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Seasonal Changes in the Ichthyoplankton of the Crimean Peninsula (Northern Black Sea) in 2023

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Abstract

The species diversity, abundance and spatial distribution of the Black Sea ichthyoplankton in the spring, summer and autumn seasons of 2023 are presented. From March to October, eggs and larvae of 45 fish species from 25 families were identified in ichthyoplankton of the Black Sea. Eggs and larvae of seven fish species from four families belonged to the temperate-water fish while 38 species from 21 families belonged to the warm-water fish

In the nearshore coastal waters of the sea, 30 species of warm-water fish were registered in ichthyoplankton, while in the shelf and deep-water areas 23 warm-water fish species and seven temperate ones were recorded.

Between March and April, mass spawning of the temperate-water *Sprattus sprattus* (Linnaeus, 1758) was observed with the maximum abundance of eggs (130.6 ind./m^2) and larvae (108.5 ind./m^2). In August, the sea surface temperature had reached the optimal limits for spawning of warm-water fish species, with the maximum number of eggs of 70.8 ind./m^2, and that of larvae of 67.7 ind./m^2. In August 2023, the number of ichthyoplankton species in the coastal waters of Karadag (20 species), and on the shelf and in the deep-water areas of the study (18 species each), was quite comparable.

Introduction

The Black Sea stands out from other inland seas by its interannual and long-term variability, it has a positive water balance, its own thermohaline structure of waters with a halocline and a cold intermediate layer, whereas the influx of the Mediterranean waters through the Bosphorus Strait brings in constant heating and salinization in the bottom layers of the sea. With a deep-water basin exceeding 2200 m, the oxygen zone is limited to a layer of 125-230 m, below which there is a hydrogen sulphide zone devoid of living aerobic organisms (86% of the sea volume). Water stratification is the main factor reducing the intensity of vertical mixing of sea waters, and the presence of a sharp pycnohalocline blocks the flow of oxygen into the lower layers of the sea (Zatsepin, 2002). In the study area, the depth at the outer edge of the shelf is 90-100 m. The southwestern part of the study area is characterized by a rapid increase in depths, so the width of the shelf does not exceed 5-7 km, whereas in the southeastern part, in the Feodosia Gulf zone, the shelf is relatively leveled and the 50 m isobath is located at a distance of 10-30 km from the coast. Due to good connectivity with the open sea, the proximity of the Main Black Sea Current, and onshore-offshore circulation, active water exchange occurs in the shelf zone of the Crimean Peninsula (Troshchenko et al., 2019).

More than 200 species and subspecies of fish have been recorded in the Black Sea, 30 of which are of commercial significance. The timing of spawning, species diversity, spatial distribution and survival of fish during early ontogenesis are determined by the season of hydrological processes. The relatively thin active layer of the Black Sea leads to low resistance of the pelagic ecosystem to both anthropogenic impact and climate change. Between 1950 and 1970, ichthyoplankton assemblage showed relative stability with reliable reproduction in the sea of 63 representatives of warm-water subtropical and tropical species and of five temperate boreal species whose eggs and larvae were found in the ichthyoplankton (Dekhnik, 1973). The spatial distribution of most ichthyoplankton species was usually confined to the shelf and coastal zones, where eggs and larvae of the pelagophilic species such as *Mullus barbatus* Linnaeus, 1758 and *Diplodus annularis* (Linnaeus, 1758), *Trachurus mediterraneus* (Steindachner, 1868), and *E. encrasicolus* and larvae of coastal species from demersal eggs predominated. In deep-water areas (depth over 300 m), the temperate-water commercial species *S. sprattus* prevailed in ichthyoplankton during the winter spawning season, while the warm-water commercial species *E. encrasicolus* prevailed in the summer spawning season (Dekhnik, 1973; Dekhnik & Pavlovskaya, 1979; Eremeev et al., 2011).

The growing anthropogenic pressure between 1980 and 1990 led to heightened water eutrophication, a changed structure of the plankton community in favour of predatory jelly macroplankton, and a depletion of the food supply of planktivorous fish. Soil dumping, bottom trawling, and knife dredging contributed to the destruction of benthic biocenoses. Uncontrolled increase in fishing reduced the spawning stock of natural fish populations. As a result, catastrophic decline in the abundance and species diversity of ichthyoplankton occurred. A tendency toward restoration of the Black Sea shelf ecosystem was noted only in the early 2000s (Klimova, 1998; Gucu, 2002; Eremeev et al., 2011). By the end of the second decade of 2000, eggs and larvae of 68 fish species from 34 families were identified in the ichthyoplankton of the northern Black Sea. And the average abundance of eggs and larvae near the Crimean Peninsula in July-August reached 176.0 and 57 ind./m^2 respectively (Klimova & Podrezova, 2018; Klimova et al., 2022, 2024).

The recovery of the ichthyoplankton assemblage coincided with climate changes occurring since the mid-1990s, which had a significant impact on the hydrological and hydrochemical regime of the Black Sea. In recent decades, there has been warming and an increase in salinity in the upper 100-meter layer of the sea, thinning and erosion of the cold intermediate layer, prolongation of winter and summer hydrological seasons into the spring and autumn, a lower speed of the Black Sea Rim Current in the summer hydrological season, increased dynamic activity in coastal shelf waters, etc. (Turan et al., 2016; Kubryakov et al., 2016; Oguz, 2017; Ginzburg et al., 2021; Artamonov et al., 2023; Korotaeva et al., 2024). In recent decades, there has been a replacement of brackish-water aquatic organisms for marine ones, an emergence of Mediterranean migrants, a reduction in the time period of embryonic and postembryonic development, and a decrease in the length and weight of fish larvae. Exceeding the optimal temperature limits for spawning and embryonic development leads to a decline in spawning activity up to its cessation. Prolongation of the summer and winter hydrological seasons to the autumn and spring interseasonal periods contributes to the resumption of productive spawning of both warm-water and temperate-water fish with a multi-batch type of spawning (Klimova & Podrezova, 2018; Klimova, Vdodovich, Podrezova, 2021; Klimova et al., 2023).

The main goal of the ichthyoplankton research in 2023 was to study the features of the dynamics of species diversity, abundance, and spatial distribution of eggs and larvae of natural fish populations in the pelagic ecosystem of the Black Sea near the Crimean Peninsula during different hydrological seasons.

Materials and Methods

Ichthyoplankton was sampled in different hydrological seasons during four cruises of the R/V *"Professor Vodyanitsky"* near the Crimean Peninsula in the shelf and deep-water areas of the sea from Laspi Bay to the Kerch Peninsula at 264 ichthyoplankton stations: from March 15 to April 3, from June 14 to July 7, on August 3-25, and on October 6-24, 2023 (Figure 1). For comparative purposes, ichthyoplankton samples collected at 56 stations in the same areas from December 2 to December 24, 2022, at the onset of the 2022–2023 winter hydrological season, are also included.

Coastal ichthyoplankton was sampled in the summer spawning season of 2023 at three stations in the coastal area (from 3 to 20 m) off the Karadag Nature Reserve are presented, where 126 ichthyoplankton samples were collected from May to October (Figure 2). Samples were collected using plankton nets Hensen (70 cm inlet diameter), Bogorov-Rass and ICN-80 (80 cm inlet diameter). The mesh size of all nets was about 400 µm. Ichthyoplankton was collected in the vertical catch mode from the bottom to surface at coastal and shelf water stations (depth of up to 100 m) and from the lower boundary of the oxygen layer (σ = 16.2, according to the profiling by Sea-Bird CTD plus probe) to the surface at deep-water stations. The samples were fixed in a 4% formaldehyde solution and processed in stationary conditions with a stereomicroscope MBS-10.

Maps of the spatial distribution of ichthyoplankton were created using the OpenLayers library (https://openlayers.org). The data on the winter spawning season of *S. sprattus* included the following periods: March-April 2023. Larvae were divided into size groups: *S. sprattus* with total length (TL) up to 5.9 mm with yolk and mixed feeding types and larvae TL more than 6 mm with exogenous feeding (Gorbunova, 1958; Dekhnik, 1973). *E. encrasicolus* larvae were divided into

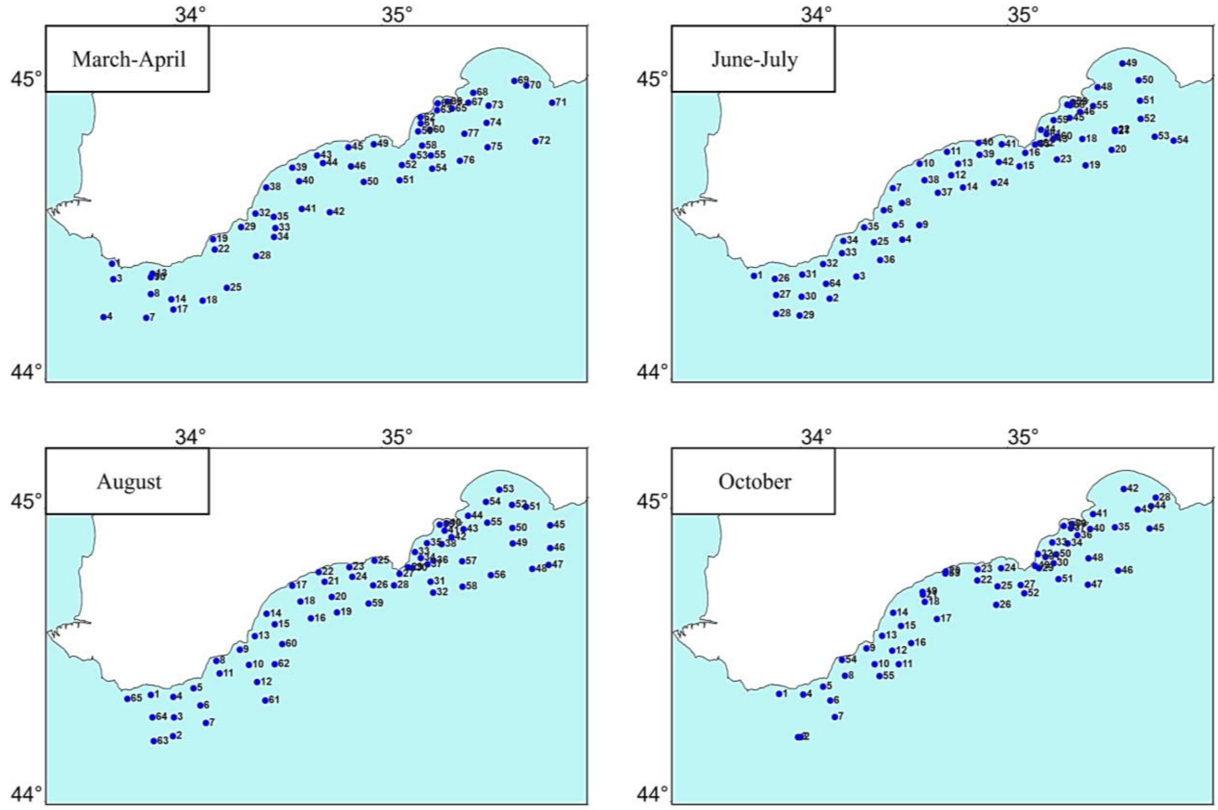

Figure 1. Location of study area and stations occupied during four cruises of the R/V *"Professor Vodyanitsky"* near the Crimean Peninsula (Northern Black Sea) in 2023.

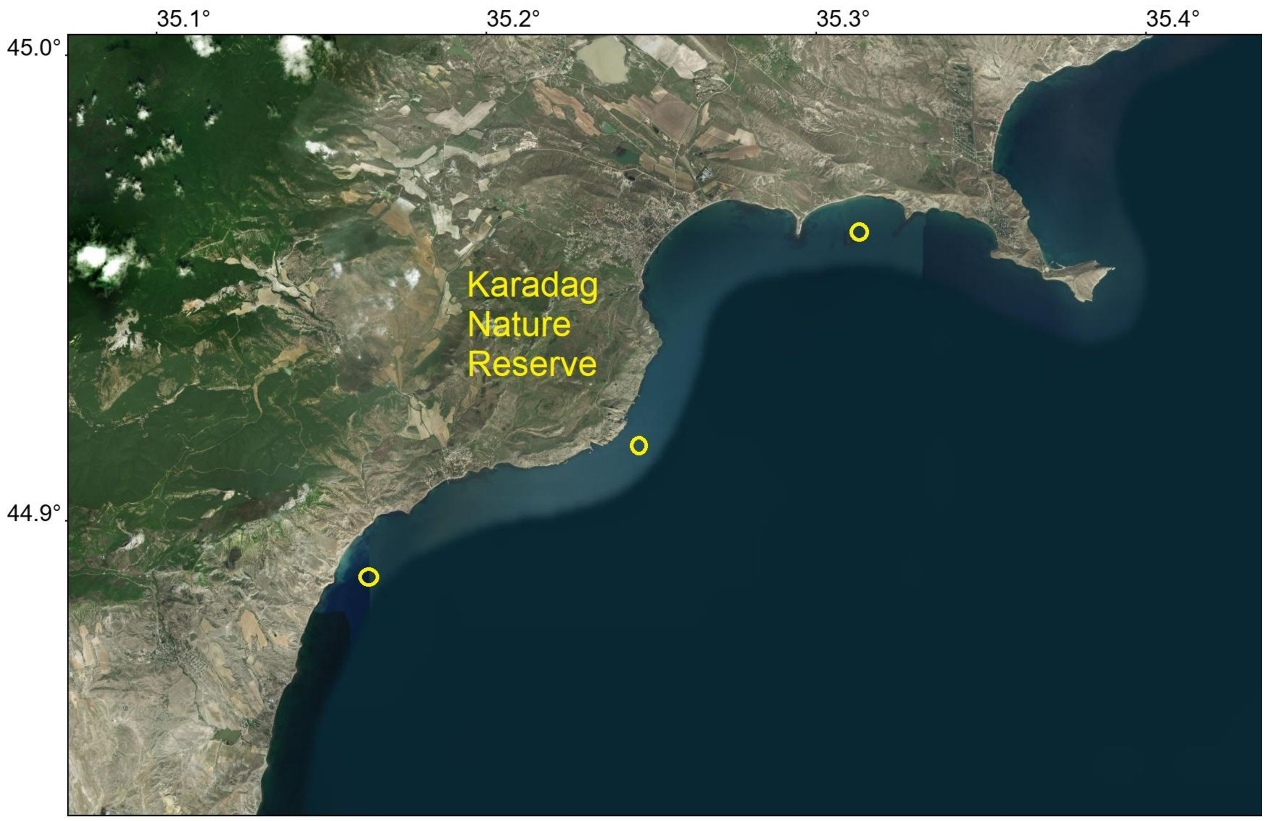

Figure 2. Map of the locations of ichthyoplankton stations off the Karadag Nature Reserve.

three size groups: (1) TL≤3.5 mm, yolk feeding type; (2) TL 3.6–6.0 mm, mixed type; (3) TL 6.1–12.0 mm, exogenous feeding (Duka & Sinyukova, 1976). The classification of ichthyoplankton into temperate-water species (spawning in the winter hydrological season and in summer within the cold intermediate layer) and warm-water species (spawning in the summer hydrological season within the surface mixed layer) is given according to Dekhnik (1973).To analyze the state of ichthyoplankton assemblage in different hydrological seasons, indices of species diversity (Shannon, Weaver, 1958), species richness (Simpson, 1949), dominance (Margalef, 1958) and evenness (Pielou, 1966) proposed by (Odum, 1986) and species similarity index by (Sörensen, 1948) were calculated. Plots of abundance of eggs and larvae of dominant species over different depths were constructed in Microsoft Excel (2019), with the confidence level of the polynomial approximation. Polynomial approximation of the data was performed in Microsoft Excel (2019), using the least squares method. All ichthyoplankton was identified to species level (D'Ancona, 1933; Dekhnik, 1973). Species names of aquatic organisms are given according to the World Register of Marine Species (WoRMS Editorial Board, 2025). Ichthyoplankton abundance is expressed as the number of individuals per square meter in the water column under the sea surface.

Results

In the winter, spring, summer, and autumn hydrological seasons of 2023, eggs and larvae of 45 fish species from 25 families were identified near the Crimean Peninsula, including seven species from four families of temperate-water fish and 38 species from 21 families of warm-water fish (Table 1).

Table 1. Species composition of fish eggs and larvae in the coastal and shelf and deep-water zones of the Crimean Peninsula (Black Sea)

Taxonomic composition	Coastal waters of the Crimean Peninsula (Karadag)		Shelf and deep-water zones of the Crimean Peninsula	
	Eggs	Larvae	Eggs	Larvae
Temperate-water species				
Family: Clupeidae *Sprattus sprattus* (Linnaeus, 1758)	-	-	+	+
Family: Gadidae *Merlangius merlangus* (Linnaeus, 1758)	-	-	+	+
Trisopterus luscus (Linnaeus, 1758)	-	-	-	+
T. minutus (Linnaeus, 1758)			-	+
Gadidae sp.	-	-	+	-
Family: Moridae *Rhynchogadus hepaticus* (Facciolà, 1884)	-	-	-	+
Family: Lotidae *Gaidropsarus mediterraneus* (Linnaeus, 1758)	-	-	+	-
Warm-water species				
Family: Engraulidae *Engraulis encrasicolus* (Linnaeus, 1758)	+	+	+	+
Family: Ophidiidae *Ophidion rochei* Müller, 1845	+	+	-	-
Family: **Syngnathidae** *Syngnathus schmidti* Popov, 1928	-	+	-	+
Family: **Scorpaenidae** *Scorpaena porcus* Linnaeus, 1758	+	-	-	-
Family: **Serranidae** *Serranus scriba* (Linnaeus, 1758)	+	+	+	+
Family: Gobiesocidae *Diplecogaster bimaculata* (Bonnaterre, 1788)	-	-	-	+
Lepadogaster candolii Risso, 1810	-	-	-	+
Family: Blenniidae *Parablennius tentacularis* (Brünnich, 1768)	-	+	-	+
P. sanguinolentus (Pallas, 1814)	-	+	-	-
P. zvonimiri (Kolombatovic, 1892)	-	+	-	+
Aidablennius sphynx (Valenciennes, 1836)	-	+	-	-
Salaria pavo (Risso, 1810)	-	+	-	-
Blennius sp.	-	+	-	-
Family: Callionymidae *Callionymus* sp.	+	+	+	+
Family: Gobiidae				
Gobius niger Linnaeus, 1758	-	+	-	+
Pomatoschistus marmoratus (Risso, 1810)	-	-	-	+
P. minutus (Pallas, 1770)	-	-	-	+
P. pictus (Malm, 1865)	-	-	-	+
Gobius sp.	-	-	-	+

Table 1. Continued

Taxonomic composition	Coastal waters of the Crimean Peninsula (Karadag)		Shelf and deep-water zones of the Crimean Peninsula	
	Eggs	Larvae	Eggs	Larvae
Warm-water species				
Family: Pomacentridae				
Chromis chromis (Linnaeus, 1758)	-	+	-	-
Family: Mugilidae				
Mugil cephalus Linnaeus, 1758	-	-	+	-
Chelon auratus (Risso, 1810)	+	-	-	-
Family: **Carangidae**				
Trachurus mediterraneus (Steindachner, 1868)	+	+	+	+
Family: Mullidae				
Mullus barbatus Linnaeus, 1758	+	+	+	+
Family: Sciaenidae				
Sciaena umbra Linnaeus, 1758	+	+	-	-
Family: Labridae				
Ctenolabrus rupestris (Linnaeus, 1758)	-	+	+	-
Symphodus cinereus (Bonnaterre, 1788)	-	+	-	-
S. ocellatus (Linnaeus, 1758)	-	+	-	-
S. roissali (Risso, 1810)	-	+	-	-
S. tinca (Linnaeus, 1758)	-	+	-	-
Family: Sparidae				
Diplodus annularis (Linnaeus, 1758)	+	+	+	+
Sparidae sp.	+	+	-	-
Family: Pomatomidae				
Pomatomus saltatrix (Linnaeus, 1766)	+	+	+	-
Family: Trachinidae				
Trachinus draco Linnaeus, 1758	+	-	+	-
Echiichthys vipera (Cuvier, 1829)	-	-	+	-
Family: Uranoscopidae				
Uranoscopus scaber Linnaeus, 1758	+	-	+	-
Family: Bothidae				
Arnoglossus kessleri Schmidt, 1915	+	+	-	-
Family: Soleidae				
Pegusa nasuta (Pallas, 1814)	+	-	-	+
Number of species, temperate water	**0**		**7**	
warm water	**30**		**23**	
Total species	**45**			

Coastal Area of Karadag

In the coastal area of the Karadag Nature Reserve (Figure 2), where the studies were carried out during the summer spawning season, eggs and larvae of 30 fish species from 20 families of exclusively warm-water species were identified. The species similarity index (Sörensen, 1948) of ichthyoplankton near the Karadag Nature Reserve and the coastal waters of Sevastopol in the summer spawning season of 2020 was 0.73 (Podrezova et al., 2021). In May 2023, when the sea water temperature was 17°C, ichthyoplankton were still absent. In early June, there was a sharp increase in the sea surface temperature and the transition to the summer hydrological season started. During the first ten days of June, the sea water temperature rose to 19.9°C. Samples contained eggs and larvae of 21 warm-water fish species. The average abundance of eggs was 10.0 ind./m² and that of larvae was 1.5 ind./m². The eggs of *M. barbatus* (51.6%) and *E. encrasicolus* (15.5%) were dominating in the samples, although their spawning was still ineffective. In July and August 2023, the ichthyoplankton species composition comprised 26 and 20 species, respectively. In July and August, fish eggs of *E. encrasicolus* dominated the samples accounting for 52% in July and 67.8% in August. At the end of the summer spawning season (in September), the share of *E. encrasicolus* eggs decreased to 6.8%, but its larvae continued dominating the ichthyoplankton, comprising approximately 65% of the total larval abundance of all species.

Shelf and Deep-Water Areas of Crimean Peninsula

In the shelf and deep-water areas of Crimean Peninsula from Laspi Bay to the Kerch Peninsula, eggs and larvae of 30 species from 20 families of warm-water and temperate-water fish were recorded in the winter, summer and autumn hydrological seasons. Temperate-water species were registered in all seasons of the studies, and warm-water species were found from April to October (Table 1).

The Winter Hydrological Season

In March–April the water temperature corresponded to the winter hydrological season. The average sea surface temperature was about 9°C, which is favourable for spawning of temperate-water fish species (Gorbunova, 1958). Eggs and larvae were observed throughout the entire study water area and were absent at only 10 stations. The average abundance of eggs was 29.8 ind./m², and that of larvae was 9.5 ind./m². The maximum abundance reached 147.9 and 108.5 ind./m², respectively (Figure 3).

Ichthyoplankton of temperate-water fish species was represented by the eggs of *S. sprattus* and *M. merlangus*, whereas larvae belonged only to *S. sprattus*. Despite a high proportion of dead eggs (76.8%), the spawning of *S. sprattus* was with a high efficiency (32.5%). Eggs and larvae of *S. sprattus* were present throughout the entire study area over the depths ranging from 30 to 1534 m, with their abundance increasing toward deep waters. The reliability level of the polynomial trend line approximation was high for eggs (0.81) and moderate for larvae (0.57) (Figure 4)

A larva of warm-water *Pomatoschistus marmoratus* (Risso, 1810) from the Gobiidae family was caught in April, at the depth of 42 m, when the temperature at the water surface was over 10°C (Table 2).

The proportion of *S. sprattus* larvae with yolk and mixed feeding types was high, reaching 93%, which indicated the continuation of effective spawning (Figure 5). For comparative reasons, the size range of *S. sprattus* larvae at the beginning of the winter spawning season (December 2022) is also shown on Figure 5.

The spring hydrological season began only in the second decade of April and was characterized by a gradual temperature increase from 11.0°C to 13.0°C in the middle and at the end of April, reaching 17.5°C by the end of May.

The Summer Hydrological Season

From June–July, there still was the initial phase of the summer hydrological season, with the average sea surface temperature not exceeding 23°C by the end of the sampling period in early July. Eggs and larvae of 20 fish species from 15 families were identified in June in the shelf and in deep-water study areas. Warm-water fishes were represented by eggs and larvae of 16 fish species, while temperate-water fishes belonged to four species (Table 2). The average egg abundance was only 6.76 ind./m² and the average abundance of larvae was 0.8 ind./m², with maximum abundance reaching 45.8 ind./m² and 7.9 ind./m², respectively. The share of eggs of temperate-water species *S. sprattus* and *M. merlangus* averaged 42%, however, their spawning was ineffective. The larvae belonged to two species from the

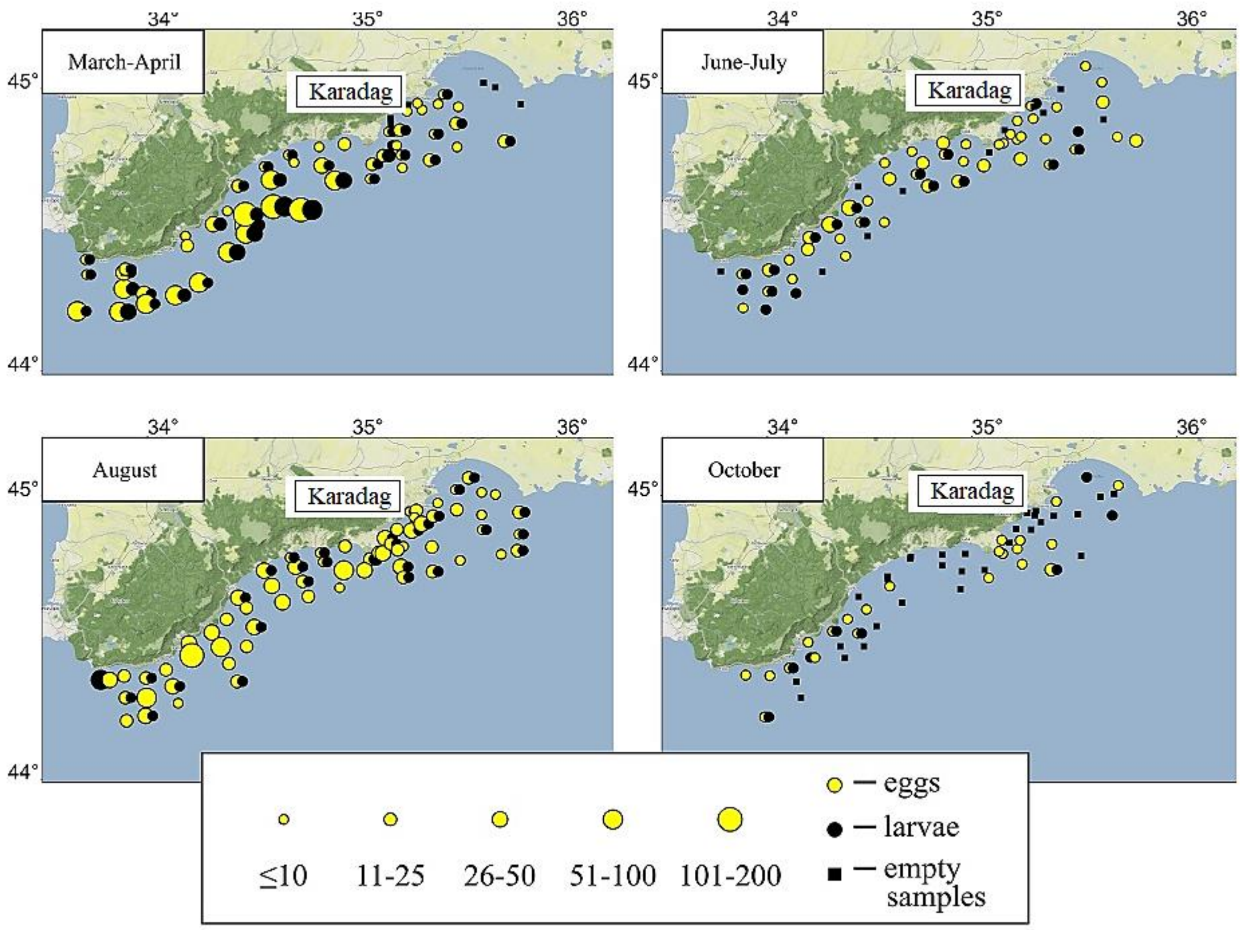

Figure 3. Schematic map of the spatial distribution of fish egg and larval abundance (ind./m²) in March–April, June–July, August, and October 2023 in the shelf and deep-water zones off the Crimean Peninsula.

family Gadidae, dominated by the Mediterranean invader *Trisopterus luscus* (Linnaeus, 1758). Among warm-water fish eggs, the commercially important species *E. encrasicolus* prevailed, accounting for 33% of the fish eggs; however, spawning was still not effective, there were no larvae in the samples. Among warm-water fish larvae, *Syngnathus schmidti* Popov, 1927 predominated, acccounting for 36.84%, and dominating in deep-water zone samples with 50.4%. Larvae from the family Gobiidae were found only on the shelf, accounting for 19.74%. The distribution of larvae of other species from the families Gobiesocidae,

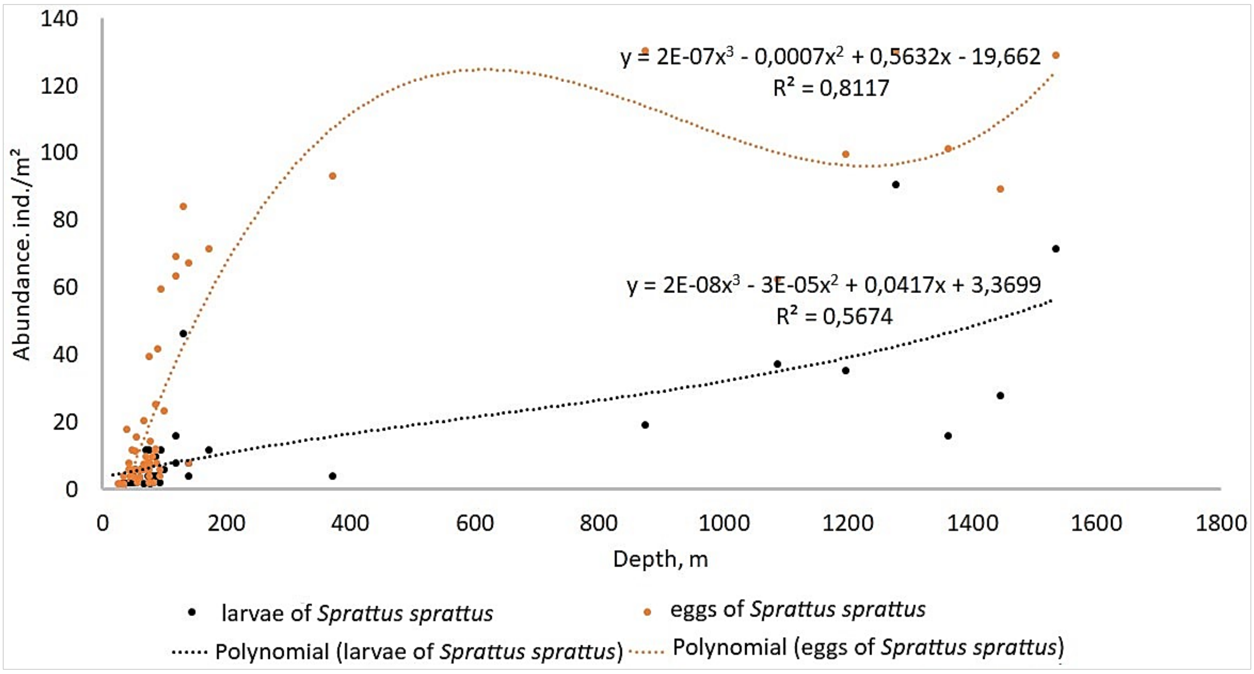

Figure 4. Abundance of eggs and larvae of *S. sprattus* (ind./m^2) in vertical catches depending on the depth of the station in March.

Table 2. Species composition (%) of fish eggs (numerator) and larvae (denominator) in shelf and deep-water areas near the Crimean Peninsula during four cruises of the R/V *Professor Vodyanitsky*: in March-April, June-July, August, and October of 2023

Species composition	March-April	June-July	August	October
Temperate-water species				
Sprattus sprattus	96.97 / 99.68	12.72 / 0	0.42 / 0	17.59 / 0
Merlangius merlangus	3.03 / 0	4.14 / 0	1.39 / 0	53.30 / 0
Trisopterus luscus	-	0 / 15.79	-	-
T. minutus	-	-	-	0 / 21.21
Gadidae sp.	-	25.14 / 7.89	2.49 / 0	-
Rhynchogadus hepaticus	-	-	0 / 1.11	-
Gaidropsarus mediterraneus	-	-	-	23.07 / 0
Warm-water species				
Engraulis encrasicolus	-	33.0 / 0	78.53 / 85.97	6.04 / 45.46
Syngnathus schmidti	-	0 / 36.84	-	-
Serranus scriba	-	1.78 / 0	1.15 / 0	-
Diplecogaster bimaculata	-	-	-	0 / 6.06
Lepadogaster candolii	-	0 / 7.89		-

Table 2. Continued

Species composition	March-April	June-July	August	October
		Warm-water species		
Parablennius tentacularis	-	0 3.95	0 0.73	-
P. zvonimiri	-	-	0 1.11	-
Callionymus sp.	-	0.44 0	0 1.11	-
Gobius niger	-	0 11.84	0 0.74	-
Pomatoschistus marmoratus	0 0.32	0 3.95	0 2.95	0 15.15
P. minutus	-	-	0 2.20	-
P. pictus	-	0 3.95	-	0 12.12
Gobius sp.	-	-	0 1.11	-
Mugil cephalus	-	-	0.14 0	-
Trachurus mediterraneus	-	10.95 0	9.23 1.11	-
Mullus barbatus	-	0.89 3.95	3.55 1.11	-
Ctenolabrus rupestris	-	0.89 0	-	-
Diplodus annularis	-	6.8 3.95	1.71 0	-
Pomatomus saltatrix	-	2.37 0	0.88 0	-
Trachinus draco	-	0.44 0	0.23 0	-
Echiichthys vipera	-	0.44 0	0.14 0	-
Uranoscopus scaber	-	-	0.14 0	-
Pegusa nasuta	-	-	0 0.74	-
Number of species	**3**	**20**	**22**	**8**
Egg abundance, ind./m²	**0-147.9*** **29,8+39.28**	**0-45.8** **6.76+8.56**	**0-70.8** **21.8+15.32**	**0-18.3** **1.8+3.10**
Larvae abundance, ind./m²	**0-108.5** **9,5+18.81**	**0-7.9** **0.8+1.60**	**0-67.7** **2.8+8.79**	**0-4.5** **0.6+1.35**

* Minimum abundance – maximum abundance. Mean abundance + standard deviation.

Blenniidae, Mullidae, and Sparidae was mainly restricted to the shelf and continental slope areas where they were encountered singly (Figure 3, Table 1, Table 2).

From the first days of July until the end of August, the average sea surface temperature increased from 23°C to 26°C. The peak of the summer hydrological season in the sea started with the formed upper surface mixed layer.

In the shelf and deep-water areas off the Crimean Peninsula 22 fish species from 16 families were identified in August. The numbers of species in summer ichthyoplankton in August 2023 in coastal waters off Karadag (20 species), shelf (18 species), and deep-water areas (18 species) were quite comparable. The average abundance of fish eggs was 21.8 ind./m² and the average abundance of larvae was 2.8 ind./m², with maximum abundances reaching 70.8 ind./m² and 67.7 ind./m², respectively (Figure 3; Table 2). Similar to the coastal waters of Karadag, warm-water *E. encrasicolus* eggs dominated in the samples (78.53%). Eggs and larvae of *E. encrasicolus* were found at all sampled stations over the depths of up to 1455 m and, unlike the temperate-water *S. sprattus*, had a "patchy" distribution with a low confidence level of polynomial trend line approximation: R^2 = 0.18 for eggs, and R^2 = 0.04 for larvae (Figure 6).

The proportion of *T. mediterraneus* eggs accounted for 9.23%, while eggs of other fish species were registered singly. Among larvae of warm-water species, *E. encrasicolus* also prevailed accounting for 85.97%, the peak of its spawning was observed. All larvae belonged to the younger age group with yolk type of feeding, with an average size of 2.4 mm. Four larval species from the family Gobiidae accounted for only 7%, and larvae of other warm-water species had single occurrence cases. Temperate-water species were represented by individual specimens of eggs from *S. sprattus, M. merlangus*, and Gadidae sp. The larva with a total length of 10.9 mm, identified as *Rhynchogadus hepaticus* (Facciolà, 1884) from the family Moridae (D'Ancona, 1933), was caught on August 18 on the traverse of Cape Meganom at a depth of 76 m. The larva had a body pigmentation (star-shaped pigment) typical of the order Gadiformes, covering the entire body except for the caudal fin. The body tapered towards the caudal peduncle. The head was concave anteriorly and massive posteriorly. The snout tip was flat (horseshoe-shaped) and slightly raised. The eyes were large of intense black colour (D'Ancona, 1933). Pelvic fins were located at eye level. This family Moridae species Inhabitant of the Northern Hemisphere, inhabiting seas

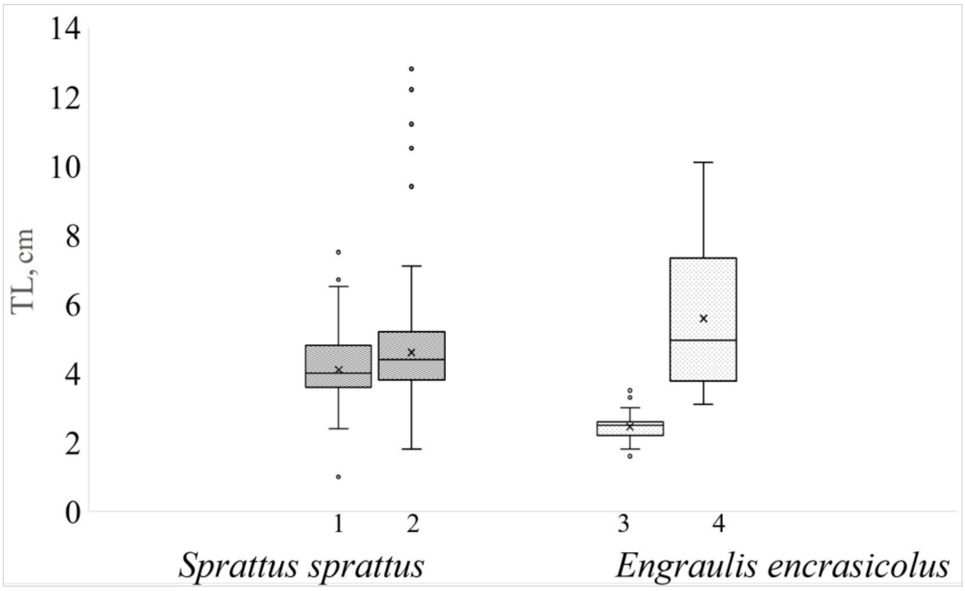

Figure 5. Size ranges of *Sprattus sprattus* and *Engraulis encrasicolus* larvae in different hydrological seasons: 1 – December 2022 (the onset of the 2022–2023 winter hydrological season); 2 – March – April 2023; 3 – August 2023; 4 – October 2023. Each box contains five horizontal lines representing the following percentiles of the data: 10 %, 25 %, 50 % (median), 75 %, and 90 % (from 25% to 75% is shown within the box); (○) — outliers, (×) — mean value.

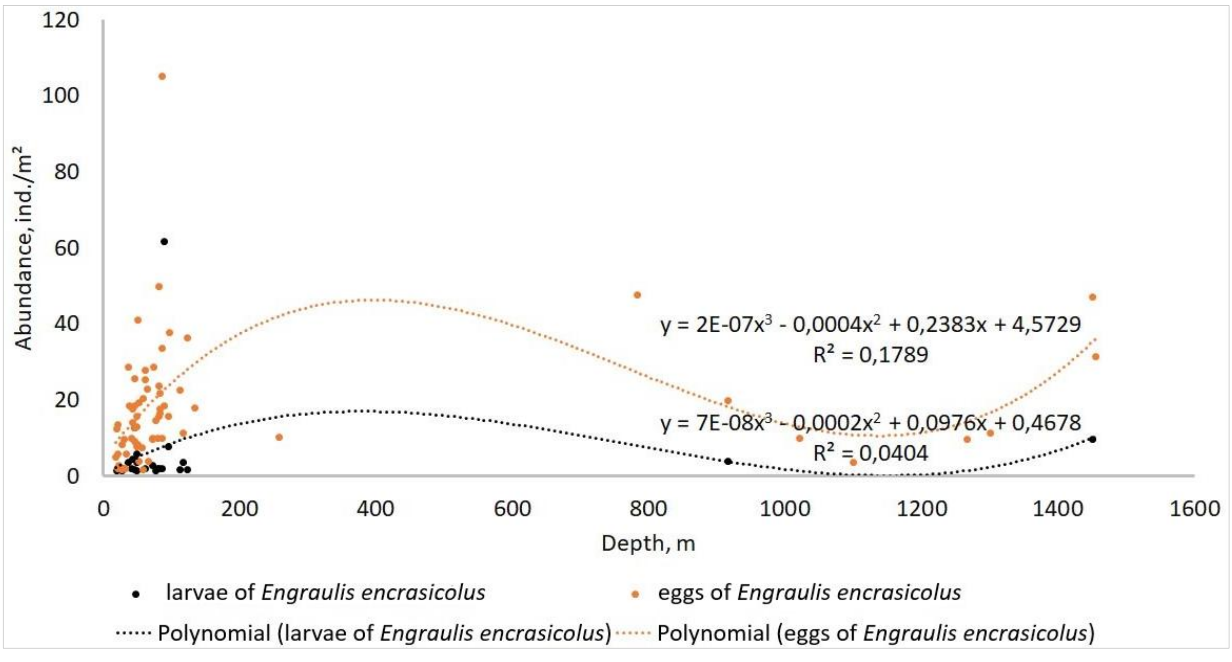

Figure 6. Abundance of eggs and larvae of *Engraulis encrasicolus* (ind./m^2) in vertical catches depending on the depth of the station in August.

of the Mediterranean basin and eastern part of the Atlantic Ocean. Unlike other species of the family Moridae, it leads a pelagic lifestyle (Figure 7).

The Autumn Hydrological Season

The transition from the summer to the autumn hydrological season in 2023 began with a gradual decrease in sea surface temperature from 22.5°C at the end of September to 21–20.5°C in mid-October. Eight fish species from 6 families continued spawning. Four species belonged to the warm-water and four species - to the temperate-water fish. The average abundance of eggs was 1.8 ind./m² and for larvae - 0.6 ind./m² (Figure 1, 3, Table 2). The eggs of three temperate-water species dominated (93.96%), although their spawning was still ineffective. Two larvae, identified as *Trisopterus minutus* (Linnaeus, 1758) from the family Gadidae (D'Ancona, 1933), were caught on October 6 near the southern coast of Crimea over a depth of 93 m (Figure 8).

T. minutus inhabits temperate latitudes in the eastern part of the Atlantic Ocean and the Mediterranean Sea. It is usually found in small schools at depths ranging from 3 to 91 meters over muddy or sandy bottom. Spawning in the Mediterranean Sea occurs from December to March (D'Ancona, 1933).

The eggs of warm-water fish species were represented only by *E. encrasicolus.* Larvae of warm-water fish dominated the samples, with *E. encrasicolus* prevailing, representing 45.46%. Compared to the August, the proportion of large larvae increased, which is characteristic of the late summer spawning season (Figure 3; Table 2).

Discussion

The winter hydrological season 2022-2023 finally settled down only by the beginning of February 2023, when the minimum sea surface temperature values were still 8.5°C. Throughout the entire winter hydrological season, the study area was under the influence of the waters of the Black Sea Rim Current. During the ichthyoplankton survey in the shelf and deep-water areas from Laspi Bay to the Kerch Peninsula from March–April, the winter hydrological season were still ongoing. It is noteworthy that in March of the 1950s–1970s, the winter spawning season of *S. sprattus* usually was over, with eggs found quite rarely and spawning being ineffective, which was confirmed by the absence of larvae from younger age groups (Dekhnik, 1973). In March 2023, in the Black Sea waters near Southern and Southeastern Crimea, the winter hydrological season was still ongoing, and as a result,

Figure 7. Larva (TL = 10.9 mm) of the family Moridae – *Rhynchogadus hepaticus* (Faciola, 1884).

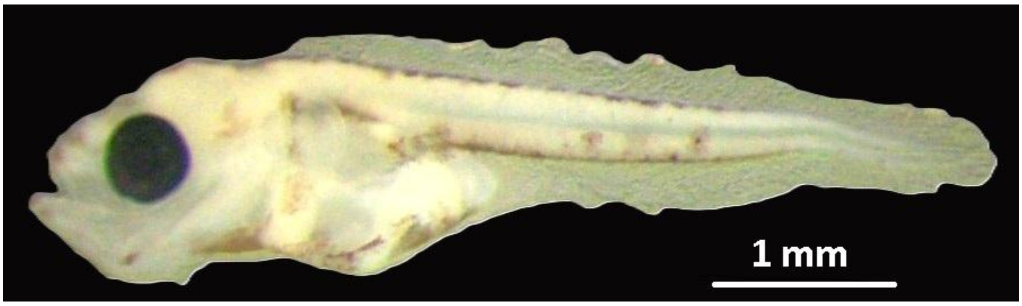

Figure 8. Larva (TL = 5.3 mm) of the family Gadidae – *Trisopterus minutus* (Linnaeus, 1758).

temperate-water *S. sprattus* dominated the samples. According to T.V. Dekhnik (1973), the maximum number of *S. sprattus* larvae for the entire winter spawning season in the Crimean Peninsula was 30 ind./m^2, then at the end of the winter spawning season, in March 2023, the maximum number of larvae reached 108.5 ind./m^2, and the predominance of larvae of the younger age group in the samples indicates the effectiveness of spawning.

According to ichthyoplankton research over recent years, mass effective spawning of *S. sprattus* begins as early as in November and continues until the end of May under favorable hydrological conditions (Klimova, Vdodovich, Podrezova, 2021; Klimova et al., 2022). During the period between 2001 and 2017, a threefold decline in the abundance of temperate-water *S. sprattus* in catches was observed due to a decrease in the abundance of older age groups in the catches (small individuals aged 0+ to 2 years dominated). However, since 2021, the status of *S. sprattus* stocks has been assessed as increasing or stable (Shlyakhov & Pyatnitsky, 2023).

The spring hydrological season 2023 began only in the second decade of April and was characterized by a gradual temperature increase from 11.0°C to 13.0°C in the middle and at the end of April, reaching 17.5°C by the end of May. The sea surface temperature was already favorable for the start of the spawning season of warm-water fish.

The ichthyoplankton assemblage of the coastal waters of Karadag (Figure 2) usually was typical of the coastal waters from the southwestern to the southeastern parts of the Crimean Peninsula.

However, in the coastal waters of Karadag, in samples collected in May 2023 when the sea surface temperature was 17°C, ichthyoplankton was still absent. In June 2023, the initial phase of the summer hydrological season was registered in the study area. In the coastal waters near Karadag, eggs and larvae of 21 species of warm-water fishes were recorded. In the summer ichthyoplankton near Karadag usually dominated *M. barbatus, D. annularis,* and *T. mediterraneus* (Bagnyukova, 1998; Podrezova et al., 2021). In June 2023, the eggs were predominantly from four common species — *M. barbatus*, *D. annularis*, and *E. encrasicolus* — which together accounted for 77.8%. However, their spawning remained ineffective. In the ichthyoplankton, as usual, more than 50% of the total population was made up of *M. barbatus*, while the share of *E. encrasicolus* did not exceed 10%. Larvae were represented by coastal species with demersal eggs.

In the shelf and deep-water areas, active wind-wave activity prevented the formation of a surface mixed layer where warm-water fish spawning occured. Ichthyoplankton included 16 species of warm-water fishes and four species of temperate-water fishes. The average abundance of ichthyoplankton was low (eggs 6.76 ind./m², larvae 0.8 ind./m²). Eggs (58%) and larvae (76.32%) of warm-water fishes dominated in the samples. Eggs of *E. encrasicolus* and *T. mediterraneus* prevailed (44%), but their spawning was ineffective. Among larvae, coastal species with demersal eggs and *S. schmidti* prevailed. Spawning of temperate-water fish continued under the thermocline layer. Eggs of three species (42%) and larvae of two species (23.79%) were identified. Due to the large number of species and low dominance of individual species (dominance index 0.17), the highest indices of species diversity (3.07), species richness (21.68), and evenness (0.71) were recorded in ichthyoplankton in June.

In early August 2023, the summer hydrological season was already observed in the shelf and deep-water research areas with a well-defined surface mixed layer. The species richness was comparable to that in June; a species similarity index was 0.71, while the abundance of eggs and larvae increased threefold. A sharp rise in sea surface temperature (exceeding 26°C) surpassed the optimal limits for spawning and embryonic development of warm-water fish, which did not contribute to mass spawning. *E. encrasicolus,* which exhibits the highest optimal temperature thresholds for spawning and embryonic development compared to other warm-water species, dominated in the samples. Its eggs share accounted for 78.5% of the samples, and larvae – for 86.7%. Its maximum abundance was observed at the shelf edge over the depths of approximately 90 m. Previously eggs and larvae of *E. encrasicolus* dominated only in the ichthyoplankton of shelf and deep-waters (Dekhnik, 1973). In coastal waters near Karadag at the height of the summer spawning season (July-August), the proportion of eggs and larvae of *E. encrasicolus* did not exceed 14 % (Podrezova et al., 2021). In 2023, the proportion of *E. encrasicolus* eggs in July being 52%, and increasing to 67.8% in August. The success of the spawning in coastal waters is confirmed by the dominance of *E. encrasicolus* larvae in September, with its share being 65%. This distribution of *E. encrasicolus* may be associated with the sharp warming of the Azov Sea water in July 2023. In recent years, by early July, water temperatures in the Azov Sea have already reached optimal levels for *E. encrasicolus* to spawn, when increased salinity promotes colonization and mass development of Black Sea warm-water jelly macroplankton and depletion of the food base, which leads to *E. encrasicolus* migration into the deep Black Sea (Yuneva et al., 2020). In early July 2023, surface water temperature of the Black Sea was as low as 16°C near the Feodosiya Bay, where upwelling was observed, and as high as 22-23°C in the South Coast region. An increase in the proportion of Azov Sea-origin *E. encrasicolus* in the Black Sea commercial fish catches is based on the data from Shlyakhov & Pyatnitsky (2023). The status of commercial stocks of *E. encrasicolus* in the Black Sea has been assessed as increasing lately: its share in catches rose from only 16.5% in 2019 to 75% in 2021. The growth in *E. encrasicolus* catches in the Black Sea is linked to an increase in bycatch of its Azov Sea population. Due to the dominance of eggs and larvae of

E. encrasicolus in August 2023 (dominance index 0.64), the species diversity index was only 1.34, species richness index was 15.14, and evenness index was 0.30.

In October 2023, the sea was still undergoing the transition from the summer to the autumn hydrological season, with sea surface temperatures exceeding 20°C. Fish eggs of three temperate-water species already dominated in the samples accounting for 93.96%; however, their spawning was ineffective, and larvae were represented only by *T. minutus* species. Favourable water temperature during the autumn interseason promotes effective spawning of warm-water fish species with multiple-batch character of egg maturation (Klimova et al*.,* 2023). In 2023, warm-water species were represented by the eggs and larvae of *E. encrasicolus* and by larvae of three demersal-spawning fish species: *P. marmaratus, P. pictus*, and *Diplecogaster bimaculata* (Bonnaterre, 1788). Larvae of warm-water fish dominated the samples, representing 78.79%, where *E. encrasicolus* prevailed, accounting for 45.46%. Effective spawning of warm-water fish during the autumn interseason was likely promted by both increased temperature in the upper 100-meter water layer and the mass development of food mesoplankton. This is supported by the high abundance of copepod nauplii of small cyclopoid species (*Oithona davisae* and *O. similis*) and appendicularians *Oikopleura (Vexillaria) dioica* during the autumn interseason along with a simultaneous decrease in biomass of gelatinous macroplankton (Anninsky et al*.,* 2023). The species diversity index in October (2.45) was comparable to that recorded in the coastal waters at Karadag in August, while species richness and evenness indices were 17.74 and 0.81, respectively.

The marked differences in the state of ichthyoplankton assemblage in shelf and deep-water areas off Southern and Southeastern Crimea during the study periods in March–April, June–July, August, and October 2023 were confirmed by cluster analysis using the unweighted pair-group method with arithmetic mean (UPGMA) (Romesburg, 1990) with dendrogram construction based on Bray-Curtis similarity index (Figure 9).

The lowest similarity was observed in the ichthyoplankton from March-April, when the winter hydrological season was still ongoing and the temperate-water species *S. sprattus* prevailed in the ichthyoplankton accounting for 96.97% and 99.68% of the total number of fish eggs and larvae, respectively. The highest similarity was registered in ichthyoplankton assemblage at the beginning and end of the summer spawning season - in June and October- with maximum evenness index values of 0.71 and 0.81, respectively.

The increase in the abundance of small pelagophilic fish species *S. sprattus* and *E. encrasicolus*, which, unlike other fish species, are widely spread throughout the Black Sea basin, contributes to the feeding migrations of temperate Mediterranean predators through the Bosphorus Strait. Additionally, rising temperatures in the upper oxygenated layer, increased salinity, and a rich food base promote their adaptation to new environmental conditions, as evidenced by the presence of their larvae in the ichthyoplankton. Besides Mediterranean predators *T. luscus* and *T. minutus* from the family Gadidae, ichthyoplankton samples also contained eggs of the coastal Mediterranean invader *Echiichthys vipera* (Cuvier, 1829) from family Trachinidae as well as of *R.*

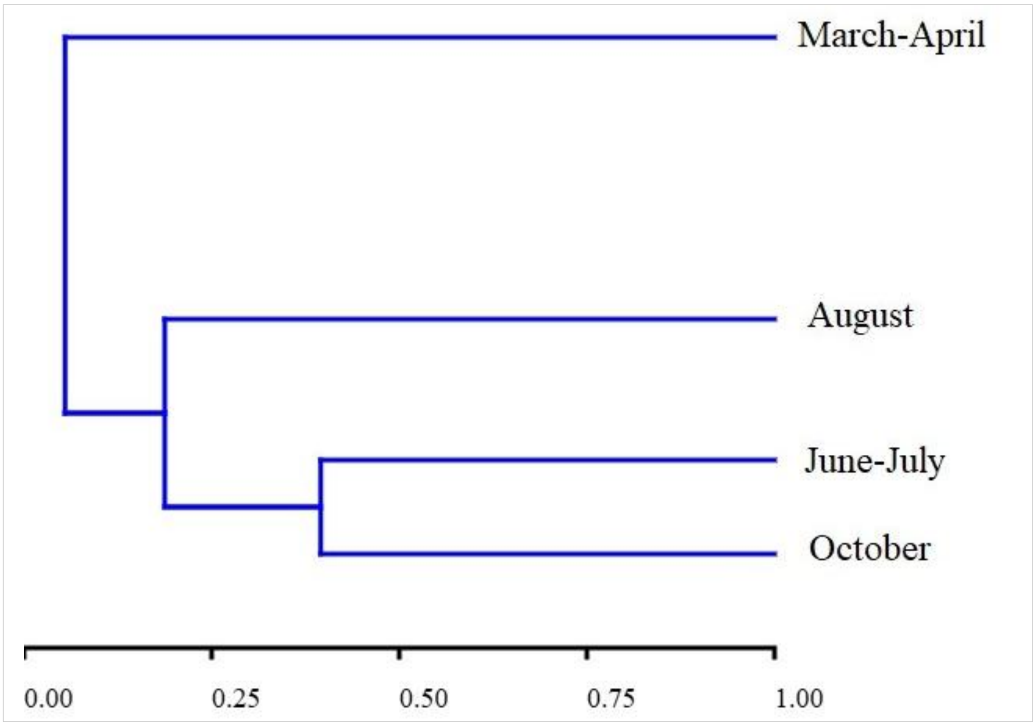

Figure 9. Dendrogram of taxonomic similarity of ichthyoplankton assemblages complexes in different seasons 2023.

hepaticus, a pelagic inhabitant from the family Moridae. While larvae of *T. luscus* have been regularly recorded throughout all seasons in ichthyoplankton near the Crimean Peninsula since 2013 (Klimova & Podrezova, 2018; Klimova et al., 2021; 2022), *T. minutus* and *R. hepaticus* were caught for the first time in 2023.

Conclusions

Off the Crimean Peninsula from March to October 2023, eggs and larvae of 45 fish species from 25 families, including seven species from four families of temperate-water fish and 38 species from 21 families of warm-water fish, were identified. From May to September, eggs and larvae of 30 species of warm-water fish were recorded in the ichthyoplankton of the nearshore waters near Karadag, while in the open waters from Laspi Bay to the Gulf of Feodosia, 23 species of warm-water and seven species of temperate-water fish were observed from March to October.

The maximum abundance of eggs and larvae of temperate-water fish species was observed in March 2023, that is the end of the winter spawning season, and it reached 147.9 and 108.5 ind./m², respectively. Eggs and larvae of *S. sprattus* dominated.

During the summer spawning season, maximum abundance of eggs and larvae was recorded in August, that is the peak of the summer spawning season, and it amounted to 70.8 and 67.7 ind./m², respectively. Eggs and larvae of *E. encrasicolus* dominated.

Cluster analysis results showed that the greatest species similarity in ichthyoplankton of shelf and deep-water areas was observed at the beginning and end of the summer spawning season, that is in June and October, with maximum evenness index values of 0.71 and 0.81, respectively.

Unlike previous years' studies, during the peak of the summer spawning season in August 2023, eggs and larvae of *E. encrasicolus* dominated across the entire study area, both in deep-water and shelf zones as well as in the coastal waters off Karadag. The dominance of *E. encrasicolus* eggs and larvae in the coastal waters off Karadag is likely associated with spawning migration of the Azov Sea population of *E. encrasicolus* into the Black Sea at the end of June, due to sea surface temperature exceeding optimal temperature limits for spawning and embryonic development in the Azov Sea.

The highest species diversity indices were recorded during periods of minimal dominance by individual species in the ichthyoplankton: in June (3.07) and October (2.45). The species similarity index between eggs and larvae of warm-water species from both shelf waters and deep-water stations and ichthyoplankton from the coastal waters stations off Karadag was 0.57 during the summer spawning season of 2023.

Previously, the number of species in summer ichthyoplankton decreased from coastal to deep-water study areas, whereas in August 2023, those values across coastal (20 species), shelf (18 species), and deep-water areas (18 species) were quite comparable.

The prolongation of the summer and winter hydrological seasons to the spring and autumn off-season promotes the resumption of fish spawning, with a continuous type of oocyte maturation. An increase in the number of small fractions of forage zooplankton and a decrease in predatory pressure from jelly macroplankton during the off-season periods favor the survival of fish larvae.

The presence of various-sized larvae of migrant fish from the Mediterranean Sea (*T. luscus*, *T. minutus*, and *R. hepaticus*) in ichthyoplankton indicates their successful adaptation to new environmental conditions in the Black Sea.

Ethical Statement

Specific permission was not required to conduct sampling for this research. No experiments have been carried out using living organisms. The authors confirm that the field studies did not involve any endangered or protected species.

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Author Contribution

Klimova T. contributed substantially to the conception and design of the study. Klimova T., Vdodovich I., Petrova T., Mashukova O. and Zabrodin D. studied ichthyoplankton samples, worked on the analysis and interpretation of the data, wrote and reviewed the manuscript. Identification of ichthyoplankton was made by Klimova T., Petrova T. and Mashukova O., larval fish nutrition was studied by Vdodovich I.

Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. All listed co-authors declare that the present study was conducted in an ethical, professional and responsible manner.

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