

Population dynamics of *Encrasicholina devisi* and *Stolephorus insularis* (Teleostei: Engraulidae) in Tegal Waters, Indonesia

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Abstract. Sulistyowati BI, Wijayanto D, Hartoko A, Purnomo PW. 2026. Population dynamics of *Encrasicholina devisi* and *Stolephorus insularis* (Teleostei: Engraulidae) in Tegal Waters, Indonesia. *Biodiversitas* 27 (3): d270319. <https://doi.org/10.13057/biodiv/d270319>. Devis anchovy (*Encrasicholina devisi*) and Hardenberg's anchovy (*Stolephorus insularis*) are small pelagic fish with strong market demand in Tegal Waters, Indonesia. The study was performed to examine the population dynamics of the anchovies based on data from fish catches from April 2024 to March 2025. A total 9,546 samples (6,294 *E. devisi* and 3,252 *S. insularis*) were used in this study. Fish length and total weight were measured to determine growth and exploitation, using von Bertalanffy's equation for growth parameters and the Beverton and Gulland's equations for mortality and exploitation rates. The growth analysis indicated maximum lengths (L_{∞}) of 103.81 mm for *E. devisi* and 49 mm for *S. insularis*, with growth coefficients (K) of 2.5 and 1.6/year, respectively. Both species were categorized as overexploited. Therefore, catch quotas need to be applied in order to ensure the fish sustainability. The maximum sustainable yields (C_{MSY}) of 485.6739 tons and 85.8343 tons have generated economic values of IDR 5.8 billion (USD 341,417) and IDR 3.7 billion (USD 217,800), respectively. The sustainable management measures include reducing fishing effort by 30-40%, increasing mesh size by 1-2 mm, adopting a 1-2 months restricted season, and reducing total capture to 60-70% of current levels, with a stricter reduction for *E. devisi* than *S. insularis*.

Keywords: Anchovy, growth, mortality, population parameters, Tegal

INTRODUCTION

Tegal waters in the northern waters of the Java Sea are the habitat of small pelagic, demersal, and benthic fish (Nugroho et al. 2016). These fish are captured for consumption by small-scale fishermen using 3-10 GT vessels (Kusumawardhani et al. 2022). Boat seines and anchovy purse seines are commonly used in Tegal Waters to catch anchovies, but anchovy purse seines have been rarely used in the last nine years (2015-2024), as fishermen prefer boat seines (Yusfiandayani et al. 2024). However, the anchovy purse seine fishing gear is specifically used to catch *Encrasicholina devisi* (Devis' anchovy), while the boat seine is used to catch both *E. devisi* and *Stolephorus insularis* (Hardenberg's anchovy). Unfortunately, the catch using the boat seine is often dominated by *S. insularis*, with only a small number of *E. devisi*. This condition indicates that differences in fishing gear selectivity may influence the composition of anchovy catches landed in Tegal and may also affect the assessment of stock conditions for each species.

Anchovies are small pelagic fish that are abundant in Central Java's coastal waters, particularly *E. devisi* and *S. insularis* in Tegal Waters (Cerna et al. 2022). In Indonesian fisheries, these anchovies are generally referred to as "teri", with local market names such as "teri jawa" and "teri nasi." The average anchovy's production from 2015 to 2024 reached 694.553 tons/year, with significant economic value IDR 6.6 billion (USD 391,050) for *E. devisi* and

88.03 tons/year with an economic value IDR 3.98 billion (USD 234,610) for *S. insularis*. These figures show that both species contribute not only to local food supply but also to the income of fishing communities and regional fish markets. Due to the high demands, the sustainability of the fish stocks due to overexploitation is under the threat (Mulya et al. 2021). Effective management should be applied to control the anchovy stocks through conservation and sustainable fishing practices (Dutta 2023). Anchovies are short-lived and fast-growing, which turnover rate enhances their survival potential (Robert et al. 2023; Yasue et al. 2024). It is necessary to examine the growth and mortality rates of the anchovy population in Tegal Waters to determine the most effective management system.

As reported in previous studies, the variability of anchovy population parameters affects the risk of overexploitation (Supeni and Dobo 2017; Juliani et al. 2019; Roul et al. 2020; Zamroni et al. 2020; Mallegowda et al. 2021; Hata et al. 2022). Most studies only estimated growth, mortality, and exploitation rates, yet the analysis on sex ratios has been overlooked (Musel et al. 2022; Hendrayana et al. 2023). This limitation leaves an important gap in understanding population dynamics because sex composition may reflect reproductive potential and population resilience under fishing pressure. In fact, the biological differences between male and female anchovies and the annual seasonal variations might also affect the population parameter estimates (Schismenou et al. 2024). Therefore, a year-long sex-differentiated study of *E. devisi*

and *S. insularis* is important to close the information gaps and strengthen the basis for sustainable fisheries management.

Considering the increasing fishing intensity and the risk of overexploitation, rigorous scientific assessment based on comprehensive biological parameters should be conducted. Such an assessment is needed to generate a more accurate picture of the stock condition of each species and to support management decisions that are responsive to field conditions. Hence, this study was performed to identify significant differences in growth parameters between *E. devisi* and *S. insularis*, highlighting the influence of local environmental conditions and fishing pressure on population dynamics. Growth metrics had been analyzed separately, without distinguishing between these two species, resulting in an incomplete evaluation of their exploitation status (Supeni and Dobo 2017; Juliani et al. 2019; Roul et al. 2020; Zamroni et al. 2020; Mallegowda et al. 2021; Hata et al. 2022; Musel et al. 2022; Hendrayana et al. 2023). In this study, the growth, sex ratio, mortality, and exploitation rate of both anchovy species were analyzed within a one-year observation in Tegal Waters, Indonesia. The results of this study are expected to provide strong scientific evidence to support adaptive and sustainable fisheries management in the region.

MATERIALS AND METHODS

Data collection

A total of 9,546 anchovy individuals were collected from Tegal Regency and Tegal City, Indonesia, including 6,294 *E. devisi* and 3,252 *S. insularis* from three sampling stations (Muarareja, Larangan, and Suradadi fish landing sites) (Table 1). The samples were caught using anchovy purse seine and boat seine fishing gear with a mesh size of 0.15 inches on 6 to 20 GT vessels (Figure 1). The data were collected monthly on April 1, 2024, to March 31, 2025. In addition to primary data, secondary data were also used (Zhang et al. 2020; Sande et al. 2022; Vilas et al. 2024). The length and weight of samples were measured using a vernier caliper (0.1 mm) and a digital scale (0.01 g). Macroscopic examination of gonads was also conducted to determine the sex of the fish, where female fish had larger, grainy, and pinkish or orange-pink gonads, while males had smaller, milky-white gonads. Female fish generally have larger gonads with better somatic conditions (Agger et al. 1974; Salazar et al. 2025).

Table 1. Fish landing sites and general description of sampling locations

Station	Fish landing site	Coordinates	Fishing gear dominance	General description
1	Muarareja	6°50.768'S, 109°6.402'E	Boat seine	Major landing site for small pelagic fisheries
2	Larangan	6°51.755'S, 109°11.621'E	Anchovy purse seine, boat seine	Important landing site with high anchovy landings
3	Suradadi	6°52.424'S, 109°16.138'E	Boat seine	Major landing site for small pelagic fisheries

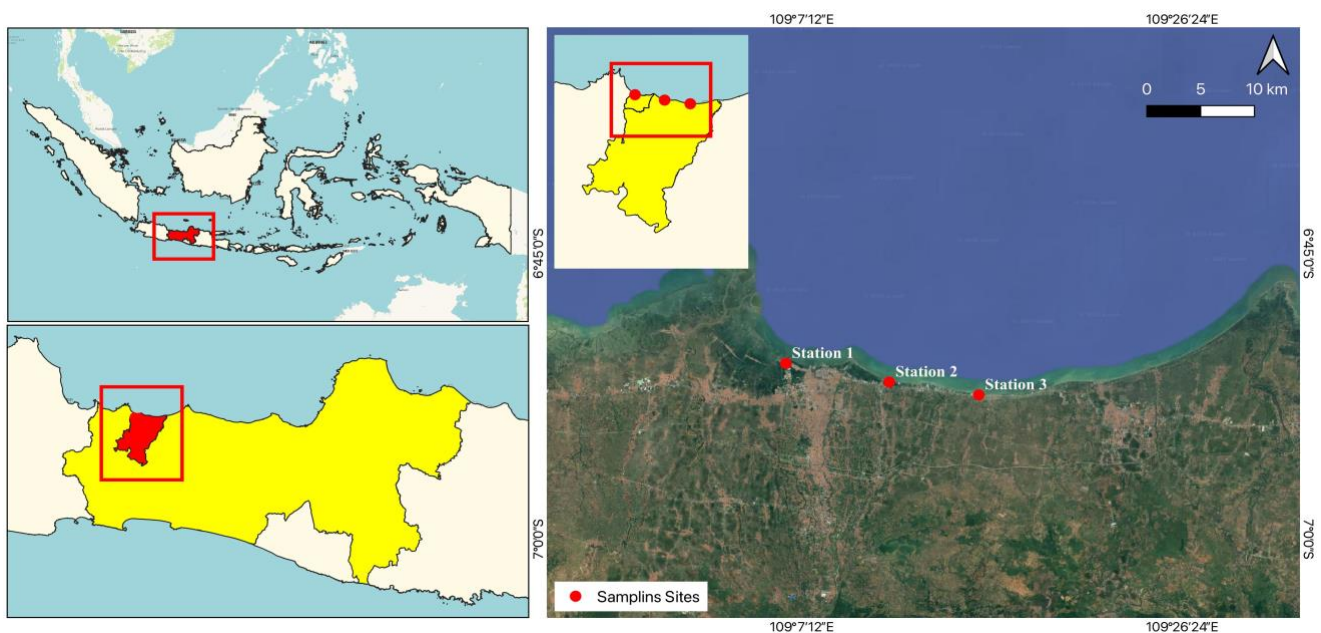


Figure 1. Research locations at the Muarareja (Station 1), Larangan (Station 2), and Suradadi (Station 2) Fish landing sites, Tegal, Indonesia

Data analysis

Population dynamics model

To assess the length-weight relationship (LWR), 3,252 *S. insularis* and 6,294 *E. devisi* specimens were examined. Data were examined using exploratory scatterplots to identify potential outliers in log-transformed length and weight values before fitting the model. The standardized residual (z_i) approach was then used to identify outliers. Observations with absolute standardized residual values (z_i) higher than 3 were deemed extreme and disqualified from additional analysis. This process reduced possible bias in the regression analysis and increased the robustness of the parameter estimate (Arimie et al. 2020; Sanjeev et al. 2023). There were 4,912 male and 1,382 female *E. devisi*, and 2,500 male and 752 female *S. insularis* in the final dataset. Growth modeling was conducted using the von Bertalanffy Growth Function (VBGF), while the length-weight relationship was analyzed with Ricker's allometric equation ($W = aL^b$). A t-test assessed whether growth is isometric ($b = 3$) or allometric ($b \neq 3$), with significance determined against t-table values using the regression slope and standard error of the b-value. (Baihaqi and Annida 2025; Lumban-Gaol et al. 2025).

The length-converted catch curve method from FISAT II was employed to estimate total mortality (Z) in fish, as described by Beverton et al. (1957). The formula for Z is as follows: Z is derived from factors such as asymptotic length (L_∞), growth coefficient (K), average fish length (L), and the smallest length caught (L_C). Pauly's (1983) equation estimates the natural mortality (M) as $\log M = -0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log T$, where T is the mean in situ sea surface temperature measurement (29°C) for a year (April 2024-March 2025) at a depth of 5-10 m at three sites. This equation presents the correlation between water temperature and M . The exploitation status of the fish was evaluated using Gulland's (1971) reference point, which indicated a balanced yield with an ideal exploitation rate (E_{opt}) of 0.5. Values above 0.5 indicate overexploitation, while values below 0.5 indicate under-exploitation.

From these figures, the fishing mortality (F) and exploitation rate (E) were then calculated to gain an equation that estimated the number of catches under conditions of maximum sustainable yield (C_{MSY}) as follows (Sparre and Venema 1999; Liang et al. 2020; Dutta 2023; Denderen et al. 2024; Wijayanto et al. 2025a; Wijayanto et al. 2025b):

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

$$\log(-t_0) = -0.3922 - 0.2752 \log L_\infty - 1.038 \log K$$

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

$$F = Z - M$$

$$E = F/Z$$

$$\text{If } E_{MSY}: 0.5, \text{ then } F_{MSY}: 0.5Z$$

$$\text{If } F_{MSY}/F = C_{MSY}/C, \text{ then } C_{MSY}: (0.5Z/F.C)$$

Estimation of Catch at Maximum Sustainable Yield (C_{MSY}) was measured by calculating the catch mortality index at maximum sustainable yield parameters with $F_{MSY}: 0.5Z$ and analyzing C_{MSY} using the formula $C_{MSY}: 0.5Z/F.C$. F represents fishing mortality, while Z is total

mortality. F_{MSY} indicates fishing mortality at MSY, C_{MSY} is the catch at MSY in tons, and C is current fishery production in tons based on statistical catch data.

Statistical analysis

Chi-square tests and Fisher's exact tests were the statistical tests used to determine the independence of variables in uncorrelated groups. The chi-square test fits larger samples, whereas Fisher's test is more recommended for smaller sample size (Piepho et al. 2022; Ozturk et al. 2023; Chechile and Barch 2025). In examining sex ratios, the chi-square formula is used to evaluate disparities in proportions of non-numeric data. The chi-square formula:

$$\chi^2 = K \sum_{i=1}^k \frac{(O_i - E_i)^2}{E_i}$$

Where, χ^2 is chi-square, O_i is the frequency of observed fish, and E_i is the expected frequency of male and female fish in a balanced sex ratio condition. The null hypothesis H_0 asserts a balanced ratio, while the alternative H_1 asserts an imbalanced ratio, with conclusions based on t-values (Rinandha et al. 2021; Sultana et al. 2023; Yusnaini et al. 2025). Length-based models rely on life-history parameters, which are evaluated using normality tests and sensitivity analyses to assess bias effects (values less than or greater than 5% and 10%) on L_∞ (asymptotic length), K (growth coefficient), F (fishing mortality), M (natural mortality), and Z (total mortality), and their influence on the exploitation rate (E) (Amorim et al. 2020; Medeiros et al. 2023; Sululu et al. 2024). Furthermore, autocorrelation (ACF) and partial autocorrelation (PACF) analyses are used to examine recruitment time series, focusing on patterns with a significant 12-month lag to better understand interspecies interactions (Crisafulli et al. 2023; Eleuterio 2023; Wade et al. 2023; Pyae et al. 2025).

RESULTS AND DISCUSSION

Small pelagic fish from the Engraulidae family include *E. devisi* and *S. insularis*. According to standard taxonomy, species identification was based on diagnostic morphological traits (Whitehead et al. 1988; Riede 2004). *E. devisi* has a cylindrical body with a rounded belly, a blue-gray back, and a bright silver stripe running the length of the body with a thin blue line above it. This species, which can grow up to 10 cm in length in females and reach sexual maturity at about 6.1 cm, is primarily found in brackish and tropical coastal waters (Whitehead et al. 1988). *S. insularis*, on the other hand, has a somewhat flattened body with a dark yellow caudal fin, a double pigment line on the back behind the dorsal fin, and the origin of the pelvic fins below about the middle of the base of the dorsal fin. This species grows to about 8 cm, reaches maturity at about 4.3 cm, and migrates oceanodromously in warm waters. It lives in neritic-pelagic and brackish environments (Riede 2004) (Figure 2). Both species are significant targets for the regional small-scale pelagic fishery and are widely distributed in the Tegal Waters. They are usually caught on one-day fishing

excursions two to three nautical miles offshore using a boat seine and an anchovy purse seine. Although environmental factors also affect success, the use of effective fishing gear can greatly increase catch rates (Sulistiyowati and Wullandari 2022; Micheli et al. 2024).

This study evaluated the sex ratio of *E. devisi* and *S. insularis* fish over a year. As found in this study, the sex ratio between male:female is of 3.55:1 for *E. devisi* and 3.32:1 for *S. insularis*. The sex ratio might also be influenced by seasonal changes (Figure 3, Table 2). Due to behavioral or migratory differences between the sexes, male anchovies dominate catches for several months in various species, such as *Stolephorus commersonii*, along the northern coast of Tanzania (Sululu et al. 2020). Fluctuations in the sex ratio can be attributed to factors such as variations in natural mortality rates between males and females, geographic mobility, and differential susceptibility to fishing gear. It is important to note that anchovy sex ratios can vary significantly across species and geographic regions. For instance, the sex ratio of European anchovies (*Engraulis encrasicolus*) in the Aegean Sea stands at 1.91:1, indicating a higher number of females than males (Taylan and Bayhan 2024). This contrasting pattern underscores how fishing pressure, sex-specific growth-rate differences, and environmental factors can affect anchovy

populations, leading to marked regional differences in population dynamics and reproductive success.



Figure 2. A. *Engrasicholina devisi*, B. *Stolephorus insularis*

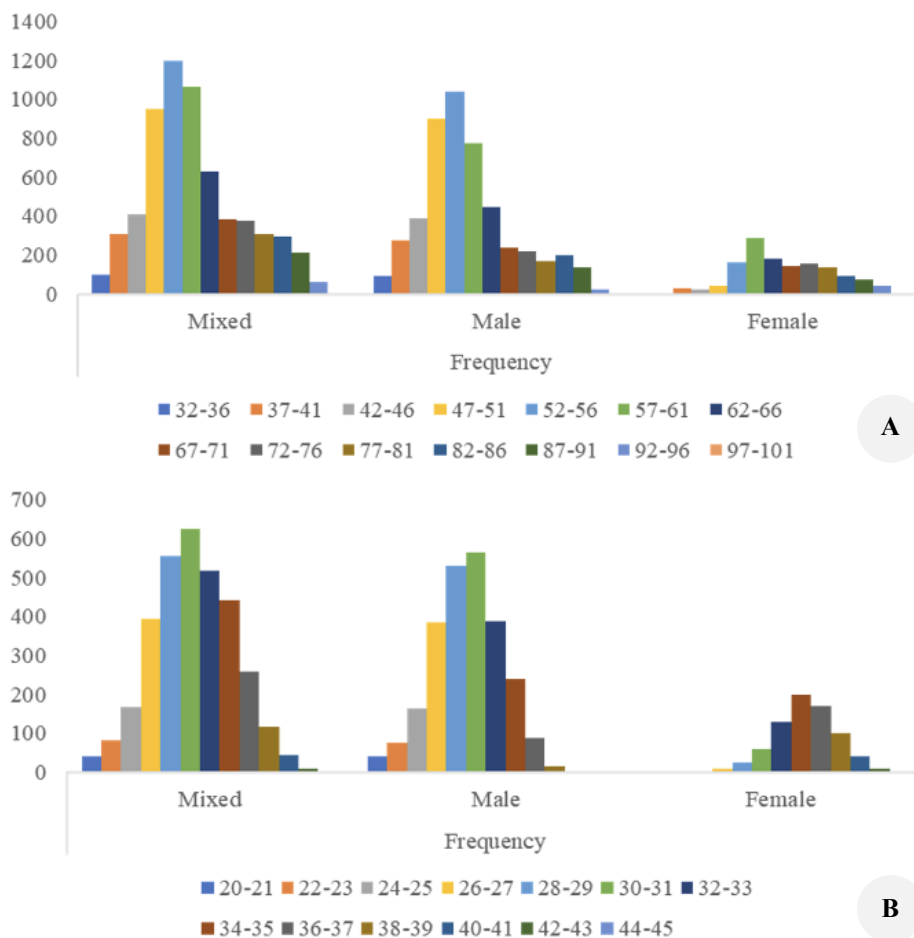


Figure 3. The total length frequency (mm) of: A. *Engrasicholina devisi*, B. *Stolephorus insularis*

Table 2. Chi-square test of sex ratio and overall catch size ratio of *Encrasicholina devisi* and *Stolephorus insularis*

Year	Month	<i>Encrasicholina devisi</i>				<i>Stolephorus insularis</i>				
		N	Sex (%)		Sex ratio	N	Sex (%)		Sex ratio	
			Male	Female	(Male:Female)		Male	Female	(Male:Female)	
2024	April	540	68.35	31.65	2.16:1	278	85.86	14.14	6.07:1	
	May	535	71.89	28.11	2.56:1	287	83.93	16.07	5.22:1	
	June	536	85.37	14.63	5.84:1	279	82.57	17.43	4.74:1	
	July	496	76.71	23.29	3.29:1	191	71.28	28.72	2.48:1	
	August	498	84.6	15.4	5.49:1	280	79.59	20.41	3.90:1	
	September	499	76.07	23.93	3.18:1	241	86.69	13.31	6.51:1	
	October	498	81.3	18.7	4.35:1	289	80.21	19.79	4.05:1	
	November	539	79.7	20.3	3.93:1	294	75.65	24.35	3.11:1	
	December	539	83.43	16.57	5.03:1	278	76.87	23.13	3.32:1	
	2025	January	540	77.96	22.04	3.54:1	283	67.27	32.73	2.05:1
		February	537	77.2	22.8	3.39:1	271	62.02	37.98	1.63:1
		March	537	73.13	26.87	2.72:1	281	74.55	25.45	2.93:1
Total		6294	78.04	21.96	3.55:1	3252	76.88	23.12	3.32:1	
95% CI	Calculate X ²	Table X ²	df	Highest % length range	95% CI	Calculate X ²	Table X ²	df	Highest % length range	
0.000	90.178	19.675	11	19.05% (52-56 mm)	0.000	95.206	19.675	11	17.3 % (28-29 mm)	

Beyond the observed skewed sex ratio, the body sizes recorded in this study were generally smaller compared to those reported in others research. *E. devisi* was most frequently found ranging from 52 to 56 mm, in contrast to the 68 to 74 mm and 70 to 110 mm ranges noted in other regions (Figure 3, Table 2) (Juliani et al. 2019; Mallegowda et al. 2021). Similarly, *S. insularis* was typically measured at 28 to 29 mm, which is below the 30.8 to 58.7 mm range documented in prior studies (Hata et al. 2022; Chu and Pauly 2024). The high fishing pressure is altering size distributions, likely due to selective fishing practices and environmental factors like rising sea temperatures that affect the juvenile growth (Boëns et al. 2021; Taboada et al. 2023). The Chi-square test reveals a continuous male dominance in the fish population of Tegal Waters, with a significant deviation from the expected 1:1 sex ratio ($p < 0.05$), which threatens recruitment and anchovy spawning (Wagiyo et al. 2023; Visser et al. 2025). Factors that include gear selectivity, overfishing, and environmental conditions also affect this condition (Conrad and Kindsvater 2024). Both *E. devisi* and *S. insularis* show male dominance, particularly during transitional monsoon periods (Juliani et al. 2019; Fabiani et al. 2022; Musel et al. 2022; Ridwan et al. 2024), where seasonal sex ratio fluctuates along with the reproductive cycles (Véron et al. 2020; Arefayne et al. 2025; Pawelek et al. 2025). Size-selective fishing also contributes to the male dominance, since this method targets larger females (Pauly and Soriano 1986; Honeycutt et al. 2019; Heikkilä 2020; Koepper et al. 2021; Mramba and Mkude 2022; Id et al. 2023; Morandini et al. 2024). In addition, rising sea temperatures worsen this situation. It is considered necessary to improve fisheries management and marine protected areas to enhance resilience to climate change (Wootton et al. 2021).

Length-weight relationship

Males and females of *E. devisi* exhibit isometric growth, whereas male *S. insularis* show positive allometric growth, while females of the same species display isometric growth. These distinct growth patterns are shaped by their feeding habits and reproductive strategies (Dias et al. 2022; Yoneda et al. 2025). The positive allometric growth observed in male *S. insularis* is tied to mating competition, whereas the isometric growth in females indicates that energy is primarily allocated towards reproduction. In various regional studies of *E. devisi*, isometric growth has been consistently recorded, aligning with findings from Sarawak (b: 3.0134) and Kutai Kartanegara (b: 3.096) (Juliani et al. 2019; Musel et al. 2022). Conversely, negative allometric growth has been noted along the Karnataka coast (b: 2.897), as reported by Mallegowda et al. (2021). This highlight regional variations in growth patterns that are influenced by factors such as food availability, predation, and habitat sustainability. Notably, isometric growth suggests an adequate food supply (Azrita et al. 2024; Kurnia and Burton 2025). For *S. insularis*, positive allometric growth was documented in Belawan (b: 3.10) and the Strait of Malacca (b: 3.004) (Gurukinayan et al. 2015; Mulya et al. 2021). In contrast, negative allometric growth was recorded in Lempasing, Lampung (b: 2.49), and Indian waters (b: 2.562) (Roul et al. 2020; Manuel 2025). In comparison to these findings, the isometric growth of *E. devisi* and the sex-specific growth patterns of *S. insularis*, demonstrating positive allometric growth in males and isometric growth in females within Tegal Waters, indicate that the growth dynamics of anchovies are notably influenced by local environmental conditions, resource availability, and fishing pressure (Caserta et al. 2025; Kelly et al. 2024; Kindong et al. 2024). The length-weight growth parameters for *E. devisi* and *S. insularis*, categorized by sex, are illustrated in Figure 4 and Table 3.

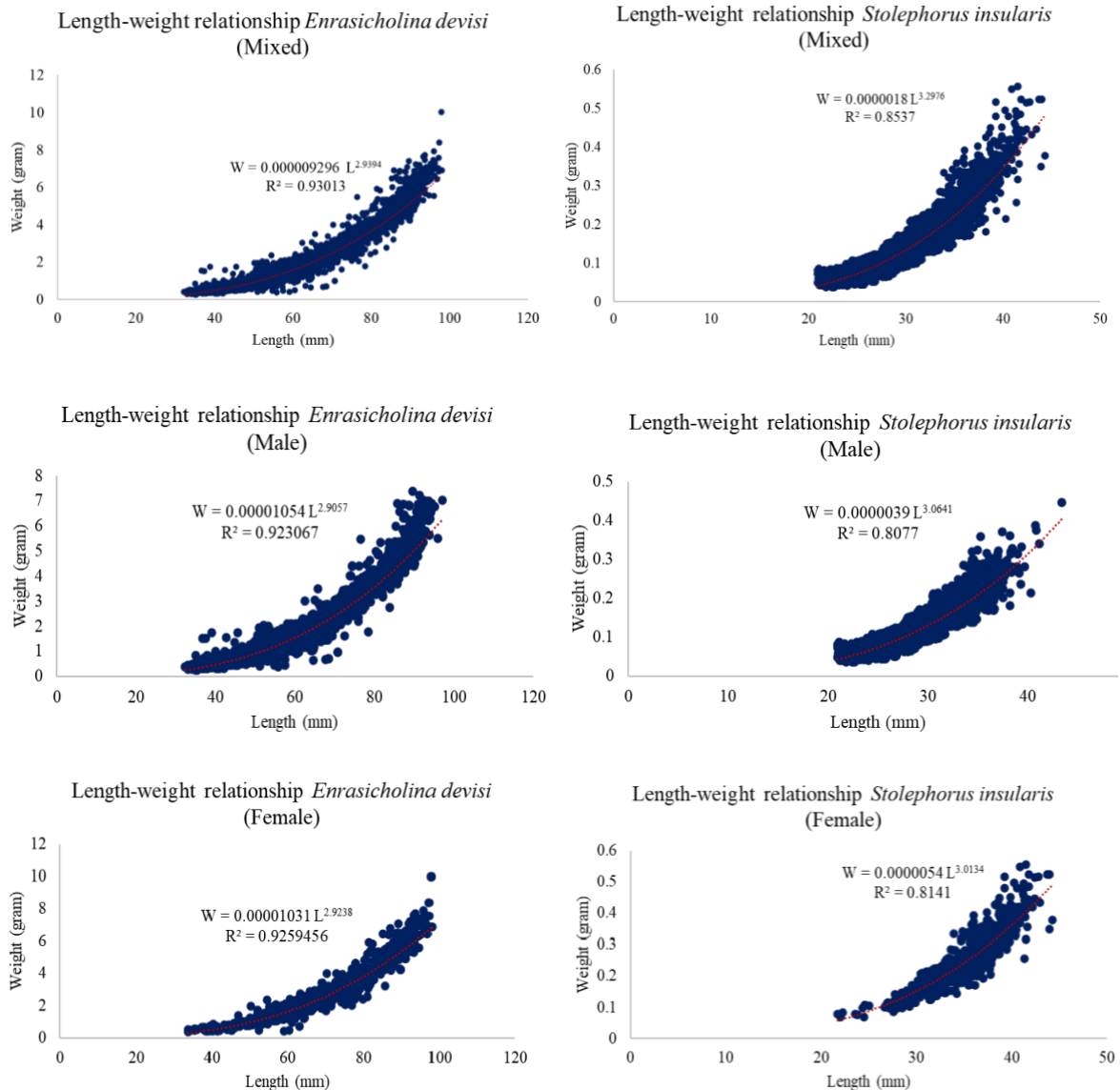


Figure 4. Length-weight relationship of *Enrasicholina devisi* and *Stolephorus insularis* in Tegal Waters, Indonesia

Table 3. Growth parameter *Enrasicholina devisi* and *Stolephorus insularis*

Species	Gender	Sample size	a	b	T-test	Growth patterns	R ²	Regression equations
<i>Enrasicholina devisi</i>	Mixed	6294	0.000009296	2.93	-5.98 < 1.97	Isometric	0.93	$W: 9.29 \times 10^{-6} L^{2.9394}$
	Male	4912	0.00001054	2.90	-7.88 < 1.97	Isometric	0.92	$W: 1.054 \times 10^{-5} L^{2.9057}$
	Female	1382	0.00001031	2.92	-3.43 < 1.97	Isometric	0.92	$W: 1.031 \times 10^{-5} L^{2.9238}$
<i>Stolephorus insularis</i>	Mixed	3252	0.00000180	3.29	12.43 > 1.96	+ Allometric	0.85	$W: 1.80 \times 10^{-6} L^{3.2975}$
	Male	2500	0.00000388	3.06	2.09 > 1.96	+ Allometric	0.80	$W: 3.88 \times 10^{-6} L^{3.0641}$
	Female	752	0.0000054	3.01	0.25 < 1.96	Isometric	0.81	$W: 5.4 \times 10^{-6} L^{3.0133}$

Growth

The Von Bertalanffy's Growth Function (VBGF) for *E. devisi* and *S. insularis* in Tegal Waters shows the rapid growth of *E. devisi* (Table 4), as shown by larger asymptotic lengths (L_{∞} of 101.81-112.22 mm) and higher growth coefficients (K of 2.0-2.9 year⁻¹) compared to *S. insularis*, which has smaller L_{∞} (44.91-51.67 mm) and a

consistent K of 1.6 year⁻¹. While growth performance indices (Φ') are similar for both species, L_{∞} is smaller, and K is larger than in previous studies, indicating variability in growth rates but comparable overall performance (Sena 2007; Boonsuk et al. 2010; Fricke et al. 2012; CMFRI 2015; Gurukinayan et al. 2015; Supeni and Dobo 2017; Eviasta et al. 2018; Juliani et al. 2019; Mulya et al. 2021;

Musel et al. 2022; Hendrayana et al. 2023; Dalzell and Lweis 2024). Species with rapid growth are at higher risk of population collapse (Wang et al. 2020; Otero 2023; Lin et al. 2025).

Anchovies in Tegal Waters have high growth rates (K) and smaller asymptotic lengths (L_{∞}). While these traits promote short-term productivity, they also elevate mortality risks due to rapid maturation and high turnover (Kamal and Teixeira 2023; Smallegange and Lucas 2023; Fellatami et al. 2024; Kutsyn 2025). Although small pelagic species tolerate moderate exploitation, they are vulnerable to overfishing and environmental changes. Several growth factors affect this situation, including temperature, habitat complexity, water quality, food availability, and density (Bang et al. 2022; Sulistyowati and Wullandari 2022; Wijayanto et al. 2022). Climate change may disrupt reproductive timing and biomass which could enhance fisheries yields but increases the mortality (Canales and Cubillos 2021; Ofelio et al. 2023). Thus, effective anchovy fisheries management in Tegal Waters should prioritize environmental quality and regulate exploitation for sustainable productivity and resilience.

Mortality and exploitation

Most of marine organisms, including *E. devisi* and *S. insularis* prefer an average water temperature of 29°C (Hartoko 2023). The population and stock of these fish are affected by fishing pressure that increases mortality rates from overexploitation (Figure 5) (Gulland 1971; Pauly 1980). Selective harvesting may also harm larger reproductive individuals, as it affects the spawning yield and population resilience (Lamarins et al. 2024). The results of comparative studies show that the exploitation rates of *E. devisi* in several regions are low, such as in Lawas and Kutai Kartanegara. However, the exploitation

rates in Tegal and the Andaman Sea are higher (Boonsuk et al. 2010; Supeni and Dobo 2017; Juliani et al. 2019; Musel et al. 2022). On the other side, *S. insularis* experiences consistently high exploitation in the Malacca Strait and Mediterranean (Sena 2007; Fricke et al. 2012; Gurukinayan et al. 2015; Mulya et al. 2021), highlighting how catch levels and environmental factors influence anchovy mortality and exploitation rates (Table 5).

The validity of population parameters for *E. devisi* and *S. insularis* was tested using the ELEFAN method and FISAT II. The normality tests confirmed normal distributions, while sensitivity analyses revealed exploitation rates that consistently exceeded 0.5 (Table 6). This value indicates significant fishing pressure and a primary role for fishing in mortality due to non-sustainable fishing practices. Non-sustainable fishing practices negatively affect juvenile catch rates and hinder recovery (Damora et al. 2018; Koniyo and Juliana 2018; Peatman et al. 2022; Campos et al. 2024). As found in previous studies done from 2012 to 2019, overfishing significantly harmed local anchovy stocks. The stock of fish affects the economic activities, since lower catches indicate stock depletion (Sutono and Susanto 2016; Dewantara et al. 2020). High fishing mortality reduces stock productivity, depletes biodiversity, and causes unstable dynamics that result in recruitment failures and evolutionary shifts toward smaller fish (Zhang et al. 2025; Link and Watson 2019; Bueno-pardo et al. 2020; Canales et al. 2020; Yan et al. 2021; Pham et al. 2023; Daphnee et al. 2024; Durant and Holt 2024; Kindong et al. 2024; Rifai 2025). These challenges threaten the food security and the livelihoods of fishing communities. Therefore, sustainable fishing practices and effective fisheries management should be encouraged (Ojo et al. 2025; Parker 2025).

Table 4. Comparison of VBGF growth parameter *Encrasicholina devisi* and *Stolephorus insularis* in different locations

Species	Gender	L_{∞} (mm)	K	Φ'	Sources
<i>Encrasicholina devisi</i>	Mixed	103.81	2.5	4.43	This study
	Male	112.22	2	4.47	This study
	Female	101.81	2.9	4.4	This study
	Mixed	130.2	1.3	4.3	Juliani et al. 2019
	Mixed	89.25	0.74	3.77	Supeni and Dobo 2017
	Mixed	105	1.8	4.29	Boonsuk et al. 2010
	Mixed	76.1	1.1	3.8	Musel et al. 2022
	Mixed	117	1.59	4.34	CMFRI 2015
	Mixed	74.4	1.59	3.94	Hendrayana et al. 2023
	Male	160	0.31	3.89	Eviasta et al. 2018
	Female	146	0.34	3.86	Eviasta et al. 2018
<i>Stolephorus insularis</i>	Mixed	49	1.6	3.58	This study
	Male	44.91	1.61	3.51	This study
	Female	51.67	1.61	3.63	This study
	Mixed	86	1.66	4.08	Dalzell and Lweis 2024
	Mixed	137.82	0.22	3.62	Sena 2007
	Mixed	58	2.8	3.97	Fricke et al. 2012
	Mixed	39.18	0.89	3.1	Gurukinayan et al. 2015
	Mixed	65.6	0.34	3.1	Mulya et al. 2021

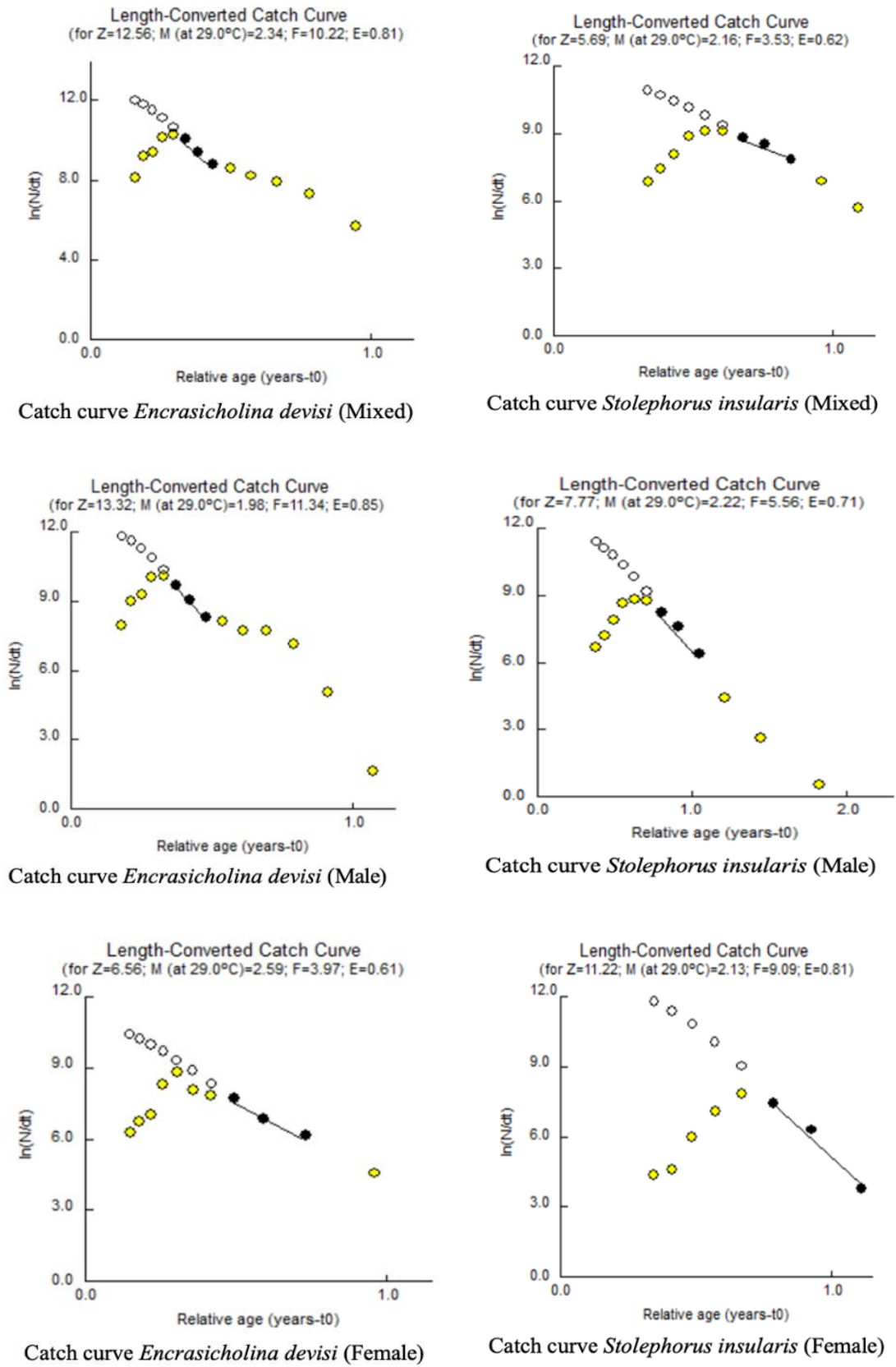


Figure 5. Total (Z), natural (M), fishing mortality (F), and exploitation rate (E) of *Encrasicholina devisi* and *Stolephorus insularis* in Tegal Waters, Indonesia

Table 5. Comparison of growth, mortality, and exploitation rate comparison of *Engrasicholina devisi* and *Stolephorus insularis* in different locations

Species	Grouping	L_{∞} (mm)	K	Z	M	F	E	Sources
<i>Engrasicholina devisi</i>	Mixed	103.81	2.5	12.56	2.34	10.22	0.81	This study
	Male	101.81	2.9	6.56	2.59	3.97	0.61	This study
	Female	112.22	2	13.32	1.98	11.34	0.85	This study
	Mixed	105	1.8	9.59	2.88	6.72	0.70	Boonsuk et al. 2010
	Mixed	89.25	0.74	2.97	1.098	1.87	0.63	Supeni and Dobo 2017
	Mixed	76.1	1.10	4.48	2.88	1.60	0.36	Musel et al. 2022
	Mixed	130.2	1.3	4.59	2.75	1.84	0.40	Juliani et al. 2019
<i>Stolephorus insularis</i>	Mixed	49	1.6	5.69	2.16	3.53	0.62	This study
	Male	44.91	1.61	7.77	2.22	5.56	0.71	This study
	Female	51.67	1.61	11.22	2.13	9.09	0.81	This study
	Mixed	58	2.8	2.76	0.9	1.86	0.67	Fricke et al. 2012
	Mixed	65.6	0.34	0.64	0.75	1.39	2.17	Mulya et al. 2021
	Mixed	39.18	0.89	4.76	1.56	3.199	0.67	Gurukinayan et al. 2015
	Mixed	137.82	0.22	0.99	0.30	0.69	0.70	Sena 2007

The monthly monitoring conducted in this study revealed clear recruitment trends for *E. devisi* and *S. insularis* (Figure 6). Changes in the average length mode each month indicate new recruitment (Roberts and Britton 2020; Yusuf et al. 2023). *E. devisi*'s length increased from 49 mm in July to 59 mm in August 2024, then stabilized at 54-64 mm until March 2025, whereas *S. insularis* peaked at 34.5 mm after beginning at 26.5 mm. Increased fishing pressure on smaller fish leads to higher mortality and disrupted recruitment (Moiron et al. 2020; Roy and Arlinghaus 2022). During peak recruitment months, fishing closure should apply (July-August for *E. devisi* and May-June for *S. insularis*) to protect juvenile and enhance stock resilience. Furthermore, overexploitation of larger individuals affects the spawning populations, success in fish recruitment, and eventual collapse (Uusi-heikkilä 2020; Wootton et al. 2021).

The ACF and PACF plots analysis for *E. devisi* and *S. insularis* revealed stationarity and significant autocorrelation which indicate an inverse relationship and seasonal peaks from July 2024 to March 2025 (July, August, September, November, January, and March) for *E. devisi* and from May 2024 to March 2025 (May, July, August, September, October, November, January, February, and March) for *S. insularis* (Figure 7). Recruitment peaks occur multiple times a year, with minimal activity from April to June. The life span of anchovies are categorized into: short lifespan (40-60 days) and indeterminate multiple-batch spawning (Bang et al. 2022; Febrianto et al. 2023). *E. devisi* shows continuous recruitment pattern (Houde et al. 2022; Dalzell and Lweis 2024), while *S. insularis* has shorter recruitment periods of about one month (Ridwan et al. 2024). The diverse recruitment timelines enhance resilience and adaptability of the fish in the habitat. Both species follow an r-strategy life-history pattern, characterized by rapid

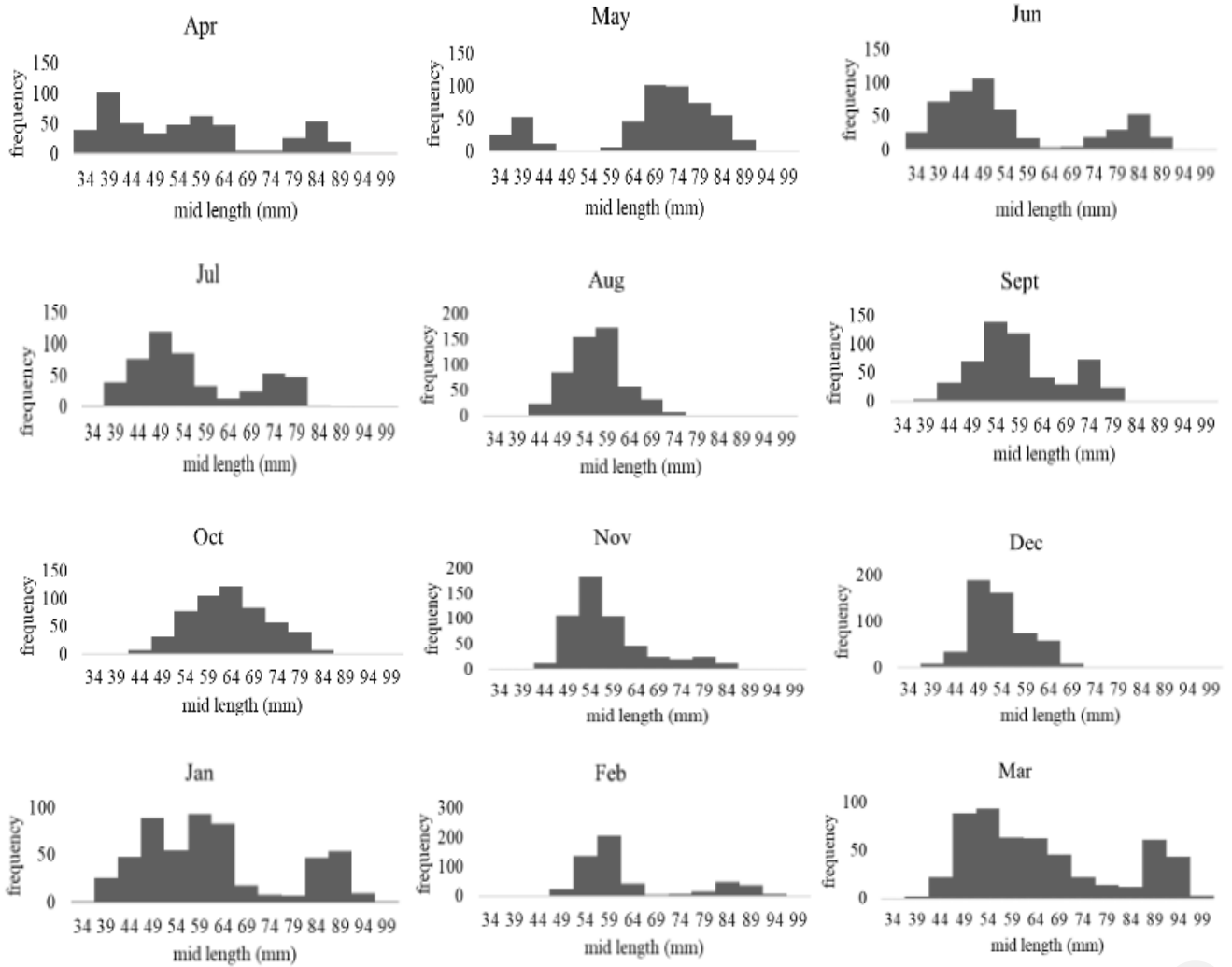
growth and early sexual maturity, with environmental factors (water temperature affecting growth and recruitment success) affecting the population resilience (Finlayson et al. 2020; Chen et al. 2023).

C_{MSY} indicates a significant difference in sustainable catch potential between the species *E. devisi* (485.6739 tons) and *S. insularis* (85.8343 tons). *E. devisi* shows a significantly higher C_{MSY} value (Table 7), implying that species-specific management approaches should be applied, instead of single regulations. The MSY production level is essential for sustainability policies as it determine the acceptable catch limits for the balance between conservation and exploitation (Wijayanto et al. 2025a). Effective stock assessments are crucial in determining C_{MSY} levels to prevent overexploitation and ensure sustainable catches (Liang et al. 2020; Denderen et al. 2024; Liu et al. 2024). Implementing C_{MSY} -based controls is vital for the sustainable exploitation of both species to maintain stock viability.

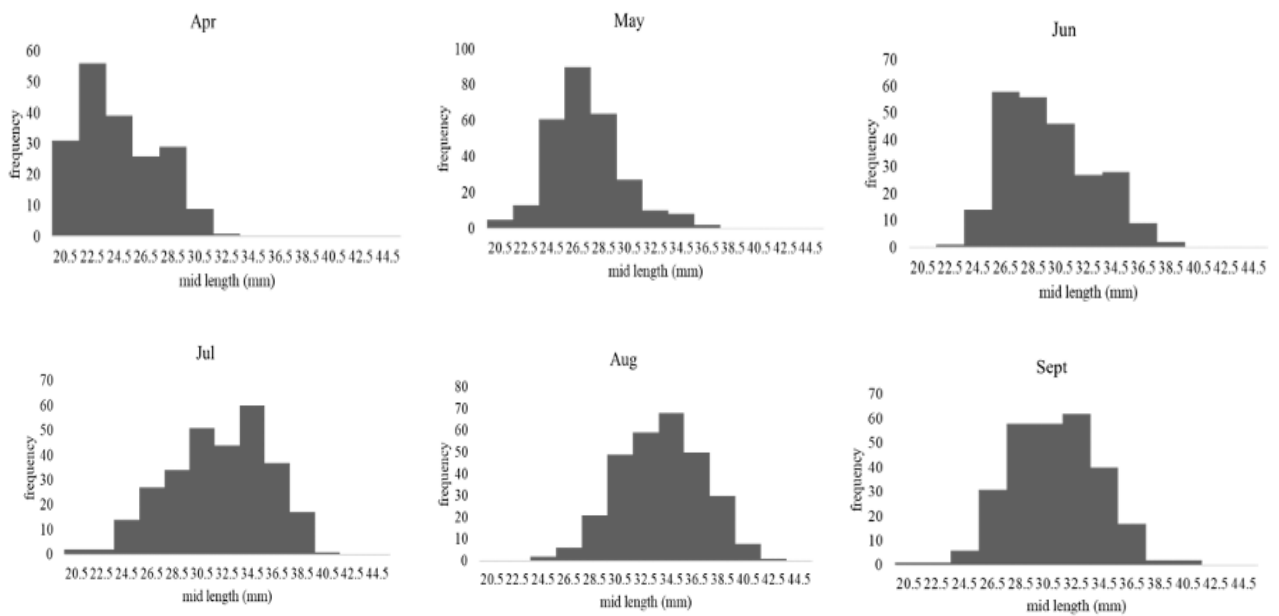
A comparative analysis of *E. devisi* and *S. insularis* reveals distinct growth patterns, exploitation rates, and fishing vulnerabilities. *E. devisi* exhibits isometric growth in both sexes, while *S. insularis* displays positive allometric growth in males and mixed-sex individuals, with isometric growth in females. Exploitation rates for *E. devisi* (E: 0.81) are higher than those of *S. insularis* (E: 0.62), particularly affecting female *E. devisi* (E: 0.85). Fishing pressure on *E. devisi* is higher, since the species can be caught using both anchovy purse seine and boat seine. The recruitment peaks varied, with *E. devisi* occurring between July-August and *S. insularis* in May-June. *E. devisi* has a substantially larger sustainable production potential (485.67 tons) than *S. insularis* (85.83 tons), thereby specific management measures for fast-growing fish should apply (Taboada et al. 2023; Uriarte et al. 2023).

Table 6. Sensitivity analysis with variations in the error values of the variable L_{∞} , K (growth coefficient), F (fishing mortality), M (natural mortality), and Z (total mortality), and their impact on the variable E (exploitation rate)

Variable	Bias variable	<i>Encrasicholina devisi</i>						<i>Stolephorus insularis</i>					
		Male	E	Female	E	Mixed	E	Male	E	Female	E	Mixed	E
L_{∞} (mm)	10%	111.991	0.612	123.442	0.855	114.191	0.815	49.401	0.721	56.837	0.814	53.900	0.628
	5%	106.9005	0.609	117.831	0.853	109.001	0.813	47.156	0.718	54.254	0.812	51.450	0.625
	0%	101.81	0.605	112.220	0.852	103.810	0.811	44.910	0.715	51.670	0.810	49.000	0.621
	-10%	91.63	0.598	100.998	0.848	93.429	0.806	40.419	0.709	46.503	0.806	44.100	0.614
	-5%	96.72	0.602	106.609	0.850	98.620	0.808	42.665	0.712	49.087	0.808	46.550	0.618
K	10%	3.19	0.590	2.200	0.844	2.750	0.801	1.771	0.702	1.771	0.801	1.760	0.607
	5%	3.05	0.598	2.100	0.848	2.625	0.806	1.691	0.709	1.691	0.805	1.680	0.614
	0%	2.90	0.605	2.000	0.852	2.500	0.811	1.610	0.715	1.610	0.810	1.600	0.621
	-10%	2.61	0.622	1.800	0.860	2.250	0.821	1.449	0.729	1.449	0.821	1.44	0.637
	-5%	2.76	0.613	1.900	0.856	2.375	0.816	1.530	0.722	1.530	0.815	1.520	0.629
F	10%	4.37	0.628	12.474	0.863	11.000	0.825	6.116	0.734	9.999	0.825	3.883	0.644
	5%	4.17	0.617	11.907	0.858	10.500	0.818	5.838	0.725	9.545	0.818	3.707	0.633
	0%	3.97	0.605	11.340	0.852	10.000	0.811	5.560	0.715	9.090	0.810	3.530	0.621
	-10%	3.57	0.580	10.206	0.838	9.000	0.794	5.004	0.693	8.181	0.794	3.177	0.596
	-5%	3.77	0.593	10.773	0.845	9.500	0.803	5.282	0.705	8.636	0.802	3.354	0.609
M	10%	2.85	0.582	2.172	0.839	2.569	0.796	2.434	0.696	2.340	0.795	2.366	0.598
	5%	2.72	0.593	2.074	0.846	2.452	0.803	2.323	0.706	2.234	0.803	2.258	0.610
	0%	2.59	0.605	1.975	0.852	2.335	0.811	2.213	0.715	2.128	0.810	2.151	0.621
	-10%	2.33	0.630	1.777	0.864	2.102	0.826	1.991	0.736	1.915	0.826	1.936	0.645
	-5%	2.46	0.617	1.876	0.858	2.219	0.818	2.102	0.726	2.021	0.818	2.043	0.634
Z	10%	7.22	0.550	14.652	0.774	13.574	0.737	8.558	0.650	12.342	0.737	6.259	0.564
	5%	6.89	0.576	13.986	0.811	12.957	0.772	8.169	0.681	11.781	0.772	5.975	0.591
	0%	6.56	0.605	13.315	0.852	12.335	0.811	7.773	0.715	11.218	0.810	5.681	0.621
	-10%	5.90	0.673	11.983	0.947	11.102	0.901	6.995	0.794	10.096	0.900	5.113	0.691
	-5%	6.23	0.637	12.649	0.896	11.719	0.853	7.384	0.753	10.657	0.853	5.397	0.654



A



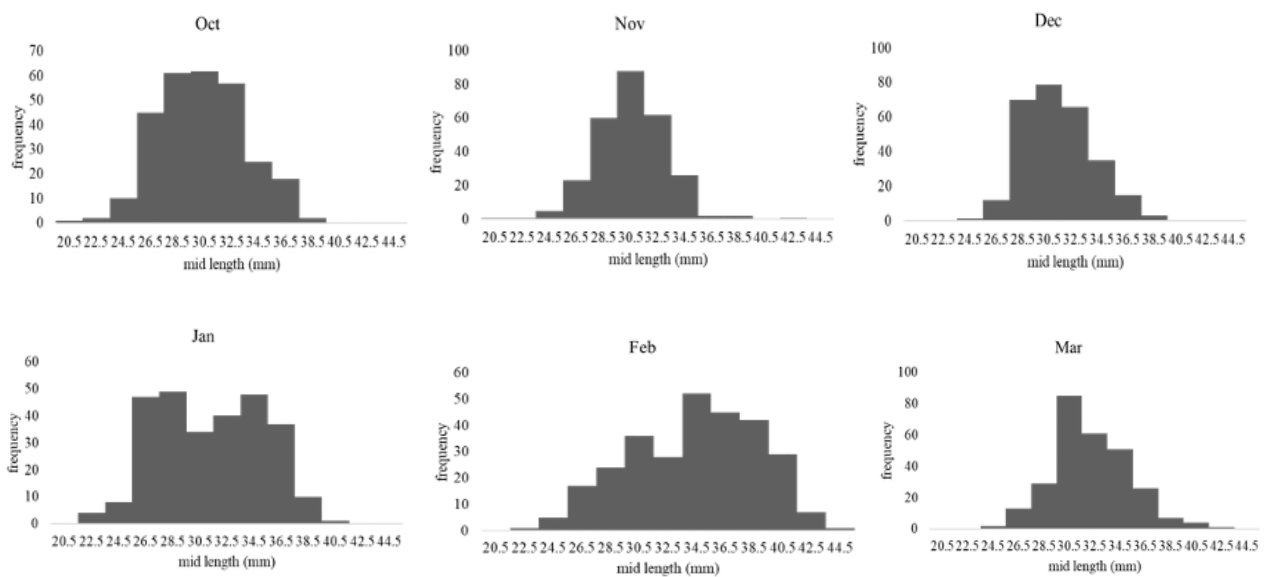
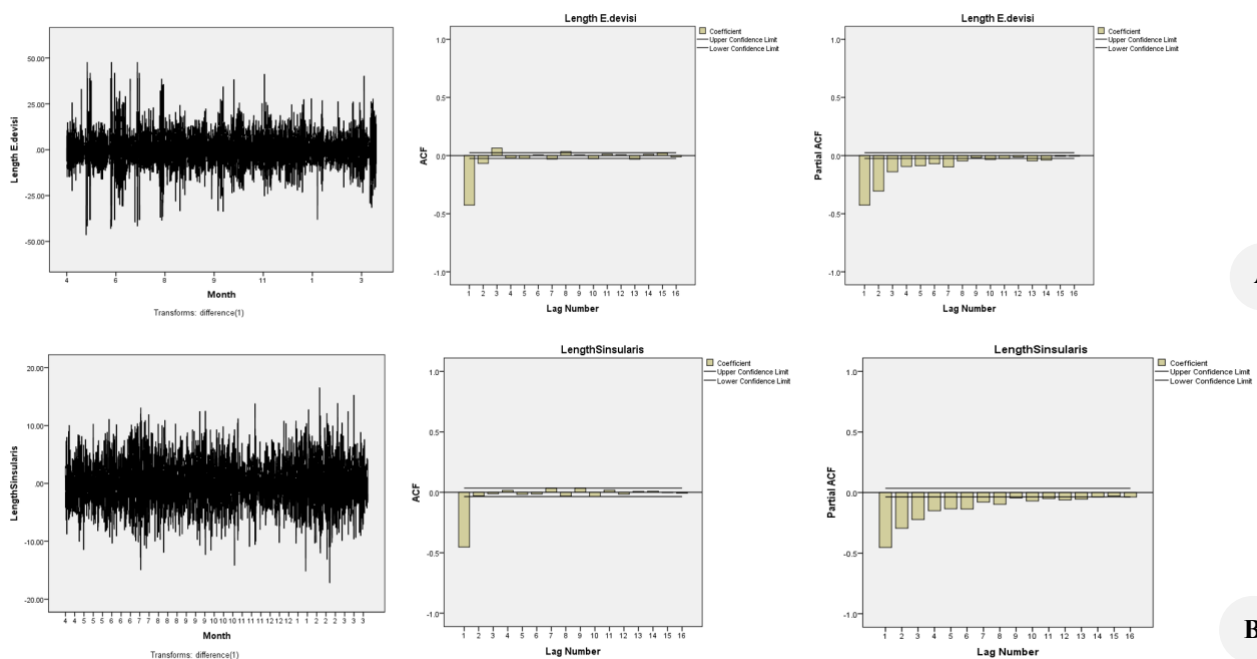


Figure 6. Monthly seasonal frequency of mid-length. A. *Encrasicholina devisi*, B. *Stolephorus insularis*

B



A

B

Figure 7. Time series of recruitment deviations, autocorrelation (ACF), and partial autocorrelation of (A) *Encrasicholina devisi* and (B) *Stolephorus insularis* in Tegal Waters. Dashed lines in autocorrelation and partial autocorrelation panels indicate 95% confidence intervals

Table 7. Estimated Catch at Maximum Sustainable Yield (C_{MSY}) and economic value

Species	C_{MSY} (tons)	Estimated economic value (Rp)
<i>Encrasicholina devisi</i>	485.6739	5.8 billion
<i>Stolephorus insularis</i>	85.8343	3.7 billion

Note: *using 2024 production data; **using the assumption of *E. devisi* price at the fisherman level of IDR 12,000 per kg, and *S. insularis* IDR 45,000 per kg

Effective management of anchovies in Tegal Waters requires adaptive strategies that integrate biological, governance, and socio-economic knowledge. The global fisheries data report that seasonal closures adjusted to the recruitment periods, recruitment-based decision-making, and reliable monitoring systems are effective management system to apply (Kroetz et al. 2019; Andr et al. 2023; Smith et al. 2023; Lahellec et al. 2024; Owusu 2024; Wang and Zhang 2025; Quezada et al. 2025). To reduce juvenile

captures in Tegal Waters, short-term seasonal closures should be conducted during recruitment maxima (May to June for *S. insularis* and July to August for *E. devisi*). It is also necessary to increase gear selectivity by increasing mesh size by 1-2 mm. Reducing fishing effort by 30-40% and keeping catches within C_{MSY} reference points (485.67 tons for *E. devisi* and 85.83 tons for *S. insularis*) will help maintain sustainable exploitation. A comprehensive approach that includes effort reduction, selective gear use, strong law enforcement, and local governance is essential to ensure the long-term sustainability of Tegal's anchovy fisheries.

In conclusion, this study demonstrates that *E. devisi* and *S. insularis*, which are often managed as a single resource, have different population dynamics, production capacities, and vulnerability to fishing pressure. Differences in growth patterns, with isometric growth in *E. devisi* and positive allometric growth in *S. insularis*, reflect different energy allocation strategies and influence their responses to exploitation. This is evident from the higher exploitation rate of *E. devisi* (E: 0.81) compared to *S. insularis* (E: 0.62). The higher vulnerability of *E. devisi* is associated with exposure to multiple fishing gears, especially anchovy purse seines and boat seine, which can negatively affect already exploited populations. These findings indicate that fishing pressure on *E. devisi* has reached a biologically risky level and requires immediate and targeted regulation. The strongly male-biased sex ratio in both species and the different peak recruitment periods, July-August for *E. devisi* and May-June for *S. insularis*, indicates species-specific vulnerabilities occurring at different life-history stages. These include reduced reproductive capacity in *E. devisi* and increased juvenile exploitation in *S. insularis*. The large difference in C_{MSY} values (485.67 tons for *E. devisi* and 85.83 tons for *S. insularis*) provides a strong quantitative basis for evidence-based fisheries management. These results highlight the need for adaptive, species-specific policies, including seasonal regulation, effort control, and catch limits, to ensure long-term sustainability and support the resilience of small-scale fisheries.

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