

Population dynamics and the spawning season of the commercial dominant species (*Encrasicholina devisi* and *Sardinella fimbriata*) from the northern region of Sarawak

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Abstract. The study explained the morphometric (length, L-weight, W) relationship ($W=aL^b$) and the spawning season of anchovy and sardine sampled from the coastal waters of Lawas, Sarawak in 2017 until 2018. In the study, the dominant species of anchovy and sardine in Lawas waters were initially determined, which were *Encrasicholina devisi* and *Sardinella fimbriata*. The length-weight relationship was estimated via the FiSAT program, while the spawning season was discovered through ovary examination. The total length (TL) ranged from 4.2 cm – 8.9 cm and 10.07 cm – 14.60 cm for *E. devisi* and *S. fimbriata* respectively. The length-weight relationships were given by $W = 0.005846L^{3.0134}$, $r^2 = 0.8$ for *E. devisi* while $W = 0.07663L^{2.1028}$, $r^2 = 0.71$ for *S. fimbriata*. The asymptotic length (L_{∞}) was estimated at 7.61 cm, growth coefficient (K) was 1.10 yr^{-1} , total mortality (Z) was 4.48 yr^{-1} , natural mortality (M) was calculated as 2.88 yr^{-1} and fishing mortality (F) was 1.60 yr^{-1} for *E. devisi*. On the other hand, *S. fimbriata* recorded the asymptotic length (L_{∞}) at 15.61 cm, growth coefficient (K) was 0.97 yr^{-1} , total mortality (Z) was 3.23 yr^{-1} , natural mortality (M) was calculated as 2.17 yr^{-1} and fishing mortality (F) was 1.06 yr^{-1} . The females reached the first sexual maturity at a size of 6.0 cm and 13.50 cm total length for *E. devisi* and *S. fimbriata*. The major spawning months were estimated to occur in June and November for *E. devisi* while March and July for *S. fimbriata*. The information obtained was important as a guideline for the management to establish a fishing regulation for a sustainable fishery in the waters of Lawas.

Key Words: anchovy, FiSAT, fishery management, sardines.

Introduction. Lawas waters with an area of approximately 401 km² is a common spot for the anchovy and sardine fisheries, with 21 jetties provided including in Kampung Awat-awat and Punang, where the research sampling was conducted. The fishing activity is operated via a small purse-seine net or locally known as *Lengkong*. The average landings of anchovy and sardine in Lawas during the previous 10 years were approximately 636 metric tonnes and 528 metric tonnes respectively (DOF 2020).

An abundance of anchovy species is found in Lawas. The most dominant species is *Encrasicholina devisi* or Devi's anchovy (locally termed as *Bilis*). Other species present are *Encrasicholina punctifer*, *Encrasicholina heteroloba*, *Stolephorus commersonii*, and *Stolephorus indicus*. While, many species of sardines including *Dussumieria elopoides*, *Dussumieria acuta*, *Sardinella gibbosa*, and *Sardinella fimbriata* are inhabiting the Lawas waters. *Sardinella fimbriata* or fringe scale sardines (locally termed as *Tamban Sisik*) are the dominant species targeted by the artisanal fishing sector in Lawas, Sarawak.

Both fishes are acknowledged as valuable resources to Sarawak as human food, mostly in the form of delicacies that are currently in the focus of exporting to the

peninsular region and even abroad. The demand for anchovies and sardines from the locals only are undoubtedly high every year. Worldwide anchovy catch production has declined day by day (Froese & Pauly 2019; Juliani et al 2019). This condition has raised the world's concern of sustainable fisheries which required an integrated collaboration of all countries (Kosamu 2015).

Feared of this condition, this research was conducted in the waters of Lawas, the productive area of anchovies and sardines fishery. The study involved analyzing data of biological parameters and mortality rate, which applied as the basis to determine biological fish stocks (Aghajanpour et al 2016). Thus, the research aimed to estimate the population parameters and the spawning season, in which the information acquired from this study will contribute to the management interventions to ensure sustainable fishery in the coastal waters of Lawas Sarawak.

Material and Method

Research site. The research was conducted from 2017 until 2018 (12 months) in the coastal waters of Lawas, approximately 3-5 NM from the shore (Figure 1).

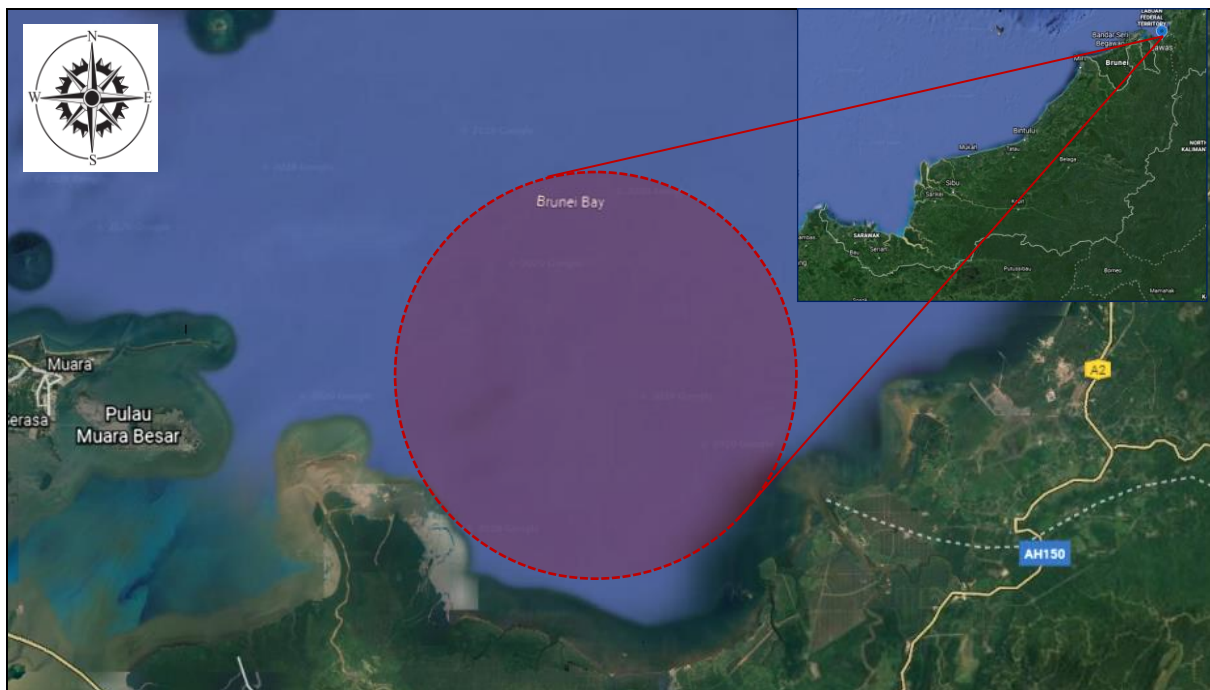


Figure 1. Sampling location of *E. devisi* and *S. fimbriata* in Lawas, Sarawak.

Sample collection. The fishing operation was conducted by using a mini purse-seine net. The samples were collected during the 12 months of the study and stored in a bottle, fixed with 10% buffered formalin as described by (Musel et al 2019). The samples were then labelled and transferred to the lab for further examination.

Length-weight measurements. 300 specimens were randomly collected monthly for one year from the preserved samples and measured using a mini measuring board (Wildco Model #118-E40) at an accuracy of ± 0.1 cm. Bodyweight was determined at ± 0.0001 g accuracy by using an electronic balance (Mettler Toledo ME 204).

FiSAT analysis. The total length (cm) and body weight (g) of 3600 individuals collected from one-year samples were incorporated into FiSAT II (FAO-ICLARM Stock Assessment) software to obtain the regression analysis (Quinn & Deriso 1999). The relationship between length and weight was analyzed according to the formula proposed by Le Cren (1951) in (Musel et al 2019):

$$W=aL^b$$

where:

W = weight (mg)

a = intercept (condition factor)

L = total length (mm)

b = slope (growth coefficient)

The growth parameters (L_∞ and K) were calculated in FiSAT II by using the ELEFAN I method (Gayaniilo et al 2005). Then, the parameters were estimated via the von Bertalanffy (VBGF) model of Sparre and Venema (1998). Theoretical age at birth (t_0) was independently calculated according to Pauly (1979):

$$\log(-t_0) = -0.3922 - 0.275 * \log L_\infty - 1.038 * \log K$$

where:

t_0 = theoretical age at birth

L_∞ = asymptotic length

K = von Bertalanffy growth coefficient

Growth performance index (Pauly & Munro 1984) method was followed for the comparisons of growth rate for the fish species in this study with other published values:

$$\Phi' = 2 \log L_\infty + \log K$$

where:

Φ' = growth performance index

L_∞ = asymptotic length

K = von Bertalanffy growth coefficient

Using the estimated K, potential longevity was calculated using Pauly's (Pauly & Munro 1984) formula in (da Costa et al 2018):

$$t_{max} = 3/K + t_0$$

where:

t_{max} = potential longevity

K = von Bertalanffy growth coefficient

t_0 = theoretical age at birth

The length converted catch curve in FiSAT II was used to estimate the mortality parameters and directly counted the total mortality (Z) (Sparre & Venema 1998). Natural mortality (M) was calculated based on Pauly's empirical formula (Pauly 1980) at Lawas water temperature, 30°C, the mean annual surface water temperature in the study area:

$$\log M = -0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log T$$

where:

M = natural mortality

L_∞ = asymptotic length

K = von Bertalanffy growth coefficient

T = temperature

Consequently, fishing mortality (F) was estimated using the formula (Gulland 1971):

$$F = Z - M$$

where:

F = fishing mortality

Z = total mortality

M = natural mortality

Exploitation rate (E) then can be estimated by using Pauly's formula (Gulland 1971):

$$E = F / Z$$

where:

E = Exploitation rate

F = Fishing mortality

Z = Total mortality

Subsequently, the length at first capture was calculated from the probability of capture analysis. The L50 is the length at first capture, L_c , while the L75 is accounted for approximately 75% of the fish that was caught in the gear.

A recruitment pattern was obtained through FiSAT II by the backward projection of the length-frequency data in a 1-year timeline.

Relative Yield-per-Recruit (Y/R) model of Beverton and Holt (1956) modified by Pauly and Soriano (1986), and Relative Biomass-per-Recruit (B/R) was performed in FiSAT II. The values of E_{max} , $E_{0.1}$, and $E_{0.5}$ were initially calculated from the ratio of M/K and L_c/L_∞ based on the knife-edge selection (Beverton & Holt 1966). Then, the exploitation rate (E) was compared to the E_{max} (maximum allowable limit of exploitation), $E_{0.1}$ (the exploitation rate at which the marginal increase in relative yield-per-recruit is 10% of its value at $E=0$) and $E_{0.5}$ (the exploitation rate corresponding to 50% of the unexploited relative biomass-per-recruit).

Yield isopleth was plotted based on the intersection values of exploitation rate and critical length ratio (L_c/L_∞) to determine the fishing status on the four quadrants (Pauly & Soriano 1986).

Reproductive biology analysis. Random fish samples were dissected to determine 40 female individuals each month for a one-year timeline. The total length and body weight were measured and weighed correspondingly. Ovaries were removed and preserved in 70% ethanol for the subsequent procedure. Ovaries were weighed ($\pm 0.0001g$) with an electronic balance (Mettler Toledo ME 204). The ovarian maturity of anchovy was defined following the method by Andamari et al (1998) while sardine was performed according to Kudale and Rathod (2016). The criteria were shown in Table 1 and Table 2.

Table 1
Criteria of female ovaries maturity stages for *Encrasicholina* spp. adapted from Andamari et al (1998)

Stage	Maturity Stages	Criteria
I	Immature/Developing	Immature: Oogonia present. Developing: Pre-vitellogenic oocytes.
II	Maturing	Yolk precursor stage; appear of some non-staining yolk.
III	Ripe	Ripe: Non-staining yolk and develop chorion. Running ripe: Red-staining yolk, hydrated oocytes. Development complete.
IV	Spent	Degeneration of ripe oocytes and previtellogenic oocytes. Presence of post-vitellogenic follicles.

Table 2

Criteria of female ovaries maturity stages for *S. fimbriata* adapted from Kudale and Rathod (2016)

Stage	Maturity Stages	Criteria
I	Immature/Developing	Immature (never spawned): Small, thread-like, translucent, and asymmetrical lobes. Oviduct - Long and thin. Ova - Diameter ranged from 0.0053 to 0.131 mm (not visible to the naked eye).
		Immature (Redeveloping): Size - 1/2 of the body cavity. Colour - Yellowish. Ova - Diameter ranged from 0.133 to 0.159 mm.
		Developing: Ovary turgid, opaque with granular. Size - 2/3 of the body cavity. Colour - Yellowish. Oviduct - Reduced. Ova - Diameter ranged from 0.161 to 0.176 mm.
II	Maturing	Maturing: The prominence of blood vessels. Colour - Reddish yellow. Ova - Diameter ranged from 0.180 to 0.201 mm. Semi-transparent and spherical.
		Mature: Ovary large, fully developed, eggs visible to naked eye. Size - Almost occupied entire body cavity. Colour - Orange. Ova - Diameter ranged from 0.204 to 0.295 mm. Yellowish and numerous filled the ovary.
III	Ripe	Ovary filled with yolk. Eggs large and opaque, ready for release. Ova - Diameter ranged from 0.322 to 0.512 mm.
IV	Spent	Partially or fully spent. Spent ovaries and residual eggs can be seen. Ovaries appeared flaccid or saggy, contracted, and empty.

The gonadosomatic index (GSI) was estimated as follows:

$$GSI = \frac{\text{Ovary weight}}{\text{Ovary-free body weight}} \times 100$$

Fecundity was calculated from the females in their mature or ripe stages. Each of the ovaries was dissected to obtain the sub-sample and weighed to the nearest 0.0001g. The oocytes were counted under a compound microscope (Olympus BX43). Fecundity of each individual was estimated as follows (Musel et al 2019):

$$F = F_s \times \frac{GW}{GW_s}$$

where:

- F = Estimated fecundity of an individual
- F_s = Number of oocytes in a sub-sample
- GW = Ovary whole weight
- GW_s = Ovary sub-sample weight

Size at sexual maturity was obtained from the first 50% of females at the ovarian maturity stage at a given total length class.

Results

Length-weight relationship. The regression between the total length (TL) and total body weight (BW) relationship for *E. devisi* and *S. fimbriata* (both sexes) were shown in Figure 2 and Table 3.

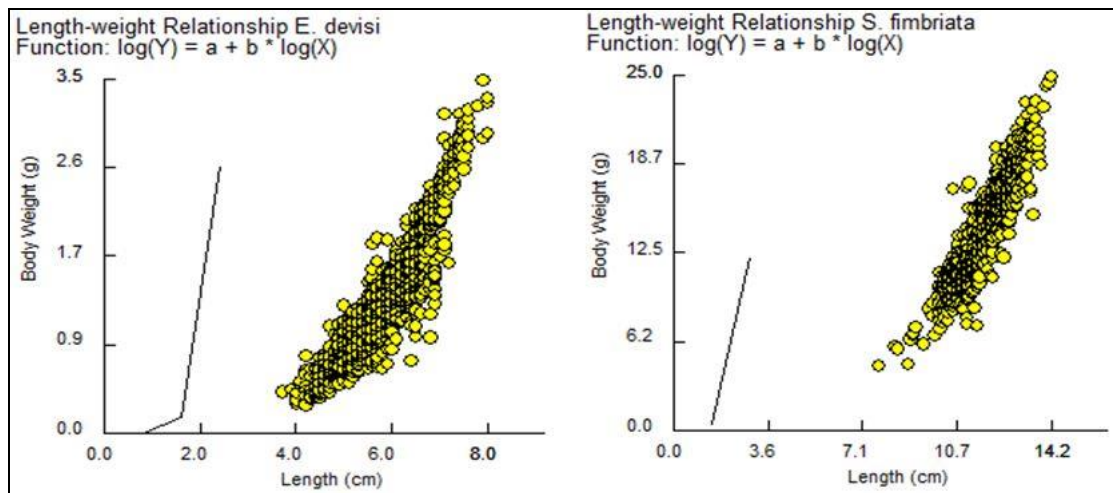


Figure 2. Regression analysis of *E. devisi* (left) and *S. fimbriata* (right) via FISAT.

Table 3

Regression analysis of *E. devisi* and *S. fimbriata*

Species	a	b	r ²	Equation
<i>E. devisi</i>	0.005846	3.0134	0.8	W = 0.005846L ^{3.0134}
<i>S. fimbriata</i>	0.07663	2.1028	0.71	W = 0.07663L ^{2.1028}

Growth parameters. The growth estimation was based on monthly length frequency. The asymptotic length, L_∞ was 7.61 cm; growth rate, K was 1.10 yr⁻¹ for *E. devisi*, while the asymptotic length, L_∞ for *S. fimbriata* was 15.61 cm; growth rate, K was 0.97 yr⁻¹ regardless of seasonal oscillation (Figure 3). The theoretical age at birth (t₀) was calculated at 0.21 and 0.20 for *E. devisi* and *S. fimbriata* correspondingly. The growth performance index was 1.80 yr⁻¹ and the potential longevity, T_{max} was 2.52 yr⁻¹ for *E. devisi*. The growth performance index for *S. fimbriata* was 2.37 yr⁻¹ and the potential longevity, T_{max} was 2.90 yr⁻¹ (Table 4).

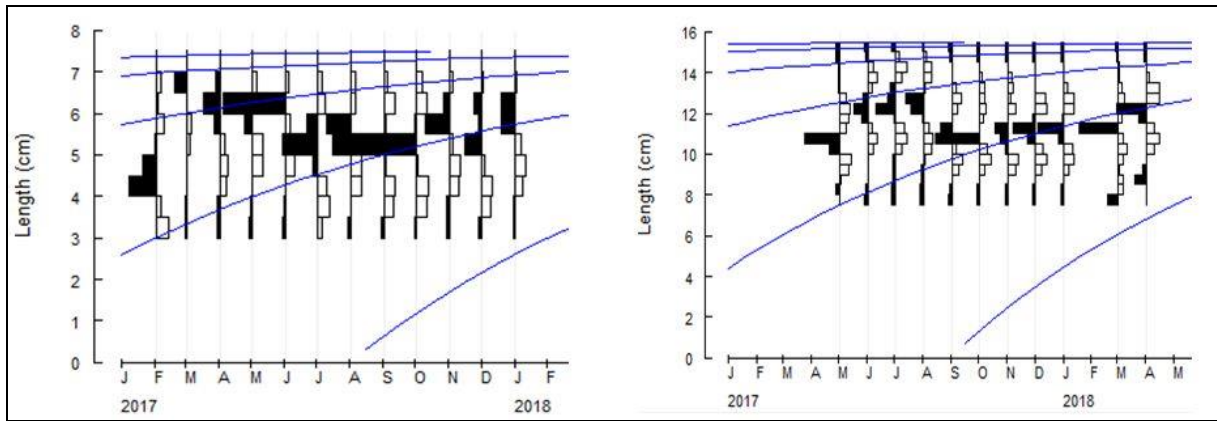


Figure 3. Von Bertalanffy growth curves overlaid on the restructured length-frequency histograms. The black and white bars indicated positive and negative deviation respectively from the "weighted" moving mean of four length classes (*E. devisi*) and five length classes (*S. fimbriata*) and they represented pseudo-cohort.

Mortality. Total mortality (Z) and natural mortality (M) for *E. devisi* were estimated at 4.48 yr^{-1} and 2.88 yr^{-1} respectively, while the total mortality (Z) and natural mortality (M) for *S. fimbriata* were 3.23 yr^{-1} and 2.17 yr^{-1} correspondingly. Based on the Z obtained, the fishing mortality (F) was found to be 1.60 yr^{-1} for *E. devisi* while 1.06 yr^{-1} for *S. fimbriata*. From the figures obtained, the current exploitation rate (E) was calculated at 0.36 for the *E. devisi* and 0.33 for *S. fimbriata*.

Length at first capture. The value for *E. devisi* ($L_{50} = 6.01 \text{ cm}$; $L_{75} = 6.38 \text{ cm}$) and *S. fimbriata* ($L_{50} = 10.67 \text{ cm}$; $L_{75} = 11.09 \text{ cm}$) was obtained.

Recruitment pattern. The results showed two peaks for *E. devisi* and *S. fimbriata*, indicated that both fishes can spawn two times per year (Figure 4).

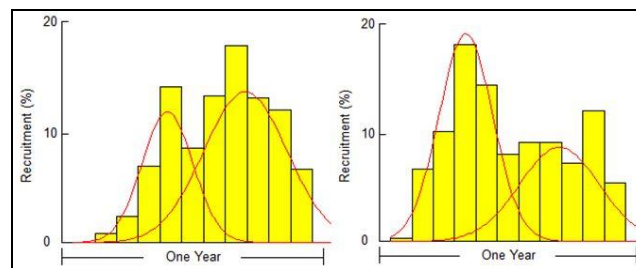


Figure 4. Recruitment pattern of *E. devisi* and *S. fimbriata* respectively.

Exploitation rate. The exploitation rate was calculated as 0.36 (*E. devisi*) and 0.33 (*S. fimbriata*), which indicated that the *E. devisi* and *S. fimbriata* fishery in the coastal waters of Lawas are under control. The maximum allowable limit of exploitation level (E_{\max}) for *E. devisi* was estimated at 1.0; $E_{0.1} = 1.0$; $E_{0.5} = 0.46$ while *S. fimbriata* were calculated at $E_{\max} = 1.00$; $E_{0.1} = 1.0$; $E_{0.5} = 0.43$ respectively (Figure 5).

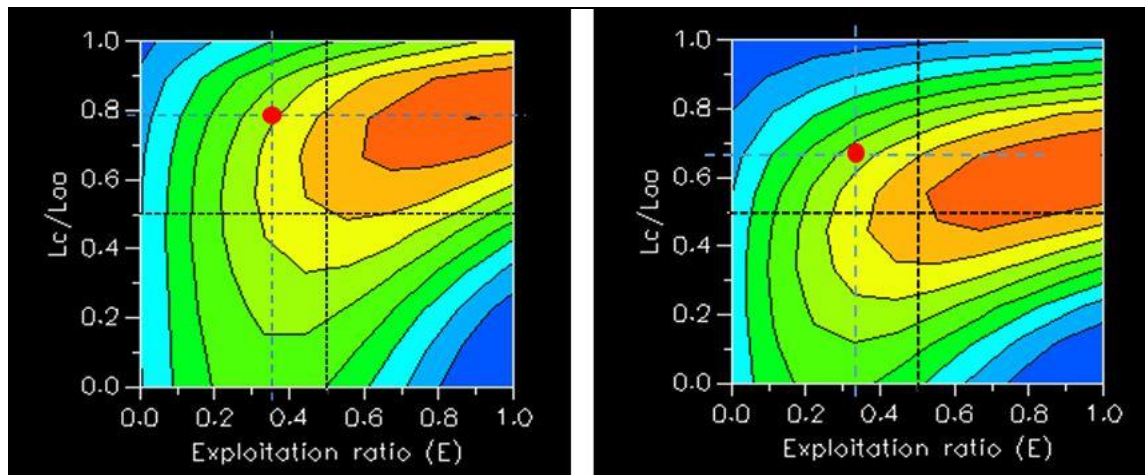


Figure 5. Yield isopleth of *E. devisi* (left) and *S. fimbriata* (right). The blue line represents the L_c/L_∞ and E ; the red dot represents the intersection of L_c/L_∞ and E . The contour indicated the fishing regime for both *E. devisi* and *S. fimbriata* lied in Quadrant A.

Table 4

The value of parameters obtained from FISAT analysis

Parameters	<i>E. devisi</i>	<i>S. fimbriata</i>
L_∞ (cm)	7.61	15.61
K (yr^{-1})	1.10	0.97
Z (yr^{-1})	4.48	3.23
M (yr^{-1})	2.88	2.17
F (yr^{-1})	1.60	1.06
E	0.36	0.33
Φ' (yr^{-1})	1.80	2.37
T_{\max} (yr)	2.52	2.90
E_{\max}	1.00	1.00
$E_{0.1}$	1.00	1.00
$E_{0.5}$	0.46	0.43
L_{50}/L_c (cm)	6.01	10.67
L_{75} (cm)	6.38	11.09

Spawning season. The mean GSI of females *E. devisi* portrayed 2 peaks, which were in June and November (Figure 6). The GSI value was at a lower level in February and July until October, where the Stage I showed dominance. The maximum value was observed in June (GSI = 1.82), where most females were found in matured stage (Stage II and Stage III = 93.33%), and the minimum was observed in February (GSI = 0.16), where most females were found to be in immature phase (100%).

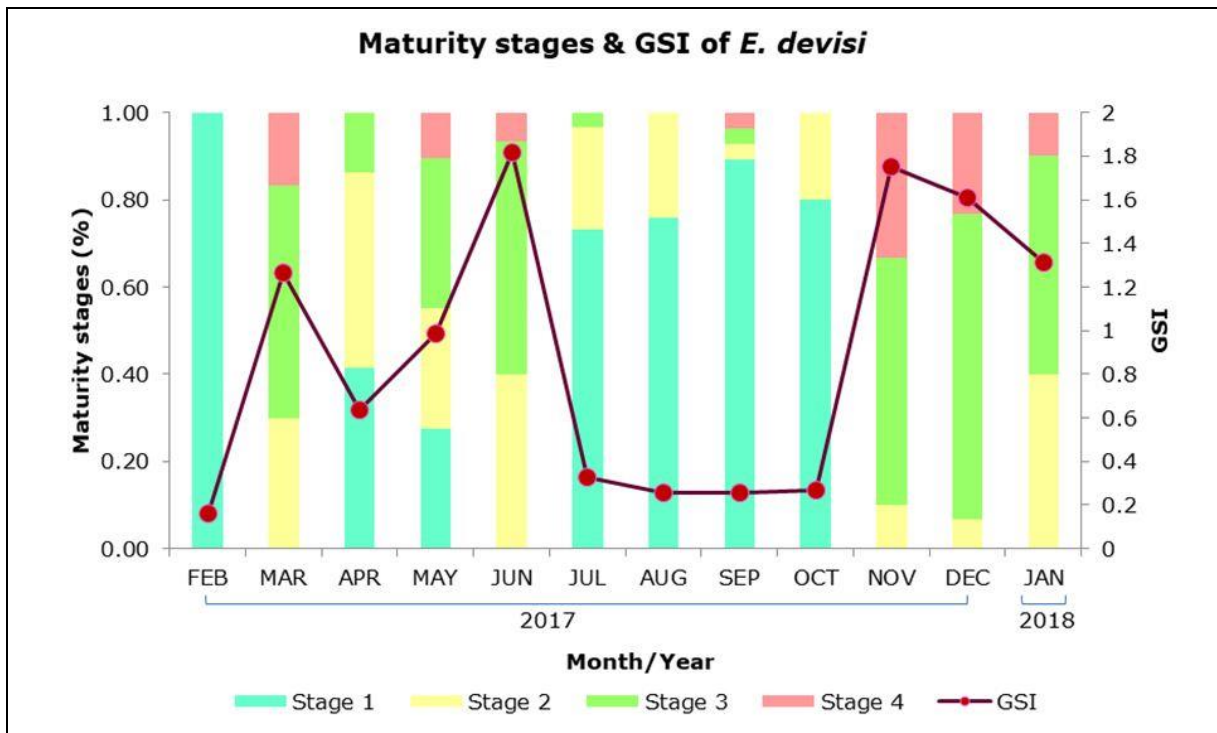


Figure 6. Variations in the GSI of female *E. devisi* and the percentage of occurrence of the ovarian maturity stages for a year-round sample.

The peak of mean GSI occurred in February, March, and July for *S. fimbriata* (Figure 7). The GSI value was lower in September until December due to the high percentage of Stage I. The maximum value was observed in July at 3.21, though most females were found in matured stage (48.23%) in February. The minimum value was observed in September (GSI = 0.19).

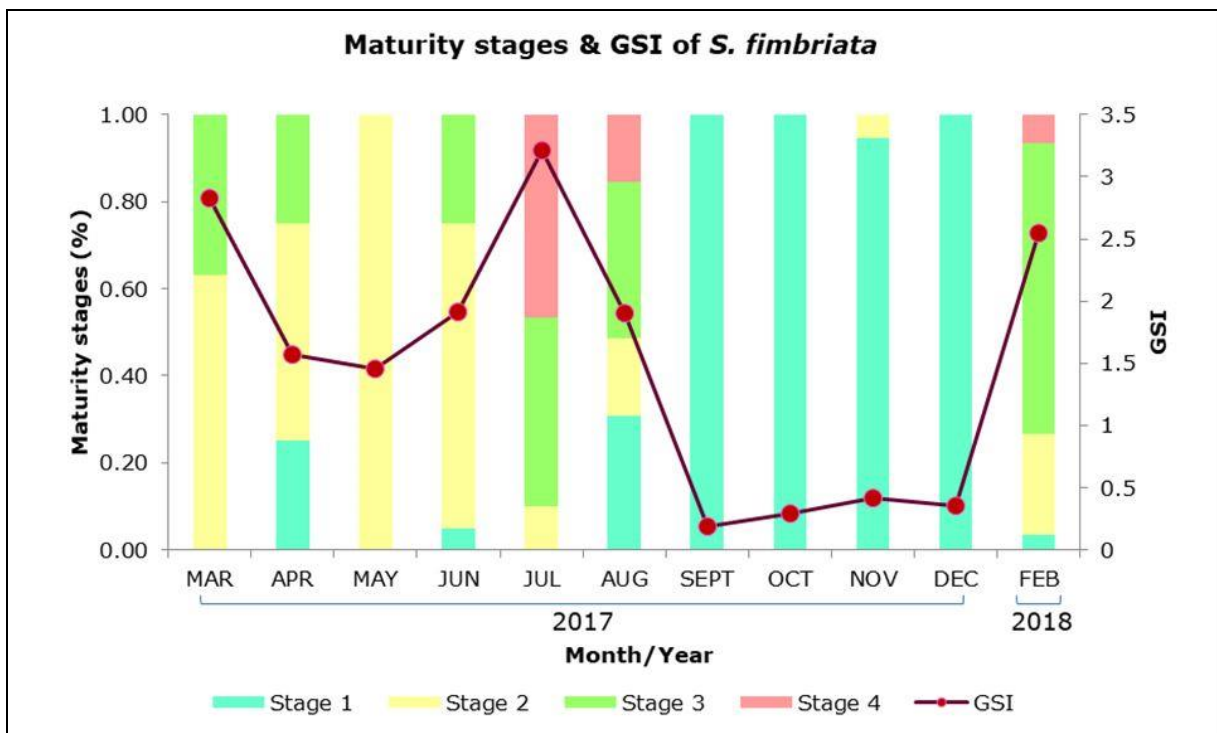


Figure 7: Variations in the GSI of female *S. fimbriata* and the percentage of occurrence of the ovarian maturity stages for a year-round sample.

Size/length at first maturity. The maturity stages (Stage II and Stage III) for *E. devisi* (Figure 8) and *S. fimbriata* (Figure 9) first occurred at >50% at a total length of 6.0 cm and 13.50 cm respectively indicated the size at sexual maturity.

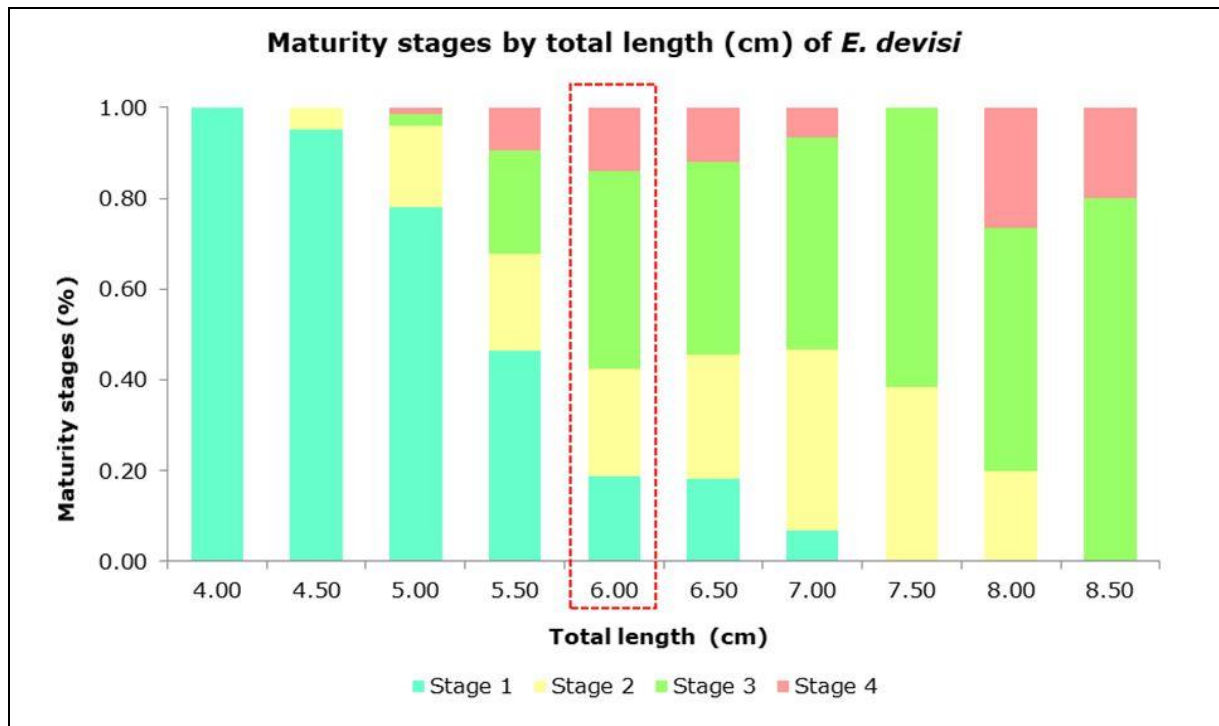


Figure 8. The percentage of occurrence of the ovarian maturity stages according to total length for *E. devisi*.

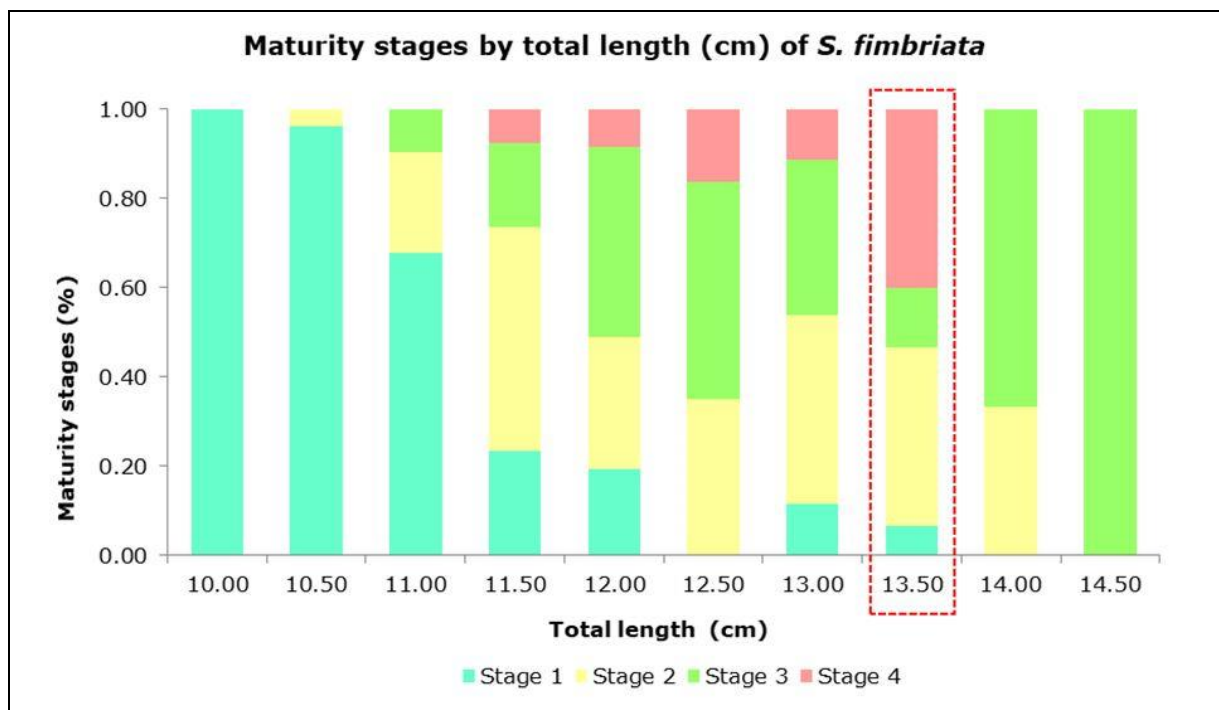


Figure 9. The percentage of occurrence of the ovarian maturity stages according to total length for *S. fimbriata*.

Fecundity. The highest mean fecundity recorded for *E. devisi* was in March with 7,723.94 ($\pm 2,175$ eggs) (Figure 10). Individual fecundity ranged at 11.33 – 46,992 eggs with fish size ranging from 4.2 cm until 8.9 cm. The highest mean fecundity recorded for

S. fimbriata was in September with 95,403.99 ($\pm 26,348$ eggs). Individual fecundity was ranged at 81.4 - 365,323.6 eggs with a total length ranging from 10.07 cm until 14.60 cm (Table 5).

Table 5

Fecundity of *E. devisi* and *S. fimbriata*

	Species	TL (cm)	BW (g)	GW (g)	Fecundity (eggs number)
Mean		6.1	1.4	11.6	1,960.82
SD	<i>E. devisi</i>	0.9074	0.8079	17.5199	4,289.04
Range		4.2 - 8.9	0.36 - 4.37	0.1 - 140	11.33 - 46,992
Mean		12.11	14.37	0.27	61,911.47
SD	<i>S. fimbriata</i>	0.88	2.62	0.2	55,387.84
Range		10.07 - 14.60	8.13 - 24.60	0.01 - 0.77	81.4 - 365,323.6

Discussion

Length-weight relationship. The values of 'b' in this study were 3.0134 and 2.1028 for *E. devisi* and *S. fimbriata* respectively. The 'b' value showed positive allometric (near to isometric) for *E. devisi*, while it was negative allometric for *S. fimbriata*. The allometric values indicated that the length and weight of the fish are not balanced. Positive allometric means that the weight of *E. devisi* increase faster than the length grows, while vice versa for *S. fimbriata*. The results comparisons with other studies in different locations as shown in Table 6 and Table 7.

Table 6

Parameters of length-weight relationship (a and b) for *E. devisi* in various locations

Area	a	b	Equation	Source
Malaysia (Lawas)	0.005847	3.0134	$W = 0.005847L^{3.0134}$	Present study
Indonesia (Makassar Strait, Kutai Kartanegara, East Kalimantan)	0.000007	3.0968	$W = 0.000007L^{3.0968}$	Juliani et al 2019
India (Mangalore-Malpe)	0.004145	3.221	$W = 0.004145L^{3.2210}$	Rohit & Gupta 2008

Table 7

Parameters of length-weight relationship (a and b) for *S. fimbriata* in various locations

Area	a	b	Equation	Source
Malaysia (Lawas)	0.07663	2.1028	$W = 0.07663L^{2.1028}$	Present
Indonesia (Prigi Waters, Trenggalek Regency)	0.014	2.804	$W = 0.014L^{2.804}$	Bintoro et al 2020
Indonesia (Alas Strait, East Lombok) - male	0.00005	2.647	$W = 0.00005L^{2.647}$	Rilani et al 2017
Indonesia (Alas Strait, East Lombok) - female	0.0004	2.68	$W = 0.0004L^{2.68}$	Rilani et al 2017

Growth parameters. The growth parameters were different throughout the areas of the study (Table 8 and Table 9). The growth rate (K) influences the length growth (L_{∞}) of fish. As the growth rate higher, the length growth lengthens faster; hence, the fish will achieve the asymptotic length faster as well as experience death earlier, and vice versa (Sparre & Venema 1999; Rilani et al 2017). The differences observed in different studies also associated with the seasons, geographical areas, environmental conditions and, fishing and industrial activities (Amponsah et al 2016).

The values of growth performance index in this study were 1.80 yr^{-1} and 2.37 yr^{-1} for *E. devisi* (Table 8) and *S. fimbriata* (Table 9) respectively. The growth performance index is a species-specific parameter; thus, the value of the related taxa is generally identical with a normal distribution (Dinh et al 2015; Tran et al 2007). Any discrepancy in the value of the same taxa is due to the unreliability in the precision of the measured growth parameters, besides environmental differences such as food availability and temperature (Salarpouri et al 2018). The value differences between species may contribute to variations in Φ' , and it appears that a longer fish may result in a higher growth index value (Dinh et al 2015).

The obtained potential longevities for both *E. devisi* and *S. fimbriata* were 2.52 and 2.7 respectively. It showed that the *E. devisi* is a short-lived species compared to *S. fimbriata*. This was supported by the fast growth rate of *E. devisi* when compared to *S. fimbriata*. According to Amponsah et al (2016) and Benchikh et al (2018), anchovy is a fast-growing species. Nonetheless, fast growth rates are a kind of defensive mechanism against predators to enhance the sustainability of fish population within the marine environment.

Table 8

Growth parameters comparison of the same species *E. devisi* in various locations

Location	L_{∞}	$K \text{ yr}^{-1}$	Φ'	T_{max}	Source
Malaysia (Lawas)	7.61 cm	1.10	1.80	2.52	Present study
Indonesia (Makassar Strait Kutai Kartanegara East Kalimantan)	130.2 mm	1.30	4.34*	2.23*	Juliani et al 2019
Indonesia (Kei Island)	89.25 mm	0.74	3.77*	3.89*	Supeni & Dobo 2017

Note: *Value was calculated based on the information given in the journal.

Table 9

Growth parameters comparison of the same species *S. fimbriata* in various locations

Location	$L_{\infty}(\text{cm})$	$K \text{ yr}^{-1}$	Φ'	T_{max}	Source
Malaysia (Lawas)	15.61	0.97	2.37	2.70	Present study
Indonesia (Prigi Waters, Trenggalek Regency)	26.75	0.92	2.82*	3.08*	Bintoro et al 2020
Philippines (Manila Bay)	18.50	0.95	2.51	2.97*	Dicdiquin et al 2017
India (Northwest Bay of Bengal)	20.70	0.85	2.56	3.51	Ghosh et al 2013

Note: *Value was calculated based on the information given in the journal.

Mortality and exploitation rate. Total mortality (Z) for *E. devisi* was estimated at 4.48 yr^{-1} . The results showed higher natural mortality (2.88 yr^{-1}) over fishing mortality (1.60 yr^{-1}), which indicated the unbalanced stock position in the study (Table 10). As for *S.*

fimbriata, the total mortality value was 3.23 yr⁻¹, also with higher natural mortality (2.17 yr⁻¹) against fishing mortality (1.06 yr⁻¹) (Table 11). The exploitation rate (E) was 0.36 and 0.33 respectively for *E. devisi* and *S. fimbriata*, which was significantly lower than the optimum level of exploitation (E=0.50), implied that the fishery activities of both fishes in Lawas were not overexploited. The fishing regime was then discovered through Pauly and Soriano (1986) as reported by (Musel et al 2019). The yield isopleths for *E. devisi* ($L_c/L_\infty = 0.79$ and $E = 0.36$) and *S. fimbriata* ($L_c/L_\infty = 0.68$ and $E = 0.33$) were fit into Quadrant A; therefore, the fishing regime were both categorized as underfishing. This signified that large fish were caught at a low effort, suggested that it should be increased strongly or remain.

Table 10

Mortality comparison of the same species *E. devisi* in various locations

Location	Z yr-1	M yr-1	F yr-1	E	Source
Malaysia (Lawas)	4.48	2.88	1.60	0.36	Present study
Indonesia (Makassar Strait, Kutai Kartanegara, East Kalimantan)	4.59	2.75	1.84	0.40*	Juliani et al 2019
India (Mangalore-Malpe)	8.19	3.11	5.08	0.62	Rohit & Gupta 2008
Indonesia (Kei Island)	2.97	1.09	1.87	0.63	Supeni & Dobo 2017

Note: *Value was calculated based on the information given in the journal.

Table 11

Mortality comparison of the same species *S. fimbriata* in various locations

Location	Z yr-1	M yr-1	F yr-1	E	Source
Malaysia (Lawas)	3.23	2.17	1.06	0.33	Present study
Indonesia (Prigi Waters, Trenggalek Regency)	1.71	1.42	0.29	0.17	Bintoro et al 2020
Philippines (Manila Bay)	5.86	1.98	3.88	0.66	Dicdiquin et al 2017
India (Northwest Bay of Bengal)	4.32	1.75	2.57	0.59	Ghosh et al 2013

Spawning season. Monthly changes in GSI resulted in 2 major peaks which revealed the major spawning month of the fishes. *E. devisi* was expected to spawn mainly in June and November (Figure 6), while *S. fimbriata* was in March and July (Figure 7). Sarawak experienced the wettest period (Northeast monsoon) in November until March, while the warmer period would be in May until September (Southeast monsoon) (Sa'adi et al 2019). In this study, both fishes have observed spawning during the warmer and the wettest month. Such flexibility is a result of the demographic plasticity behavior of anchovy and sardinella (Malavolti et al 2018; Baali et al 2017).

Size/length at 1st maturity. The length at first maturity initially occurred at the length of 6.0 cm for *E. devisi* and 13.50 cm for *S. fimbriata*. It appeared that the length at first capture of 75% ($L_{75} = 6.38$ cm) was higher than the length at first maturity of *E. devisi*, indicated that the fish were harvest at an appropriate period after spawning. Conversely,

for *S. fimbriata*, the $L_{75} = 11.09$ cm was smaller than the length at first maturity showed that the fish were caught at pre-spawning. However, this fishery practice may result in catch declination in the future. Therefore, the fish should be allowed to breed at least once in their lifetime so that the population could be restocked and to achieve equilibrium.

Fecundity. The mean fecundity of *E. devisi* and *S. fimbriata* were 1,960.82 eggs with the range of 11.33 – 46,992 eggs and 61,911.47 eggs with a range of 81.4 - 365,323.6 eggs correspondingly. Comparisons with other local studies could not be accomplished due to no published data of *E. devisi* and *S. fimbriata* that were previously recorded. As compared to the neighbor country, a study by Andamari et al (2002) showed a low range of fecundity for *E. devisi*, while a study of *S. fimbriata* by Rilani et al (2017) revealed a higher range of fecundity than this study. The variation in fecundity in different locations has been known that the clupeoid fishes are able to efficiently adjust their reproductive behavior to the environment; thus, producing eggs in the preferable condition of the offspring survival (Doring 2018).

Conclusions. The population of *E. devisi* and *S. fimbriata* in Lawas showed a sustainable fishery. The management could maintain the fishery management plan in the area or suggesting other intervention plans to increase fishery efforts in the waters of Lawas.

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