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Modelling of the Spawning Pattern of European Anchovy (*Engraulis encrasicolus*, Linnaeus, 1758) with Using Bootstrap Regression of Frequent Ichthyoplankton Sampling Data

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Abstract

To understand rapid temporal fluctuations during the spawning period, weekly ichthyoplankton sampling was conducted in the Çanakkale Strait (North Aegean Sea) between April and December 2023 using a WP-2 net. The anchovy spawning period was estimated to last 22 weeks (May 23-October 30). Weekly observations revealed that monthly averages smoothed short-term fluctuations and masked major abundance peaks. Due to the asynchronous spawning pattern, 7-8 spawning peaks and 2 major spawning peaks were detected during spawning. A bootstrap-based resampling approach was applied to analyze the relationship between biological and environmental variables. According to bootstrap regression, each 1 unit increase in temperature led to an increase in egg abundance by 337.722 units on average, whereas every 1 unit increase in salinity led to an average decrease of 36.456 units in the number of larvae.

Introduction

Small-scale fisheries are a vital source of nutrition and livelihood, with 40% of total global catch and 90% of capture fishery work power (FAO, 2024). The total landings harvested from the General Fisheries Commission for the Mediterranean (GFCM) area has decreased from 2 million tons to 1.1 million tons in the last 25 years. The primary species constituting this harvest were small pelagic species such as European anchovy, *Engraulis encrasicolus* (Linnaeus, 1758), European pilchard, *Sardina pilchardus* (Walbaum, 1792) and European sprat, *Sprattus sprattus* (Linnaeus, 1758). Between all landings in the GFCM area, 32.2% of the total catch comprised European anchovy with a catch of 342 000 tons. Anchovy landings constitute 20.1%, 13%, 14.2% and 65% of the total landings in the Adriatic, Western Mediterranean, Eastern Mediterranean and the Black Sea subregions, respectively. Türkiye was declared the main producer in the GFCM area, constituting 18% and 28% of the total fishing capacity and the total landings, respectively. Additionally, 61.9% of the total landing weight from the Black Sea was obtained by the Turkish fishing fleet. Of the total catch from the GFCM area, 37.5% was landed from the Black Sea region (FAO, 2023). According to this landing and fishing capacity data, the significance of anchovy is substantial for both the GFCM and other areas. It was reported that the balance between sustainable exploitation and socioeconomic development of small pelagic fish species must be achieved correctly (FAO, 2024).

Hilborn et al. (2020) compared the status of well-managed and non-managed fishery stocks and identified more catch records in non-managed areas, although with a declining trend. For sustainability, sufficient fishery management implementations should be performed. For this purpose, some valuable precautions were applied for anchovy species in various geographical areas and management bodies (Pacific

Fisheries Management Council (PFMC); Scientific, Technical and Economic Committee for Fisheries (STECF); Coastal Pelagic Species Fisheries Management Plan (CPSFMP)), such as quota implementation, marine protection areas, closed seasons, etc. (PFMC, 1978; STECF, 2011; CPSFMP, 2024). For the 2024-2025 fishery season, a quota program for anchovies was implemented for the first time in Türkiye by the Ministry of Agriculture and Forestry within the scope of the agricultural production planning program. In some papers, science-based management plans (SBMP) were stated to be mandatory for sustainable use of fishery research (Cooke et al., 2017). Mostly, management plans are prepared using inaccurate scientific data. SBMPs should include quality-assured data, fishery policy formulations, true analysis, and the best selected data (Su et al., 2021).

Ichthyoplankton are defined as the meroplanktonic stage of fish eggs and the nektonic stage of fish larvae, which are mostly distributed in the pelagic ecosystem above the thermocline (Odum, 1971). Ichthyoplankton have become a useful tool for fishery managers due to revealing scientific knowledge about life cycle, recruitment, spawning area, spawning time and stock capacity (Auth et al., 2018). To obtain the best quality-assured scientific data with lower costs and effort compared to other fishery techniques or acoustic data, the importance of ichthyoplankton cannot be ignored.

Several monitoring studies have been carried out in different geographical areas using the ichthyoplankton method in order to provide accurate data for fishery managers. Most of these studies were performed as long-term monitoring studies in a certain area (Moser et al., 2001; Tucker et al., 2018; Chang et al., 2023; Hunt et al., 2024) in order to understand the effects of climate change and anthropogenic effects on marine species. However, the results of frequent sampling intervals have not been adequately evaluated in relation to the ichthyoplankton community structure. Limited studies were conducted related to the effects of ichthyoplankton sampling frequency (Daban and İşmen, 2020; Pompeu et al., 2023). Thus, the aim of this study is to understand the effects of sampling interval during the entire spawning season on processes (such as abundance, detection of the onset, peak and the end time of spawning, egg sizes etc.) and test the sufficiency of collect ichthtyoplankton data with a monthly sampling interval within whole spawning season.

Materials and Methods

In the present study, frequent weekly sampling was carried out to obtain all detailed information related to European anchovy reproduction. In addition, sampling was carried out in a way that would determine the exact beginning and end dates for reproduction. Therefore, the dates on which first and last eggs were observed in the study area were accepted as the spawning interval for *E. encrasicolus.*

The vertical plankton tows were completed with weekly intervals around Çanakkale Straits, North Aegean Sea, between 18th April and 7th December 2023 (Figure 1). Fish egg and larvae samples were collected with a WP-2 type plankton net (57 cm mouth diameter, 500 µm mesh size, and 3 m total length) in coastal areas. Plankton samples were fixed with 4% buffered formaldehyde, European anchovy eggs and larvae were

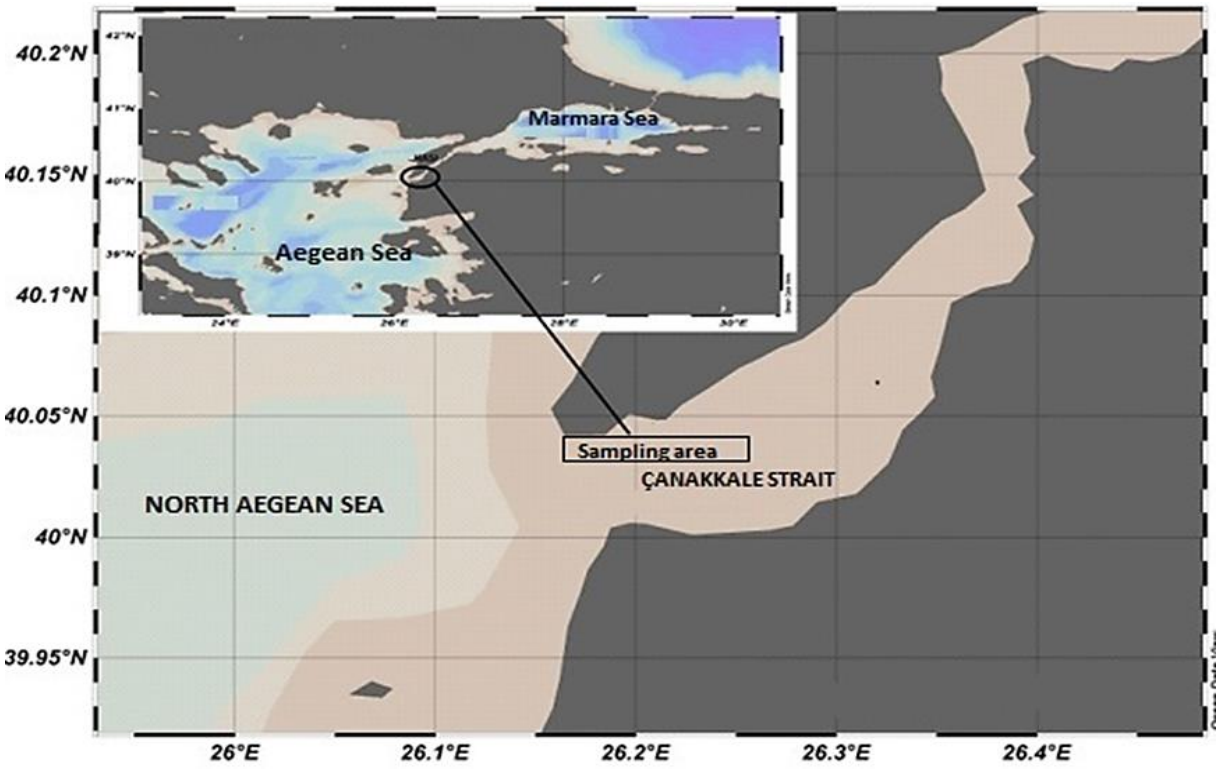


Figure 1. Study area.

sorted with an SZX7 stereo microscope. The egg diameter and larvae lengths were measured with Q-Capture Pro digital imaging tool. The sea surface temperature (SST; °C), salinity (S; ppt) and dissolved oxygen (DO; mg/L) values were measured with a YSI 6600 multiparameter device.

Mean European anchovy eggs and larvae from vertical tows were standardized in a unit area (n/10 m^2) according to the formula given in the "Vertical Distribution" section of FAO Fisheries Technical Papers No: 175;

$$C = Cv \times (SR/V)$$

where C is the number of individuals in a unit area (n/10 m^2), Cv is the number of individuals in unit volume (n/1000 m^3), S is the unit of area (10 m^2), R is the depth of sampling (m) and V is the unit of volume (1000 m^3) (Smith and Richardson, 1977).

The numerical data about the physicochemical properties of sea water and the number of fish eggs and larvae obtained from sampling were transferred to the R programming language (RSTUDIO IDE) and the necessary data pre-processing steps were performed. The boot, corrplot, car and ridge packages of R programming language were used and the probability of making a type I error in the analyses was accepted as 0.05.

Considering the limited sample size represented by the dataset used in this study, the normality assumption was assessed using the Shapiro–Wilk test, which is regarded as one of the most suitable and powerful tests for small samples. Outlier detection was performed using Tukey's interquartile range (IQR) method and was supported by visual inspection of boxplots. Observations identified as extreme values were not treated as measurement or data-entry errors by default; instead, they were evaluated in the biological context of the spawning season.

The results showed that the variables did not satisfy the normality assumption. Therefore, the nonparametric Spearman correlation coefficient was used to evaluate the relationships between variables, taking the limited sample size into account (Xia and Shen, 2024). This method allowed the evaluation of the strength and direction of monotonic relationships between variables. In modelling egg and larval abundance according to environmental parameters, a bootstrap-based resampling approach was applied, considering the limited sample size, the high short-term variability in abundance values, and the methodological constraints of the dataset. This approach is especially useful when distributional assumptions are not strictly met and sample size is limited (Kostanek et al., 2024).

In order to examine the temporal variations in fish egg and larval abundance, bootstrap confidence intervals were calculated on a monthly basis using B= 1000. A fixed random seed (seed = 123) was used to ensure reproducibility. In addition, to evaluate the effect of sampling interval, weekly observations and monthly mean values were compared using time-series graphs. These graphs were used to illustrate how monthly summaries smooth short-term fluctuations and peak events detected in weekly sampling, thereby providing a more intuitive comparison of temporal patterns (Melià et al., 2012).

Although non-linear relationships between individual environmental variables and egg or larval abundance may be biologically plausible, especially in the presence of short-term abundance peaks during the spawning season, the diagnostic plots presented in S1 Figure did not provide clear evidence of a strong non-linear structure in the present dataset. Component-plus-residual plots showed only slight curvature in some predictor–response relationships, and residuals-versus-fitted plots did not indicate a pronounced systematic departure from linearity. Therefore, a linear specification was retained for the exploratory regression analyses. In this context, ordinary least squares (OLS), ridge regression, and bootstrap regression were treated as complementary approaches rather than competing methods for selecting a single best model (Sahinler and Topuz, 2007). The regression model for n observations was defined as

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \epsilon$$

where Y denotes the dependent variable (egg abundance or larval abundance), X_1 denotes sea surface temperature (SST), X_2 salinity (S) and X_3 dissolved oxygen (DO). The design matrix is $X = [1, x_1, x_2, x_3]_{n\times 4}$ and the parameter vector is $\beta\ is\ [\beta_0, \beta_1, \beta_2, \beta_3]'_{4\times 1}$. In the first step, OLS regression was applied as a baseline linear modeling approach, and the regression coefficients were estimated as

$$\hat{\beta}_{LS} = (X'X)^{-1}X'y.$$

Because the explanatory variables showed evidence of multicollinearity, ridge regression was additionally used as a shrinkage-based complementary approach. The ridge estimator was obtained as

$$\hat{\beta}_{Ridge} = \left(X'X + kI_p\right)^{-1}X'y,\ k > 0$$

where k denotes the ridge parameter. Ridge regression was not treated as a definitive or superior model, but rather as a supplementary approach to evaluate coefficient stability under multicollinearity.

Since the dataset consisted of a limited number of weekly observations, exhibited high short-term variability, and did not satisfy the normality assumption, bootstrap regression was further applied to assess parameter uncertainty under the observed data structure. In the bootstrap procedure, B resamples of size N were generated by sampling observations with replacement from the original weekly dataset. For each

bootstrap sample, regression coefficients were re-estimated using the least squares estimator, and the bootstrap estimate of the regression coefficient was obtained by averaging the estimates across all resamples (Fox, 1997).

An N-dimensional bootstrap sample $\left(w_1^{(b)}, w_2^{(b)}, \dots, w_n^{(b)}\right)$ is created by reselecting the observations with probability $1/n$ for each w_i. The elements of each vector are labeled as,

$$w_i^{(b)} = \left(y_i^{(b)}, x_{ji}^{(b)}\right)', i = 1,2, \dots, n \ and \ j = 1,2, \dots, k$$

From these, $Y_i^{(b)} = \left(y_1^{(b)}, y_2^{(b)}, \dots, y_n^{(b)}\right)'$ vector and $X_{ji}^{(b)} = \left(x_{j1}^{(b)}, x_{j2}^{(b)}, \dots, x_{jn}^{(b)}\right)'$ matrix are created. The least squares estimator is applied to the data obtained from the bootstrap sample as many times as the number of bootstrap iterations (B) where;

$$\hat{\beta}^{(b_1)} = \left(X^{(b)\prime} X^{(b)}\right)^{-1} X^{(b)\prime} Y^{(b)}$$

in each iteration, and the bootstrap estimate of the regression coefficient is obtained from the average of these estimates (Fox, 1997);

$$\hat{\beta}^{(Boost)} = \frac{\sum_{r=1}^{B} \hat{\beta}^{(b_r)}}{B}.$$

Results

Physicochemical Parameters

As can be seen in Figure 2, the SST and S temporally varied in a similar way, whereas DO changed in inverse fashion. The DO% ranged between 6.64 mg/l and 10.31 mg/l, with a mean of 7.66±0.15 mg/lt. The S values were distributed from 23.2 ppt to 29.5 ppt (mean: 25.5±0.23 ppt) and the SST values ranged from 14.9°C to 24.4°C (mean: 20.6±0.52°C). The SST was measured as a 15.5°C, when the first European anchovy eggs were found on 17th May 2023. Lower SST values were recorded during the period when anchovy eggs had not yet appeared in the sampling area. In addition, the occurrence of European anchovy eggs relatively decreased and/or disappeared when the S values increased towards 27-29 ppt. No different DO values were detected before or after spawning compared to those observed during spawning (Figure 2).

Eggs and Larvae Characteristics

The width and height of the elliptically shaped anchovy eggs were measured. The egg widths ranged from 0.991 to 1.484 µm (mean: 1.212±0.033 µm) and the egg heights were distributed from 0.488 to 0.750 µm (mean: 0.618±0.017 µm). Statistically significant monthly variations in the mean width and height of the eggs were observed, and larger eggs were seen in May and June. According to ANOVA, the mean width in May and June and the mean height in June were statistically different from the other months for European anchovy eggs (df: 5; F: 32.07; P<0.05).

The pre-larvae ranged in length between 1.558 mm and 3.220 mm, with a mean of 2.342±0.438 mm. The pre-flex larvae and the flex larvae had lengths between 1.717 mm and 4.059 mm, with a mean of 2.483±0.038 mm. The post-larvae were 2.950 mm to 10.078 mm long (mean: 4.067±0.285 mm). In total, post-larvae constituted only 17% of the total larvae abundance. In addition, larvae larger than 5 mm and 7 mm constituted 1.9% and 0.6% of the total larvae abundance. Temporally, all development stages of anchovy larvae were found during the entire spawning season. Additionally, the pre-larvae decreased and other stages increased after the 6th July.

Spawning Season

Sampling began before the first anchovy eggs were seen and continued until it was certain that the eggs had disappeared from the environment to ensure that the beginning and the end of the spawning were included. Thus, weekly ichthyoplankton samplings were completed over 29 sampling observations collected over 27 calendar weeks, from 18th April 2023 to 7th December 2023. The first and the last anchovy eggs were seen on 17th May and 10th November,

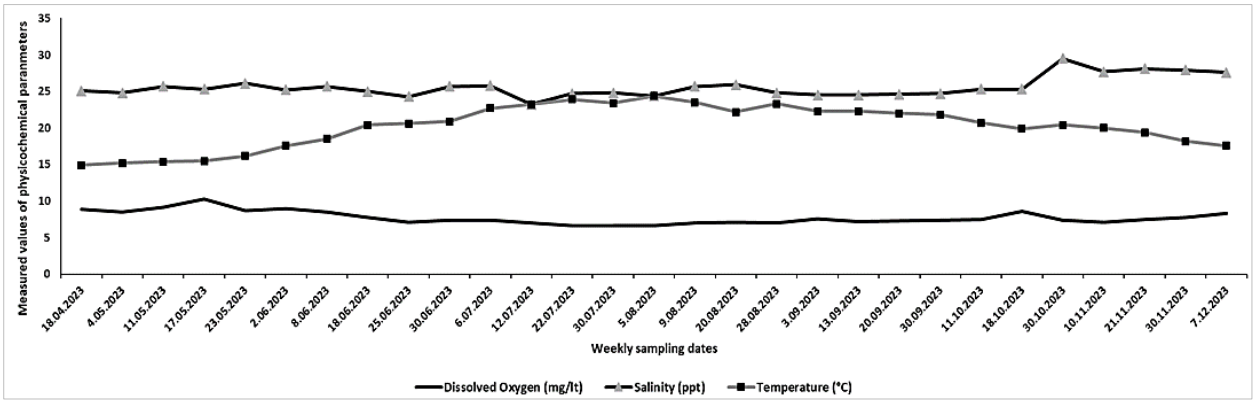


Figure 2. Physical-chemical parameters of the sea water in the study area.

respectively. Also, the first and the last anchovy larvae were detected on 23rd May and 30th October, respectively. Thus, the spawning interval for anchovy was estimated to be between 23rd May and 30th October, spanning over 22 weeks.

Fish Egg and Larvae Abundance

The mean abundance of anchovy eggs during the 22-week spawning season was detected as 2656.7±821.2 n/10 m^2. At the beginning of spawning, mean fish egg abundance was calculated as 274.4 n/10 m^2. Mean abundance peaked two times on 30th June and 13th September, with abundance of 15072.4 n/10 m^2 and 8428.1 n/10 m^2, respectively. Although two major peaks were detected, mean abundance of fish eggs showed a fluctuating pattern. Mean abundance was found 39.2 n/10 m^2 on 10th November, when the last eggs were seen (Figure 3). According to physical evaluation (integrity of vitellus and egg periphery) of the eggs the moment that sampled, the ratio of dead eggs via alive eggs was detected as 49%.

European anchovy larvae were detected during 16 weeks in the 22-week spawning season. The mean abundance during the season was 189.5±44.3 n/10 m^2. As in the case of fish eggs, one major abundance peak was observed on 30th June with abundance of 803.6 n/10 m^2 for fish larvae. In contrast to fish eggs, a relatively high larvae abundance was detected on 22nd July. This may be a result of hatching of the dense egg production on 30th June. The last larvae was detected on 30th October. According to development phases, the majority (82%) the pre-flex larvae were found between 2nd June and 7th July. On 7th July, the occurrence of pre-flex larvae peaked, with abundance of 157.6 n/10 m^2. The other development phases peaked on 30th June and 13rd September (Figure 3).

Modelling of the Temporal Changes during European Anchovy Spawning

A total of 29 sampling observations collected over 27 calendar weeks covering the 2023 spawning season were used in this study. The dataset included biological measurements of egg and larval abundance, as well as environmental variables such as temperature, salinity, and dissolved oxygen. The dataset was first examined using boxplots for the detection of extreme observations. Figure 4 shows the overall distribution of anchovy egg abundance and the dates on which extreme observations occurred. Accordingly, the high values observed on 25.06.2023, 30.06.2023, and 13.09.2023 indicate short-term biological peaks. Figure 5 shows that the distribution of larval abundance also included several dates with clearly elevated peak values. In particular, the extreme values observed in late June, July, and September reflect short-term biological increases in larval abundance.

Descriptive statistics were calculated for the dataset used in this study, and the distributional properties of the variables were evaluated using the Shapiro-Wilk test (Table 1). High variability was observed in both egg and larval abundance, with egg abundance showing a more heterogeneous distribution than larval abundance. In contrast, the physicochemical variables, namely temperature, salinity, and dissolved

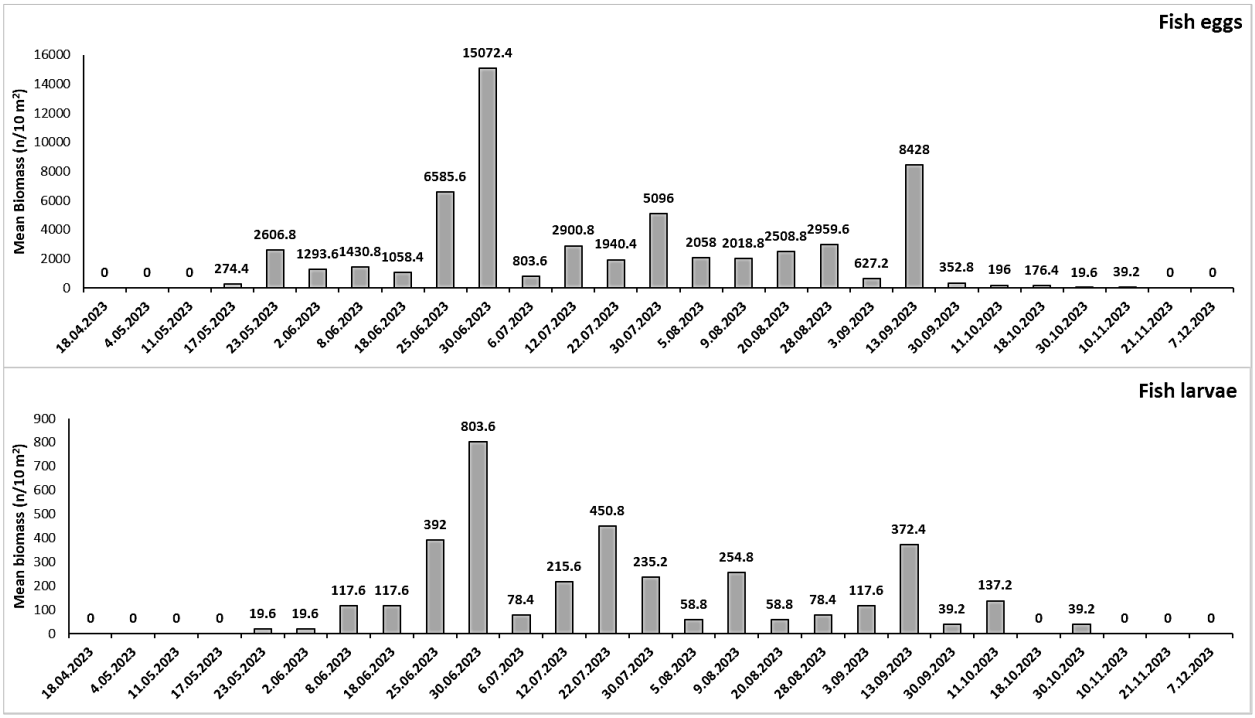


Figure 3. Mean European anchovy fish egg and larvae abundance in the study area.

oxygen, exhibited more stable distributions with lower coefficients of variation. According to the Shapiro-Wilk test results, the variables in the dataset did not satisfy the normality assumption ($P<0.05$). Therefore, given the limited sample size and the high short-term variability, resampling-based confidence intervals were used to evaluate temporal variation.

The 95% confidence intervals for egg and larval abundance are presented in Table 2. In May, the 95% confidence interval for egg abundance ranged from 0 to 1955 n/10 m², whereas for larval abundance it ranged from 0 to 14.7 n/10 m². This indicates that larval abundance remained low and showed relatively limited variability during this period. In June, the confidence interval for egg abundance was considerably wider, ranging from 1227 to 9889 n/10 m², while the confidence interval for larval abundance remained narrower, between 78.4 and 564 n/10 m². This finding suggests that egg abundance was both higher and more variable in June. In August, the confidence intervals for both variables became narrower, indicating a more stable distribution. In September, the confidence interval for egg abundance ranged from 157 to 6409 n/10 m², whereas the interval for larval abundance ranged from 9.8 to 289 n/10 m². This pattern indicates that egg abundance became more variable again in September. In October, the narrowing of the confidence intervals for both egg and larval abundance suggests lower variation in both parameters during this period.

To evaluate the effects of weekly and monthly sampling intervals on egg and larval abundance, data obtained from both sampling approaches were compared using time-series graphs (Figures 6 and 7). These graphs clearly demonstrate how monthly mean values alter the temporal pattern of variation relative to weekly measurements. As shown in Figure 6, egg abundance exhibited pronounced short-term fluctuations throughout the spawning season. The sharp increases observed in late June and September represent the most striking examples of this pattern. In

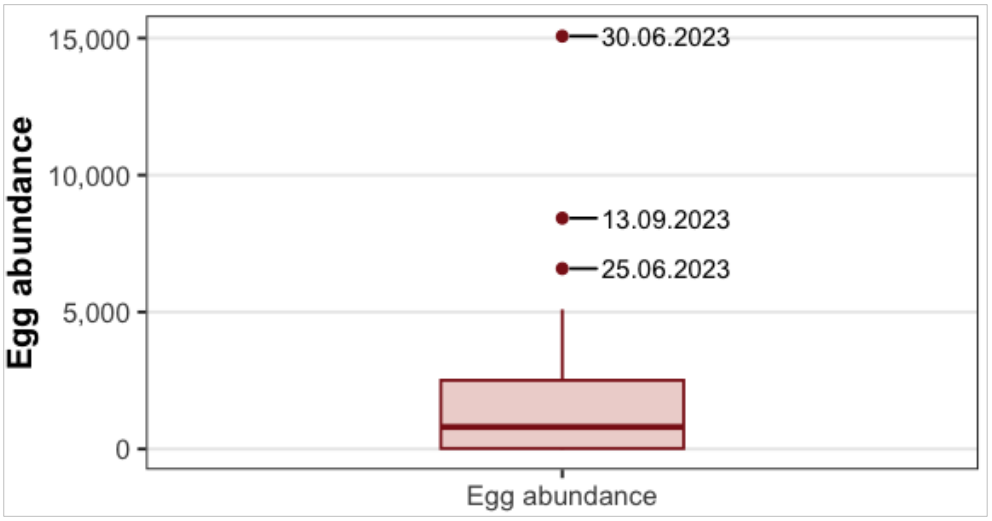


Figure 4. Boxplot of Anchovy egg abundance with labeled extreme observations.

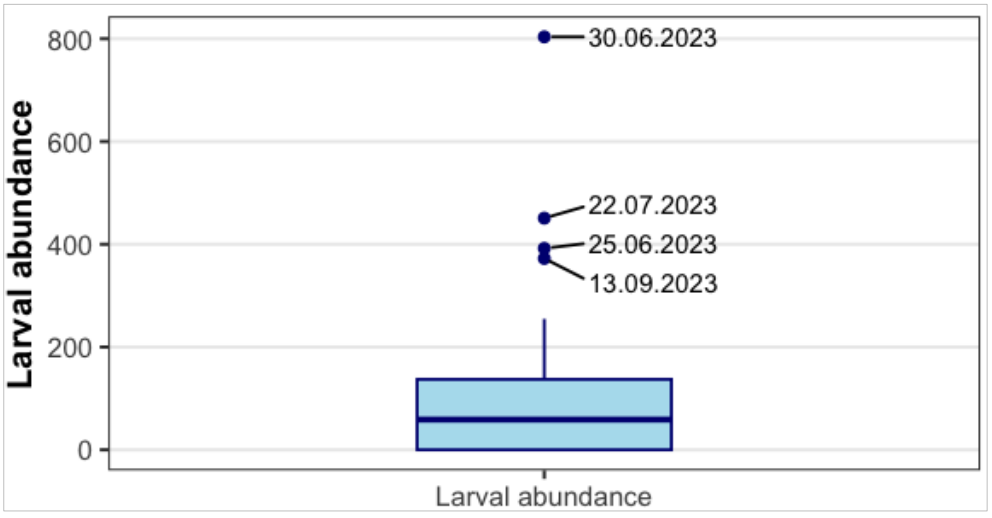


Figure 5. Boxplot of Anchovy larval abundance with labeled extreme observations.

contrast, the monthly mean values followed a much smoother course during the same period and substantially attenuated the magnitude of these abrupt peaks. This suggests that summaries based on monthly sampling may conceal sudden increases in abundance and therefore underestimate temporal variability during critical phases of the spawning season. The divergence between weekly and monthly values became particularly evident in June and September, highlighting the importance of high-frequency sampling during these months.

A similar pattern was observed for larval abundance (Figure 7). The pronounced peak in June, together with additional fluctuations in July and September, shows that short-term variability can be tracked more clearly in weekly observations. In contrast, when monthly mean values were used, these fluctuations were largely smoothed; although the general seasonal trend remained visible, the intensity of the peaks was reduced and the representation of within-month variation became weaker. Taken together, these findings indicate that sampling frequency plays a decisive role in accurately representing the abundance pattern of the early life stages of European anchovy. Although monthly means may reflect the broader seasonal pattern, they are insufficient to preserve the short-term fluctuations and peak events captured by weekly measurements. Therefore, all subsequent analyses were based on weekly observations in order to provide a more detailed and biologically meaningful representation of temporal variability.

The relationships between egg and larval abundance and the physical and chemical parameters of seawater were evaluated using a heatmap based on the Spearman correlation coefficient, since the variables did not conform to the normality assumption (Figure 8).

The analysis showed a positive correlation of 79% between egg and larval abundance. Among the environmental variables, the strongest relationship with egg abundance was observed for dissolved oxygen, and

Table 1. The descriptive statistics of the data used in this study

	Egg	Larvae	Temperature	Salinity	Dissolved oxygen
Mean	2015.421	124.359	20.276	25.583	7.738
Std. Error of Mean	606.048	34.077	0.544	0.254	0.164
Std. Deviation	3263.667	183.511	2.928	1.369	0.884
Coefficient of variation	1.619	1.476	0.144	0.054	0.114
Shapiro-Wilk	0.649	0.712	0.922	0.874	0.894
P-value of Shapiro-Wilk	< .001	< .001	0.034	0.002	0.007
Minimum	0.000	0.000	14.900	23.200	6.640
Maximum	15072.400	803.600	24.400	29.500	10.310

Table 2. %95 Bootstrap confidence interval of European anchovy eggs and larvae

Month	Egg		Larvae	
	Lower	Upper	Lower	Upper
May	0	1955	0	14.7
June	1227	9589	78.4	564
July	1328	4307	118	392
August	2038	2734	58.8	206
September	157	6409	9.8	289
October	19.6	196	0	137
November	0	39.2	0	0

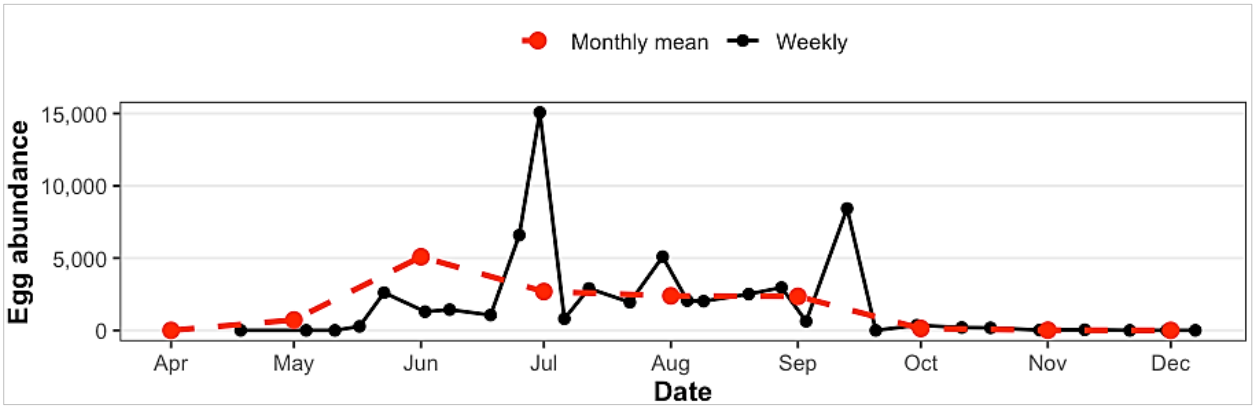


Figure 6. Temporal variation in Anchovy egg abundance: Weekly observations and monthly means.

this relationship was moderately negative (r_s = -0.50). Larval abundance, on the other hand, showed the strongest association with temperature among the environmental variables, and this relationship was found to be moderately to strongly positive (r_s = 0.65).

In addition, the relationships among the physical and chemical parameters of seawater were examined in detail, and a negative correlation of 86% was found between temperature and dissolved oxygen (Figure 8). This suggests that the interrelationships among environmental variables may lead to a multicollinearity problem in modelling egg and larval abundance. Supporting this finding, the variance inflation factor (VIF) values calculated for the OLS models, when egg abundance was taken as the dependent variable, were 5.544, 1.367, and 4.986 for temperature, salinity, and dissolved oxygen, respectively. When larval abundance was used as the dependent variable, the VIF values remained unchanged because the explanatory variables were the same. These results indicate a moderate level of multicollinearity, particularly between temperature and dissolved oxygen.

Therefore, the effects of environmental variables on egg and larval abundance were initially examined using the ordinary least squares (OLS) method; however, these results were interpreted cautiously

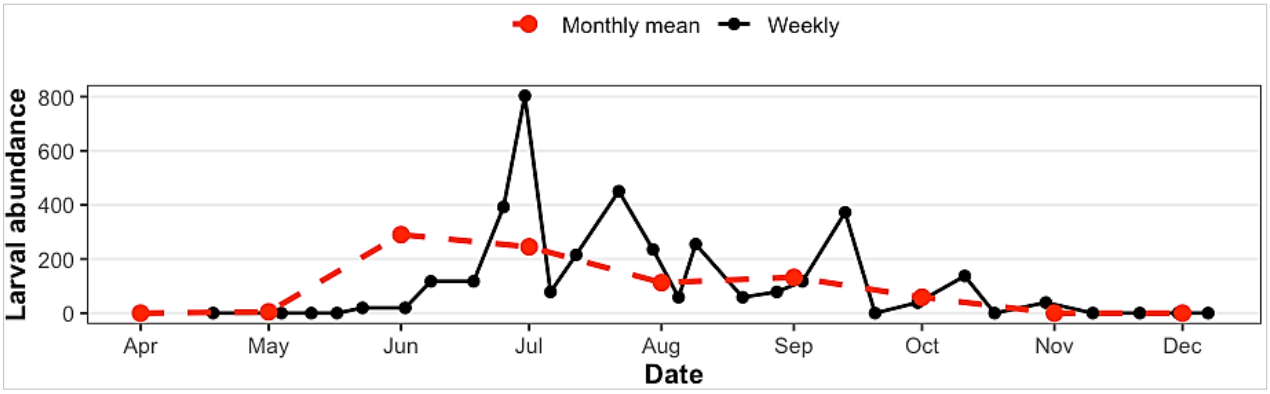


Figure 7. Temporal variation in Anchovy larval abundance: Weekly observations and monthly means.

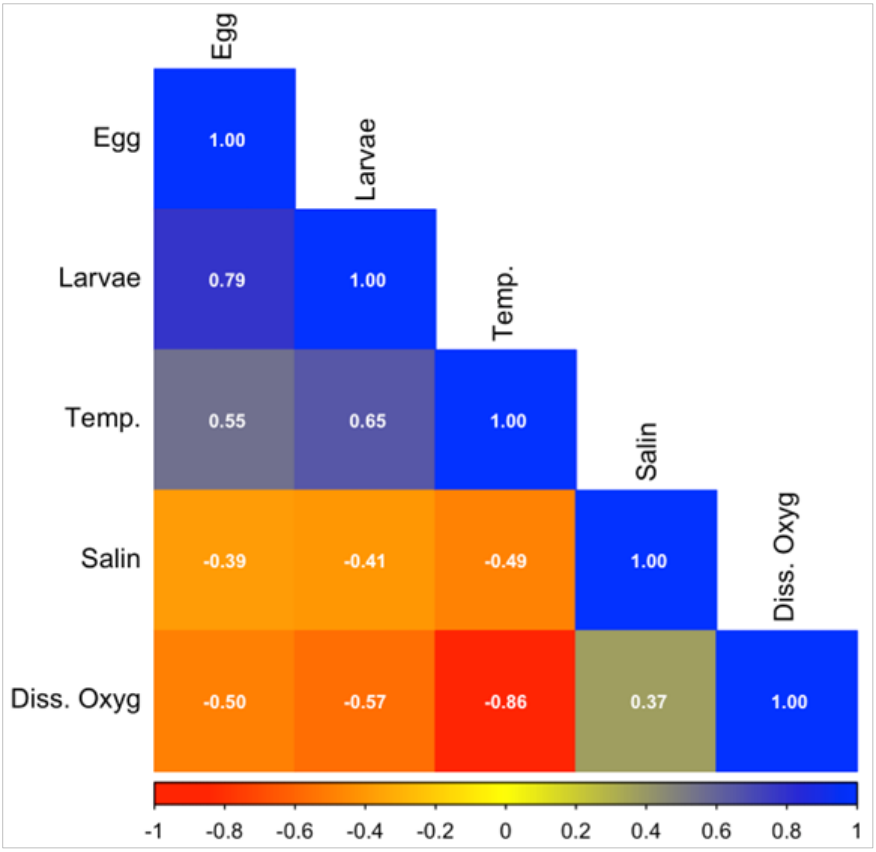


Figure 8. Correlation heat map for the European anchovy.

because of the limited sample size, the high short-term variability in abundance values, some violations of model assumptions, and the multicollinearity among the explanatory variables. In addition, ridge regression was applied as a complementary approach in order to reduce the effect of multicollinearity on coefficient estimates and to assess the stability of the estimates. Nevertheless, in this study, OLS and ridge regression analyses were not treated as tools for identifying a final or superior model, but rather as supportive exploratory analyses aimed at examining possible relationships between environmental variables and abundance. The main comparisons and subsequent evaluations in the study were based on weekly sampling data, and bootstrap-based analyses were likewise performed using weekly observations. Detailed results of the OLS and ridge regression analyses are provided in the supplementary material.

Tables S1 and S2 present the results of modelling anchovy egg abundance using OLS and ridge regression, respectively. According to the OLS results, the effects of temperature, salinity, and dissolved oxygen on egg abundance were not statistically significant at the 5% significance level. Similarly, in the ridge regression results obtained with a ridge parameter of 0.657, the coefficients of temperature, salinity, and dissolved oxygen were also not found to be statistically significant at the 5% level. Tables S3 and S4 present the results of modelling larval abundance using OLS and ridge regression, respectively, and in both methods the coefficients of temperature, salinity, and dissolved oxygen were likewise not statistically significant at the 5% level. However, the results presented in Tables S1-4 should not be interpreted as definitive evidence that environmental variables have no effect on egg and larval abundance. The limited sample size, the high short-term variability in abundance values, and the multicollinearity among the explanatory variables may have reduced the statistical power of these analyses.

The extreme observations in the dataset were not treated as measurement or data-entry errors, but rather as biologically meaningful peak events specific to the spawning season. For this reason, robust methods that reduce the influence of such observations were not preferred as the main analytical approach. This is because such methods may suppress the short-term abundance peaks that constitute the central focus of the study and may therefore lead to an underrepresentation of the true biological variability. Instead, a bootstrap approach was applied in order to evaluate the uncertainty of parameter estimates under conditions of limited sample size and high short-term variability. By resampling from the weekly observations, the bootstrap procedure made it possible to obtain the empirical distribution of the regression coefficients; thus, biologically meaningful peak values were retained within the data structure, while the relationships between environmental variables and egg and larval abundance were evaluated by taking estimation uncertainty into account.

Tables 3 and 4 present the results of bootstrap regression models for egg and larval abundance, respectively, in relation to the physical and chemical properties of seawater. According to Table 3, the coefficient of temperature was found to be statistically significant in the egg abundance model, whereas the effects of salinity and dissolved oxygen were not significant. Accordingly, a 1-unit increase in temperature, while holding the other variables constant, was associated with an average increase of 337.722 units in egg abundance. This finding suggests that egg abundance may tend to increase under warmer sea conditions. However, this relationship should not be interpreted as a causal effect, but rather as a positive association observed within the scope of the present dataset.

According to the bootstrap regression results for larval abundance, salinity was found to be statistically significant, whereas temperature and dissolved oxygen did not make a significant contribution to the model (Table 4). Based on the estimated coefficient, a 1-unit increase in salinity, while holding the other variables constant, was associated with an average decrease of 36.456 units in larval abundance. This finding suggests that there may be a negative relationship between larval abundance and salinity. Overall, the bootstrap regression results indicate a positive association between egg abundance and temperature, and a

Table 3. Modelling of European anchovy eggs with bootstrap regression

Model	Unstandardized	Bias	Standard Error	p
Temperature	337.722	-13.931	135.234	0.008
Salinity	-218.630	27.712	232.513	0.385
Dissolved Oxygen	71.262	-51.240	468.303	0.929

Table 4. Modelling of European anchovy larvae with bootstrap regression

Model	Unstandardized	Bias	Standard Error	p
Intercept	1970.252	322.360	1266.673	0.047
Temperature	-5.542	-5.930	21.815	0.975
Salinity	-36.456	-2.084	17.423	0.026
Dissolved Oxygen	-101.683	-19.203	70.408	0.079

negative association between larval abundance and salinity. Nevertheless, these findings should be interpreted cautiously in light of the methodological limitations of the study.

Discussion

This study examines the temporal spawning dynamics of European anchovy with a specific focus on the effect of sampling frequency. The results indicate that the spawning season in the study area lasts approximately 22 weeks, characterized by distinct pulses in egg and larval abundance. A comparison between weekly and monthly data shows that monthly sampling intervals tend to smooth out short-term abundance peaks, leading to an underestimation of temporal variability. Literature documented worldwide indicates that ichthyoplankton assemblages exhibit considerable temporal variability (Doyle et al., 1993). Our decision to implement a weekly sampling strategy, rather than a standard monthly approach, was driven by the need to capture these rapid changes in community structure, which are often overlooked in less frequent surveys.

Although the study was limited by a small-scale sampling grid and sample size, the use of a bootstrap-based regression approach allowed for the identification of key environmental associations. Specifically, a positive relationship was observed between egg abundance and sea surface temperature. These findings suggest that weekly monitoring provides a more detailed representation of anchovy spawning compared to monthly intervals, particularly in environments where hydrographic structures may cause rapid fluctuations in egg and larval retention.

The observed pulses in anchovy egg and larval abundance may reflect not only biological spawning intensity but also the influence of complex hydrographic structures within the sampling area. In a strait environment characterized by strong currents and meso-scale eddies, changes in drift and retention patterns can significantly concentrate or disperse ichthyoplankton. As noted by Smith et al. (1999), ichthyoplankton assemblages can function as biological tracers of short-term hydrographic variability. In highly dynamic environments like straits, localized retention cells or current fields may concentrate eggs and larvae, which aligns with the sudden abundance peaks recorded in our weekly samplings. Because our study utilized a fixed sampling grid rather than covering the entire spawning ground, these short-term peaks might be partially attributed to the transport of eggs and larvae into the study area from adjacent waters. Factors such as frontal zones or localized upwelling events, common in such dynamic maritime passages, are known to influence the spatial distribution and aggregation of fish eggs. While these physical processes act as confounding factors, their rapid nature further emphasizes the necessity of high-frequency monitoring. Since hydrographic shifts and biological pulses can occur within days, a monthly sampling strategy would likely fail to capture these transient events, masking the true temporal variability of the spawning season. Such limitations in sampling frequency directly impact the accuracy of ichthyoplankton assessments and necessitate a closer examination of sampling strategies.

Although lots of scientific ichthyoplankton surveys have been completed all around the world, the investigations of variabilities on sampling accuracy remain limited. By means of spatial distribution of mean ichthyoplankton abundance, physical variables such as eddies and currents, ontogenic variations of mortality, and species behavior such as swimming and schooling should be taken in consideration (Helbig and Pepin, 1998; Leis et al., 2007; Pepin and Helbig, 2012). The selection of sampling points within a broad geographical area becomes important for systematic smaller, equal-area sampling units (Ma et al., 2025). In several ichthyoplankton studies, classical monthly or seasonal sampling was implemented. In this pattern, the timing of the spawning processes may be overlooked; hence, the estimation of spawned species richness and/or mean spawned abundance values can be estimated incorrectly. Pompeu et al. (2023) revealed that the detection of fish eggs of some migratory freshwater species could be performed efficiently by using a three-day sampling interval in a São Francisco River in South America. Daban and İşmen (2020) revealed that the occurrence of some larvae species with shorter spawning duration increased with frequent weekly sampling intervals in North Aegean Sea. Frequent sampling is understood to allow the collection of fish eggs and larvae from species with relatively lower mean abundance and/or short spawning duration.

Owing to the frequent weekly sampling interval and varied time-based models in the present study, for the first time in the literature the results were found to reduce the bias of time-dependent variations. It was observed that weekly sampling intervals can be useful in reducing bias encountered by estimating monthly mean abundance values outside the peak spawning months within the entire spawning period. During the initial and final months of spawning, the results from monthly sampling were insufficient due to the high temporal variance. Reducing this effect may only be possible by averaging the weekly sampling abundance data.

In addition, frequent weekly sampling enabled us to understand the relationship between abundance values and physical and chemical parameters. According to several studies completed in the Mediterranean, anchovy are able to lay eggs in high temperature and salinity ranges. Anchovy prefer to spawn between 25°C and 27°C around the southern coasts of the Mediterranean (Zarrad et al., 2018), 16°C and 21°C in the southeastern Atlantic (van der Lingen et al., 2001), and 17°C and 23°C in the northwestern Mediterranean (Palomera et al., 2007). In addition, Somarakis et al. (2007) revealed that spawning intensified where the SST

was higher than 21.5 °C, the salinity was lower than 35 ppt and in current areas enriched with high zooplankton values. When compared to the results of the present study, the anchovy eggs were seen between at 15.5°C and 24.4°C and peaked at 20.9°C on 30th June and at 22.3°C on 13rd September. Maynou et al. (2020) revealed that the SST range between 20°C and 24 °C had positive effect for anchovy egg and larvae abundance, whereas it had the opposite effect at SST values higher than 24°C. Due to the highest SST being measured as 24.4°C, the potential negative effect was excluded in the present study based on Maynou's hypothesis. Also, negative relationships between salinity and European anchovy egg and larvae abundance were found in many studies (Sabatés et al., 2007; Palomera et al., 2007; Martín et al., 2008). Positive relationships were detected between salinities lower than 37.85 ppt and anchovy egg and larvae abundance (Maynou et al. 2020). In addition, the fish eggs decreased and/or disappeared when the salinity increased from 27 ppt to 29 ppt. The salinity values were measured as 25.7 ppt and 24.3 ppt in the weeks when fish egg abundance peaked. According to the bootstrap regression model, each 1 unit increase in temperature led to an increase in the egg abundance by 337,722 units on average, whereas every 1 unit increase in salinity led to an average decrease of 36,456 units in the number of larvae. Thus, the results coincide with the findings of Somarakis et al. (2007) in terms of SST and salinity. The opposite temporal variations of DO% compared to SST and salinity were previously seen and explained by Türkoğlu (2010) as being the result of vertical mixing of the stratification of Çanakkale Strait, in which heavy southwestern winds cause the displacement of lower layer low DO% waters with water from upper layers with high DO%. None of the models used in this study found these inverse relationships were statistically significant. According to this, the Black Sea and the Marmara Sea seem to be favorable spawning areas for the European anchovy with lower temperate and saline-enriched waters. Due to the sampling area being located at the end of the Sea of Marmara and at the start of the North Aegean Sea, dense Black Sea Water (BSW) flows carry non-motile and/or semi-motile organisms like anchovy eggs and some larvae from favorable areas to non-favorable areas. In the Northern Aegean Sea, the anchovy larvae and juveniles concentrate in areas influenced and enriched by the BSW flow direction. Thus, the BSW water is crucial both in the Black Sea, Sea of Marmara and the North Aegean Sea, especially for small pelagic fish species like anchovy.

Fish egg sizes were grouped according to the sampling months and larger eggs were obtained at the beginning of the spawning season (May and June). Due to larger eggs being produced by older age groups, it is thought that older age classes start to spawn earlier than younger age classes. The physiological conditions of older cohorts may have caused this situation due to higher energy capacity. The mean mortality rate of the European anchovy eggs was 49%. According to previous studies, when compared to the findings of the present study, mean mortality rate for European anchovy was higher in the Black Sea with values above 80% (Satilmis et al., 2006; Şahin and Hacımurtazaoglu, 2013; Klimova et al., 2024), whereas the rate was similar around the Aegean Sea (Çakır and Hoşsucu, 2006; Çoker, 2003). The lower mortalities around Dardanelles and the Aegean Sea compared to the Black Sea may be attributed to lower oxygen values related to high hydrogen sulfide formation in deeper parts of the Black Sea.

The mean abundance values of fish eggs and larvae were 265 n/m^2 and 18.9 n/m^2, respectively. Mean abundances of European anchovy eggs and larvae were previously detected as 81.5 n/m^2 and 55.9 n/m^2 (Klimova et al., 2022); 360 n/m^2 (Uygun and Üstün, 2024), 90 n/m^2 and 4.3 n/m^2 (Kideys et al., 1999); and 31 n/m^2 and 5 n/m^2 (Satilmis et al., 2003) in the Black Sea. The results of the present study coincide with the findings previously reported from the Black Sea. The mean fish eggs and larvae abundance values were previously found to be lower near the study area. The mean fish egg abundance was 19.3 n/m^2 in the Çanakkale Strait, 33.5 n/m^2 at Gökçeada Island, (Daban et al., 2020), and 36.5 n/m^2 in Edremit Bay (Taylan and Hoşsucu, 2015) in the North Aegean Sea. When the results are compared, the mean abundance values for anchovy eggs seems to be increased. Although this situation is good news, it may be the result of reduced estimation bias related to frequent sampling intervals.

Conclusions

Based on our findings, it is recommended that fishery management authorities consider extending the closed season for the seine-net fishery until November to better align with the European anchovy's protracted spawning biology. Our data show pronounced spawning activity in September, followed by a significant recruitment effort of juveniles in November.

Furthermore, to improve the accuracy of future ichthyoplankton assessments, researchers should prioritize high-frequency (weekly) sampling intervals during peak spawning periods. However, given the complex hydrographic structure of the strait and the potential for egg transport via currents, future studies should transition from fixed-point monitoring to broader geographical sampling grids. Integrating such multi-point sampling designs with hydrodynamic modeling would allow for a more holistic understanding of both spawning intensity and the physical processes governing larval retention. Such a combined spatial and temporal approach is essential for developing more robust and representative models for fisheries management.

Ethical Statement

Not applicable.

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Author Contribution

I.B.D: Writing– review & editing, Writing– original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. T.S.A.: Writing– original draft, Methodology, Data curation, Validation, Software. O.A.: Methodology, Investigation. A.İ.: Writing– original draft, Supervision, Conceptualization.

Conflict of Interest

The authors declare that they have no known competing financial or non-financial, professional, or personal conflicts that could have appeared to influence the work reported in this paper.

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SUPPLEMENTARY MATERIALS

S1 Table. Modelling of European anchovy eggs with using LS (Least Squares)

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	35156.7	32491.4	1.082	0.290
Temperature	-205.2	546.8	-0.375	0.711
Salinity	-659.8	556.0	-1.187	0.247
Dissolved oxygen	-1554.3	1640.7	-0.947	0.353

F-statistic: 1.211 on 3 and 23 DF, P-value: 0.328.

S2 Table. Modelling of European anchovy eggs with Ridge

	Estimate	Std. Error	t value	Pr(>|t|)
Temperature	87.43	1529.40	0.812	0.417
Salinity	-315.93	1907.35	1.148	0.251
Dissolved oxygen	-480.18	1585.05	1.359	0.174

Ridge parameter: k=0.657.

S3 Table. Modelling of European anchovy larvae with using LS (Least Squares)

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	2014.104	1725.686	1.167	0.255
Temperature	-7.056	29.042	-0.243	0.810
Salinity	-38.045	29.530	-1.288	0.210
Dissolved oxygen	-99.580	87.140	-1.143	0.265

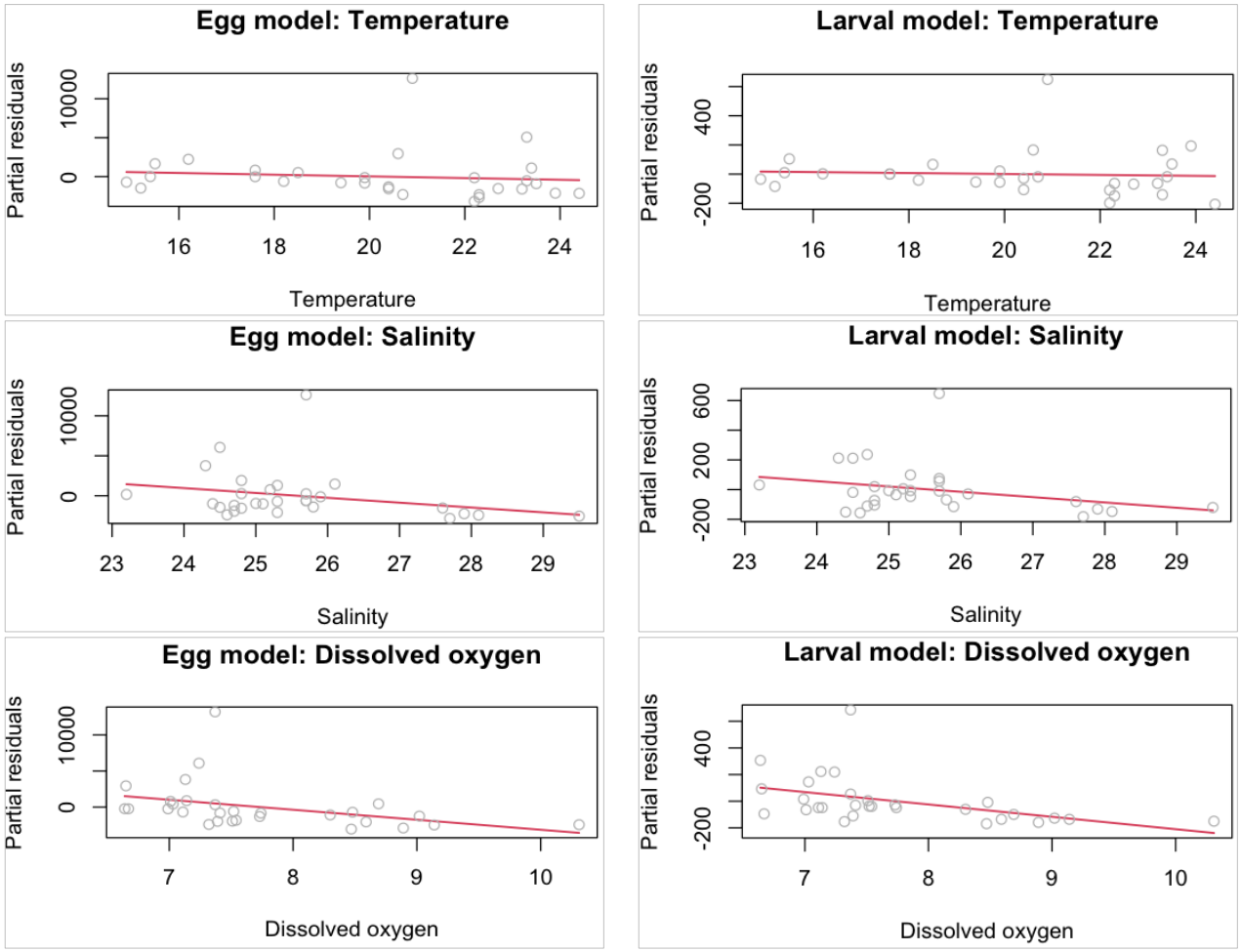
F-statistic: 2.222 on 3 and 23 DF, P-value: 0.1128.

S4 Table. Modelling of European anchovy larvae with ridge

	Estimate	Std. Error	t value	Pr(>|t|)
Temperature	957.230	119.135	0.869	0.3847
Salinity	-23.917	130.147	1.274	0.2026
Dissolved oxygen	-47.332	120.663	1.760	0.0784

Ridge parameter: k=0.309.

SUPPLEMENTARY MATERIALS



S1 Figure. Model diagnostic plots (component-plus-residual and residuals-versus-fitted) for assessing the linearity assumption in the exploratory regression analyses of European anchovy egg and larval abundance.