark with the size at 25 %, 50 % (size at first capture), and 75 %, Chiloscyllium plagiosum, in Sabah, Malaysia.

	L ₅₀ (cm)	L ₂₅ (cm)	L ₇₅ (cm)
Male	68.20	65.07	70.72
Female	47.17	42.92	50.98

first capture refers to the age at which the observed fishing gear can catch 50 % of the population. The probability of capture is shown in Figure 6. The $t_{\rm c}$ for males and females was estimated to be 8.12 and 3.15 years, respectively.

For YPR, the analyses provide the contour line plots at various F and t_c values, which, for YPR, are shown in Figure 7. The results indicate that both male and female sharks have not reached maximum YPR yet. Target and limit reference points are estimated from the YPR and SPR for the current t_c , indicating that the current F was not reached for both target and limit reference points (Table 6).

At current t_c , the F_{curr} are smaller than $F_{0.1}$ for 60 % of male and 54 % of female sharks. For F_{max} , the F_{curr} is 66 % smaller for female sharks and <12 % for male sharks because the peak of the YPR curve for males is >2.0. The YPR curve for males and females is shown in Figure 8. The figure shows no peak found for males as the YPR seems to get higher at this t_c . For females, the peak corresponds to a smaller t_c than for males. However, the current *F* still be in the acceptable range as lower than BRPs.

For SPR, results focus only on the female stock capable of producing offspring. The SPR contour line of t_c against F is shown in Figure 9, and the contour line for % SPR at constant t_c is presented in Figure 10. The smaller current F than those limit and target BRPs of YPR and SPR indicate that the whitespotted bambooshark stock is healthy in growth and recruitment overfishing.

Figure 10 shows that the fishing ground's current spawning biomass was approximately 50 % during the study period. This result indicates that the stock of whitespotted bambooshark in Sabah water is still in abundance compared to the target reference point.

Discussion

The information on the population structure of the whitespotted bambooshark is still now limited. However, the study of the related species, such as

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Fig. 6. Probability of capture with the size at 25 %, 50 % (size at first capture), and 75 % of whitespotted bambooshark, *Chiloscyllium plagiosum*, in Sabah, Malaysia.

Fig. 7. Yield-per-recruit contour lines for male and female whitespotted bamboosharks, *Chiloscyllium plagiosum*, in Sabah, Malaysia. The oval represents the situation at current t_c and F_{curr} .

Fig. 8. Yield-per-recruit curve at current age at first capture (t_c) the black dot is the SPR at current fishing mortality (F_{curr}) for male and female whitespotted bambooshark, *Chiloscyllium plagiosum*, in Sabah, Malaysia.

Table 6. Age at first maturity, age at first capture, current fishing mortality, target, and limit reference points for whitespotted bambooshark, *Chiloscyllium plagiosum*, in Sabah, Malaysia.

t _m (years)	tm	t _m t (users)	Fcurr	YPR	YPR		SPR	
	tc(years)	(year ⁻¹)	Target	Limit	Target	Limit		
Male	4.5	8.1	0.24	0.40	>2.0	-	-	
Female	4.5	3.8	0.10	0.21	0.34	0.21	0.31	

YPR: yield-per-recruit, SPR: spawning-per-recruit.

Fig. 9. Contour plot of per cent spawning-per-recruit for whitespotted bambooshark *Chiloscyllium plagiosum* in Sabah, Malaysia.

While the migratory pattern of demersal elasmobranchs remains unclear, only larger individuals migrate short distances from the shoreline to forage (Speed et al., 2016). As reported in the Taiwanese waters, small whitespotted bambooshark prefers shallower water (Chen et al., 2007). Thus, the fisheries data collected in this study covered all possible ranges of adult sharks. The length composition of this shark in this study is deemed to represent the adult population occurring in coastal waters and recruited into the fishing ground from within 30 nm to the high sea according to fishing zone C.

The LFD of a sample reflects growth. In this study, various models provided in the R-package have been selected by R_n score. The score in equation (5) is based on the number of monthly peaks in the LFD to peaks crossed by the growth curve. Growth parameters are more reliable if the score is higher (Gayanilo et al., 2005; Taylor and Mildenberger, 2017). Because the highest ELEFAN_SA male and female scores were 0.36 and 0.37, these two parameters were set as the highest R_n scores.

ELEFAN_SA uses a simulated annealing optimisation algorithm. It examines the range of growth parameters and finds the most reliable results in a shorter simulation time, even if the function is not linear or smooth (Xiang et al., 2013; Taylor and Mildenberger, 2017). Taylor and Mildenberger (2017) also suggest that an advantage of using ELEFAN_SA is its ability to find the best set of L_{∞} and k.

The previous study about the growth of whitespotted

Fig. 10. Line plot of per cent spawning-per-recruit (SPR) at current age at first capture (t_c) the black dot is the SPR at current fishing mortality (F_{curr}) for whitespotted bambooshark, *Chiloscyllium plagiosum*, in waters off Sabah, Malaysia.

bambooshark was provided by Chen et al. (2007). Their study was conducted in Taiwanese waters, where all of the sharks were caught by longline and lobster trap fisheries. The growth parameter determination showed that L_{∞} and k of Taiwanese male and female sharks were 98.5 cm and 0.212 year⁻¹ for males and 93.2 cm and 0.224 year⁻¹ for females, respectively, using age determination method from vertebrae. The larger L_{∞} and k compared to the present study can be influenced by the difference in geographic distribution (Yamaguchi et al., 1998) and the size composition of the catch, which can be affected by the size distribution of the species in the natural habitat. The maximum size can be roughly observed from the fit plot of the growth curve (Fig. 4) as well. As the fish grow older, the growth rate will become slower, and the growth curves become closer around the large individual (Campana et al., 2002), which, in the present study, was the size larger than 70 cm.

Moreover, the age determination in the elasmobranch can be difficult, especially for those species without a dorsal spine, since the growth band from the vertebrae can be hard to find the true centric area (Goldman, 2005). Thus, in the tropical region where age determination is difficult to be determined, the length-based growth parameter determination can be an appropriate alternative method (Sparre and Venema, 1998; Zischke and Griffiths, 2015).

Length-converted catch curves have been widely used in various regions because models can estimate mortality and gear selectivity based on LFD, including elasmobranchs in the tropical region (Pauly, 1983, 1984; Cortés and Parsons, 1996; Özbilgin et al., 2004; Chang and Liu, 2009; Windsland, 2014). For gear selectivity, the L_c can be affected by sex dimorphism between male and female size and the differences in habitat usage, as reported for leopard shark, *Triakis semifasciata* Girard, 1855 (Carlisle and Starr, 2009) sicklefin lemon shark, *Negaprion acutidens* (Rüppell, 1837) (Pillans et al., 2021) and Haller's round stingray, *Urobatis halleri* (Cooper, 1863)(Mull et al., 2010). The fitting of female selectivity in Figure 6 resulted from the number of sharks in each length class where the smallest length class was far from the next larger length class without any sample shown in between. The length-converted catch curve was used to reconstruct the catch's size composition by pooling the number of each length class from each observed month (Zischke and Griffiths, 2015). This was done to enable the model to estimate the selectivity based on the major pooled size classes available.

The natural mortality was estimated from maximum age (t_{max}), although information on t_{max} values for Hemiscyllid elasmobranchs is limited. In the results, LCCV provided the highest t_{max} for both sexes compared to the other models. This is because LCCV estimates the age based on the length of the individual using equation (3) which the estimated age can be increased as long as the input length does not exceed the L_{∞} , thus, the value can be increased depending on the increasing length and lead to overestimation. Therefore, the results from other models were essential to compare the results together.

Chen et al. (2007) suggest that the longevity of whitespotted bambooshark using the traditional von Bertalanffy growth function is 13.7 years for males and 14.2 years for females. Krajangdara (2017) indicates this species lives for 15 to 22 years, with a maximum reported age of 25 years in captivity (Chen et al., 2007). A median t_{max} was used of 15.07 years for males and 17.65 years for females. These values were slightly greater than Chen et al. (2007) reported but within the range of those reported by Krajangdara (2017). This age range was similar to that of the relative species occurring in the same area, *C. punctatum*, in which the t_{max} was up to 14 years (Fahmi et al., 2021b).

YPR indicates that the stock status of whitespotted bambooshark is healthy in terms of growth overfishing. Exploitation obtains a high yield of males, and higher fishing pressure with lower t_c is acceptable (Fig. 6). The YPR curve at the current t_c (Fig. 7) has no peak within F < 2.0 at this selectivity. Age at first capture, t_c , is a controllable parameter in YPR and SPR. For a healthy stock, a reduction in tc will not negatively affect YPR and SPR because recruitment compensates for a catch from fishing. According to Figure 6, the whitespotted bambooshark stock off Sabah can handle higher F with a lower t_c to reach maximum YPR. YPR and SPR suggest the stock is also healthy for female stock SPR, but with less room to increase F_{curr} at the current t_c .

Despite the useful amount of data input into the model, the per recruit method still has the disadvantage on the equilibrium fishery condition, which assumes that the F_{curr} will be constant throughout the stock. However, the compensation between natural and fishing mortality is also involved

in the realistic condition model (Sparre and Venema, 1998; Chang and Liu, 2009). For the large size with low fecundity, such as the thresher shark (Alopias spp.) or other large-pelagic shark species, conservative BRPs for per recruit model such as $F_{50\%}$ and $F_{60\%}$ were suggested. However, it is known that the smallbenthic or coastal shark species, such as the family Hemiscyllium have more resilience toward fishing pressure regarding the higher fecundity. Thus, the per recruit model can be applied for these species with conservative BRPs than the less usually recommended level, which is used for 30-40 % or more of BRPs for elasmobranch species (Tsai et al., 2011; Liu et al., 2015).

Most YPR and SPR, and other related models such as length-based spawning potential ratio, are applied to teleost species (Griffiths, 1997; Peixer et al., 2007; Zischke and Griffiths, 2015; Charernnate et al., 2021) or invertebrate, such as freshwater shrimp, and sea scallop (Etim and Sankare, 1998; Hart, 2003), proves that the model is flexible and can be applied to a wide range of species and at various stages of the life cycle. The per recruit model has also been suggested for elasmobranchs as well with some modifications of the reference points (Zhou et al., 2020). For example, the stock assessment of shortfin mako, Isurus oxyrinchus Rafinesque, 1810, uses a combination of YPR and virtual population analysis (Chang and Liu, 2009), YPR for grey sharpnose shark, Rhizoprionodon oligolinx Springer, 1964 (Purushottama et al., 2017), and the YPR for Halmahera epaulette shark Hemiscyllium halmahera Allen & Erdmann, 2013, in Indonesia (Jutan et al., 2018). Therefore, YPR and SPR for elasmobranch are applicable under some assumptions (Sparre and Venema, 1998).

For the fishery management measures in the area, catch quota system, and coastal states with jurisdiction over waters have recently implemented fisheries zonation, and fisheries data are now continuously collected for particular taxa (Department of Fisheries Malaysia, 2014; Abd Haris Hilmi et al., 2020). Monitoring and surveillance of these activities could assist with the maintenance of healthy regional elasmobranch stocks. However, should the stock decline, control overfishing effort, measured using F, could be implemented by establishing marine protected areas (MPAs) (MacKeracher et al., 2019; Dwyer et al., 2020).

Conclusion

The length-based growth parameter estimation is one of the important alternatives for fish stock assessment in Southeast Asia, as the age data for fish is limited and difficult to achieve. Results of stock assessment using yield-per-recruit (YPR) and spawning-per-recruit (SPR) suggest that stocks of whitespotted bambooshark, *Chiloscyllium plagiosum*, remain in good condition with F_{curr} lower than any reference points ($F_{0.1}$ and F_{max} for YPR and F_{30} % and

 $F_{20\%}$ for SPR). This also suggests that the management of this species in the study area could continue at current levels of fishing pressure. Moreover, this approach can work together with the other approaches as the monitoring model, for example, the amount of spawning stock of a particular species that remained in the area or the current level of fishing pressure. However, the stock status of this shark species can vary by area based on the natural habitat, local fishing pressure, and local management measure. Thus, the stock status determination of whitespotted bambooshark and other elasmobranch species should be expanded into other parts of the region.

Acknowledgements

We thank Steve O'Shea, PhD, from Edanz (https://jp .edanz.com/ac) for editing a draft of this manuscript.

Conflict of interest: The authors declare that they have no conflict of interest.

Author contributions: Supapong Pattarapongpan: Data validation and analysis and writing the manuscript. Sukchai Arnupapboon: Supervision and authorisation on the data usage and data validation. Abdul Haris Hilmi bin Ahmad Arshad: Local enumerator collaboration, data validation, and data authorisation. Takashi Fritz Matsuishi: Supervision on data validation and analysis and manuscript revision.

References

- Abd Haris Hilmi, A.A., Hamizahm N.A., Ahmad, A., Kissol, L., Rosdi, M.N., Sukri, M. 2020. Terminal report data collection on sharks and rays by species in Tawau, Sabah (Phase I) October 2018-September 2019. SEAFDEC/MFRDMD, Kuala Terengganu, Malaysia. 34 pp.
- Arai, T., Azri, A. 2019. Diversity, occurrence and conservation of sharks in the southern South China Sea. PLoS ONE 14:e0213864. https://doi.org/10.1371/journal.pone.0213864
- Beverton, R.J.H., Holt, S.J. 1957. On the dynamics of exploited fish populations. Ministry of Agriculture and Food, London. 538 pp.
- Brey, T., Pauly, D. 1986. Electronic length frequency analysis: a revised and expanded user's guide to ELEFAN 0, 1 and 2. Berichte aus dem Institut für Meereskunde an der Christian-Albrechts-Universität Kiel, Kiel. 76 pp. https://doi.org/10.3289/IFM_BER_149
- Caddy, J.F., McGarvey, R. 1996. Targets or limits for management of fisheries? North American Journal of Fisheries Management 16:479–487. https://doi.org/10.1577/1548-8675(1996)016<0479:TOLFM0>2.3.C0;2
- Campana, S.E., Natanson, L.J., Myklevoll, S. 2002. Bomb dating and age determination of large pelagic sharks. Canadian Journal of Fishery and Aquatic Sciences 59:450-455.
- Carlisle, A.B., Starr, R.M. 2009. Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. Marine Ecology Progress Series 380:213–228. https://doi.org/10.3354/meps07907
- Chang, J.H., Liu, K.M. 2009. Stock assessment of the shortfin mako shark (*Isurus oxyrinchus*) in the Northwest Pacific Ocean using per recruit and virtual population analyses. Fisheries Research 98:92– 101. https://doi.org/10.1016/j.fishres.2009.04.005

- Charernnate, K., Noranarttragoon, P., Jutagate, T. 2021. Length-based stock assessment of Smith's barb, Puntioplites proctozytron (Bleeker, 1865) (Cyprinidae) and Asian redtail catfish, Hemibagrus nemurus, (Valenciennes, 1840), (Bagridae) in multipurpose reservoir in Thailand. Asian Fisheries Science 34:159-167 https://doi.org /10.33997/j.afs.2021.34.2.005
- Chen, W.K., Chen, P.C., Liu, K.M., Wang, S. Bin 2007. Age and growth estimates of the whitespotted bamboo shark, *Chiloscyllium plagiosum*, in the northern waters of Taiwan. Zoological Studies 46:92–102.
- Cortés, E., Parsons, G.R. 1996. Comparative demography of two populations of the bonnethead shark (*Sphyrna tiburo*). Canadian Journal of Fisheries Aquatic Sciences 53:709–718. https://doi.org /10.1139/f95-240
- Davidson, L.N.K., Krawchuk, M.A., Dulvy, N.K. 2015. Why have global shark and ray landings declined: Improved management or overfishing? Fish and Fisheries 17:438–458. https://doi.org /10.1111/faf.12119
- Department of Fisheries Malaysia 2014. National plan of action for the conservation and management of shark (Plan 2), Ministry of Fisheries and Agriculture. Ministry of Agriculture and Agro-based Industry Malaysia, Putrajaya, Malaysia. 49 pp.
- Dwyer, R.G., Krueck, N.C., Udyawer, V., Heupel, M.R., Chapman, D., Pratt, H.L., Garla, R., Simpfendorfer, C.A. 2020. Individual and population benefits of marine reserves for reef sharks. Current Biology 30:480-489.e5. https://doi.org/10.1016/j.cub.2019.12.005
- Ebert, D.A., Dando, M., Fowler, S. 2021. Sharks of the World: A complete guide. Princeton University Press, New Jersey. 608 pp. https://doi.org/doi:10.1515/9780691210872
- Etim, L., Sankare, Y. 1998. Growth and mortality, recruitment and yield of freshwater shrimp, *Macrobranchium völlenhovenii*, Herklots 1851 (Crustacea, Palaemonidae) in the Fahe reservoir, Côte d'Ivoire, West Africa. Fisheries Research 38:211–223. https://doi.org/10.1016 /S0165-7836(98)00161-1
- Fahmi, Kurniawan, W., Tibbetts, I.R., Oktaviyani, S., Dudgeon, C.L., Bennett, M.B. 2021b. Age and growth of the tropical oviparous shark, *Chiloscyllium punctatum* in Indonesian waters. Journal of Fish Biology 99:921–930. https://doi.org/10.1111/jfb.14778
- Fahmi, Tibbetts, I.R., Bennett, M.B., Ali, A., Krajangdara, T., Dudgeon, C.L. 2021a. Population structure of the brown-banded bamboo shark, *Chiloscyllium punctatum* and its relation to fisheries management in the Indo-Malay region. Fisheries Research 240:105972. https://doi.org/10.1016/j.fishres.2021.105972
- Froese, R., Binohlan, C. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. Journal of Fish Biology 56:758-773. https://doi.org/10.1111/j.1095-8649.2000.tb00870.x
- Gayanilo Jr., F.C., Sparre, P., Pauly, D. 2005. FAO-ICLARM Stock Assessment Tools II (FiSAT II). Revised version. Users guide. FAO Computerized Information Series (Fisheries). FAO, Rome. 168 pp.
- Goldman, K.J. 2005. Age and growth of elasmobranch fishes. In: Management techniques for elasmobranch fisheries. FAO, Rome, pp. 97-132.
- Goodyear, C.P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. In: Risk evaluation and biological reference points for fisheries management, Smith, S.J., Hunt, J.J., Rivard, D. (Eds.), Canadian Special Publication of Fisheries and Aquatic Sciences, Ottawa, pp. 67–81.
- Grabowski, R., Chen, Y. 2004. Incorporating uncertainty into the estimation of the biological reference points $F_{0.1}$ and F_{max} for the Maine green sea urchin (*Strongylocentrotus droebachiensis*) fishery.

Fisheries Research 68:367-371. https://doi.org/10.1016 /j.fishres.2003.12.005

- Griffiths, M.H. 1997. The application of per-recruit models to Argyrosomus inodorus, an important South African sciaenid fish. Fisheries Research 30:103-115. https://doi.org/10.1016/S0165-7836(96)00552-8
- Hart, D.R. 2003. Yield- and biomass-per-recruit analysis for rotational fisheries, with an application to the Atlantic sea scallop (*Placopecten magellanicus*). Fishery Bulletin 101:44–57.
- Jutan, Y., Restraubun, A., Khouw, A., Nikijuluw, V., Pattikawa, J. 2018. Study on the population of Halmahera walking shark (*Hemiscyllium halmahera*) in Kao Bay, north Maluku, Indonesia. International Journal of Fisheries and Aquatic Studies 6:36–41.
- Katsukawa, T. 2005. Evaluation of current and alternative fisheries management scenarios based on spawning-per-recruit (SPR) and revenue-per-recruit (RPR), and yield-per-recruit (YPR) diagrams. ICES Journal of Marine Science 62:841-846.
- Krajangdara, T. 2017. The cartilaginous fishes (sharks, rays and chimeras) found in Thai waters and the adjacent areas. Marine Fisheries Research and Development Division, Department of Fisheries, Bangkok, Thailand. 331 pp.
- Kyne, P.M., bin Ali, A., Fahmi, Finucci, B., Herman, K., Manjaji Matsumoto, B.M., VanderWright, W.J. 2021. *Chiloscyllium plagiosum*, [WWW Document]. IUCN Red List Threat. Species 2021 e.T124554059A124453319. https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T124554059A124453319.en (Accessed 06 October 2021).
- Lam, V.Y.Y., Sadovy De Mitcheson, Y. 2011. The sharks of South East Asia - unknown, unmonitored and unmanaged. Fish and Fisheries 12:51-74. https://doi.org/10.1111/j.1467-2979.2010.00383.x
- Liu, K.M., Chin, C.P., Chen, C.H., Chang, J.H. 2015. Estimating finite rate of population increase for sharks based on vital parameters. PLoS ONE 10:e0143008. https://doi.org/10.1371/journal.pone.0143008
- Mace, P.M., Sissenwine, M.P. 1993. How much spawning per recruit is enough? Canadian Special Publication of Fisheries and Aquatic Sciences, Ottawa, pp. 101–118.
- Mackay, D., Moreau, J. 1990. A note in the inverse function of the von Bertalanffy growth function. Fishbyte 8(1):28-31.
- MacKeracher, T., Diedrich, A., Simpfendorfer, C.A. 2019. Sharks, rays and marine protected areas: A critical evaluation of current perspectives. Fish and Fisheries 20:255-267. https://doi.org /10.1111/faf.12337
- Mull, C.G., Lowe, C.G., Young, K.A. 2010. Seasonal reproduction of female round stingrays (*Urobatis halleri*): Steroid hormone profiles and assessing reproductive state. General and Comparative Endocrinology 166:379–387. https://doi.org/10.1016/J.YGCEN.2009 .12.009
- Özbilgin, H., Tosunoglu, Z., Bilecenoglu, M., Tokaç, A. 2004. Population parameters of *Mullus barbatus* in Izmir Bay (Aegean Sea), using length frequency analysis. Journal of Applied Ichthyology 20:231– 233. https://doi.org/10.1111/j.1439-0426.2004.00555.x
- Pauly, D. 1983. Length-converted catch curves: a powerful tool for fisheries research in the tropics (Part 1). Fishbyte 1:9–13.
- Pauly, D. 1984. Length-converted catch curves: A powerful tool for fisheries research in the tropics (Part 2). Fishbyte 2:17-19.
- Pauly, D., Munro, J.L. 1984. Once more on the computation of growth in fish and invertebrates. Fishbyte 2(1):1-21.
- Peixer, J., Catella, A., Petrere Jr, M. 2007. Yield per recruit of the pacu *Piaractus mesopotamicus* (Holmberg, 1887) in the pantanal of Mato Grosso do Sul, Brazil. Brazilian Journal of Biology 67:561–567.
- Pillans, R., Rochester, W., Babcock, R.B., Thomson, D.P., Haywood, M.D.E., Vanderklift, M.A. 2021. Long-term acoustic monitoring reveals site fidelity, reproductive migrations, and sex specific

differences in habitat use and migratory timing in a large coastal shark (*Negaprion acutidens*). Frontiers in Marine Science 8:616633. https://doi.org/10.3389/fmars.2021.616633

- Powell, D.G. 1979. Estimation of mortality and growth parameters from the length frequency of catch. Rapports et Proces-verbaux des Reunions. Conseil International pour L'Exploration de la Mer 175:167-169.
- Prager, M.H., O'Brien, J.F., Saila, S.B. 1987. Using life time fecundity to cpmpare management strategies: a case study from striped bass. North American Journal of Fisheries Management 7:409–409.
- Prager, M.H., Porch, C.E., Shertzer, K.W., Caddy, J.F. 2003. Targets and limits for management of fisheries: A simple probability-based approach. North American Journal of Fisheries Management 23:349–361. https://doi.org/10.1577/1548-8675(2003)023<0349 :TALFM0>2.0.C0;2
- Preecha, C. 2012. Biology and population dynamics of Bocourti's catfish (*Pangasius bocourti* Sauvage, 1880) in the Mekong River, Nong Khai area. Kasetsart University, Bangkok. 94 pp.
- Purushottama, G., Dash, G., Thakurdas, Akhilesh, K.V., Kizhakudan, S.J., Zacharia, P.U. 2017. Population dynamics and stock assessment of grey sharpnose shark *Rhizoprionodon oligolinx* Springer, 1964 (Chondrichthys: Carcharhinidae) from the north-west coast of India. Indian Journal of Fisheries 64:8–17. https://doi.org/10.21077 /ijf.2017.64.3.67657-02
- Ramli, M.F.S. 2015. False alarm: Is fishing rezoning necessary in Malaysia? IOSR Journal of Agriculture and Veterinary Science Ver. II 8:2319-2372. https://doi.org/10.9790/2380-081125863
- Ricker, W. 1940. Relation of "Catch per unit effort" to abundance and rate of exploitation. Journal of the Fisheries Research Board of Canada 5a:43-70. https://doi.org/10.1139/f40-008
- Ricker, W. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada. Department of the Environment Fisheries and Marine Service, Ottawa. 382 pp. https://doi.org/10.1038/108070b0
- Sparre, P., Venema, S.C. 1998. Introduction to tropical fish stock assessment Part I: Manual. FAO Fisheries Technical Paper, Rome. 407 pp.
- Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Harcourt, R.G., Stevens, J.D., Babcock, R.C., Pillans, R.D., Bradshaw, C.J.A. 2016.
 Reef shark movements relative to a coastal marine protected area.
 Regional Studies in Marine Science 3:58–66. https://doi.org/10.1016 /j.rsma.2015.05.002
- Sun, C.L., Wang, S.P., Porch, C.E., Yeh, S.Z. 2005. Sex-specific yield per recruit and spawning stock biomass per recruit for the swordfish, *Xiphias gladius*, in the waters around Taiwan. Fisheries Research 71:61-69. https://doi.org/10.1016/j.fishres.2004.07.010
- Sun, C.L., Wang, S.P., Yeh, S.Z. 2002. Age and growth of the swordfish (*Xiphias gladius* L.) in the waters around Taiwan determined from anal-fin rays. Fishery Bulletin 100:822–835.
- Tanaka, S. 1960. Studies on the dynamics and management of fish populations. Bulletin of Tokai Regional Fisheries Research Laboratory 28:1-200.
- Taylor, C.C. 1958. Cod growth and temperature. ICES Journal of Marine Science 23:366–370. https://doi.org/10.1093/icesjms/23.3.366
- Taylor, M.H., Mildenberger, T.K. 2017. Extending electronic length frequency analysis in R. Fisheries Management and Ecology 24:330– 338. https://doi.org/10.1111/fme.12232
- Tsai, W.P., Sun, C.L., Wang, S.P., Liu, K.M. 2011. Evaluating the impacts of uncertainty on the estimation of biological reference points for the shortfin mako shark, *Isurus oxyrinchus*, in the north-western Pacific Ocean. Marine and Freshwater Research 62:1383-1394. https://doi.org/10.1071/MF11010

- Wanchana, W., Ali, A., Sulit, V.T., Chanrachkij, I., Arnupapboon, S., Sayan, S. 2020. Terminal report regional sharks, rays and skates data collection. SEAFDEC, Bangkok. 348 pp.
- Wetherall, J.A. 1986. A new method for estimating growth and mortality parameters from length-frequency data. Fishbyte 4(1):12–14.
- Windsland, K. 2014. Total and natural mortality of red king crab (Paralithodes camtschaticus) in Norwegian waters: catch-curve analysis and indirect estimation methods. ICES Journal of Marine Science 72:642-650. https://doi.org/10.1093/icesjms/fsu138
- Xiang, Y., Gubian, S., Suomela, B., Hoeng, J. 2013. Generalized simulated annealing for global optimization: The GenSA package. The R Journal 5:13–28. https://doi.org/10.32614/rj-2013-002
- Yamaguchi, A., Taniuchi, T., Shimizu, M. 1998. Geographic variation in growth of the starspotted dogfish *Mustelus manazo* from five localities in Japan and Taiwan. Fisheries Science 64:732-739. https://doi.org/10.2331/fishsci.64.732
- Zhou, S., Punt, A.E., Lei, Y., Deng, R.A., Hoyle, S.D. 2020. Identifying spawner biomass per-recruit reference points from life-history parameters. Fish and Fisheries 21:760–773. https://doi.org /10.1111/faf.12459
- Zischke, M.T., Griffiths, S.P. 2015. Per-recruit stock assessment of wahoo (Acanthocybium solandri) in the southwest Pacific Ocean. Fishery Bulletin 113:407-418. https://doi.org/10.7755/FB.113.4.4

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