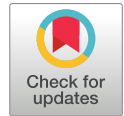


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Ichthyoplankton in the Strait of Istanbul (Bosphorus) and Northern Sea of Marmara: Summer Snapshot of Spatial Distribution and Satellite Modeled Hydrographic Drivers



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Abstract

The Strait of Istanbul (Bosphorus, Sol) system, which serves as a biological corridor between the Black Sea and the Sea of Marmara, plays a critical role in the transport of fish during their early life stages. This study examined the structure, distribution, and relationship with environmental factors of the surface ichthyoplankton assemblage in the transition zone between the Strait of Istanbul and the Northern Marmara Sea, beginning at the Black Sea entrance. The research was conducted at 13 stations determined between 22 and 29 July 2023, representing the summer period. Sampling was performed using a WP2 plankton net, while hydrographic data (temperature, salinity and current velocity) were obtained in high resolution from the Copernicus Marine Service (CMEMS) satellite database. A total of 21 taxa were identified in the assemblage, with *Engraulis encrasicolus* (European anchovy) and *Trachurus mediterraneus* (Mediterranean horse mackerel) identified as the dominant species in the upper layer. The results of the Distance-Based Linear Model (DistLM) and dbRDA analyses indicate that temperature and salinity gradients are the main explanatory variables for variation in species composition. Additionally, the observed spatial patterns and the model's sensitivity to current velocity suggest that the Strait of Istanbul surface current system could potentially act as a supportive mechanism for the localized transport of *E. encrasicolus* early life stages. In turn, this transport process is thought to have potential implications for the local recruitment dynamics of the species in the Sea of Marmara.

Keywords

Fish eggs and larvae • *Engraulis encrasicolus* • Assemblage Structure • Remote Sensing • Upper Layer • Northern Marmara



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Introduction

The Sea of Marmara possesses a distinctive two layer flow regime formed by the Black Sea origin low salinity upper water mass and the Mediterranean origin dense lower water mass. This permanent stratification, driven by salinity differences, is demarcated by a sharp pycnocline located at a depth of approximately 25 meters (Beşiktepe et al., 1994). Situated in the critical transition zone between the Aegean and Black Seas, the basin exhibits a dynamic biogeochemical cycle shaped by nutrient fluxes, in which primary production and food-web efficiency depend on seasonal inputs (Tugrul et al., 2002). Morphometrically, the Sea of Marmara covers an area of approximately 11,110 km² and is characterized by a complex basin ridge system consisting of broad shelf areas and deep tectonic depressions, with maximum depths reaching about 1,270 m in the Çınarcık Basin (Gazioğlu et al., 2002).

The confinement of primary production in the Sea of Marmara is largely limited to a narrow band in the upper layer, determining the vertical distribution of biological productivity (Polat et al., 1997). In this context, while the upper layer exhibits high mesozooplankton abundance (Isinibilir et al., 2008; Bedikoğlu and Demirel, 2025), the water column immediately below the halocline is characterized by the formation of suboxic conditions and a distinct subsurface oxygen minimum (Tuğrul and Polat, 1995; Ediger et al., 2016). This severe hypoxic environment limits the survival of the early life stages of fish. However, these natural cycles are under pressure from pollution from intense urbanization and industrial activities surrounding the basin, leading to eutrophication-related water quality problems, particularly in semi enclosed bays and the upper layer (Burak et al., 2009). The mucilage events experienced in 2021, as a cumulative result of increasing environmental stress, global warming, and pollution load, have negatively impacted the survival rates of fish eggs and larvae by altering the pelagic food web and habitat quality (Yüksek et al., 2024). Since the early life stages of fish are the biological units with the lowest tolerance and fastest response to environmental changes, examining the structure of the ichthyoplankton assemblage serves as a vital indicator for determining the instantaneous state of ecosystem health and predicting the future of fish stocks (Moser and Smith, 1993; Govoni, 2005). In this context, the relationship of ichthyoplankton with environmental parameters is a fundamental tool not only for fisheries management but also for monitoring the health of the marine ecosystem (Olivar and Sabatés, 1997; Uygun and Hoşsucu, 2024).

Research on ichthyoplankton in Turkish seas and the Sea of Marmara dates back to the pioneering study by Arım (1957).

In the ensuing period, particularly through studies conducted from the 1990s to the present, eggs and/or larvae of 76 distinct fish species belonging to 32 families have been identified in the Sea of Marmara; it has been revealed that biodiversity increases in the southwestern Marmara and that *Engraulis encrasicolus* is dominant during the summer season (Yüksek et al., 2024). Studies conducted on ichthyoplankton in the region have provided significant contributions to the literature by documenting species composition and seasonal changes across a wide area extending from the entrance of the Sol to the exit of the Dardanelles (Demirel et al., 2007; Daban and Yüksek, 2017; Demirel, 2015; Yüksek and Gül, 2016; Kara and Yüksek, 2023; Daban et al., 2024). The Sea of Marmara ecosystem has recently been affected by large scale ecological changes, including increasing anthropogenic pressures and the 2021 mucilage event; however, ichthyoplankton studies examining the effects of these stress factors on coastal fish communities are quite limited and have primarily been conducted during the winter period (Daban et al., 2024). There is a need for up to date datasets that comprehensively capture summer dynamics in conjunction with physical oceanographic parameters, especially in the upper layer, where the system is most hydrodynamically active and biological production is concentrated (Isinibilir et al., 2008). Monitoring the current status of these surface waters, which is critical for the sustainability of pelagic fish stocks under changing ecosystem conditions, is important for fisheries management.

In this context, the aim of the study is to investigate the structure and distribution of ichthyoplankton assemblage in the upper layer waters of the Black Sea entrance, the Sol, and the Northern Sea of Marmara during the summer period. The study aims to examine spatial variations in ichthyoplankton abundance, the distribution patterns of dominant species, and the relationship between the ichthyoplankton assemblage and fundamental environmental variables (temperature, salinity, current velocity) in this transition zone under the influence of Black Sea surface waters.

Material and Methods

Study Area

This study was conducted between July 22 and 29, 2023, representing the summer period, at 13 stations designated within the transition region covering the Black Sea entrance, the Strait of Istanbul (Bosphorus, Sol) and the Northern Sea of Marmara (Figure 1). These stations were spatially distributed across the region to provide a representative coverage of the summer ichthyoplankton assemblage.



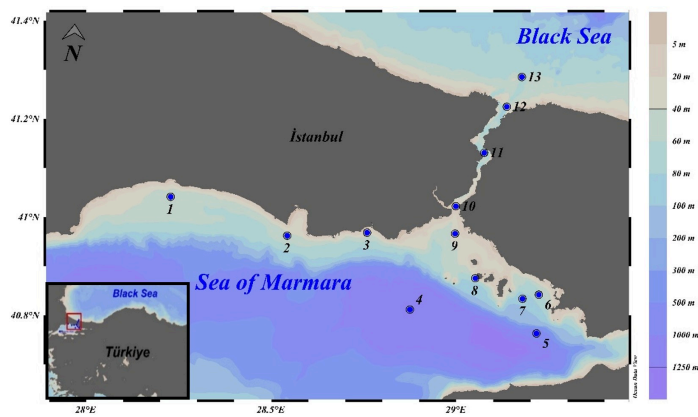


Figure 1. Study area

Sampling and Laboratory Procedures

Ichthyoplankton samples were collected by vertical hauls from 20 m to the surface, representing the upper water layer at each station. A WP2 standard plankton net with a 57 cm mouth diameter and 200 μ m mesh size was used for sampling, and the obtained material was fixed with a 4% buffered formaldehyde-seawater solution.

Taxonomic identifications of fish eggs and larvae sorted in the laboratory were performed to the lowest possible taxonomic level based on fundamental references such as Arim (1957), D'Ancona (1931-1956), Dekhnik (1973), and Rodríguez et al. (2017); current nomenclature was verified using the World Register of Marine Species database (Ahyong et al., 2026). Abundance data for species were standardized using the method of Smith and Richardson (1977) and expressed as the number of individuals per unit area ($\text{ind. } 10 \text{ m}^{-2}$). The egg mortality rate (%) was determined by calculating the percentage of dead eggs relative to the total number of eggs collected at each station:

$$\text{Egg Mortality (\%)} = (n_{\text{dead egg}} / n_{\text{total egg}}) \times 100 \quad (1)$$

To accurately assess mortality, eggs that were already dead prior to fixation were distinguished based on characteristic morphological features, including a turbid perivitelline space, an opaque and dispersed vitellus, and embryo abnormalities. To determine assemblage structure, the frequency of occurrence (FO%) and dominance indices (D) were calculated for the species. The frequency of occurrence was calculated using the formula:

$$\text{FO\%} = (m_i / M) \times 100 \quad (2)$$

Where m_i is the number of stations at which species i occurred, and M is the total number of sampled stations. The dominance index (Bellan-Santini, 1981) was calculated using the formula:

$$D = (n_i / N) \times 100 \quad (3)$$

where n_i is the total number of individuals of species i , and N is the total number of individuals of all species.

Processing of Environmental Data

To characterize the hydrographic structure of the study area, high-resolution ($L4, 0.025^\circ \times 0.025^\circ$) daily data for potential temperature, salinity, and current velocity were obtained from the Copernicus Marine Service database (Jansen et al., 2024). The processing of hydrodynamic model output (NetCDF) was carried out in R 4.5 statistical software (R Core Team, 2025) using the "ncdf4" (Pierce, 2019) and "raster" (Hijmans, 2025) packages through two different procedures. For use in statistical analyses, environmental data were extracted corresponding to the sampling day at each station, and the values at 0, 10, and 20 m depths were averaged to represent the upper layer. Whereas for spatial mapping, daily data covering the entire study period (July 22–29, 2023) were averaged across both time and the 0–20 m layer to illustrate the general oceanographic conditions of the study area.

Data Analyses and Mapping

Assemblage diversity and structure were measured using the Shannon-Weaver (H') and Pielou's evenness (J') indices. The Shannon-Weaver index was calculated using the following formula:

$$H' = -\sum (p_i \times \ln p_i) \quad (4)$$

where p_i represents the proportion of total individuals belonging to the i -th species. Pielou's evenness index was calculated to assess how evenly the individuals were distributed among the species, using the formula:

$$J' = H' / \ln S \quad (5)$$

where H' is the calculated Shannon-Weaver diversity value and S is the total number of species at the given station.

To assess the complete ichthyoplankton assemblage, egg and larval abundance data were consolidated into a single matrix before conducting multivariate analyses. Early developmental stages (e.g., yolk sac and preflexion) constituted 99.2% of the collected larvae. Due to their restricted active swimming capabilities, both eggs and these early stage larvae were considered subject to the same passive hydrodynamic transport within the upper water column (Sabatés et al., 2007). Despite this physical pooling, eggs and larvae of the same species were maintained as separate independent variables within the matrix to preserve their distinct ecological roles. For instance, the eggs and larvae of the *E. encrasicolus* were coded (Eenc_E and Eenc_L) and analyzed as two distinct variables rather than a single aggregated taxon.

To reduce the dominance of highly abundant species, biological data were $\log(x+1)$ transformed, while environmental data were normalized to eliminate unit differences (Clarke & Warwick, 2001; Clarke & Gorley, 2015). Spearman rank correlation matrix was used to evaluate multicollinearity among three environmental variables. While parameters with $r > 0.7$ were retained if ecologically significant (Dormann et al., 2013; Santos et al., 2024). To explore and visualize the spatial groupings of the assemblages, the similarities between stations were examined using Cluster and Non-Metric Multidimensional Scaling (nMDS) analyses based on the Bray-Curtis similarity matrix. The Distance-Based Linear Model (DistLM) was utilized to explicitly quantify how much of the variation in the ichthyoplankton composition could be explained by environmental drivers (temperature, salinity, current velocity). In model selection, the *All specified* procedure, which evaluates all possible models using the *Adjusted R^2* criterion, was applied, and the results were visualized in a dbRDA (Distance-Based Redundancy Analysis) ordination diagram to illustrate these species-environment relationships. The calculation of the biodiversity indices (Shannon-Weaver and Pielou's evenness) and all multivariate analyses (Cluster, nMDS, DistLM, and dbRDA) were performed using PRIMER v7 with the PERMANOVA+ add-on (Anderson et al., 2008; Clarke and Gorley, 2015). In addition, Spearman's correlation analysis was performed using the "stats" package in R to determine the degree of association between mortality rates, biodiversity indices and environmental factors, without requiring the assumption of a normal distribution; the significance level was accepted as $p < 0.05$. Spatial distribution maps of biological and environmental parameters were created in the R 4.5 environment using the packages "ggplot2" (Wickham, 2016) for visualization, "sf" (Pebesma, 2018) for data management, "rnatuarearth" (South, 2017) for map baselayers, and "gridExtra" (Auguie, 2017) for multi-panel arrangements.

Results

Environmental Parameters

Mean environmental parameter values calculated for the upper layer (0-20 m) in the study area are shown in Figure 2 based on the geographic locations of the stations. Upper layer (0-20m) temperatures ranged from 17.46°C to 23.19°C. While the highest temperature value was measured at Station (St.) 1 in the western coastal area, the lowest temperatures were recorded at the entrance to the Sol in the Sea of Marmara (St. 9 and 10; 17.46-17.70°C) (Figure 2a). Salinity values decreased to minimum levels (18.13-18.29‰) at the Sol line and Black Sea entrance stations (St. 11, 12, and 13) due to the influence of

the low-salinity upper water mass originating from the Black Sea. Salinity increased moving southwestward and offshore, reaching a maximum value of 24.7‰ in the open waters of the Sea of Marmara (St. 5). Similarly, salinity was observed to remain at levels of 24.5-24.6‰ at stations offshore Tuzla (St. 6 and 7) (Figure 2b).

When the current velocity was examined, the highest velocity was recorded at St. 10 (0.88 m/s), which is influenced by the Sol Current. High velocities were also observed at St. 9 (0.61 m/s) and St. 11 (0.64 m/s). Furthermore, at the Black Sea entrance stations, current velocities were recorded as 0.20 m/s and 0.13 m/s for Sts. 12 and 13, respectively. In contrast, current velocities were observed to be 0.02-0.03 m/s at Sts. 2 and 3, located in areas where current influence diminished (Figure 2c).

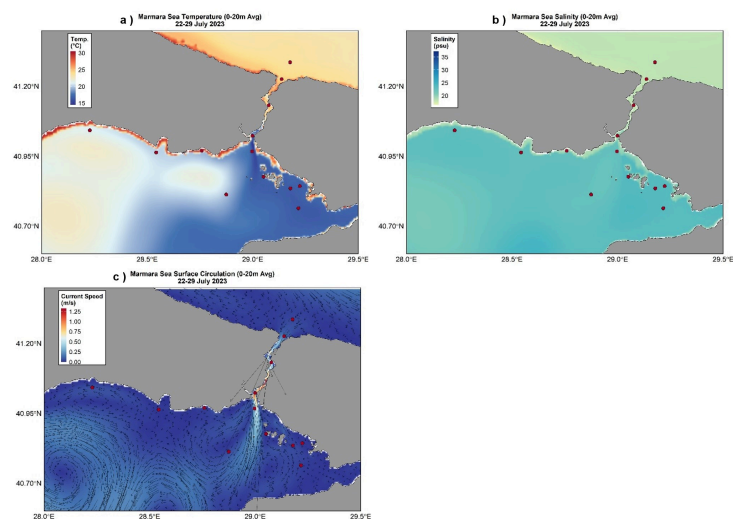


Figure 2. Distribution maps of environmental parameters in the study area averaged for the 0-20 m depth layer during July 22-29, 2023: a) temperature, b) salinity and c) current velocity

Ichthyoplankton Assemblage Structure and Dominant Species

As a result of the research, 21 distinct taxa belonging to 16 families were identified. A total of 17 taxa, comprising 16 species and 1 morphotype, were identified in the egg stage, while 11 distinct species were identified in the larval stage. The mean egg abundance in the study area was calculated as 1515 ind. 10 m⁻², whereas the mean larval abundance was calculated as 837 ind. 10 m⁻². When the percentage distribution of the sampled larvae according to their developmental stages was examined, the assemblage was found to consist of prelarva (70.8%), preflexion (28.4%), flexion (0.4%), and postflexion (0.4%) stages, respectively.

When the ichthyoplankton composition is examined, a dominance of *E. encrasicolus* is observed in both egg and

Table 1. Mean abundance, dominance, and frequency values of the ichthyoplankton taxa identified in the study area.

Family	Code	Species	Mean Abundance		Dominance		Frequency Occurrence	
			individual.10m ⁻²		%		%	
			Egg	Larvae	Egg	Larvae	Egg	Larvae
Blennidae	Pten	<i>Parablennius tentacularis</i>	0	27	0.0	3.2	0.0	23.1
Bothidae		<i>Arnoglossus</i> sp.1	3	0	0.2	0.0	7.7	0.0
		<i>Arnoglossus</i> sp.2	0	3	0.0	0.4	0.0	7.7
Callionymidae		<i>Callionymus</i> sp.	0	3	0.0	0.4	0.0	7.7
Carangidae	Tmed	<i>Trachurus mediterraneus</i>	193	87	12.7	10.4	92.3	46.2
	Ttra	<i>Trachurus trachurus</i>	66	6	4.4	0.7	30.8	7.7
Engraulidae	Eenc	<i>Engraulis encrasicolus</i>	1049	633	69.2	75.5	100.0	46.2
Gobiidae	Gnig	<i>Gobius niger</i>	0	60	0.0	7.2	0.0	53.8
Mugilidae		<i>Chelon auratus</i>	15	0	1.0	0.0	7.7	0.0
		<i>Chelon saliens</i>	6	0	0.4	0.0	7.7	0.0
Mullidae		<i>Mullus barbatus</i>	15	9	1.0	1.1	7.7	7.7
Pomacentridae		<i>Chromis chromis</i>	0	3	0.0	0.4	0.0	7.7
Sciaenidae		<i>Sciaena umbra</i>	3	0	0.2	0.0	7.7	0.0
Scophthalmidae		<i>Scophthalmus maximus</i>	18	0	1.2	0.0	15.4	0.0
Scorpaenidae		<i>Scorpaena porcus</i>	3	0	0.2	0.0	7.7	0.0
Serranidae	Sscr	<i>Serranus scriba</i>	84	0	5.6	0.0	30.8	0.0
		<i>Serranus hepatus</i>	12	0	0.8	0.0	15.4	0.0
Soleidae		<i>Buglossidium luteum</i>	3	3	0.2	0.4	7.7	7.7
		<i>Microchirus variegatus</i>	3	0	0.2	0.0	7.7	0.0
Sparidae	Dann	<i>Diplodus annularis</i>	36	3	2.4	0.4	15.4	7.7
Triglidae		<i>Trigla lucerna</i>	3	0	0.2	0.0	7.7	0.0
Unknown		Morphotype Egg	3	0	0.2	0.0	7.7	0.0

larval abundance (Table 1). *E. encrasicolus* constituted 69.2% of the total egg abundance, with a mean value of 1049 eggs 10 m⁻², and 75.5% of the total larval abundance, with a mean of 633 larvae.10 m⁻². The second dominant species, *Trachurus mediterraneus*, was represented by a mean of 193 eggs.10 m⁻² (12.7%) in the egg stage and 87 larvae.10 m⁻² (10.4%) in the larval stage. Following these species, *Serranus scriba* ranked third in egg dominance, while *Gobius niger* ranked third in the larval stage. The abundances and contributions to the composition of other species are presented in Table 1.

Spatial Distribution

When the spatial distribution of ichthyoplankton abundance was examined, it was notable that eggs and larvae were not evenly distributed across the study area, with distinct differences between the eastern and western stations of the Sea of Marmara (Figure 5).

It was determined that the most productive areas in terms of total egg abundance were the regions near the Marmara exit of the Sol and around the Prince Islands. The highest egg density was observed particularly offshore of the Prince Islands region

(St. 8), with 5604 eggs. 10 m⁻² and at St. 13 at the Black Sea entrance with 4663 eggs.10 m⁻². This density stems from the extreme dominance of *E. encrasicolus* eggs (4585 eggs.10 m⁻²) at St. 13 in the Black Sea (J': 0.377). Due to its high dominance, the distribution map of *E. encrasicolus* eggs (Figure 4c) almost overlaps with the total egg distribution (Figure 4a). *T. mediterraneus* eggs, the second dominant species following *E. encrasicolus* eggs showed a concentration at stations around the Prince Islands in the northeastern Sea of Marmara (Sts. 4-8) (Figure 4e).

Larval distributions showed spatial limitations compared to eggs. Total larval abundance peaked at St. 12 at the Black Sea boundary, reaching a remarkably high value of 5369 larvae.10 m⁻² (Figure 4b). This situation displayed a similar pattern for *E. encrasicolus* and *T. mediterraneus* larvae, while *E. encrasicolus* reached 4820 larvae.10 m⁻² at this station (Figure 4d), *T. mediterraneus* was recorded at an abundance of 509 larvae.10 m⁻² (Figure 4f). Conversely, the lowest productivity, in terms of both egg and larval densities, was observed at the stations in the northwestern Sea of Marmara (Sts. 1, 2 and 3).

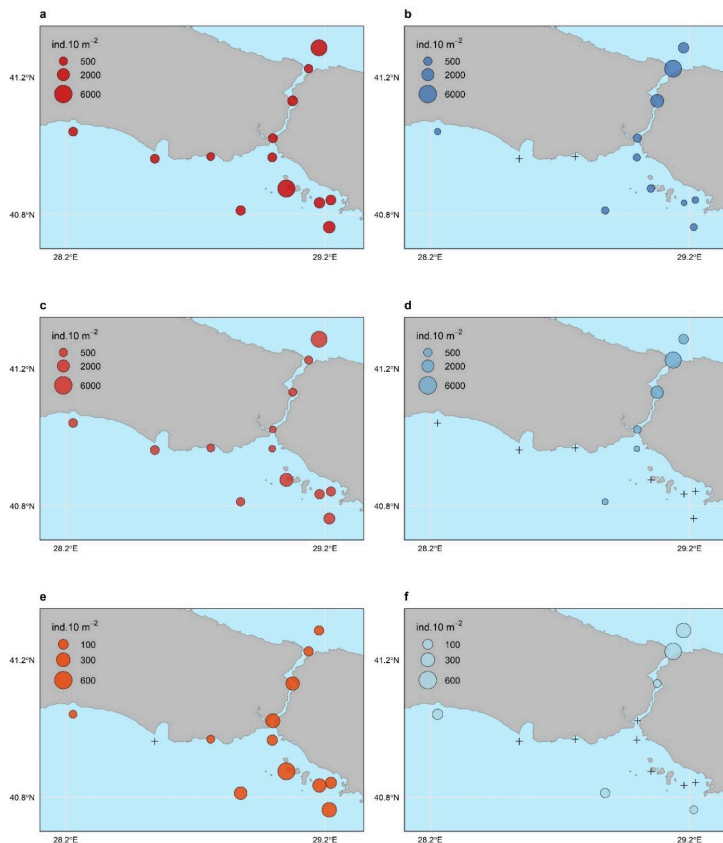


Figure 4. Distribution maps of total egg and larval abundances and dominant species in the study area (ind. 10 m⁻²): (a) Total eggs, (b) Total larvae, (c) *E. encrasicolus* eggs, (d) *E. encrasicolus* larvae, (e) *T. mediterraneus* eggs, (f) *T. mediterraneus* larvae

Biodiversity Indices and Mortality

Biodiversity index values by station are presented in Figure 3. Accordingly, species diversity was suppressed at certain stations by the extreme dominance of *E. encrasicolus*. In terms of the number of species (S), St. 8 (Prince Islands) had the highest diversity (15 species), followed by Sts. 10 and 11, each with 8 species. In contrast, only 1 species was detected at St. 2 (Küçükçekmece), located in the southwestern section of the study area. Notably, low biodiversity indices were observed at all stations located in the southwestern section (St. 1, 2, and 3) (S: 1-2; H': 0-0.5).

While the Shannon diversity index (H') reached its maximum value of 1.93 at St. 8, it remained at very low levels at St. 12 and 13 (0.36 and 0.26, respectively), where dominance was high. Reflecting the imbalance in the number of individuals among species, the evenness index (J') showed a decrease at stations near the Sol exit, where *E. encrasicolus* abundance peaked.

When the spatial distribution of mortality rates on the ichthyoplankton assemblage was examined, distinct differences were observed across the study area. The lowest

Sample	S	N	J'	H'
1	2	784	0.722	0.5
2	1	666	0	0
3	2	392	0.469	0.325
4	4	1097	0.747	1.036
5	3	1959	0.692	0.761
6	5	1136	0.675	1.086
7	5	1293	0.61	0.981
8	15	5917	0.715	1.937
9	6	941	0.889	1.593
10	8	1136	0.791	1.645
11	8	3449	0.498	1.036
12	3	5917	0.33	0.363
13	2	5917	0.377	0.261

Figure 3. Variation of ecological indices belonging to the ichthyoplankton assemblage (S: Number of species, N: Number of individuals, J': Evenness, H': Diversity) by stations

mortality rates were recorded at St. 12 (%35.7) at the Black Sea entrance, and at St. 8 (%58.0) near the Prince Islands, where biodiversity is highest. In contrast, mortality was over 75% at most stations. Notably, mortality reached 100% at the western coastal stations (Sts. 2 and 3(Figure S1).

According to the Spearman correlation analysis conducted to identify factors affecting mortality rates, a statistically significant negative relationship was detected between current velocity and mortality ($R = -0.595$, $p < 0.05$). This indicates that mortality rates decrease in areas with strong current systems in the Sol, while they increase in stagnant waters. Furthermore, a significant negative relationship was found between the number of species (S), which reflects ecological importance, and mortality ($R = -0.589$, $p < 0.05$), suggesting that mortality rates are lower in habitats with high species number.

Multivariate Assemblage Analyses

Cluster and nMDS analyses (Stress: 0.07) based on the Bray-Curtis similarity matrix were used to evaluate the spatial structure of the ichthyoplankton assemblage (Figure 5). The results revealed a detailed spatial pattern, grouping the stations into three main clusters (Groups A, B, and C) at approximately 60% similarity. Group A included the relatively shallow stations on the northwestern coast (Sts. 1, 2 and 3), as well as St. 6 located on the Tuzla coast in the northeast, which clustered within this group due to a similar distribution pattern characterized by lower abundance and diversity values. Group B (Sts. 7, 8 and 9) constituted the northeastern line of the Sea of Marmara, encompassing the Prince Islands region, where abundance and biodiversity were relatively high;

notably, St. 9 clustered within this group rather than with the other strait stations. Finally, Group C encompassed the remaining stations and was divided into two distinct sub-groups based on their spatial positions: the first sub-group consisted of stations located at the Black Sea entrance (Sts. 12 and 13), while the second sub-group included the stations located along the main Sol line (Sts. 4, 10, 11 and 5).

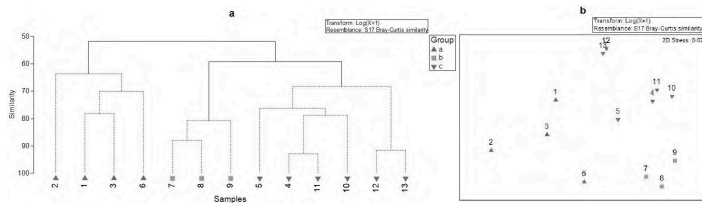


Figure 5. (a) Cluster Dendrogram and (b) nMDS ordination plot showing similarity relationships of stations based on ichthyoplankton species abundance data

Environmental Influence on Assemblage Structure

Based on the DistLM results used to identify the environmental factors affecting the spatial distribution of the ichthyoplankton assemblage during the summer period, marginal tests revealed that temperature, salinity and current velocity were all statistically significant variables. Temperature was the most explanatory factor, explaining 28.3% of the variation alone (Pseudo-F = 4.34, $p = 0.008$), followed by salinity, with an explanatory rate of 25.4% (Pseudo-F = 3.75, $p = 0.016$). In addition, the current velocity showed significance in a marginal test (Pseudo-F = 2.81, $p = 0.042$), it explained 20.3% of the variation.

The multivariate relationship between environmental variables and the ichthyoplankton assemblage was visualized using a dbRDA ordination diagram (Figure 6). The constructed model explained 52.46% of the total variation, revealing the importance of environmental factors on species distribution ($Adjusted R^2 = 0.366$). The dbRDA plot showed that the first two axes accounted for 53.2% of the total variation. When the positions of environmental factors are on the axis, the first axis clearly separates the water masses in the study area by salinity and temperature gradients (Figure 6a). Stations on the right side of the graph (Sts. 5, 6, 7, 8 and 9), showing a positive relationship with the salinity vector, represented more saline waters. In contrast, stations clustered on the left side of the graph (Sts. 11, 12, 13) exhibited a relationship with the temperature vector. Furthermore, stations located in the lower section of the plot (Sts. 9, 10 and 11) were closely aligned with the current vector.

The vectors of dominant species (Figure 6b) were examined, and it was observed that *E. encrasicolus* (*Eenc_L*) and *T.*

mediterraneus larvae (*Tmed_L*) were located in the left region of the graph, indicating a close relationship with temperature vectors. Conversely, *Serranus scriba* eggs (*Sscr_E*) were observed to be associated with right side of the plot, representing the stations with high salinity. Also, the alignment of *E. encrasicolus* larvae (*Eenc_L*) with the current vector revealed a strong positive relationship.

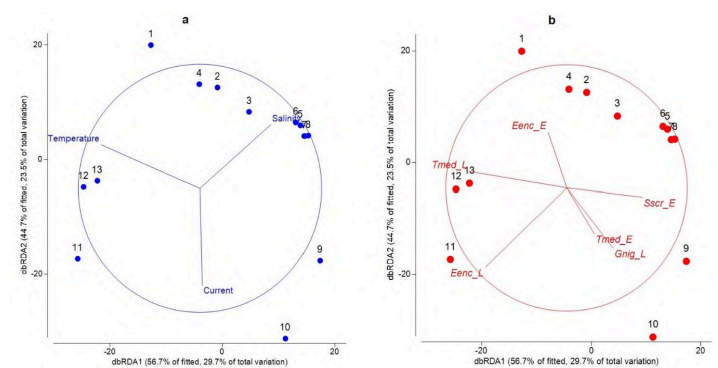


Figure 6. dbRDA ordination diagram showing the relationship between ichthyoplankton assemblage and environmental variables in the study area. (a) Distribution of environmental vectors in the ordination, (b) Positions of vectors belonging to dominant taxa in the ordination. Abbreviations: *Eenc*: *E. encrasicolus*, *Tmed*: *T. mediterraneus*, *Gnig*: *G. niger*, *Sscr*: *S. scriba*, *_E*: Egg, *_L*: Larvae

Discussion

Species Composition and Biodiversity

In this study, which reflects the current status of the Sea of Marmara pelagic ecosystem during the summer period, a total of 21 distinct taxa belonging to 16 families were identified, including 16 eggs and 11 larvae. Although 76 fish species have been reported in the long-term inventory, which compiles all data from 1993 to 2022 in the basin (Yüksek et al., 2024), studies covering a single sampling period are expected to report fewer species. Indeed, the number of taxa obtained in the present study is consistent with past studies conducted in the Sea of Marmara during the summer period. For instance, in research conducted under similar seasonal conditions, 19 species were reported (Demirel et al., 2007), and a total of 23 species were recorded in the Golden Horn, a eutrophic system, with increasing diversity in the summer months (Demirel, 2015). In the annual monitoring study conducted in the Sol, the highest biodiversity indices (15 species) were recorded in July (Yüksek and Gül, 2016), confirming that the summer season is a critical window for the reproductive strategies of pelagic fish. These findings indicate that, despite the intense pollution pressure and ecological stressors such as mucilage to which the Sea of Marmara has been exposed in recent years (Daban et al., 2023), it maintains its pelagic production capacity at a certain level during the summer period.

The notably high species diversity and relatively low mortality rates recorded at station 8 (Prince Islands) can be attributed to the unique benthic habitat structure of this region. The Prince Islands are a biodiversity “safe haven” hosting rich octocoral assemblages (soft corals and gorgonians) within their benthic habitats. These benthic features create structurally complex and diverse reef like habitats (Topcu et al., 2024). It is well established in marine ecology that habitat biodiversity and structural complexity are primary determinants of fish community structure, providing essential shelter and spawning grounds for a wide array of species (Gratwicke and Speight, 2005; Messmer et al., 2011). Consequently, the rich ichthyoplankton composition observed at this station is likely a reflection of the diverse adult fish community supported by these complex benthic habitats.

In contrast to the highly diverse transition zones, St. 6 clustered with the northwestern coastal stations (Sts. 1-3) regardless of the geographical distance between them. When evaluated against the dynamic, structurally complex Sol influenced areas (Sts. 7 and 8), both St. 6 and the northwestern sites exhibit a coastal composition. Habitat conditions in these coastal areas typically restrict overall species diversity while promoting the high dominance of a few taxa specifically adapted to shallow waters (Palomera et al., 2007; Sabatés et al., 2007).

Dominant Species and Abundance Dynamics

The mean egg abundance in the study area ($1516 \text{ ind.} \cdot 10\text{m}^{-2}$) remains below the value of $3360 \text{ ind.} \cdot 10\text{m}^{-2}$ reported for the same period in previous years (Demirel et al., 2007). This difference can be explained by interannual natural fluctuations in fish stocks (Govoni, 2005) and by changes in the carrying capacity of the marine ecosystem between the Black Sea and the Sea of Marmara (Yüksek and Gül, 2016; Yüksek et al., 2024). Additionally, the disparities in abundance and taxonomic composition compared to Demirel (2007) likely stem from mesh-size selectivity. While our 200 μm mesh effectively retains smaller early life stages, it is highly susceptible to rapid clogging in the eutrophic Sea of Marmara. Conversely, the 500 μm mesh employed in previous studies (Demirel, 2007; Yüksek and Gül, 2016) maintains a more consistent filtration efficiency in such particle rich waters, which may have the potential to alter the catch rates of larger or more active larvae (Pepin and Shears, 1997; Uygun and Hoşsucu, 2024).

It is observed that the ichthyoplankton assemblage in the study area is dominated by *E. encrasicolus* and *T. mediterraneus*, which are specific to the summer period (Arim, 1957; Yüksek and Gül, 2016). *E. encrasicolus* constitutes

the main component of the assemblage. In this context, the highest egg and larval abundance values for *E. encrasicolus* in our study were obtained from Sts. 11-13, starting from the Black Sea boundary and along the Sol. The dense clusters formed by the eggs and larvae of the species at the Black Sea entrance and stations along the Sol line are consistent with the high abundance values reported in a study conducted in the Sol (Yüksek and Gül, 2016). These high abundance data, which exhibit continuity in the direction of the current starting from the entrance region, imply that the early life stages of the species in question are transported towards the Sea of Marmara by the strong upper current system in the Sol. Additionally, the notable accumulation of larvae at the Black Sea boundary (St. 12) raises the possibility that the immediate entrance of the Sol could potentially act as a temporary retention area for larval development, alongside its known role as a transport corridor. Similarly, as observed in the northwestern Mediterranean, small pelagics prefer hydrodynamically active areas with high productivity, such as river inputs or continental shelf currents, as spawning grounds (Palomera et al., 2007; Sabatés et al., 2007). In the Sea of Marmara ecosystem, this resource, which is essential for the reproduction and larval development of the species, consists of nutrient rich Black Sea origin waters (Tugrul et al., 2002) that support dense mesozooplankton assemblages serving as primary prey for fish larvae (Üstün et al., 2024). Therefore, the dense presence of *E. encrasicolus* in this region may reflect the relationship of the species' reproductive strategy with hydrographic productivity.

Yet, the overall spatial distribution of the summer assemblage exhibits a more multifaceted pattern. In contrast to the distribution of *E. encrasicolus*, the second dominant species, *T. mediterraneus*, showed eggs concentrated primarily around the Prince Islands (Sts. 5-8) (Figure 4e). This distinct local concentration implies the presence of active spawning or retention zones within the Sea of Marmara itself and suggests a potential spatial segregation from the main anchovy spawning grounds. Furthermore, regional research suggests that summer ichthyoplankton assemblages may undergo significant structural oscillations even within weekly timescales (Uygun, 2026). Consequently, given the brief sampling period, this distribution may reflect transient fine scale patchiness rather than a persistent hydrodynamic feature, and should be interpreted as a temporal snapshot.

Regarding the *Trachurus* genus in the study area, *T. mediterraneus* was dominant, whereas *T. trachurus* was represented at low rates. This situation can be explained by differences in the two species' reproductive phenology and vertical distribution strategies within the Sea of Marmara

ecosystem. Regional studies in the region show that the reproductive activity of *T. trachurus* mainly occurs in the March-June period, whereas *T. mediterraneus* continues to spawn during the summer months (Arim, 1957; Yüksek and Gül, 2016; Yüksek et al., 2024). In addition to temporal differences, the species' vertical distribution preferences may also be decisive in this result. Arim (1957) reported that the early life stages of *T. trachurus* concentrate in the 30-60 m depth range rather than at the surface, in layers where the temperature is lower and salinity is relatively higher. The fact that samplings in our study were carried out only in the upper layer (0-20 m) and that this layer has high temperatures during the summer period explains why *T. trachurus* eggs and larvae, which prefer below the thermocline and cooler waters, were detected at low density.

Environmental Drivers

Temperature and salinity were identified as the primary environmental drivers shaping the spatial distribution of the ichthyoplankton assemblage. Temperature represents a fundamental abiotic factor in marine ecosystems, directly controlling the reproductive phenology, egg development duration, and larval growth rates of poikilothermic fish (Pepin, 1991; Sabatés et al., 2007). In our analysis, the fact that thermal variation accounted for the highest share in explaining the assemblage structure (28.3%) can be attributed to this thermal control mechanism in the life cycle of fish. Temperature not only dictates reproductive phenology and spawning timing (Tsikliras et al., 2010) but also governs survival rates during early life stages, where warmer summer conditions potentially accelerate metabolic processes and shorten larval development time (Fuiman and Werner, 2009). Consistent with observations across various marine environments, temperature appears to be the primary factor shaping the distribution dynamics of these early life stages (Demirel, 2015; Mavruk et al., 2018; Uygun and Hoşsucu, 2024; Uygun et al., 2026).

Salinity variations, identified as the secondary explanatory variable for the ichthyoplankton assemblage within the scope of our study, reflect the complex hydrography of the Sea of Marmara's upper layer, which is distinctly characterized by the continuous inflow of low salinity, nutrient rich Black Sea waters (Tugrul & Polat, 1995; Tugrul et al., 2002). Since our sampling was restricted to the upper 20 m, the significant influence of salinity in the model likely reflects a horizontal gradient between the Sol plume and the relatively more saline coastal waters rather than a vertical stratification barrier. This horizontal differentiation may ecologically distinguish hydrodynamically active zones from

more sheltered areas, such as the Prince Islands (Topcu et al., 2024), thereby potentially defining the spatial boundaries of habitat suitability for different taxa. Furthermore, the statistical significance of current velocity in the model points to the possibility that the Sol Current and associated coastal circulations may be hydrodynamic drivers influencing the transport (Oguz et al., 1990; Beşiktepe et al., 1994) and contributing to a possible retention mechanism for eggs and larvae (Sabatés et al., 2007) within the region. However, given the brief sampling period, these environmental relationships and transport dynamics should be interpreted cautiously as a short term spatial snapshot of the community rather than as a representation of persistent long term basin dynamics.

Conclusion

Although limited to the upper layer during July, this study provides a valuable snapshot of the pelagic ecosystem in the Sea of Marmara. The findings indicate that temperature and salinity are key drivers of ichthyoplankton distribution, while the Sol current plays an active role in their regional transport. Furthermore, the Prince Islands region stands out as a critical local habitat, harboring a notably high abundance and diversity of commercially important species. However, these results inherently reflect a specific short-term condition rather than absolute long-term basin dynamics. Future studies incorporating multi-seasonal sampling are essential to fully understand the broader temporal variability of these early life stages.



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