International Journal of Design & Nature and Ecodynamics
Vol. 21, No. 10, October, 2026, pp. 2861-2882
Journal homepage: http://iieta.org/journals/ijdne

Sea Surface Temperature, Monthly Spatial Variation and Population Dynamics of Flying Fish *Exocoetidae* in the Ombai Strait, Belu Regency, East Nusa Tenggara, Indonesia

Raymundus Putra Situmorang[1,2*], Agus Hartoko[3], Anindya Wirasatriya[4], Kunarso[4], Yosy Gustasya[5]

[1] Doctoral Program - Aquatic Resources Management, Faculty of Fisheries and Marine Science, Diponegoro University, Semarang 50275, Indonesia
[2] Capture Fisheries Department, Faculty of Military Logistics Vocational Studies, The Republic of Indonesia Defense University, Belu 85752, Indonesia
[3] Department of Aquatic Resources Management, Faculty of Fisheries and Marine Science, Diponegoro University, Semarang 50275, Indonesia
[4] Department of Oceanography, Faculty of Fisheries and Marine Science, Diponegoro University, Semarang 50275, Indonesia
[5] Aquaculture Study Program, Faculty of Military Logistics Vocational Studies, The Republic of Indonesia Defense University, Belu 85752, Indonesia

Corresponding Author Email: raymundusp@gmail.com

Copyright: ©2026 The authors. This article is published by IIETA and is licensed under the CC BY 4.0 license (http://creativecommons.org/licenses/by/4.0/).

https://doi.org/10.18280/ijdne.211003

Received: 4 August 2026
Revised: 28 September 2026
Accepted: 8 October 2026
Available online: 31 October 2026

Keywords:
flying fish, population dynamics, reproductive biology, sea surface temperature, spawning zone, fisheries management

ABSTRACT

Flying fish of the family *Exocoetidae* are an important small pelagic fishery resource in eastern Indonesian waters, including the Ombai Strait. This study aimed to characterize the monthly and spatial variation of sea surface temperature (SST), analyze flying fish population characteristics, and identify potential reproductive or spawning zones. Field observations were conducted at 12 fishing stations located at 2, 4, 6, and 12 nautical miles during June–November 2024 and May 2025. Five flying fish species were identified. Mean SST ranged from 27.81 °C in August 2024 to 31.13 °C in November 2024 across the available sampling periods, spanning the East Monsoon and the available November observation of the West Monsoon. Male flying fish exhibited significantly negative allometric growth (b = 2.7184, p < 0.001), whereas female growth was statistically consistent with isometric growth (b = 2.9358, p = 0.062). The female-to-male ratio was 1.00:1.52, and immature gonads dominated the catch (72.95%). Female Lm_{50} ranged from 17.8–27.0 cm total length (TL), while female Lc_{50} was lower than Lm_{50} at seven of eleven comparable stations. Spatial integration of gonadal maturity, female size relative to Lm_{50}, and environmental SST context identified areas with potential reproductive characteristics, particularly around 6–12 nautical miles. These findings support spatially adaptive fisheries management based on reproductive characteristics, fishing selectivity, and environmental conditions.

1. INTRODUCTION

Marine capture fisheries continue to face increasing challenges in maintaining the biological sustainability of exploited fish stocks. The most recent global assessment reported that approximately 35.5% of assessed marine fish stocks were overfished, while 64.5% were exploited within biologically sustainable levels [1]. These conditions highlight the importance of fisheries management approaches that consider not only catch production and exploitation rates, but also population structure, reproductive characteristics, and the capacity of exploited stocks to maintain their productivity over time. Sustainable fisheries management therefore requires biological information that can identify changes in population structure and reproductive status before substantial declines in overall production become apparent.

In Indonesia, these challenges are particularly relevant for small pelagic fisheries, which contribute substantially to food security, livelihoods, and the economy of coastal communities. Flying fish Exocoetidae are an important small pelagic resource in eastern Indonesian waters and are particularly relevant in the border region between Indonesia and Timor-Leste. The Ombai Strait represents an important fishing ground for flying fish and is also a transboundary marine system in which the resource is utilized by fishing communities from both countries [2]. Identified flying fish as an important fisheries commodity in the Indonesia–Timor-Leste border region and reported that the flying fish stock in the Ombai Strait is shared by fishermen from both countries. Their study estimated an exploitation rate of approximately 0.11, which was considered to be within a rational utilization range at the time of their study.

At the national management scale, the status of flying fish resources in Fisheries Management Area (FMA)-573 also does not currently indicate a high level of utilization. According to Decree of the Minister of Marine Affairs and

Fisheries of the Republic of Indonesia Number 76 of 2024 concerning the Flying Fish Fisheries Management Plan, the utilization level of flying fish in FMA-573 was estimated at 0.12, whereas the utilization level of small pelagic fish in the same FMA was 0.60. The flying fish value represents a 2023 pro-rata estimate by the Indonesian National Research and Innovation Agency (BRIN) [3]. This relatively low utilization level indicates that, at the FMA scale, flying fish resources in FMA-573 were not classified as fully utilized. However, an aggregated utilization estimate at the FMA scale may not adequately represent spatial differences in fishing intensity, population structure, reproductive condition, and fishing selectivity among individual fishing grounds.

This distinction is particularly important in the Ombai Strait, where fishing activities occur across geographically heterogeneous fishing grounds. A relatively low exploitation or utilization level at a broad management-unit scale does not necessarily mean that all fishing grounds have similar biological characteristics or that all components of the population experience the same level of fishing vulnerability. Changes in size composition, the proportion of immature individuals, length at first maturity (Lm_{50}), and length at first capture (Lc_{50}) may provide additional information regarding the biological condition of an exploited population that cannot be fully described by an aggregated exploitation indicator alone. Therefore, biological assessment at the fishing-ground scale is necessary to complement existing FMA-level fisheries assessments.

Previous studies have provided important information on the biology and population dynamics of flying fish in eastern Indonesia [4]. The previous research documented species diversity and differences in length distribution of flying fish between the Flores Sea and Sulawesi Sea, demonstrating spatial variability in the size characteristics of flying fish populations. Similarly reported differences in size structure among flying fish populations from the Makassar Strait, Sulawesi Sea, and Arafura Sea were reported, indicating that biological characteristics can vary among geographic areas [5]. These findings demonstrate that flying fish populations should not necessarily be considered biologically homogeneous across eastern Indonesian waters.

The biological characteristics and distribution of pelagic fish are also closely associated with oceanographic variability. The previous research emphasized that Indonesian waters possess distinct oceanographic characteristics and ecosystem conditions, which influence the occurrence, abundance, diversity, and spatial distribution of plankton resources. The interaction between oceanographic conditions and plankton distribution is also relevant to the spatial occurrence of plankton-feeding organisms, including juvenile and small pelagic fish, and may contribute to the identification of spawning, nursery, and fishing grounds [6]. Therefore, environmental variables that characterize the oceanographic conditions of fishing grounds should be considered when interpreting spatial and temporal variability in small pelagic fish populations.

Among oceanographic variables, sea surface temperature (SST) is an important indicator of the thermal condition of marine habitats and exhibits substantial seasonal and spatial variability. In the Indonesian Seas, seasonal SST variability is strongly influenced by monsoonal forcing and ocean dynamics, including the upwelling of subsurface water, resulting in distinct spatial and seasonal temperature patterns [7]. Therefore, in the present study, SST is treated primarily as an environmental indicator of the surface thermal habitat rather than as a sole determinant of flying fish distribution.

Oceanographic conditions are also relevant to the biological and reproductive characteristics of flying fish. Nur et al. [8] reported that the reproductive strategy of flying fish is associated with environmental variability may influence reproductive activity, such as temperature, flows, sea levels, lunar phase, and spawning. Thus, examining monthly spatial SST together with biological observations can provide an environmental context for understanding spatial differences in flying fish population characteristics and reproductive condition.

From an ecological perspective, flying fish are components of pelagic ecosystems, and their distribution and biological characteristics may vary in relation to environmental conditions. Oceanographic variability, including fluctuations in SST, can provide information on changes in habitat conditions that may be associated with food-resource availability, habitat use, growth, reproduction, and fish distribution. Therefore, interpretation of flying fish population characteristics should consider not only biological indicators but also the spatial and monthly environmental conditions of the fishing grounds where fish are captured. This perspective is consistent with ecosystem-based fisheries management (EBFM), which considers the interrelationships among fish resources, environmental conditions, habitats, and fishing activities. In this context, integrating environmental information with size structure, gonadal maturity, length at first maturity, and length at first capture can provide a more comprehensive understanding of spatial heterogeneity and reproductive vulnerability of flying fish resources.

For fisheries resource management, spatial information on reproductive characteristics is particularly important because areas with a high occurrence of reproductively mature individuals may have greater ecological importance for maintaining the reproductive potential of the resource. The spatial distribution of gonadal maturity stages, particularly mature and reproductively advanced individuals, together with fish size relative to Lm_{50}, can provide an initial basis for identifying areas with potential reproductive importance. When these biological indicators are considered together with the corresponding monthly SST conditions and geographic location of fishing grounds, they can be used to identify potential reproductive or spawning zones that may warrant further ecological verification, monitoring, and consideration in spatial fisheries management. Such identification should be regarded as a preliminary assessment rather than confirmation of spawning grounds, because direct evidence of spawning activity, eggs, or larvae would be required for definitive designation.

Several studies have specifically investigated flying fish in the Ombai Strait. Rehatta et al. [2] examined growth, mortality, recruitment, and exploitation rate using flying fish obtained from landings in Belu, Indonesia, and Bobonaro, Timor-Leste. The study reported an asymptotic length of 330.5 mm total length (TL), a growth coefficient of 0.99 $year^{-1}$, and year-round recruitment, with relatively high recruitment occurring during May–September. Although this study provided important population-dynamic information for the Ombai Strait, the biological samples were obtained from fish landed at fishing sites rather than from fish sampled directly at geographically referenced fishing locations.

This represents an important research gap because landing-based biological data may integrate fish originating from

multiple fishing grounds and therefore potentially obscure spatial differences in population characteristics. Direct sampling at sea, accompanied by recording of fishing coordinates, provides an opportunity to associate biological characteristics with specific fishing grounds and the environmental conditions prevailing at the time and location of capture. Such an approach is particularly relevant in the Ombai Strait because its oceanographic environment is influenced by monsoonal forcing and the Indonesian Throughflow, potentially generating spatial and monthly variability in SST and other environmental conditions.

The scientific advancement of the present study therefore lies not in the individual measurement of SST, size structure, or reproductive characteristics, as these parameters have been examined in previous studies, but in their spatially referenced integration at the fishing-ground scale. By obtaining fish directly from geographically referenced fishing locations and linking biological observations with the SST conditions corresponding to the sampling period and location, this study provides a finer-scale environmental–biological perspective than assessments based solely on aggregated landing data. This approach enables biological indicators, including size structure, gonadal maturity, Lm_{50}, and Lc_{50}, to be evaluated in relation to the spatial and temporal context of individual fishing grounds.

Despite these previous studies, spatially explicit information on the biological and reproductive characteristics of flying fish in relation to geographically referenced fishing grounds and monthly oceanographic conditions in the Ombai Strait remains limited. In particular, previous assessments have generally described biological characteristics at broader spatial or landing-based scales, whereas information linking population characteristics, reproductive indicators, and environmental conditions to specific fishing grounds remains scarce. Furthermore, the spatial identification of areas with potential reproductive importance based on the integration of SST, population characteristics, gonadal maturity, and Lm_{50} has not been sufficiently addressed. The present study addresses this gap by integrating monthly spatial SST information with spatially referenced biological and reproductive observations to characterize population dynamics and identify potential reproductive or spawning zones in the Ombai Strait.

The novelty of this study does not lie in the individual measurement of SST, size structure, or reproductive characteristics of flying fish, as these aspects have been examined in previous studies. Rather, the scientific contribution of this study lies in integrating environmental information and population and reproductive characteristics at the fishing-ground scale based on geographically referenced fishing locations. Unlike landing-based approaches that may aggregate fish originating from multiple fishing grounds, this study obtained fish samples directly from fishing locations recorded using geographic coordinates and linked them with SST conditions corresponding to the sampling location and month. This approach allows variation in population structure, gonadal maturity, Lm_{50}, and Lc_{50} to be interpreted within the environmental context of individual fishing grounds. Furthermore, the integration of reproductive indicators with spatial SST and fishing-ground information provides a preliminary basis for identifying areas with potential reproductive importance and prioritizing them for further monitoring and conservation-oriented fisheries management.

Therefore, this study aimed to: (1) characterize the monthly spatial variation of SST in the Ombai Strait; (2) analyze the spatial dynamics of flying fish population characteristics based on size structure, species composition, length–weight relationship, sex ratio, condition factor, gonadal maturity, length at first maturity (Lm_{50}), and length at first capture (Lc_{50}); and (3) identify potential reproductive or spawning zones by integrating monthly spatial SST information with population and reproductive indicators, particularly gonadal maturity, fish size relative to Lm_{50}, and the spatial occurrence of reproductively mature individuals. The resulting spatial information is intended to provide a basis for fisheries resource management, including the prioritization of areas for further reproductive-ground verification, spatial monitoring, and conservation measures in the Ombai Strait.

2. MATERIAL AND METHOD

2.1 Study area and sampling design

This study was carried out in the Ombai Strait coastal waters of Belu Regency, East Nusa Tenggara, with twelve observation stations that have active flying fish catches, regarded as different fishing ground areas. The twelve stations' coverage is: (St 1,2,3) distance from the fishing base at Belu coast is 2 nautical miles; (St 4,5,6) distance from the fishing base is 4 nautical miles; (St 7,8,9) distance from the fishing base is 6 nautical miles; and (St 10,11,12) distance from the fishing base is 12 nautical miles, as illustrated in Figure 1. The sampling locations were geographically referenced using GPS coordinates recorded during fishing operations. These geographic coordinates were used to associate biological observations with their corresponding fishing grounds and to examine spatial variation in fish size structure, reproductive characteristics, and environmental conditions. Accordingly, spatial analyses were interpreted not only according to distance from the coast but also according to the geographic distribution of the sampling stations.

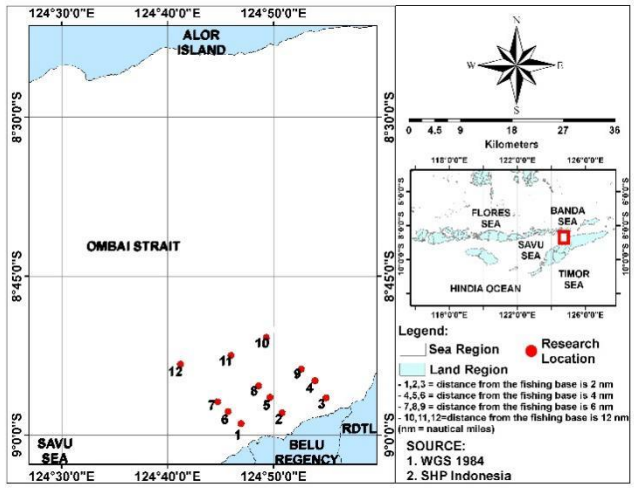


Figure 1. Research location in Ombai Strait

The research method applied in this study was a survey method [9]. Twelve fishing stations were established at the beginning of the study and maintained as fixed sampling stations throughout the observation period. The stations represented four nominal fishing-distance categories from the coastline: 2, 4, 6, and 12 nautical miles, with three stations

assigned to each category (ST1–ST3, ST4–ST6, ST7–ST9, and ST10–ST12, respectively). Repeated observations were conducted at the same designated stations during each available sampling month to maintain a consistent spatial sampling design and facilitate temporal comparisons among fishing grounds [9]. A total of 3087 individual samples were obtained from twelve observation stations; flying fish were collected directly from fishing operations using gillnets operated by fishing vessels at the designated sampling stations. The fishing gear had a TL of 95.96 m and a width of 2.22 m, with a soaking duration of approximately 2 h. Because biological observations were obtained from gillnet fishing operations, the sampled individuals represent the fishery-available component of the flying-fish assemblage and may be subject to gear-related size selectivity. The *Exocoetidae* samples were taken proportionally using the following criteria:

1) If the number of flying fish caught was <10 kg, the number of fish samples taken was 100% of the fish catch from each field station and month;

2) If the number of flying fish caught was >10 kg, the number of samples taken was 10 kg of the production landed from each field station and month;

Actual fish catch data as primary data were collected during seven sampling months, namely June–November 2024 and May 2025. Sampling was not conducted during December 2024–April 2025 because of unfavorable sea conditions and high waves, resulting in a five-month interruption in field observations. Therefore, the dataset does not provide continuous monthly coverage across the entire annual cycle. The biological characteristics used to characterize the flying fish population included TL, body weight, sex, and gonad maturity level, following parameters commonly used in studies of flying fish biology and population characteristics [10]. Fish length measurement, weighing of flying fish samples were conducted at the Capture Fisheries Laboratory, Faculty of Vocational Military Logistic, The Republic of Defense University, Belu Regency, East Nusa Tenggara Province.

Species identification. Flying fish specimens were identified based on external morphological characteristics and taxonomic references. Species identification was subsequently verified using the FishBase database. Five species were identified during the study: *Cypselurus poecilopterus*, *Cheilopogon abei*, *Cheilopogon spilopterus*, *Hirundichthys oxycephalus*, and *Cheilopogon intermedius*. Five flying fish species were identified during the study. The subsequent biological analyses, including length–weight relationship, sex ratio, condition factor, gonadal maturity, Lm_{50}, and Lc_{50}, were conducted using pooled *Exocoetidae* samples rather than species-specific datasets. The analytical design focused on characterizing the spatial biological and reproductive characteristics of the sampled flying-fish assemblage across fishing grounds.

Satellite-derived SST. SST data were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard the Aqua satellite. Level-3 SST products with a spatial resolution of 4 km and 8-day temporal composites were used to characterize the surface thermal conditions of the Ombai Strait during the sampling period. The 8-day composite products were used to reduce the effects of cloud cover and obtain more spatially continuous SST observations.

SST data covering the study area were extracted for each sampling period and processed to obtain the minimum, maximum, mean, and standard deviation (SD) of SST for each sampling month. SST values corresponding to the geographically referenced fishing stations were also extracted to characterize the thermal conditions of the fishing grounds at 2, 4, 6, and 12 nautical miles from the coast. The monthly SST values were subsequently compared descriptively to identify temporal and spatial variability in the surface thermal conditions during the observation period.

2.2 Relationship between sea surface temperature and fish size

To evaluate the association between environmental conditions and fish size, Pearson's correlation analysis was applied to paired station-month observations of SST and mean TL. Only station-month observations with complete SST and mean TL data were included in the analysis. The analysis was intended to assess the strength and direction of association between SST and fish size rather than to infer a causal relationship.

Fish size structure. The fish size structure reflects the size composition of the fish and was presented in the form of a histogram graph. In addition, descriptive statistical calculations were carried out to the minimum, maximum and mode sizes [11].

TL-weight relationship. The increase in fish body weight (W) at each life stage is a function of length increase (L). Therefore, to calculate the relationship between TL and fish weight, the general formulae proposed by researchers [11, 12] used in this study are as follows:

$$W = a \times L^b$$

where, W = weight of fish (grams); L = total length (TL) of fish (cm); a and b = constants obtained from the regression results of the length-weight relationship.

Transformation into a linear equation using logarithm as follows:

$$\log W = \log a + b \log L$$

The equation is used to determine the relative growth curve of the fish. If the value of growth coefficient (b) = 3 indicates that the pattern of relative growth is isometric; the increase in weight is proportional to the increase in length. If the b value $\neq 3$, it indicates an allometric relative growth pattern, i.e., the increase in weight is not proportional to the increase in length.

The value of b was statistically tested against the theoretical value of 3 using a t-test to determine whether the observed growth pattern differed significantly from isometric growth. The standard error and 95% confidence interval (CI) of b were also calculated. The null hypothesis (H_0) assumed that $b = 3$ (isometric growth), whereas the alternative hypothesis (H_1) assumed that $b \neq 3$ (allometric growth). Statistical significance was evaluated at $\alpha = 0.05$. When b was significantly lower than 3, the growth pattern was classified as negative allometric, whereas a significantly higher b indicated positive allometric growth. If the test was not significant, the growth coefficient was considered not significantly different from isometric growth.

Fish condition factor (K). If the b value = 3, the condition factor is calculated using the following formula [11]:

$$k = \frac{10^3 \times W}{L^3}$$

But if $b \neq 3$, the condition factor is calculated using the formula as follows:

$$k = \frac{W}{aL^b}$$

where, K = condition factor; W = weight (grams); L = total length (cm); a and b = constants obtained from the regression results of the length-weight relationship. For consistency, L was expressed in cm in the length–weight relationship and condition-factor calculations.

In this study, we use this formula because the b value $\neq 3$. K value is used to identify the conditions where the species live. When the K value is greater than or equal to 1, the fish is in good growth condition; but when K is less than 1, the fish is in poor growth condition [12].

Sex ratio. The sex ratio of *Exocoetidae* was obtained from the equation [12]:

$$SR = \frac{Nm}{Nf}$$

where, SR = sex ratio; Nm = number of male fish (individuals); Nf = number of female fish (individuals).

Sex ratio analysis. The observed sex ratio was tested against the expected 1:1 ratio using a Pearson chi-square goodness-of-fit test. The null hypothesis assumed an equal proportion of males and females. Statistical significance was evaluated at $\alpha = 0.05$.

The Pearson chi-square goodness-of-fit test was used to determine whether the observed sex ratio differed significantly from the expected 1:1 ratio. Because two sex categories (male and female) were compared, the test had one degree of freedom (df = 1).

Estimation of the size of the first caught fish (Lc50). Estimating the size of the first caught fish uses a graph of the relationship between the class length distribution (X-axis) and the number of fish expressed by estimating the cumulative normal distribution (Y-axis). The first size (Lc_{50}) of flying fish is obtained from the equation of [13]:

$$Slest = \frac{1}{(1 + Exp\ (S_1 - S_2)x\ L)}$$
$$Lc_{50} = \frac{S_1}{S_2}$$

where, $Slest$ = maximum slope of the logistic curve; S_1 = intercept value a (intersection between the linear line and the y-axis); S_2 = slope b value (the slope angle of the regression line).

Station-level estimates of Lm_{50} and Lc_{50} were calculated separately for each sampling station. For Lm_{50}, the analysis used female flying fish recorded at each station, whereas Lc_{50} was estimated separately for males and females using the corresponding station-level length-frequency data. The sample size used for each estimate is reported in the section results Lm_{50} and Lc_{50}. Estimates were interpreted with caution when the available sample size was limited or when the distribution of fish among length classes and gonadal maturity stages was insufficient to provide a reliable estimate. At ST3, Lm_{50} was not estimated because the available female sample was limited and did not provide sufficient information for a reliable maturity-size estimate.

Gonad maturity index (GMI) and size of the first mature gonad (Lm). Observation of the GMI was carried out using the morphological method [13]; the gonad maturity level of flying fish takes place in five stages, and the morphological characteristics used to classify the five gonadal maturity stages are summarized in Table 1.

Table 1. Gonad maturity index (GMI) of the *Exocoetidae*

Stage	Ovaries	Testes
GMI 1 (Young Fish phase)	The gonads are very small, thread-like, white, and transparent.	Opaque testicles
GMI 2 (Initial maturity phase)	Ovaries are round, light yellow in color; new ova are visible.	Thick, flat, whitish testicles
GMI 3 (Mature phase)	The ovaries are swollen, measuring approximately 30–60% of the abdominal cavity, and are clearly visible, yellow in color.	The testes are full, thick, convex, and triangular in shape. They occupy approximately 25–50% of the abdominal cavity and are increasingly white.
GMI 4 (Spawning phase)	Ovaries are full size, ±60–90% of the abdominal cavity. The egg drops out with a little pressure; color is reddish yellow.	The testicles are fully extended, approximately 50–85% of the abdominal cavity. Semen fluid is released when slightly pressed and is thick and white in color.
GMI 5 (spent phase)	The ovaries shrink to approximately 5–30% of the abdominal cavity, with visible blood vessels in the abdominal cavity, and reddish-colored residual eggs.	The testicles shrink to approximately 5–25% of the abdominal cavity, with visible blood vessels and a small amount of thick white fluid remaining.

The size of the first mature gonad is calculated using the Spearman-Karber equation developed by [13]:

$$m = x_k + \frac{d}{2} - (d\Sigma \mathrm{Pi})$$

where,

m = logarithm of the fish length when they first mature gonads;

X_k = logarithm of the median value of the length class when all fish have 100% or completely mature gonads;

d = difference in the logarithm of the median value;

p_i = proportion of mature gonads in the i-th class ($p_i = r_i/n_i$).

Thus, the average L of flying fish at the time of reaching the first mature gonad is M = antilog m.

3. RESULTS

3.1 Monthly spatial variation in sea surface temperature

Descriptive analysis of the available SST observations showed monthly and spatial variation across the sampling stations (Figure 2). During the East Monsoon (May–October), mean SST varied from 27.81 ℃ in August 2024 to 29.80 ℃ in May 2025, with an overall mean of approximately 28.88 ℃

across the six sampling periods. The lowest monthly mean SST occurred in August 2024 (27.81 ℃), followed by July 2024 (27.88 ℃), whereas the SST increased during September and October, reaching 29.56 ℃ in October. In contrast, the November 2024 observation, representing the available sampling period within the West Monsoon (November–April), showed a substantially higher mean SST of 31.13 ℃, with values ranging from 30.97 to 31.55 ℃.

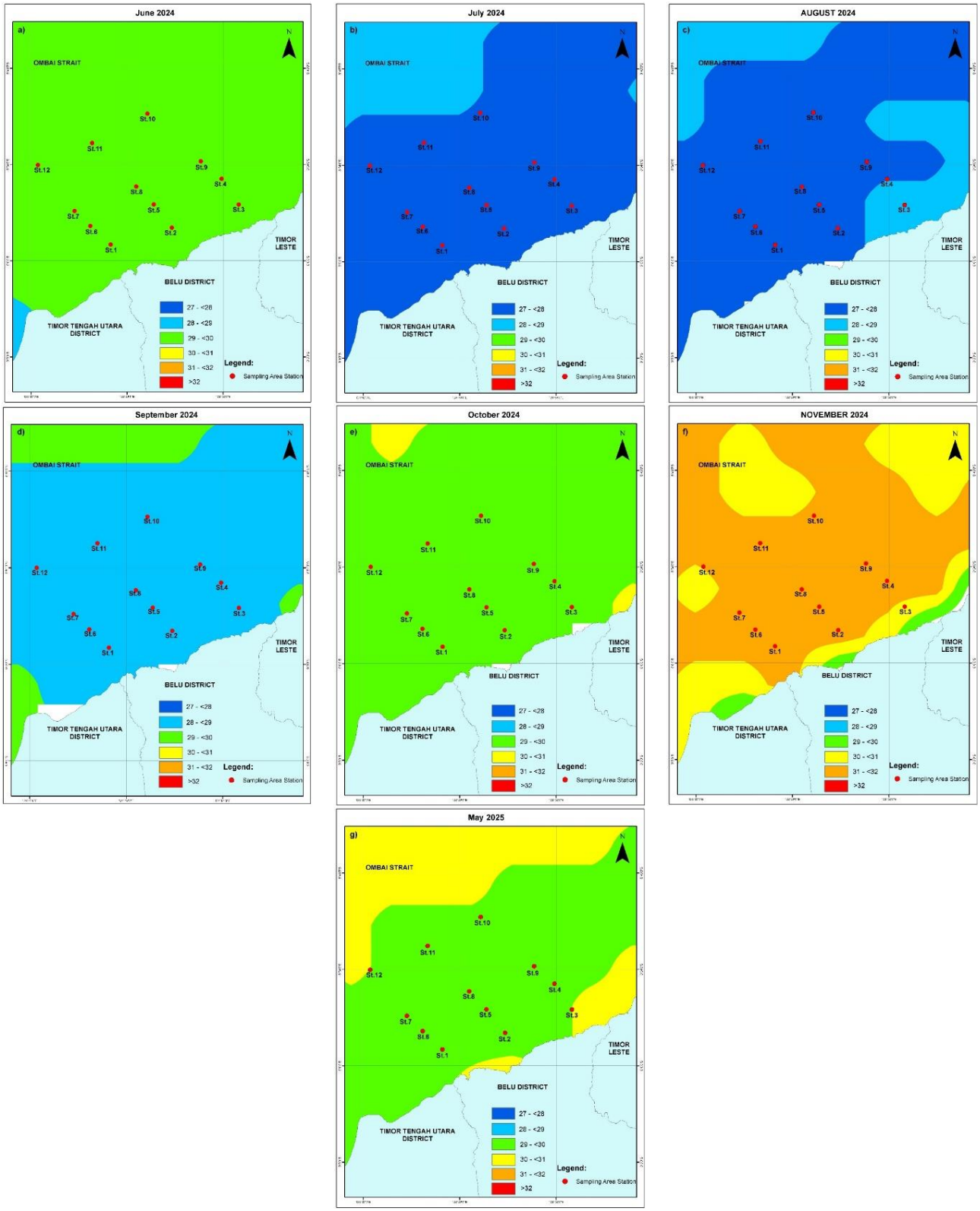


Figure 2. The Spatial distribution of satellite-derived sea surface temperature (SST) in the Ombai Strait, Belu Regency, East Nusa Tenggara, during the study period. Panels show SST conditions in (a) June 2024, (b) July 2024, (c) August 2024, (d) September 2024, (e) October 2024, (f) November 2024, and (g) May 2025
Note: Red dots indicate sampling stations.

At the fishing-ground scale, SST also showed spatial heterogeneity among the four sampling-distance categories. However, the spatial pattern was not consistent across all sampling months. Differences among stations were more

evident during periods of relatively strong thermal variability, whereas SST distributions were relatively homogeneous during some sampling periods. The observed spatial heterogeneity indicates that the thermal conditions experienced by flying fish differed among geographically distinct fishing grounds and were not represented solely by a uniform nearshore–offshore gradient.

Table 2. Monthly variation in satellite-derived SST during the sampling period

Month	Min SST	Max SST	Mean SST	SD
June 24	29.25	29.79	29.49	0.17
July 24	27.70	28.00	27.88	0.07
August 24	27.60	28.07	27.81	0.16
September 24	28.19	28.96	28.75	0.20
October 24	29.31	29.80	29.56	0.14
November 24	30.97	31.55	31.13	0.16
May 25	29.66	30.07	29.80	0.14

Note: Sea surface temperature (SST), standard deviation (SD).

The spatial distribution of SST also showed differences among sampling periods (Figure 2). During July and August 2024, relatively lower SST values dominated much of the sampling area, particularly in the offshore stations. SST subsequently increased during September and October, while the highest temperatures were observed in November 2024. In May 2025, SST ranged from 29.66 to 30.07 °C and showed a relatively warm distribution across the sampling area. These spatial patterns indicate that SST variability in the Ombai Strait was characterized by both seasonal changes and spatial heterogeneity across the sampling area. Overall, the available observations indicate a relatively cooler SST period during the middle of the East Monsoon (July–August), followed by progressive warming toward October and the available West Monsoon observation in November.

Satellite-derived SST exhibited clear seasonal variation throughout the sampling period (Figure 2; Table 2). During the East Monsoon (May–October), mean SST ranged from 27.81 ± 0.16 °C in August 2024 to 29.80 ± 0.14 °C in May 2025. Relatively high SST was observed in June 2024 (29.49 ± 0.17 °C), followed by a marked decrease in July (27.88 ± 0.07 °C) and August (27.81 ± 0.16 °C). SST subsequently increased in September (28.75 ± 0.20 °C) and October (29.56 ± 0.14 °C). The November 2024 observation, representing the available sampling period during the West Monsoon (November–April), showed the highest mean SST of 31.13 ± 0.16 °C, with values ranging from 30.97 to 31.55 °C.

3.2 Monthly variation in length structure of flying fish

Across all sampled individuals, TL ranged from 15.2 to 32.3 cm. The mean TL of flying fish varied among sampling periods (Figure 3). During the East Monsoon (May–October), mean TL ranged from 19.66 cm in August 2024 to 21.57 cm in May 2025. Mean TL decreased from 21.35 cm in June to 20.46 cm in July and reached the lowest value in August (19.66 cm). Subsequently, mean TL increased in September (20.29 cm) and October (20.50 cm). The mean TL recorded in November 2024, representing the available sampling period during the West Monsoon (November–April), was 20.51 cm. The highest mean TL across the sampling periods was observed in May 2025 (21.57 cm).

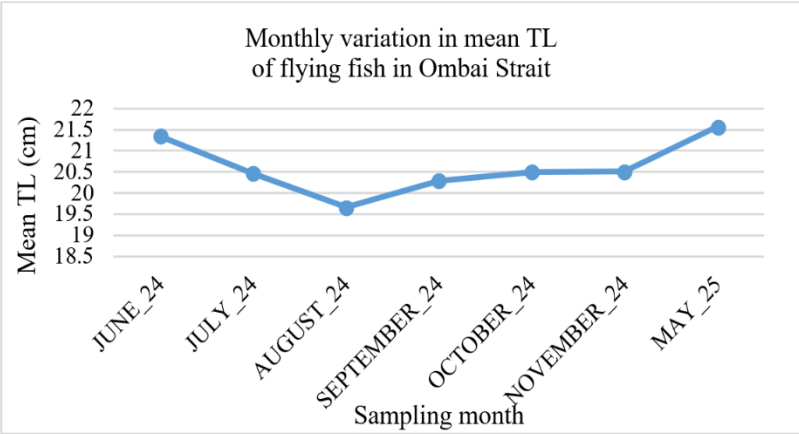


Figure 3. Monthly variation in mean total length (TL) of flying fish *Exocoetidae* in the Ombai Strait during June–November 2024 and May 2025

The length-frequency composition also showed distinct temporal changes among sampling periods (Figure 4). During June 2024, the catch was distributed across a relatively broad range of size classes, with relatively high proportions of fish in the 19–<20, 20–<21, and 21–<22 cm classes. In July, the distribution remained relatively broad, although the 20–<21 and 21–<22 cm classes contributed substantially to the catch. A marked shift toward smaller individuals occurred in August and September, when the 18–<19 cm class accounted for 33.43% and 35.46% of the catch, respectively. This shift toward smaller size classes corresponded with the lower mean TL observed during these months.

In October and November, the length-frequency distribution became relatively concentrated in the 18–<21 cm size range, although individuals from a wider range of size classes were still present. In May 2025, the distribution shifted toward relatively larger size classes, with the highest proportions occurring in the 21–<22 cm (16.06%) and 22– <23 cm (15.33%) classes. The observed variation in length composition indicates temporal changes in the size structure of flying fish in the Ombai Strait.

Considering the seasonal classification, the available East Monsoon observations showed a temporal shift in size structure, characterized by a decrease in mean TL from June toward August, followed by an increase toward October and May 2025. The available November observation during the West Monsoon showed a mean TL of 20.51 cm and was dominated by the 18–<19 and 19–<20 cm size classes.

However, because sampling was not conducted from December to April, the present data do not allow a complete characterization of length-structure dynamics throughout the West Monsoon. Accordingly, the observed temporal pattern should be interpreted as variation among the available sampling periods rather than as a complete seasonal cycle of flying fish size structure.

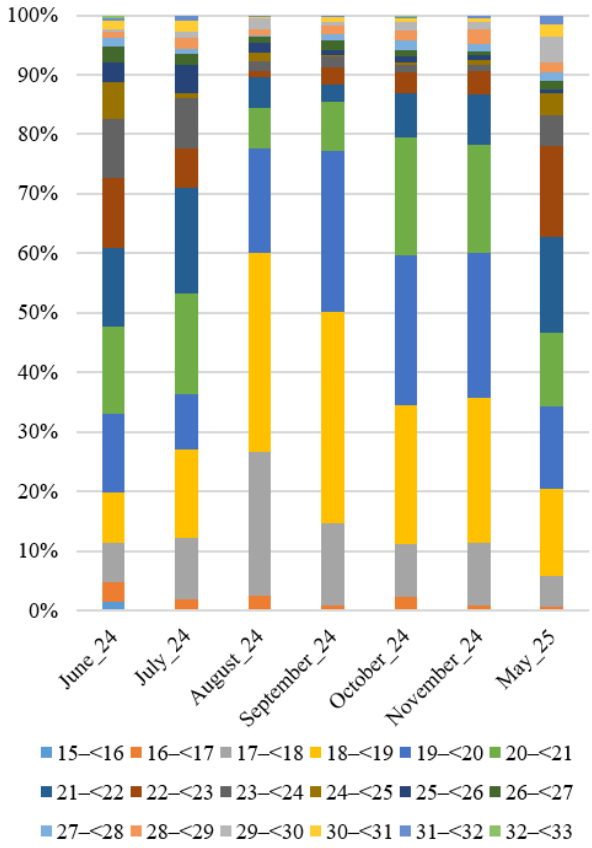


Figure 4. Monthly variation in length-frequency composition of flying fish *Exocoetidae* in the Ombai Strait during June–November 2024 and May 2025

The observed monthly size structure also provides an important context for evaluating reproductive status. Several dominant size classes during the sampling period were close to or below the estimated female Lm_{50} at several fishing grounds, indicating that the fishery encountered substantial numbers of individuals that had not yet reached the estimated size at first maturity. This size-based pattern was subsequently evaluated together with gonadal maturity and Lc_{50} to identify fishing grounds with potential reproductive importance.

3.3 Spatial variation in mean total length

The spatial distribution of mean TL showed considerable variation among sampling distances and months (Table 3). In June 2024, mean TL was relatively similar across the four sampling distances, ranging from 21.01 cm at 6 nautical miles to 21.49 cm at 4 nautical miles. In July, mean TL ranged from 18.87 cm at 12 nautical miles to 21.57 cm at 6 nautical miles. The lowest mean TL values across the sampling period were generally observed during August at 2 nautical miles (18.80 cm) and during September at 2 nautical miles (19.44 cm).

A different spatial pattern was observed in October, when mean TL increased with sampling distance, from 19.04 cm at 2 nautical miles to 22.24 cm at 12 nautical miles. In November, the highest mean TL was recorded at 2 nautical miles (22.22 cm), whereas the lowest value occurred at 6 nautical miles (19.65 cm). In May 2025, mean TL was relatively consistent among sampling distances, ranging from 21.36 cm at 6 nautical miles to 21.98 cm at 12 nautical miles. Overall, mean TL varied spatially among sampling distances, but the pattern was not consistent across months, indicating temporal variation in the spatial distribution of fish size.

The spatial pattern of fish size did not show a uniform increase or decrease with increasing distance from the coast. Instead, the distribution of mean TL varied among months, with relatively similar sizes across distances in June and May, while bigger spatial differences occurred in July, September, October, and November. This suggests that the spatial distribution of flying fish size was temporally variable rather than being determined solely by sampling distance. The absence of a consistent distance-related pattern suggests that spatial variation in fish size may reflect localized differences among fishing grounds rather than a simple nearshore–offshore gradient. Because each station represented a geographically referenced fishing ground, the observed differences indicate that the spatial distribution of size groups was heterogeneous across the study area and changed among sampling periods.

3.4 Relationship between sea surface temperature and mean total length

Pearson's correlation analysis showed a very weak and non-significant association between SST and mean TL across the available station-month observations ($r = -0.051$, $p = 0.675$). The negative correlation coefficient indicates a very weak inverse association, but the non-significant result suggests that variation in SST was not statistically associated with variation in mean TL during the observation period.

Table 3. Spatial variation in mean TL of flying fish by sampling distance and month

Mean Total Length (cm) by Sampling Distance and Month	2 nautical miles	4 nautical miles	6 nautical miles	12 nautical miles
June 24	21.48 ^{D}	21.49 ^{D}	21.01 ^{D}	21.41 ^{D}
July 24	21.04 ^{D}	20.38 ^{C}	21.57 ^{D}	18.87 ^{A}
August 24	18.80 ^{A}	19.74 ^{B}	20.45 ^{C}	—
September 24	19.44 ^{B}	19.46 ^{B}	19.57 ^{B}	22.69 ^{E}
October 24	19.04 ^{B}	20.10 ^{C}	20.62 ^{C}	22.24 ^{E}
November 24	22.22 ^{E}	20.11 ^{C}	19.65 ^{B}	20.05 ^{C}
May 25	21.54 ^{D}	21.43 ^{D}	21.36 ^{D}	21.98 ^{D}

Note: Superscript letters indicate mean TL classes: A = 18–<19 cm; B = 19–<20 cm; C = 20–<21 cm; D = 21–<22 cm; E = 22–<23 cm. — = no observation available.

The absence of a significant SST–TL relationship is consistent with the spatial and temporal variability observed in fish size. Mean TL varied among sampling months and fishing distances, but the spatial pattern was not consistent across months (Table 3).

3.5 Biological aspects of flying fish

3.5.1 Species identification

In this study, five flying fish species were identified in the samples, namely *Cypselurus poecilopterus*, *Cheilopogon abei*, *Cheilopogon spilopterus*, *Hirundichthys oxycephalus*, and *Cheilopogon intermedius* which is shown in Figure 5. These species represented the dominant flying-fish taxa observed during the sampling period. However, the quantitative composition or relative abundance of each species was not determined in the present study. Therefore, the subsequent biological analyses were conducted using pooled *Exocoetidae* samples. Accordingly, the biological results presented below describe the sampled flying-fish assemblage rather than species-specific characteristics. Species identification was based on morphological characteristics and verified using FishBase as a taxonomic reference. In the image below, we show a photo of the lateral fin of the fish, TL, standard length (SL), and head length (HL).



(a) *Cypselurus poecilopterus*
TL = 18.2 cm
SL = 13.2 cm
HL = 3.1 cm



(b) *Cheilopogon abei*
TL = 26.5 cm
SL = 21.3 cm
HL = 5.1 cm



(c) *Cheilopogon spilopterus*
TL = 20.5 cm
SL = 14.8 cm
HL = 3.3 cm



(d) *Hirundichthys oxycephalus*
TL = 18.6 cm
SL = 13.8 cm
HL = 3.2 cm



(e) *Cheilopogon intermedius*
TL = 27.4 cm
SL = 20.6 cm
HL = 4.7 cm

Figure 5. The 5 species of *Exocoetidae* were found in Ombai Strait Waters
Note: Total length (TL), standard length (SL), head length (HL).

3.5.2 Length–weight relationship

The length–weight relationship showed a strong positive relationship between TL and body weight in both male and female flying fish (Table 4 and Figure 6). For males, the estimated relationship was $W = 0.0189L^{2.7183}$ ($R^2 = 0.9117$; N = 1864), whereas for females it was $W = 0.0095L^{2.9357}$ ($R^2 = 0.8563$; N = 1223). The estimated length–weight relationships were 2.7184 ± 0.0196 (95% CI: 2.6799–2.7568) for males and

2.9358 ± 0.0344 (95% CI: 2.8682-3.0033) for females. The t-test showed that the male coefficient differed significantly from 3 ($t = -14.364$, $p < 0.001$), indicating negative allometric growth. In contrast, the female coefficient did not differ significantly from 3 ($t = -1.867$, $p = 0.062$), indicating that the female growth pattern was statistically consistent with isometric growth.

Table 4. Length–weight relationship and statistical test of the growth coefficient (*b*)

Parameter	Male	Female
N	1864	1223
a	0.0189	0.0095
b	2.7184	2.9358
SE(*b*)	0.0196	0.0344
95% CI of *b*	2.6799–2.7568	2.8682–3.0033
t	−14.364	−1.867
p-value	<0.001	0.062
Growth pattern	Negative allometric	Isometric*

Note: The female growth coefficient was not significantly different from 3 (α = 0.05).

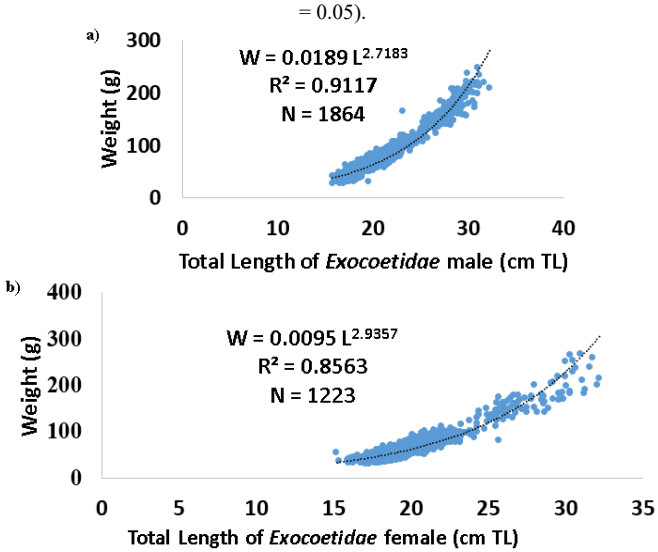


Figure 6. Relationship between TL and weight of *Exocoetidae* in the Ombai Strait: (a) male, and (b) female
Note: In the length–weight equations, W is expressed in grams (g) and L represents total length (TL) in centimeters (cm).

3.5.3 Sex ratio and condition factor

The sex composition of the sampled flying fish population was dominated by males. Of the 3087 individuals analyzed, 1864 (60.38%) were males and 1223 (39.62%) were females, resulting in a female-to-male sex ratio of 1.00:1.52 (Table 5). The mean condition factor was relatively similar between sexes, with values of 1.0595 for males and 1.0571 for females.

The condition factor also varied among sampling months (Figure 7). The highest mean condition factor was recorded in July 2024 (1.07267), followed by June 2024 (1.07122). The condition factor subsequently decreased from August (1.06717) to September (1.06216) and reached its lowest value in October (1.04715). A similarly low value was observed in November (1.04736), before increasing again in May 2025 (1.06530). This temporal variation indicates changes in the somatic condition of flying fish throughout the sampling period. During the available observations of the East Monsoon (May–October), the condition factor generally decreased from June toward October, although May 2025 showed a relatively high value (1.06530). The November 2024 observation, representing the available sampling period during the West Monsoon, showed a low condition factor of 1.04736.

Table 5. Sex ratio and condition factor of flying fish *Exocoetidae* in the Ombai Strait

Sex	N	Proportion (%)	Sex Ratio	Condition Factor (K)
Male	1864	60.38	1.52	1.0595
Female	1223	39.62	1	1.0571
Total	3087	100	1.00:1.52	1.0595: 1.0571

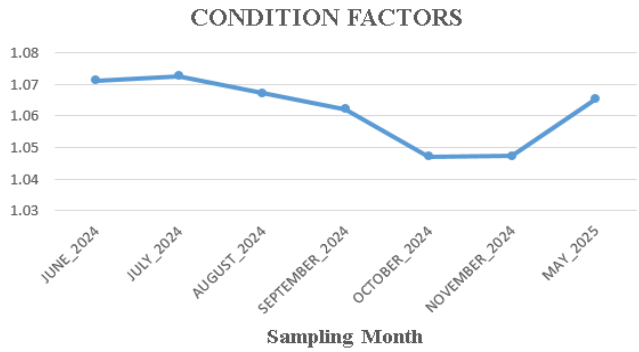


Figure 7. Monthly variation in condition factor (CF) of flying fish (*Exocoetidae*) in the Ombai Strait

The sex composition of the sampled flying fish population was dominated by males. Of the 3087 individuals analyzed, 1864 (60.38%) were males and 1223 (39.62%) were females, resulting in a female-to-male sex ratio of 1.00:1.52. The Pearson chi-square goodness-of-fit test showed that the observed sex ratio differed significantly from the expected 1:1 ratio ($X^2 = 133.13$, df = 1, $p < 0.001$), confirming significant male dominance in the sampled catch. The mean condition factor was relatively similar between sexes, with values of 1.0595 for males and 1.0571 for females.

3.5.4 Gonad maturity level

Gonadal maturity composition varied among sampling months (Figure 8; Table 6). Immature individuals (GML I–II) dominated the catch throughout the sampling period, accounting for 72.95% of the total 3,087 individuals, whereas mature individuals (GML III–V) accounted for 27.05%. The proportion of immature individuals was highest in August 2024 (90.65%), followed by July (78.50%), while the lowest proportion was observed in June 2024 (64.15%).

Table 6. Gonad maturity level composition of flying fish *Exocoetidae* by sampling month in the Ombai Strait

Month	I	II	III	IV	V	n
June 24	73	63	28	13	35	212
July 24	30	54	11	3	9	107
August 24	128	192	13	1	19	353
September 24	67	403	165	3	19	657
October 24	125	402	113	16	57	713
November 24	176	448	136	20	128	908
May 25	38	53	24	4	18	137
Total	637	1615	490	60	285	3087

GML II was the most prominent maturity stage during most sampling months, particularly in September (61.34%), August

(54.39%), October (56.38%), and July (50.47%). The highest proportion of mature individuals was recorded in June 2024 (35.85%), followed by May 2025 (33.58%) and November 2024 (31.28%). Overall, the dominance of immature individuals indicates that a substantial proportion of the sampled flying fish had not yet reached advanced gonadal maturity during the sampling period.

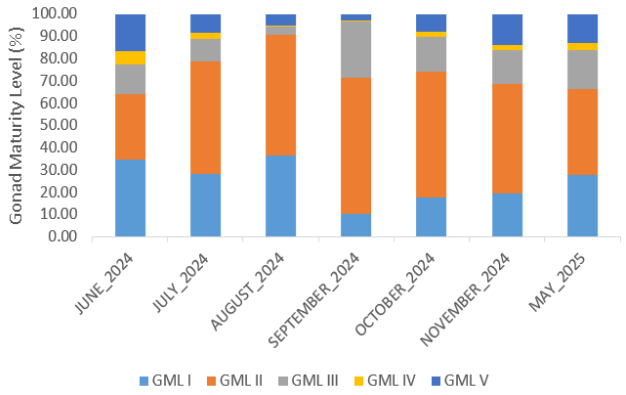


Figure 8. Gonad maturity level percentage of flying fish *Exocoetidae* by sampling month in the Ombai Strait

During the East Monsoon observations (May–October), immature individuals remained dominant, ranging from 64.15% in June to 90.65% in August. The available November observation, representing the West Monsoon, also showed a predominance of immature individuals (68.72%). However, because sampling was not conducted from December to April, the present data cannot fully characterize gonadal maturity patterns throughout the West Monsoon.

3.5.5 Spatial variation in gonadal maturity

The spatial distribution of gonadal maturity showed substantial variation among fishing grounds (Table 7). The proportion of individuals at gonadal maturity levels III–V (GML III–V) ranged from 13.18% to 39.50% among the twelve sampling stations. The lowest proportion was observed at ST10 (12 nautical miles), whereas the highest proportion occurred at ST8 (6 nautical miles), where 39.50% of the sampled individuals were classified as GML III–V. Other stations with relatively high proportions of GML III–V included ST11 (39.42%), ST7 (35.59%), ST9 (31.06%), and ST2 (30.95%). These results indicate that the occurrence of reproductively advanced individuals varied considerably among geographically distinct fishing grounds.

A more spatially restricted pattern was observed for GML IV–V, representing advanced reproductive stages. The proportion of GML IV–V individuals ranged from 3.97% at ST2 to 26.14% at ST11. ST8 also showed a relatively high proportion of GML IV–V individuals (21.27%), followed by ST11 (26.14%), ST6 (13.23%), and ST9 (12.71%). The occurrence of GML IV–V at several fishing grounds indicates that individuals in advanced reproductive condition were present at specific locations rather than being uniformly distributed throughout the study area.

The spatial distribution of gonadal maturity did not show a consistent increase or decrease with increasing distance from the coast. At 2 nautical miles, the proportion of GML III–V varied from 13.79% to 30.95%, while at 4 nautical miles it ranged from 17.65% to 25.07%. At 6 nautical miles, the proportion increased to 31.06–39.50%, whereas at 12 nautical miles it ranged from 13.18% to 39.42%. Thus, fishing grounds located at the same nominal distance from the coast could exhibit substantially different reproductive characteristics.

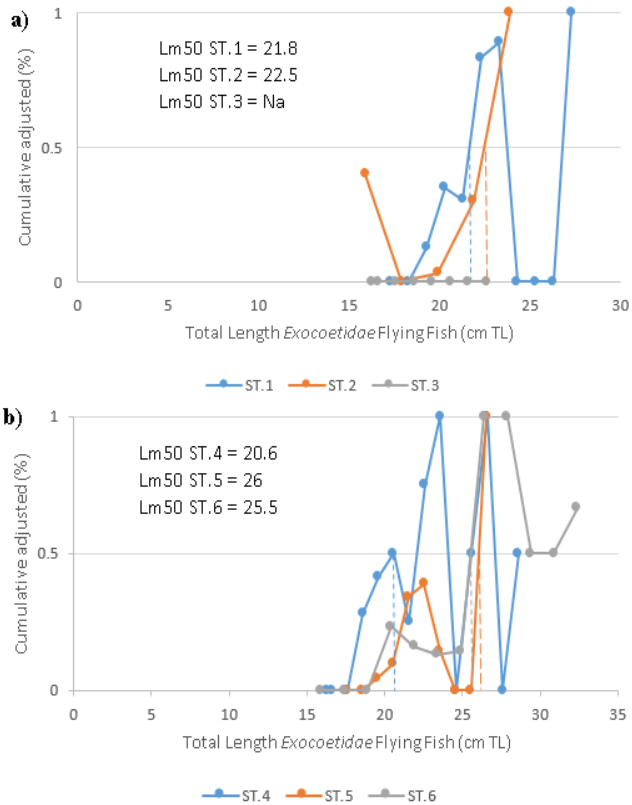
Table 7. Spatial variation in gonadal maturity of flying fish *Exocoetidae* among sampling stations in the Ombai Strait

Distance	ST	GML III–V, n (%)	GML IV–V, n (%)
2 nautical miles	1	62 (15.01)	19 (4.60)
2 nautical miles	2	39 (30.95)	5 (3.97)
2 nautical miles	3	4 (13.79)	2 (6.90)
4 nautical miles	4	51 (17.65)	19 (6.57)
4 nautical miles	5	91 (25.07)	23 (6.34)
4 nautical miles	6	62 (24.12)	34 (13.23)
6 nautical miles	7	79 (35.59)	13 (5.86)
6 nautical miles	8	143 (39.50)	77 (21.27)
6 nautical miles	9	132 (31.06)	54 (12.71)
12 nautical miles	10	17 (13.18)	12 (9.30)
12 nautical miles	11	95 (39.42)	63 (26.14)
12 nautical miles	12	60 (25.97)	23 (9.96)

The relatively high occurrence of GML III–V and GML IV–V at several offshore fishing grounds, particularly ST8 at 6 nautical miles and ST11 at 12 nautical miles, provides an important spatial indication of areas with potential reproductive importance. However, gonadal maturity alone does not confirm that these locations represent spawning grounds. Therefore, the spatial distribution of gonadal maturity was subsequently evaluated together with fish size relative to Lm_{50}, Lc_{50}, SST, and fishing-ground characteristics to identify potential reproductive or spawning zones.

3.5.6 Length at first maturity (Lm_{50})

The estimated length at first maturity (Lm_{50}) of female flying fish varied among sampling stations and distances from the coast (Figure 9 and Table 8).



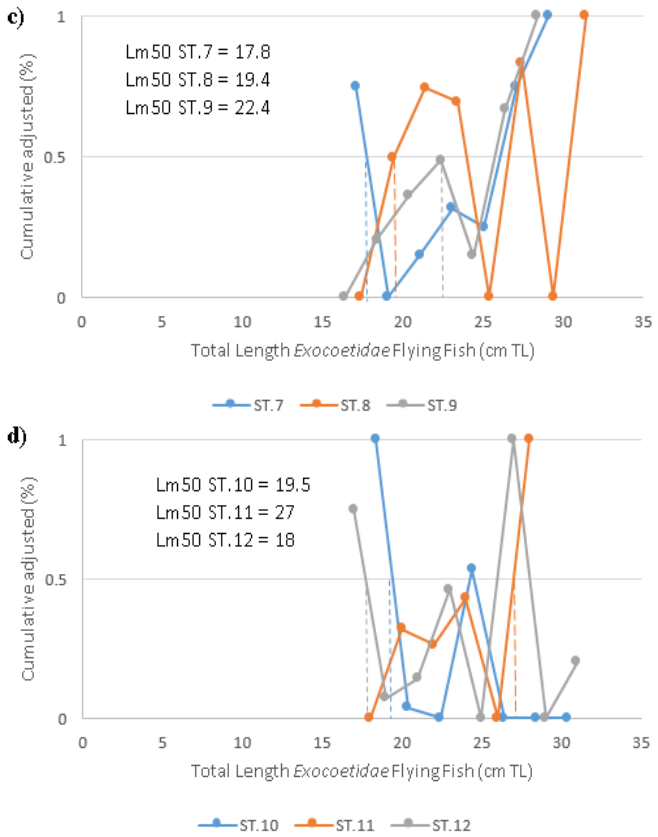


Figure 9. Length at first maturity (Lm_{50}) of female flying fish *Exocoetidae* at different sampling distances in the Ombai Strait, Belu Regency, East Nusa Tenggara, Indonesia. (a) 2 nautical miles, (b) 4 nautical miles, (c) 6 nautical miles, and (d) 12 nautical miles
Note: ST = sampling station.

At 2 nautical miles, Lm_{50} values at ST.1 and ST.2 were 21.8 and 22.5 cm TL, respectively, whereas Lm_{50} could not be estimated at ST.3. At 4 nautical miles, Lm_{50} ranged from 20.6 cm at ST.4 to 26.0 cm at ST.5. At 6 nautical miles, Lm_{50} ranged from 17.8 cm at ST.7 to 22.4 cm at ST.9. At 12 nautical miles, Lm_{50} ranged from 18.0 cm at ST.12 to 27.0 cm at ST.11. Overall, the estimated Lm_{50} values ranged from 17.8 to 27.0 cm TL among stations where estimation was possible.

The spatial pattern did not show a consistent increase or decrease in Lm_{50} with increasing sampling distance. Instead, substantial variation occurred among stations within the same distance category, particularly at 4 and 12 nautical miles. This indicates that the size at first maturity of female flying fish varied spatially across the sampling area. The spatial heterogeneity in Lm_{50} is ecologically important because stations located at the same distance from the coast did not necessarily exhibit similar maturity sizes. For example, substantial differences were observed among stations within the 4 and 12 nautical mile groups. This indicates that reproductive characteristics cannot be adequately described by distance from the coast alone and supports the interpretation of individual stations as biologically distinct fishing grounds.

Table 8. Length at first maturity (Lm_{50}) of female flying fish at each sampling station in the Ombai Strait

Distance	Station	n	Lm_{50} (cm TL)
2 nautical miles	ST.1	120	21.8
2 nautical miles	ST.2	32	22.5
2 nautical miles	ST.3	8	NA
4 nautical miles	ST.4	91	20.6
4 nautical miles	ST.5	177	26
4 nautical miles	ST.6	122	25.5
6 nautical miles	ST.7	105	17.8
6 nautical miles	ST.8	149	19.4
6 nautical miles	ST.9	155	22.4
12 nautical miles	ST.10	63	19.5
12 nautical miles	ST.11	102	27
12 nautical miles	ST.12	99	18

Note: *n* represents the number of female fish used for the station-level estimation of Lm_{50}. NA indicates that Lm_{50} could not be reliably estimated at ST3.

3.5.7 Length at first capture (Lc_{50})

The estimated length at first capture (Lc_{50}) varied among sampling stations and between sexes (Figure 10; Table 9). For males, Lc_{50} ranged from 18.5 to 21.5 cm TL, while female Lc_{50} ranged from 19.0 to 21.0 cm TL. The highest male Lc_{50} was recorded at ST.10 (21.5 cm), whereas the lowest occurred at ST.7 (18.5 cm). For females, Lc_{50} ranged from 19.0 cm at ST.2 to 21.0 cm at ST.6.

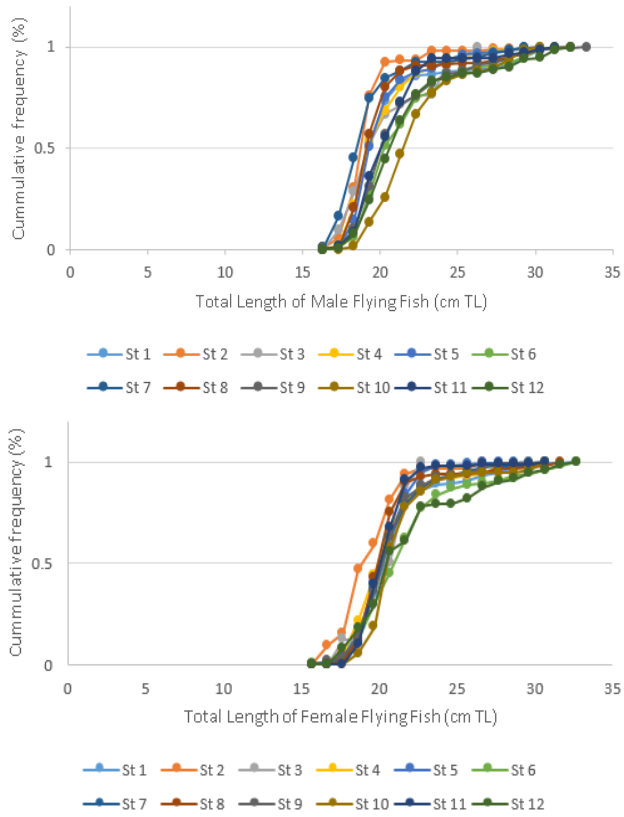


Figure 10. Curve of size at first capture (Lc50) of flying fish in Ombai Strait at the twelve stations

Table 9. Length at first capture (Lc_{50}) of male and female flying fish at each sampling station in the Ombai Strait

ST	Distance	n male	Lc_{50} Male (cm)	n female	Lc_{50} Female (cm)
ST.1	2 nautical miles	293	19.3	120	20.3
ST.2	2 nautical miles	93	18.7	32	19
ST.3	2 nautical miles	21	19.3	8	20.7

ST.4	4 nautical miles	198	19.2	91	20
ST.5	4 nautical miles	186	19.3	177	20.1
ST.6	4 nautical miles	134	20.3	122	21
ST.7	6 nautical miles	117	18.5	105	20.2
ST.8	6 nautical miles	214	19	149	20
ST.9	6 nautical miles	270	20	155	20.2
ST.10	12 nautical miles	66	21.5	63	20.5
ST.11	12 nautical miles	140	20	102	20.1
ST.12	12 nautical miles	132	20.6	99	20.5

Note: *n* represents the number of fish of each sex used for the station-level estimation of Lc_{50}.

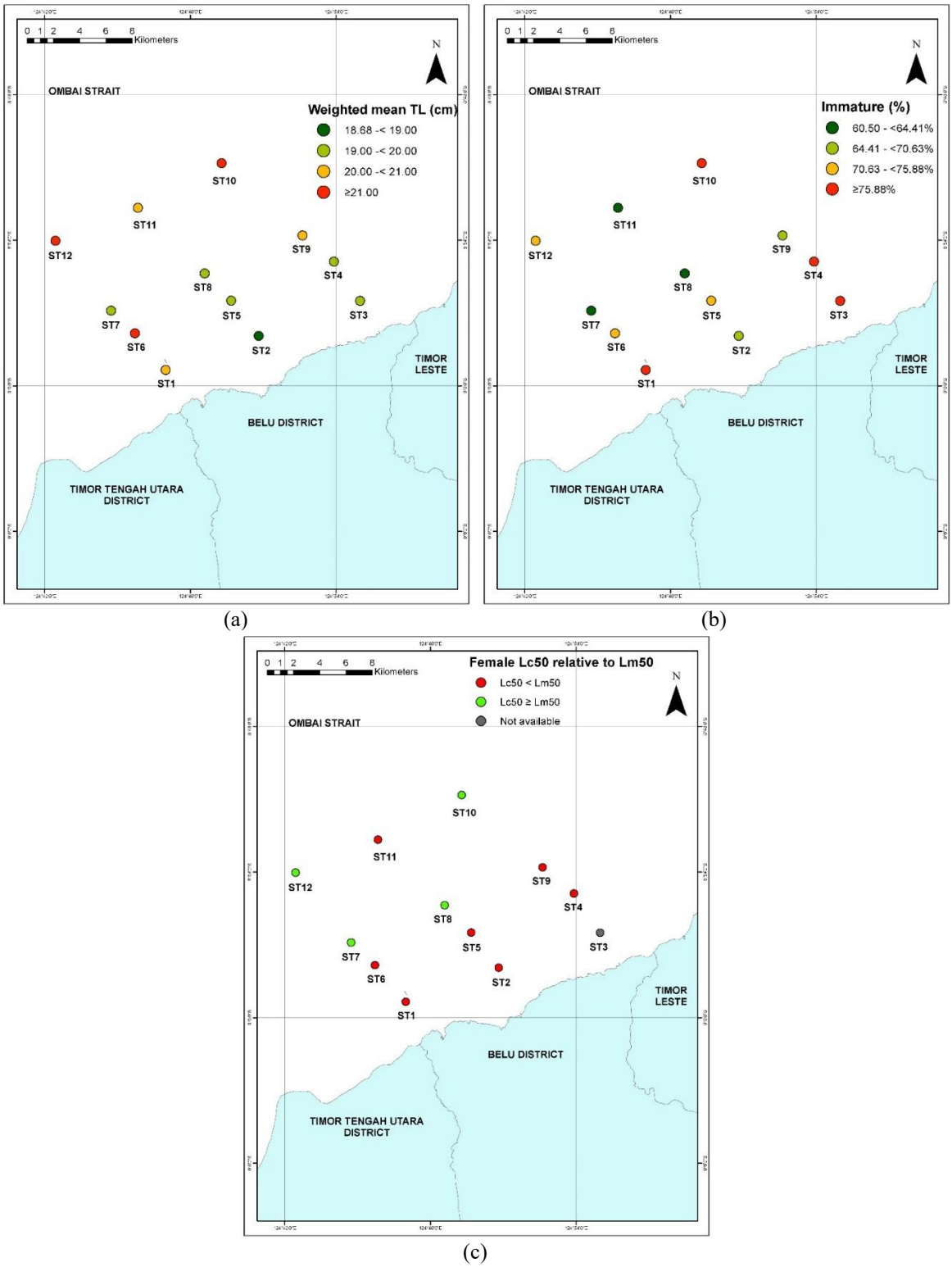


Figure 11. Spatial variation in biological and reproductive characteristics of flying fish across fishing grounds in the Ombai Strait. (a) Weighted mean total length (TL); (b) proportion of immature fish; and (c) female length at first capture (Lc_{50}) relative to length at first maturity (Lm_{50})

Comparison between female Lc_{50} and Lm_{50} showed spatially variable patterns. At seven stations (ST.1, ST.2, ST.4, ST.5, ST.6, ST.9, and ST.11), female Lc_{50} was lower than the corresponding Lm_{50}, indicating that the estimated capture size was smaller than the estimated size at first maturity, indicating potential vulnerability to capture before reaching gonadal maturity (Table 9). In contrast, female Lc_{50} exceeded Lm_{50} at ST.7, ST.8, ST.10, and ST.12. Lm_{50} could not be estimated at ST.3, and therefore a comparison was not possible at this station. These results indicate that the relationship between size at first capture and size at first maturity varied spatially across the Ombai Strait, rather than showing a consistent pattern with increasing distance from the coast. The station-level pattern further demonstrates that reproductive vulnerability was spatially heterogeneous. Stations with Lc_{50} below Lm_{50} were interspersed among stations where Lc_{50} exceeded Lm_{50}, rather than being concentrated within a single distance category. This spatial distribution suggests that differences in fishing selectivity and the availability of size groups may occur among fishing grounds independently of their distance from the coast.

The distribution at the station level further illustrates this spatial heterogeneity (Figure 11(a)). Weighted mean TL values vary across georeferenced fishing areas, and stations located at the same nominal fishing distance do not necessarily exhibit similar average sizes. This indicates that the spatial structure of fish size is heterogeneous across fishing areas and cannot be accurately represented solely based on distance from the coastline.

In addition to temporal variation, the distribution of immature individuals across stations reveals spatial heterogeneity throughout the fishing area (Figure 11(b)). The proportion of immature fish ranged from 60.50% to 86.82% across the various stations. This variation did not follow a simple gradient pattern from nearshore to offshore waters, indicating that the occurrence of immature individuals differs among geographically distinct fishing areas.

The spatial distribution of female Lm_{50}, along with the patterns of mean TL and the proportion of immature individuals at the station level shown in Figure 11, indicates that biological characteristics vary among fishing locations rather than following a uniform gradient related to distance.

This station-level pattern is visualized in Figure 11(c), which shows that fishing locations with $Lc_{50} < Lm_{50}$ values are distributed across various distance categories rather than being concentrated in specific coastal or offshore zones. Thus, this spatial distribution indicates that the potential risk of capture prior to reaching maturity varies across different fishing locations.

The relationship between SST and mean TL was weak and not statistically significant ($r = -0.051$, $p = 0.675$), indicating that the spatial variation in fish size observed among fishing grounds was not explained by SST alone.

3.6 Spatial identification of potential reproductive or spawning zones

The identification of potential reproductive or spawning zones was conducted by integrating spatial information on gonadal maturity, fish size relative to the length at first maturity (Lm_{50}), SST, and fishing-ground characteristics. The integration was intended to identify areas where multiple reproductive indicators occurred concurrently, rather than relying on a single biological parameter. In particular, the proportions of individuals at GML III–V and GML IV–V, together with the proportion of female fish attaining or exceeding Lm_{50}, were used as the primary biological indicators of reproductive characteristics.

Spatial integration showed that reproductive characteristics were not uniformly distributed across the Ombai Strait. The occurrence of GML III–V individuals was relatively high at several offshore stations, particularly ST7 and ST8 at 6 nautical miles and ST11 at 12 nautical miles. ST8 recorded the highest proportion of GML III–V individuals (39.50%), followed closely by ST11 (39.42%) and ST7 (35.59%). The proportion of GML IV–V individuals, representing more advanced reproductive conditions, was also relatively high at ST8 (21.27%) and ST11 (26.14%), while ST6 and ST9 recorded 13.23% and 12.71%, respectively.

The distribution of female fish relative to Lm_{50} provided additional spatial information. A relatively high proportion of females attaining or exceeding Lm_{50} was observed at ST7 (95.24%), ST12 (89.90%), ST10 (76.19%), and ST8 (52.03%). In contrast, the proportion was very low at ST5 (0.56%) and ST11 (0.98%), despite the relatively high occurrence of GML III–V and GML IV–V at ST11. This contrast indicates that gonadal maturity and fish size relative to Lm_{50} provide complementary information and should therefore be considered together when identifying potential reproductive zones.

The spatial pattern was also considered in relation to SST. The mean SST associated with reproductively advanced individuals varied among stations, with GML IV–V individuals occurring under SST conditions ranging from approximately 28.8 to 31.1 °C. However, these observations represent the environmental conditions recorded during the sampling period and do not demonstrate an optimum spawning temperature or a causal relationship between SST and spawning activity. SST was therefore considered as supporting environmental information rather than as a direct determinant of spawning habitat.

Based on the convergence of the biological and environmental indicators, the 6-nautical-mile fishing grounds, particularly ST7–ST9, showed a greater concentration of reproductive characteristics, while the 12-nautical-mile fishing grounds, particularly ST10–ST12, also showed important reproductive characteristics. Among the individual stations, ST8 showed a combination of a high proportion of GML III–V (39.50%), GML IV–V (21.27%), and females attaining or exceeding Lm_{50} (52.03%). ST7 was characterized by a high proportion of females $\geq Lm_{50}$ (95.24%) and GML III–V (35.59%), while ST12 showed a high proportion of females $\geq Lm_{50}$ (89.90%) and 25.97% GML III–V. The spatial distribution of these reproductive indicators is summarized in Table 10.

These patterns suggest that the 6–12 nautical mile fishing grounds may represent potential reproductive or spawning zones requiring further verification (Table 10). However, the identified areas should not be interpreted as confirmed spawning grounds because direct evidence of spawning, such as the spatial occurrence of spawning females, eggs, or larvae, was not collected in the present study. The identified zones should therefore be regarded as potential reproductive or spawning areas based on the convergence of biological, environmental, and fishing-ground indicators. These areas may subsequently be prioritized for direct reproductive surveys, spatial monitoring, and fisheries management measures in the Ombai Strait.

Table 10. Spatial distribution of reproductive indicators of flying fish *Exocoetidae* in the Ombai Strait

ST	Distance (Nautical Miles)	GML III–V (%)	GML IV–V (%)	Female ≥ Lm_{50} (%)	SST (°C)
1	2	15.01	4.60	16.67	28.97
2	2	30.95	3.97	3.13	30.06
3	2	13.79	6.90	NA	29.49
4	4	17.65	6.57	30.77	29.37
5	4	25.07	6.34	0.56	29.00
6	4	24.12	13.23	11.38	29.31
7	6	35.59	5.86	95.24	29.01
8	6	39.50	21.27	52.03	29.72
9	6	31.06	12.71	10.97	29.91
10	12	13.18	9.30	76.19	30.29
11	12	39.42	26.14	0.98	30.81
12	12	25.97	9.96	89.90	30.30

Note: GML = gonadal maturity level; Lm_{50} = length at first maturity; SST = sea surface temperature; NA = not available because Lm_{50} could not be estimated at ST3.

4. DISCUSSION

4.1 Monthly and spatial variation of sea surface temperature

The available observations showed monthly and spatial variation in SST across the Ombai Strait. Mean SST decreased from 29.49 °C in June 2024 to 27.88 °C in July and 27.81 °C in August, followed by a progressive increase to 28.75 °C in September, 29.56 °C in October, and 31.13 °C in November. The mean SST recorded in May 2025 was 29.80 °C. The observed pattern indicates that the thermal environment of the Ombai Strait was not temporally homogeneous, with the most pronounced cooling occurring during July–August and warming occurring from September toward November.

Regional oceanographic studies in the Alor–Pantar region have also documented pronounced SST variability and recurrent cold-seawater events associated with upwelling and seasonal oceanographic processes [14]. Martono [15] reported that seasonal SST variability is particularly pronounced in the Timor Sea, Arafura Sea, and Banda Sea, where seasonal cooling has been associated with monsoonal processes and upwelling. The southeast monsoon generally produces stronger southeasterly winds over the southern Indonesian region, enhancing vertical mixing and potentially bringing relatively cooler subsurface water toward the surface. During the northwest monsoon, the reversal of atmospheric forcing produces contrasting oceanographic conditions, generally associated with warmer surface waters [15]. Thus, the cooling observed during July–August in the present study is consistent with the expected influence of southeast monsoon forcing, although the available observations do not cover the complete annual monsoonal cycle.

The pronounced cooling during July–August is particularly relevant because the Ombai Strait is characterized by complex ocean circulation and topography. Regional observations from the neighboring Alor–Pantar region have documented recurrent cold-seawater events and strong SST gradients associated with upwelling and the interaction between ocean circulation and complex bathymetry [14]. Hartoko et al. [14] demonstrated that the integration of satellite and in-situ SST data was able to resolve small-scale thermal variability associated with cold-seawater events in Pantar Strait. These findings provide regional evidence that SST variability in the waters of eastern Nusa Tenggara can be strongly influenced by localized oceanographic processes and bathymetric characteristics. Moore and Marra [16] documented persistent cooling events and associated fronts in the Ombai Strait using satellite observations, with some events characterized by strong SST gradients and enhanced chlorophyll concentrations. They attributed these cooling events to variability in flow through the strait and its interaction with complex bathymetry, while also demonstrating that the occurrence and intensity of these events were related to monsoonal variability and changes in thermocline depth. Thus, the lower SST observed during July–August in the present study is consistent with the previously documented oceanographic characteristics of the Ombai Strait.

Such spatial heterogeneity is expected in a strait characterized by strong throughflow, complex bathymetry, and interactions between regional and local circulation. Sprintall et al. [17] and subsequent studies have demonstrated that the Indonesian Throughflow (ITF) and monsoon-driven circulation interact strongly in the Ombai Strait, producing spatial and temporal changes in surface flow and thermal structure. During the southeast monsoon, the westward ITF reaches its annual maximum near the surface in the southern part of the strait, while other circulation features occur in the northern portion, generating heterogeneous surface conditions [17].

The spatial variability observed in this study should therefore not be interpreted simply as a uniform offshore temperature gradient. The Ombai Strait is an important pathway of the Indonesian Throughflow, and its thermal structure is influenced by the interaction among ITF transport, monsoon-driven Ekman dynamics, bathymetry, and frontal processes. Sprintall et al. [17] showed that during the southeast monsoon, a surface thermal front can develop in the Ombai Strait, with its position related to the interaction between local wind forcing, ITF flow, and topography. This mechanism provides an oceanographic explanation for the heterogeneous SST patterns observed among the 2, 4, 6, and 12 nautical-mile fishing grounds in the present study.

However, because chlorophyll-a and nutrient dynamics were not directly analyzed in the present study, the potential link between the observed SST variability and biological productivity in the Ombai Strait remains to be further investigated. Moore and Marra [16] reported that cooling events in the Ombai Strait were associated with enhanced ocean-color signals and phytoplankton blooms, suggesting that physical processes responsible for surface cooling can also modify nutrient availability and biological productivity. In addition, studies of the Timor Sea have indicated that seasonal upwelling and mixing during the southeast monsoon

can enhance nutrient supply and influence biological productivity, although the intensity and spatial extent of these processes vary considerably across the region. Alongi et al. [18] documented subsurface upwelling associated with the Indonesian Throughflow along the southern Timor-Leste shelf during the southeast monsoon, while emphasizing that the expression of upwelling near the coast can be spatially heterogeneous.

The SST pattern observed in the present study also corresponds broadly with previous observations using Aqua-MODIS in the Ombai Strait. Maulana et al. [19] reported substantial monthly and spatial variability in SST during 2024, with the lowest monthly mean SST occurring in July (27.77 °C) and August (28.02 °C), followed by increasing temperatures toward October–November. Their spatial maps also showed considerable heterogeneity in SST distribution across the Ombai Strait. These patterns are broadly consistent with the cooling observed during July–August and subsequent warming toward November in the present study, although differences in spatial domain, temporal sampling, and data processing may account for differences in absolute SST values.

The lower SST observed during July–August is consistent with previously reported seasonal cooling in the Ombai Strait, which has been associated with monsoonal oceanographic processes and possible upwelling activity [19]. A recent study of monthly Aqua-MODIS SST in the Ombai Strait reported the highest spatial SST distribution in June and the lowest in July, with an annual mean of approximately 29.52 °C for 2024 [19]. Although the absolute values differ from those obtained in the present analysis because of differences in spatial domain, temporal compositing, and data processing, both studies identify June as a relatively warm period and July as a pronounced cooling period. This agreement provides additional support for the monthly thermal variability identified in the present study.

The observed SST variability is also relevant to the biology of flying fish. Nur et al. [8] reported that the reproductive strategy of flying fish in Indonesian waters is associated with oceanographic conditions, particularly temperature and salinity, and that environmental changes during the southeast monsoon may influence reproductive activity. In the present study, the period of lowest SST in July–August coincided with changes in the size structure of the flying fish catch and subsequent variation in gonadal maturity composition. However, this temporal coincidence should not be interpreted as evidence that SST alone controlled the biological response. Rather, SST should be regarded as one component of a broader environmental system involving circulation, productivity, food availability, reproduction, and fish distribution.

The integration of SST and biological observations in the present study provides an environmental context for interpreting biological variability at the fishing-ground scale. The value of this integration is particularly evident because the biological characteristics were obtained directly from geographically referenced fishing locations rather than from aggregated landings. Consequently, differences in size composition and reproductive characteristics can be examined together with the environmental conditions prevailing at the corresponding fishing grounds and sampling periods. This provides information that complements broader-scale assessments based on catch, landing, or exploitation data.

The temporal interpretation must, however, consider the sampling limitation of the present study. Field observations were unavailable from December 2024 to April 2025 because of unfavorable sea conditions. Consequently, the November 2024 observation should not be considered representative of the entire west monsoon period, and the May 2025 observation represents an additional observation from the following southeast monsoon period rather than a complete seasonal transition. The five-month gap may introduce temporal sampling bias because environmental conditions and biological characteristics during December–April were not directly observed. Therefore, the monthly patterns reported here represent the variability observed during the available sampling periods and should not be generalized to the entire annual cycle.

Overall, the available observations showed a temporal SST pattern characterized by cooling during July–August and progressive warming from September to November, together with spatial heterogeneity across the fishing grounds. The observed pattern is consistent with the influence of the Asian–Australian monsoon, Indonesian Throughflow, local circulation, and complex bathymetry on the thermal structure of the Ombai Strait. These oceanographic dynamics provide an important environmental context for interpreting the spatial and temporal variability in flying fish size structure and reproductive characteristics observed in the present study.

4.2 Relationship between sea surface temperature and fish size

The Pearson correlation analysis showed no significant relationship between SST and mean TL (r = -0.051, p = 0.675, n = 69). Therefore, the observed spatial and monthly variation in fish size cannot be attributed to SST based on the present analysis. SST should instead be regarded as environmental context for interpreting the spatial distribution of flying fish and their reproductive characteristics.

Fish size may be influenced by multiple ecological and fisheries-related factors, including population composition, recruitment, food availability, habitat use, movement patterns, reproductive dynamics, and fishing selectivity. The spatial variation in mean TL among fishing distances and sampling months, without a consistent nearshore-offshore gradient, further indicates that fish size structure may reflect the interaction of several biological and environmental processes rather than a simple response to SST.

The absence of a significant correlation should not be interpreted as indicating that temperature has no ecological relevance to flying fish. Rather, the result indicates that SST, when considered alone, was not a significant predictor of mean TL at the spatial and temporal scale examined in this study. Fish may respond to environmental conditions through processes that are not directly reflected by surface temperature, including prey availability, water-column structure, current dynamics, habitat suitability, and reproductive movements.

Therefore, SST in the present analysis is best interpreted as an environmental context for understanding the spatial and temporal dynamics of flying fish rather than as a direct determinant of fish size. A more comprehensive assessment of environmental effects would require additional variables, such as chlorophyll-a, prey or plankton availability, current dynamics, bathymetry, and habitat characteristics, together with longer and more continuous observations.

4.3 Monthly and spatial variation in length structure

The size structure of flying fish in the Ombai Strait exhibited clear monthly variability during the available sampling periods. Mean TL decreased from 21.35 cm in June 2024 to 20.46 cm in July and 19.66 cm in August, before increasing to 20.29 cm in September, 20.50 cm in October, and 20.51 cm in November, and reaching 21.57 cm in May 2025. The monthly length-frequency distribution showed a corresponding shift in the dominant size classes. Fish measuring 20–<21 cm TL predominated in June and July, whereas the 18–<19 cm TL class became dominant in August and September. In October, the 19–<20 cm TL class became more prominent, while November was characterized by relatively similar proportions of fish in the 18–<19 and 19–<20 cm classes. In May 2025, the dominant size shifted toward the 21–<22 cm TL class. These changes indicate that the size composition of flying fish available to the fishery varied among sampling periods.

The observed variability in flying fish size composition is consistent with previous observations from eastern Indonesian waters. Tuapetel and Tupan [4] reported differences in the length distribution of flying fish among the Ambon, with dominant size characteristics differing between sampling areas. Similarly, Indrayani et al. [5] found differences in the size structure of *Cheilopogon spilopterus, Cheilopogon abei, Cypselurus poecilopterus,* and *Hirundichthys oxycephalus* in the Makassar Strait. These findings indicate that flying fish populations may exhibit spatial and temporal variability in size structure rather than maintaining a uniform size composition across Indonesian waters.

The temporal pattern observed in the present study was particularly notable during August–September, when smaller individuals became dominant. The proportion of the 18 - ≤ 19 cm TL class reached 33.43% in August and 35.46% in September, while the mean TL declined to its lowest value of 19.66 cm in August. Previous research in the Ombai Strait [2] identified a recruitment pattern occurring throughout the year, with relatively important recruitment during May–September. The relatively high proportion of smaller individuals during August–September in the present study is therefore consistent with the previously documented recruitment pattern in the same fishing area. However, because recruitment was not estimated directly in the present analysis, the increase in smaller size classes should be interpreted as a change in size composition rather than definitive evidence of recruitment.

The subsequent increase in mean TL from August toward May 2025 indicates a change in the size composition of fish available to the fishery following the period dominated by smaller individuals. Mean TL increased from 19.66 cm in August to 20.29 cm in September, 20.50 cm in October, 20.51 cm in November, and 21.57 cm in May 2025. This pattern may reflect the combined effects of individual growth, changes in cohort composition, movement among fishing grounds, and differential availability of size groups to the fishing gear. The previous study [2] estimated an asymptotic length of 330.53 mm TL and a growth coefficient of 0.99 $year^{-1}$ for flying fish in the Ombai Strait, indicating substantial growth potential within the size range observed in the fishery.

The spatial component of the size structure is also important. The sampling stations were distributed across four fishing-distance strata (2, 4, 6, and 12 nautical miles), allowing differences in size composition among fishing grounds to be examined. The spatial distribution of mean TL did not show a consistent increase or decrease with distance from the fishing base. This absence of a simple offshore gradient suggests that the distribution of size groups was spatially heterogeneous within the Ombai Strait. Such heterogeneity may reflect differences in habitat use, movement patterns, cohort distribution, food availability, reproductive condition, and local fishing pressure among fishing grounds.

Seasonal or monthly environmental variability may provide additional context for these changes, but the relationship between SST and fish size was not statistically significant in the present study. Mean SST decreased from 29.49 °C in June to 27.81 °C in August, while mean TL also decreased during the same period. However, the Pearson correlation analysis showed a very weak and non-significant relationship between SST and mean TL (r = -0.051, p = 0.675). Therefore, the temporal correspondence between SST and size structure should not be interpreted as evidence that SST directly determined fish size. Instead, the observed size structure likely resulted from the combined effects of biological processes and spatial availability of different size groups.

The occurrence of different size groups across the sampling period may also reflect the spatial organization of the flying fish population within the Ombai Strait. Because the sampling stations represented several fishing grounds rather than a single fixed habitat, temporal changes in the observed length structure may reflect both changes in population composition and changes in the distribution of fish among fishing grounds. This spatial component is particularly relevant for flying fish because previous studies have demonstrated differences in size characteristics among geographic areas in eastern Indonesian waters [4, 5].

The temporal interpretation must nevertheless consider the sampling limitation of the present study. Field observations were unavailable from December 2024 to April 2025 because of unfavorable sea conditions. Consequently, the observed decrease and subsequent increase in mean TL describe the pattern during the available sampling periods and should not be interpreted as a complete annual cycle. In particular, the November observation cannot be considered representative of the entire November–April period, while May 2025 represents an observation from the subsequent sampling period. The absence of observations during December–April may have obscured additional changes in size composition that occurred during this interval.

Overall, the present study demonstrates that the size structure of flying fish in the Ombai Strait varied both temporally and spatially, with a shift toward smaller individuals during August–September followed by an increase in mean TL during the subsequent available sampling periods. The occurrence of smaller size groups during August–September is consistent with the previously reported recruitment period in the Ombai Strait, although recruitment was not directly estimated in the present study. The spatial variation among fishing grounds and the absence of a significant relationship between SST and mean TL further indicate that size structure is influenced by multiple interacting biological and spatial processes rather than by a single environmental factor. These patterns provide an important basis for interpreting the reproductive characteristics of the population, particularly gonadal maturity, Lm_{50}, and Lc_{50}, discussed in the following sections.

4.4 Biological characteristics and reproductive status

The biological characteristics of flying fish in the Ombai Strait indicate a population with relatively consistent somatic

condition but substantial spatial and temporal variation in reproductive characteristics. The length–weight relationship showed different growth patterns between sexes. Male flying fish exhibited significantly negative allometric growth, with a growth coefficient of $b = 2.7184$ ($p < 0.001$), whereas the female coefficient of $b = 2.9358$ was not significantly different from 3 ($p = 0.062$) and was therefore statistically consistent with isometric growth. Differences in length–weight relationships among fish populations can arise from variation in environmental conditions, food availability, reproductive status, sex, and population characteristics. Similar variation in growth coefficients has been reported for flying fish in Indonesian waters [5]. The relatively high coefficients of determination obtained in the present study indicate a strong relationship between TL and body weight, suggesting that TL provides a reliable predictor of body weight for the sampled population.

The difference in growth pattern between sexes should be interpreted in relation to the biological condition of the sampled population. The length–weight relationship integrates individuals from different maturity stages, sampling periods, and fishing grounds. Variation in gonadal development can also contribute to differences in body mass relative to body length, particularly during reproductive development [12]. Therefore, the observed sex-specific growth patterns should not be interpreted as fixed characteristics of the species but as characteristics of the sampled population under the conditions observed during the study period.

The condition factor further indicates relatively comparable somatic condition between sexes. The mean condition factor was 1.0595 for males and 1.0571 for females, showing only a small difference between the two groups. Condition factor can vary with food availability, environmental conditions, and reproductive development [12]. The relatively similar values between sexes suggest that neither sex exhibited a pronounced difference in overall somatic condition during the study period. However, the monthly variation in condition factor, with higher values during June–July and lower values during October–November, indicates temporal changes in physiological condition that may be associated with feeding conditions, reproductive allocation, or environmental variability.

The sex composition was male-biased, with 1,864 males (60.38%) and 1,223 females (39.62%), corresponding to a female-to-male ratio of 1.00:1.52. The significant deviation from the expected 1:1 ratio indicates that males were more frequently represented in the sampled catch. However, this pattern should not be interpreted as definitive evidence of a male-biased population structure because sex composition in catches may be influenced by habitat use, reproductive behavior, mortality, recruitment, and fishing selectivity. Such mechanisms were not independently evaluated in the present study. Therefore, the observed ratio should be interpreted primarily as the sex composition of the sampled catch during the study period. Spatial and temporal differences in biological characteristics among flying fish fishing grounds have also been reported in Indonesian waters [4].

The biological results presented in this study represent the sampled catch or fishery-available component of the flying-fish assemblage rather than the entire natural population in the Ombai Strait. Because the fish were collected through gillnet fishing operations, the observed size structure, sex composition, and gonadal maturity composition may be influenced by gear selectivity, fishing location, fishing operation, and the availability of different biological groups to the fishing gear. Therefore, the observed proportions of males and females, size distributions, and maturity stages should be interpreted as characteristics of the sampled catch during the study period rather than direct estimates of the population structure of the entire natural stock.

The reproductive structure provides a more direct indication of the biological status of the sampled population. Immature gonadal stages (GML I–II) accounted for 72.95% of the 3,087 individuals, whereas mature stages (GML III–V) accounted for 27.05%. Immature fish predominated throughout the sampling period, although their proportion varied among months. The highest proportion of immature fish occurred in August (90.65%), whereas the lowest occurred in June (approximately 64%). The predominance of immature individuals indicates that the sampled fishing grounds contained a substantial component of the population that had not yet reached advanced gonadal maturity.

The occurrence of immature fish is also relevant when considered together with the previously reported recruitment pattern in the Ombai Strait. Previous research identified recruitment throughout the year, with a relatively important recruitment period during May–September [2]. The relatively high proportion of smaller fish and immature gonadal stages during August–September in the present study is therefore consistent with the previously reported recruitment period. Nevertheless, recruitment and gonadal maturity represent different biological processes. The present observations should consequently be interpreted as evidence of the presence of smaller and immature components of the population rather than direct evidence of recruitment during the same months.

Female Lm_{50} showed substantial spatial variation, ranging from 17.8 to 27.0 cm TL among stations where the parameter could be estimated. The lowest Lm_{50} was recorded at ST7 (17.8 cm), whereas the highest occurred at ST11 (27.0 cm). Considerable differences were also observed among stations located at the same fishing distance, with Lm_{50} ranging from 20.6 to 26.0 cm at 4 nautical miles and from 18.0 to 27.0 cm at 12 nautical miles. The absence of a consistent increase or decrease in Lm_{50} with increasing fishing distance indicates that maturity size was not governed simply by distance from the coast. Spatial differences in Lm_{50} may reflect variation in population structure, food availability, physiological condition, and local environmental conditions among fishing grounds [8]. However, these factors were not directly tested against Lm_{50} in the present study and therefore remain potential explanations rather than demonstrated causes.

The precision of these station-level estimates should nevertheless be interpreted in relation to the available sample size. Female sample sizes used for Lm_{50} estimation ranged from 8 to 177 individuals among stations. The inability to obtain an Lm_{50} estimate at ST3, where only eight females were available, illustrates the effect of limited sample size on the estimation of maturity size. Therefore, the observed range of Lm_{50} should be interpreted as station-level estimates that may differ in precision, rather than as definitive evidence of population-level differences in maturity size.

The spatial variation in Lm_{50} becomes particularly important when considered together with Lc_{50}. Female Lc_{50} ranged from 19.0 to 21.0 cm TL, while male Lc_{50} ranged from 18.5 to 21.5 cm TL. Female Lc_{50} was lower than female Lm_{50} at seven of the eleven stations where both parameters could be compared. This indicates that at these stations a substantial proportion of females may become vulnerable to the fishery

before reaching the estimated size at first maturity. However, Lc_{50} exceeded Lm_{50} at four stations, demonstrating that the relationship between capture size and maturity size was not spatially uniform throughout the fishing grounds.

Similarly, the precision of Lc_{50} estimates may vary among stations because the number of fish used for the sex-specific length-frequency analysis ranged from 21 to 293 males and from 8 to 177 females. Estimates based on smaller samples should therefore be interpreted cautiously. The station-level Lc_{50} values are presented as empirical estimates of the observed catch structure and should not be interpreted as definitive estimates of population-wide fishing selectivity.

The Lc_{50} estimates should also be interpreted in the context of fishing selectivity. Because the samples were obtained using gillnets, the observed length-frequency distribution reflects both the fish available in the fishing grounds and the size-selection characteristics of the gear. Consequently, the station-level Lc_{50} values should be regarded as empirical estimates derived from the observed catch structure under the fishing conditions of the study, rather than as direct estimates of the size structure of the entire natural population. Differences among stations may therefore reflect variation in fish availability and gear selectivity in addition to spatial differences in the sampled fish assemblage.

The difference between Lc_{50} and Lm_{50} is relevant to the reproductive vulnerability of the population. When Lc_{50} is lower than Lm_{50}, fish may become vulnerable to fishing before reaching the estimated size at first maturity, potentially reducing the opportunity for reproductive contribution. In the present study, this condition occurred at several fishing stations, but its spatial distribution was heterogeneous. Such variation may reflect differences in fishing selectivity, size composition, and the availability of different size groups among fishing grounds. Because the fishery uses gillnets, mesh size is an important component of size selectivity, and the observed Lc_{50} values provide a biological basis for evaluating whether the existing gear configuration permits adequate escapement of immature individuals.

Another limitation of the present study is that the main biological analyses were conducted using pooled *Exocoetidae* samples despite the identification of five flying fish species. Although five dominant species were identified, their quantitative species composition or relative abundance was not determined. Consequently, species-specific differences in growth, maturity size, reproductive timing, and fishing selectivity could not be evaluated separately in the present analysis. Therefore, the Lm_{50}, Lc_{50}, and length–weight parameters reported here should be interpreted as characteristics of the sampled flying-fish assemblage rather than as species-specific population parameters. Similarly, the identified potential reproductive or spawning zones represent areas where reproductive characteristics of the pooled assemblage were observed and should not be interpreted as species-specific spawning grounds. Species-specific analyses, including quantitative assessment of species composition, would provide additional resolution for evaluating differences in biological characteristics and fishing vulnerability among the five identified species.

Importantly, the spatial variation in gonadal maturity, Lm_{50}, and the relationship between Lc_{50} and Lm_{50} demonstrates that reproductive characteristics were not uniformly distributed throughout the Ombai Strait. Stations differed in the occurrence of mature individuals and in the proportion of females attaining the estimated size at first maturity. These differences provide a basis for examining reproductive characteristics at the fishing-ground scale rather than treating the entire Ombai Strait as a homogeneous reproductive habitat. When combined with the spatial distribution of SST and fishing-ground characteristics, these biological indicators can be used to identify areas where multiple reproductive characteristics occur concurrently.

From a fisheries management perspective, these findings indicate that management should consider not only total catch but also the spatial distribution of size structure and reproductive status. Fishing grounds where immature fish are prevalent or where Lc_{50} is below Lm_{50} may require particular attention in evaluating gear selectivity and fishing pressure. At the same time, areas characterized by a relatively high occurrence of mature individuals and females attaining or exceeding Lm_{50} provide important biological information for the identification of potential reproductive or spawning zones. The spatial integration of these indicators with environmental information is therefore relevant for subsequent identification and verification of potential reproductive areas in the Ombai Strait.

The areas identified as potential reproductive or spawning zones should be considered as areas for further investigation rather than immediately designated as protected spawning grounds. Direct reproductive surveys, including observations of spawning activity and the occurrence of eggs or larvae, are needed to verify the reproductive function of these areas. Similarly, nursery habitats were not directly identified in the present study; therefore, recommendations for nursery-area protection should be considered only after specific nursery-habitat assessments are conducted. Habitat conservation and area-based management measures may subsequently be evaluated based on the results of such additional assessments.

Climate-adaptive fisheries management should also be considered as a future management direction rather than as a direct implication of the present study. Although SST was characterized spatially and temporally, the available observations do not allow assessment of long-term climate effects on SST or flying fish population dynamics. Longer-term environmental and fisheries datasets are required to evaluate climate-related changes and their potential implications for flying fish distribution, reproduction, and fishery productivity.

4.5 Implications for fisheries management

The biological and spatial characteristics observed in the present study provide several implications for the management of the flying fish fishery in the Ombai Strait. The predominance of immature individuals, which accounted for 72.95% of the sampled fish, together with spatial variation in length at first maturity (Lm_{50}) and length at first capture (Lc_{50}), indicates that management should consider not only catch production but also the size and reproductive composition of the catch. In particular, female Lc_{50} was lower than female Lm_{50} at seven of the eleven stations where both parameters could be compared, indicating that females at several fishing grounds may become vulnerable to capture before reaching the estimated size at first maturity.

The relationship between Lc_{50} and Lm_{50} provides a useful biological reference for evaluating fishing selectivity. When Lc_{50} is lower than Lm_{50}, fish may become vulnerable to fishing before reaching the size at which approximately 50% of the population is sexually mature. This condition is particularly

relevant to gillnet fisheries because mesh size influences the size composition of retained fish. Previous studies of flying fish have demonstrated differences in selectivity among mesh sizes, including reported optimum selection lengths of approximately 20.34 cm for *Cheilopogon suttoni*, 22.16 cm for *Cheilopogon abei*, and 18.67 cm for *Hirundichthys oxycephalus* using a 1.25-inch mesh, with larger mesh sizes generally shifting the selected length toward larger fish [20]. These findings demonstrate that mesh size should be evaluated in relation to the size structure and species composition of the local fishery.

The relevance of this issue is particularly apparent because the gillnet used in the present fishery has a 1.25-inch mesh size. The observed female Lc_{50} of 19.0–21.0 cm TL and its lower value relative to Lm_{50} at several stations suggest that the current mesh configuration warrants further evaluation in relation to the reproductive characteristics of the local flying fish assemblage. However, the present results do not provide sufficient evidence to recommend an immediate replacement or prohibition of the 1.25-inch mesh. Different *Exocoetidae* species may exhibit different selectivity responses to the same mesh size [20]. Therefore, comparative or experimental fishing trials using alternative mesh sizes are needed to evaluate the trade-off between catch efficiency, species composition, and the retention of immature fish.

Previous studies have similarly indicated that increasing gillnet mesh size can reduce the capture of smaller flying fish. In Majene waters, increasing mesh size from approximately 1–1.25 inches toward 1.5 inches was associated with a reduction in the number of young flying fish captured [21]. Experimental fishing in the Makassar Strait also demonstrated differences in catch performance among 1-, 1.25-, and 1.5-inch gillnets. Together, these findings indicate that modification of mesh size may be considered as one component of a broader size-selective management strategy, but its application in the Ombai Strait should be supported by local selectivity experiments.

The spatial variation observed in the present study further indicates that management should consider differences among fishing grounds. This spatial perspective is consistent with previous satellite-based research in the northern waters of Belu, which identified monthly potential fishing areas extending from the coastal waters toward the Ombai Strait based on the distribution of SST and chlorophyll-a [22]. The present study extends this environmental perspective by incorporating geographically referenced biological and reproductive indicators, allowing fishing-ground characteristics to be evaluated together with fish size and reproductive status. Female Lm_{50} ranged from 17.8 to 27.0 cm TL, without a consistent increase or decrease with increasing fishing distance, while Lc_{50} also varied among stations and between sexes. Consequently, a single biological indicator may not adequately represent reproductive vulnerability across all fishing grounds. The relevance of SST as an environmental indicator for fisheries management is also supported by previous research in Indonesian waters. Maulana et al. [22] reported a negative statistical relationship between SST and small pelagic fish catches in WPP 573, indicating that variations in SST were associated with changes in catch yields. However, their study also recognized the contribution of other factors, including chlorophyll-a, upwelling intensity, climate variability, and fishing pressure, to catch fluctuations [22]. These findings support the use of SST as one component of an integrated fisheries-management approach rather than as a sole determinant of fish abundance. Continued monitoring of catch size composition, maturity structure, and Lc_{50} relative to Lm_{50} across the 2, 4, 6, and 12 nautical miles fishing grounds would provide a basis for identifying areas where fishing pressure may have greater implications for reproductive potential.

In addition to gear-based measures, the spatial distribution of reproductive characteristics provides an important basis for area-based management. The present study identified spatial heterogeneity in gonadal maturity and the proportion of females attaining or exceeding Lm_{50}. Stations ST7–ST9 at 6 nautical miles showed a relatively high concentration of reproductive characteristics, particularly ST8, which recorded 39.50% of individuals at GML III–V, 21.27% at GML IV–V, and 52.03% of females at or above Lm_{50}. ST7 also showed a high proportion of females attaining or exceeding Lm_{50} (95.24%) and 35.59% at GML III–V. At 12 nautical miles, ST10–ST12 also showed important reproductive characteristics, including high proportions of females ≥ Lm_{50} at ST10 (76.19%) and ST12 (89.90%), while ST11 recorded relatively high proportions of both GML III–V (39.42%) and GML IV–V (26.14%).

These spatial patterns, together with the SST conditions observed at the corresponding fishing grounds, provide a basis for identifying potential reproductive or spawning zones. The identified areas should, however, be interpreted as potential rather than confirmed spawning grounds because direct evidence of spawning, such as spawning females, eggs, or larvae, was not collected in the present study. Nevertheless, areas where mature individuals, females attaining or exceeding Lm_{50}, and appropriate environmental conditions occur concurrently can be considered priority areas for further reproductive surveys and spatial monitoring. This approach allows management attention to be directed toward areas with convergent biological indicators rather than assuming that the entire Ombai Strait functions as a homogeneous reproductive habitat.

Temporal monitoring is also important because the proportion of immature and mature fish varied among the available sampling months. The predominance of immature fish throughout the observed period, particularly during August, indicates that fishing activity may interact with different reproductive components of the population at different times. However, because field observations were unavailable from December 2024 to April 2025, the present data do not represent a complete annual cycle. Therefore, temporal management measures should be developed cautiously and supported by longer-term monitoring before specific closed seasons or monthly restrictions are established.

A minimum landing size (MLS) may also be considered as a complementary management measure. However, the wide spatial variation in female Lm_{50} (17.8–27.0 cm TL) indicates that a single MLS should not be adopted solely from the present Lm_{50} estimates without considering local maturity characteristics, species composition, catch size structure, and gear selectivity. Instead, the Lm_{50} and Lc_{50} information generated in this study can serve as biological references for evaluating alternative size-based management measures at the local scale.

The need for biological and spatial information is consistent with the broader direction of flying fish fisheries management in Indonesia. The issuance of Ministerial Regulation No. 76 of 2024 concerning the Flying Fish Fisheries Management Plan provides a national management framework within which local biological information can contribute to resource

assessment and management planning. The present study adds spatially referenced information on size structure, maturity, maturity size, capture size, and environmental conditions that can complement broader fisheries production and management information.

Overall, sustainable management of the flying fish fishery in the Ombai Strait should integrate size-selective fishing, monitoring of immature catches, spatial monitoring of reproductive characteristics, and continued environmental observation. The comparison between Lc_{50} and Lm_{50} provides a biological basis for evaluating fishing selectivity, while the spatial distribution of mature individuals and females attaining or exceeding Lm_{50} provides a basis for identifying areas requiring further reproductive-ground verification. In particular, the 6–12 nautical miles fishing grounds, where several reproductive indicators converged, may be prioritized for subsequent surveys and spatial management assessment. Such an approach links population characteristics and reproductive biology with spatial environmental information and provides a practical basis for developing adaptive fisheries management and conservation measures in the Ombai Strait.

5. CONCLUSIONS

The flying fish (*Exocoetidae*) in the Ombai Strait exhibited clear monthly and spatial variability in SST, size structure, and reproductive characteristics during the available sampling periods. SST decreased from June to July–August and subsequently increased toward November, while the size structure varied among sampling months and fishing grounds. However, because field observations were unavailable from December 2024 to April 2025, the present dataset does not represent a complete annual cycle and should not be interpreted as representative of the entire monsoonal cycle.

The biological characteristics of the sampled population showed sex-specific growth patterns, with males exhibiting significantly negative allometric growth, whereas the female growth coefficient was not significantly different from 3 and was therefore statistically consistent with isometric growth. The population showed relatively similar condition factors between sexes and a male-biased sex composition. Immature individuals predominated in the sampled catch, accounting for 72.95% of the total individuals. Female Lm_{50} varied substantially among fishing stations (17.8–27.0 cm TL), while female Lc_{50} was lower than Lm_{50} at seven of the eleven stations where both parameters could be compared, indicating that females at several fishing grounds may become vulnerable to capture before reaching the estimated size at first maturity. The biological estimates should be interpreted as characteristics of the sampled catch or fishery-available component because the observations were obtained through gillnet fishing operations and may therefore be influenced by gear selectivity and fish availability.

The spatial integration of reproductive indicators showed that reproductive characteristics were heterogeneous among fishing grounds. The 6-nautical-mile stations, particularly ST7–ST9, showed a relatively high concentration of reproductive indicators, while important reproductive characteristics were also observed at several 12-nautical-mile stations. ST8, in particular, showed a combination of relatively high proportions of GML III–V (39.50%), GML IV–V (21.27%), and females attaining or exceeding Lm_{50} (52.03%). These spatial patterns, considered together with the environmental SST context, provide supporting information for identifying potential reproductive or spawning zones in the Ombai Strait. However, these areas cannot be considered confirmed spawning grounds because direct evidence of spawning, eggs, or larvae was not collected.

From a fisheries-management perspective, the findings demonstrate the importance of integrating size structure, reproductive status, fishing selectivity, and spatial environmental information into flying fish fisheries management. Evaluation of gillnet mesh-size selectivity, monitoring and reduction of immature fish capture, and continued spatial and temporal monitoring are recommended to support reproductive sustainability. Areas showing a convergence of mature individuals, females attaining or exceeding Lm_{50}, and relevant environmental conditions should be prioritized for further reproductive surveys and spatial management assessment. Such areas should be regarded as priorities for further reproductive surveys and spatial monitoring rather than as confirmed spawning or nursery grounds. Specific area-based protection, habitat conservation, or nursery-area management measures should be considered only after additional reproductive and habitat assessments provide sufficient evidence. Rather than applying a uniform management measure across the entire Ombai Strait, management strategies should consider spatial differences in biological characteristics and fishing-ground conditions. Continued long-term environmental and biological monitoring is also necessary to evaluate temporal variability and provide evidence for future climate-adaptive and spatially adaptive management of the flying fish fishery in the Ombai Strait.

ACKNOWLEDGEMENTS

The authors would like to express our thanks for the research funding from the Indonesian Education Scholarship (BPI), Center for Higher Education Funding and Assessment (PPAPT), Ministry of Higher Education, Science, and Technology (KEMDIKTISAINTEK) of the Republic of Indonesia; Indonesian Endowment Fund for Education (LPDP), Ministry of Finance of the Republic of Indonesia as funders/sponsors.

REFERENCES

[1] Sharma, R., Barange, M., Agostini, V., et al. (eds) (2025). Review of the State of World Marine Fishery Resources–2025. FAO Fisheries and Aquaculture Technical Paper, No. 721. Rome. https://doi.org/10.4060/cd5538en

[2] Rehatta, B.M., Kamal, M.M., Boer, M., Fahrudin, A., Ninef, J.S.R. (2021). Growth, mortality, recruitment pattern, and exploitation rate of shared stock flying fish (Exocoetidae) at border area of Indonesia and Timor Leste in Ombai Strait. IOP Conference Series: Earth and Environmental Science, 744(1): 012062. https://doi.org/10.1088/1755-1315/744/1/012062

[3] Ministry of Marine Affairs and Fisheries of the Republic of Indonesia (MMAF). (2024). Decree of the Minister of Marine Affairs and Fisheries of the Republic of Indonesia Number 76 of 2024 concerning the Flying Fish Fisheries Management Plan. https://jdih.kkp.go.id/Homedev/DetailPeraturan/6682.

[4] Tuapetel, F., Tupan, C. (2021). Distribution of flying fish species (*Exocoetidae*) in the waters of Ambon Island. E3S Web of Conferences, 322: 01011. https://doi.org/10.1051/e3sconf/202132201011

[5] Indrayani, Sambah, A.B., Kurniawan, A., Pariakan, A., Jufri, A., Wiadnya, D.G.R. (2020). Determination species flying fishes (*exocoetidae*) in Makassar Strait. IOP Conference Series: Earth and Environmental Science, 441: 012110. https://doi.org/10.1088/1755-1315/441/1/012110

[6] Hakim, A., Wiryawan, B., Purbayanto, A., et al. (2025). Spawning and nursery areas of Decapterus *macarellus*: siting pelagic fisheries marine protected area (MPA) in the Sulawesi Sea, Indonesia. Frontiers in Marine Science, 12: 1606963. https://doi.org/10.3389/fmars.2025.1606963

[7] Kida, S., Richards, K.J. (2009). Seasonal sea surface temperature variability in the Indonesian Seas. Journal of Geophysical Research: Oceans, 114(C6): C06016. https://doi.org/10.1029/2008JC005150

[8] Nur, M., Ihsan, M.N., Ayuandiani, W., et al. (2025). Aspects of reproductive biology of flying fish, Hirundichthys oxycephalus (Bleeker, 1853) in Majene Waters, West Sulawesi Province, Indonesia. Malaysian Journal of Science, 44(3): 1-8. https://doi.org/10.22452/mjs.vol44no3.1

[9] Maceina, M.J., Bettoli, P.W., DeVries, D.R. (1994). Use of a split-plot analysis of variance design for repeated-measures fishery data. Fisheries, 19(3): 14-20. https://doi.org/10.1577/1548-8446(1994)019<0014:UOASAO>2.0.CO;2

[10] Oliveira, M.R., Carvalho, M.M., Silva, N.B., Yamamoto, M.E., Chellappa, S. (2015). Reproductive aspects of the flyingfish, *Hirundichthys affinis* from the Northeastern coastal waters of Brazil. Brazilian Journal of Biology, 75(1): 198-207. https://doi.org/10.1590/1519-6984.11513

[11] Sparre, P., Venema, S.C. (1992). Introduction to tropical fish stock assessment. Part 1: Manual. FAO Fisheries Technical Paper No. 306. https://openknowledge.fao.org/handle/20.500.14283/w5449e.

[12] Ragheb, E. (2023). Length-weight relationship and well-being factors of 33 fish species caught by gillnets from the Egyptian Mediterranean waters off Alexandria. Egyptian Journal of Aquatic Research, 49(3): 361-367. https://doi.org/10.1016/j.ejar.2023.01.001

[13] Tuapetel, F. (2021). Reproductive biology of the flying fish Cheilopogon abei Parin, 1996 in the waters of Geser Strait, East Seram. Jurnal Iktiologi Indonesia, 21(2): 167-184. https://doi.org/10.32491/jii.v21i2.555

[14] Hartoko, A., Maro, J.F., Helmi, M., Syafina, H.A.Z., Ashari, A.R., Ariyanto, D. (2025). Detecting cold seawater upwelling in Pantar Strait via multi-source satellite data integration and assessing its ecological impacts. International Journal of Design & Nature and Ecodynamics, 20(9): 2011-2019. https://doi.org/10.18280/ijdne.200906

[15] Martono. (2016). Seasonal and interannual variations of sea surface temperature in the Indonesian waters. Forum Geografi, 30(2): 120-129. https://doi.org/10.23917/forgeo.v30i2.1530

[16] Moore, T.S., Marra, J. (2002). Satellite observations of bloom events in the Strait of Ombai: Relationships to monsoons and ENSO. Geochemistry, Geophysics, Geosystems, 3(2): 1017. https://doi.org/10.1029/2001GC000174

[17] Sprintall, J., Wijffels, S.E., Molcard, R., Jaya, I. (2010). Direct evidence of the South Java Current system in Ombai Strait. Dynamics of Atmospheres and Oceans, 50(2): 140-156. https://doi.org/10.1016/j.dynatmoce.2010.02.006

[18] Alongi, D.M., Brinkman, R., Trott, L.A., da Silva, F., Pereira, F., Wagey, T. (2013). Enhanced benthic response to upwelling of the Indonesian Throughflow onto the southern shelf of Timor-Leste, Timor Sea. Journal of Geophysical Research: Biogeosciences, 118(1): 158-170. https://doi.org/10.1029/2012JG002150

[19] Maulana, G., Situmorang, R.P., Afrisal, M., et al. (2025). Spatial distribution of sea surface temperature in the Ombai Strait based on Aqua-MODIS satellite imagery [in Indonesian]. Jurnal Kelautan, 18(3): 191-198. https://journal.trunojoyo.ac.id/jurnalkelautan/article/view/31623/0.

[20] Hutubessy, B.G., Syahailatua, A. (2010). Performance of gillnet-mesh size selectivity for three flyingfish species in Ambon waters, Moluccas Province. Marine Research in Indonesia, 35(2): 39-46. https://doi.org/10.14203/mri.v35i2.476

[21] Najamuddin, N., Assir, A., Palo, M., Najamuddin, A.A. (2018). Penerapan perubahan ukuran mata jaring dalam penangkapan ikan terbang secara berkelanjutan di Kecamatan Sendana Kabupaten Majene. Journal of Indonesian Tropical Fisheries, 1(1): 17-27. https://doi.org/10.33096/joint-fish.v1i1.16

[22] Maulana, G., Situmorang, R.P., Gustasya, Y. (2026). The effect of sea surface temperature on small pelagic fish catches in WPP 573. Fisheries Journal, 16(1): 52-58. https://doi.org/10.29303/jp.v16i1.1934