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MARINE BIOLOGY

# Features of the Distribution of Black Sea Ichthyoplankton in Conditions of Activation of Atmospheric Processes in the Summer Hydrological Season of 2021

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**Abstract**—The article presents the species diversity, abundance, and distribution features of ichthyoplankton and fodder zooplankton in the northern Black Sea in summer 2021. The intensification of cyclonic activity over the Black Sea in June–July slowed the formation of summer-type thermal stratification in the studied water area. At the beginning of July, only 13 species of eggs and fish larvae were observed in ichthyoplankton of the Crimean Peninsula, and their average abundance was 29 and 2 ind./$m^2$, respectively. At the beginning of August, summer-type vertical thermal stratification off the coast of the Caucasus had already formed. The number of ichthyoplankton species increased to 20. Activation of atmospheric processes in June–July intensified the intraseasonal wind "pumping" of the upper layer of the sea. The Black Sea Rim Current transformed into a pronounced jet over the continental slope, oriented alongshore, partially extending to the shelf. This did not affect the spawning activity of mass fish species. The average abundance of eggs in the shelf and deep-water zone was about 160 ind./$m^2$, and the average abundance of larvae on the shelf was almost five times higher, 452 ind./$m^2$.

**Keywords:** ichthyoplankton, species diversity, spatial distribution, fodder zooplankton, feeding of fish larvae, hydrological regime, Black Sea

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## INTRODUCTION

Regular ichthyoplankton studies of the northern Black Sea within Russia's economic zone aboard the R/V *Professor Vodyanitsky* began in 2016. The data obtained, in addition to individual surveys from 2005 to 2013, made it possible to assess the current state of ichthyoplankton assemblages, the nature of their changes after degradation of the sea's ecosystem since the late 1980s [23, 30], as well as the level of correspondence to the steady state of the 1950s–1970s. [6].

Climate change in the hydrological regime and dynamics of the Black Sea waters and its individual water areas since the 1990s to the present [2, 4, 13, 14, 19, 26, 35, 36, 39] has led to changes in the parameters of established hydrological seasons. The seasonality of hydrological processes and phenomena, affecting changes in living conditions and reproduction of marine organisms, ultimately determines their biological cycles, including spawning phenology, species diversity, abundance, spatial distribution, and trophic relationships in the planktonic community [16, 29]. In the Black Sea, a shift and overlap in the timing of spawning of warm- and temperate-water fish in the initial and final phases of the hydrological seasons were noted, which led to the simultaneous presence of their eggs and larvae in ichthyoplankton. A decrease in the size and weight characteristics of larvae and an increase in the share of eggs and larvae of coastal fish species in open shelf waters were noted. Since the beginning of the 2000s, changes have been observed in the species diversity of the hydrobionts that form the food supply of fish larvae and their trophic relationships in the planktonic community [31–33, 41].

These changes affected the state of ichthyoplankton in the summer spawning season, since the regional conditions of heating of the upper layer of the sea and the formation of summer-type vertical thermal stratification in the initial phase of the summer hydrological season are the main limiting factors of spawning efficiency, survival of fish in the early stages of development, and replenishment of future generations. In the development of spawning, with a decrease in spatial sea surface temperature inhomogeneities, the role of dynamic factors increases, primarily the seasonal weakening of the Rim Current, activation of synoptic and regional quasi-stationary thermodynamic formations, and current convergence/divergence zones. On the one hand, activation of coastal shelf quasi-stationary anticyclonic eddies (AEs) contributes to the formation of stable zones with thermodynamic and feed-

ing conditions favorable for efficient spawning and survival of fish larvae. On the other hand, the water circulation system in AEs contributes to the active water exchange of coastal shelf waters and open sea waters, expansion of spawning areas, and exchange of species between individual water areas [28, 32, 33].

In addition to the main limiting environmental factors that determine the life cycle of Black Sea fish during the breeding season, a number of other abiotic factors also become limiting, directly or indirectly, among which wind-wave activity plays an important role. On the one hand, increased wind affects the structure and intensity of surface currents, and on the other, it deforms the vertical thermal structure of water due to the breaking of wind waves, and in both cases limits the behavioral reactions and physiological state of spawning fish [12, 32, 33].

In the eastern Black Sea, in recent decades predominant northern winds in the warm period periodically creates a "blocking" effect in the overall water circulation system, weakens northwestern transport, promotes increased meandering of the Rim Current jet, and changes the localization zones of coastal AEs [10, 24]. On the other hand, as a result of intensification of cyclonic activity over the studied water area, intraseasonal wind pumping of the upper water column occurs, which leads to inertial transformation of the Rim Current into a pronounced flow, oriented along the continental slope and in some places penetrating onto the shelf [9, 10]. Increased wind-wave mixing during strong storms transforms the thermal structure of the upper layer of the sea due to entrainment of colder waters from the seasonal thermocline (ST), can lower the water temperature to values unfavorable for the spawning of warm-water fish species, and thereby slow the onset of the summer spawning season or even interrupt it for a while [20, 27, 33]. In addition, the dynamic impact of wave breaking leads to increased mortality of fish eggs and larvae [6, 12].

The aim of this study was to analyze the species composition and spatial distribution of summer ichthyoplankton and the food supply of fish larvae during formation of the vertical thermal structure of summer-type waters under conditions of intensified atmospheric processes over the central and eastern Black Sea.

## MATERIALS AND METHODS

The material was collected from June 29 to August 9, 2021, in the northern Black Sea near the Crimean Peninsula and the coast of the Caucasus on the cruise 117 of the R/V *Professor Vodyanitsky*. Sampling of ichthyoplankton was done with a Hensen net (inlet diameter 0.7 m, sieve mesh 400 μm), and zooplankton were sampled with a Juday net (inlet diameter 36 cm, sieve mesh 145 μm). Samples were collected in vertical fishing mode from the bottom to the sea surface in the shallow shelf zone and from the lower boundary of the oxic zone ($\sigma_t$ = 16.2 according to data from a CTD probe of the IDRONAUT OCEAN SEVEN 320 PlusM complex) to the surface of the sea in the deep-sea part. Zoo- and ichthyoplankton were fixed in 4% borate-buffered solution of formaldehyde and processed under stationary conditions under an MBS-10 at a magnification of 8 × 2 and 8 × 4. Ichthyoplankton were identified according to [5]; zooplankton, according to [17, 18]. The species names of aquatic organisms are given according to the World Register of Marine Species [40]. The abundance of ichthyoplankton is given per $m^2$ of the surface. The abundance and biomass of zooplankton are given per $m^3$ of the entire fished layer.

The feeding of fish larvae was studied according to the method [8]. Anchovy and horse mackerel larvae were divided into size groups based on morphological parameters [7, 22]. The body weight of fish larvae was measured on a torsion bar scale, and juveniles were weighed on an AXIS ADG500C electronic scale. In studying the feeding of larvae, they were opened under an MBS-9 microscope; the gut contents were removed, in which food objects were identified; then they were counted and measured under a Nikon Eclipse 200 microscope at 40× magnification.

To analyze the hydrological regime and structure of surface currents, we used expeditionary data of vertical sounding by a CTD with IDRONAUT OCEAN SEVEN 320 PlusM complex, as well as materials from satellite observations of sea surface temperature (SST) and calculated maps of geostrophic and wind currents [15].

## RESULTS

**Hydrological characteristics of the study areas.** Difficult weather conditions with alternating periods of active wind-wave activity and relative calm with stable radiation heating of the upper layer of the sea, observed in the central and eastern Black Sea in June–July 2021, determined the specific features of the formation of the thermodynamic structure of waters and progress of research on cruise 117. As a result, the ichthyoplankton survey was carried out in two stages under relatively calm weather conditions in different areas of the sea off the coast of Crimea and the Caucasus. The rapid change in weather conditions and regional inertia of warming the upper layer of the sea led to identification of separate research sectors within the corresponding stages. The first stage of the survey took place from June 29 to July 7 in the vicinity of the Crimean Peninsula, where three sectors were identified: southwestern (the water area of Sevastopol and Vekovoy transect), the sector of the southern coast of Crimea (from Laspi Bay to the city of Alushta) and eastern (from Sudak Bay to Cape Chauda). The second stage of the survey was carried out from July 30 to

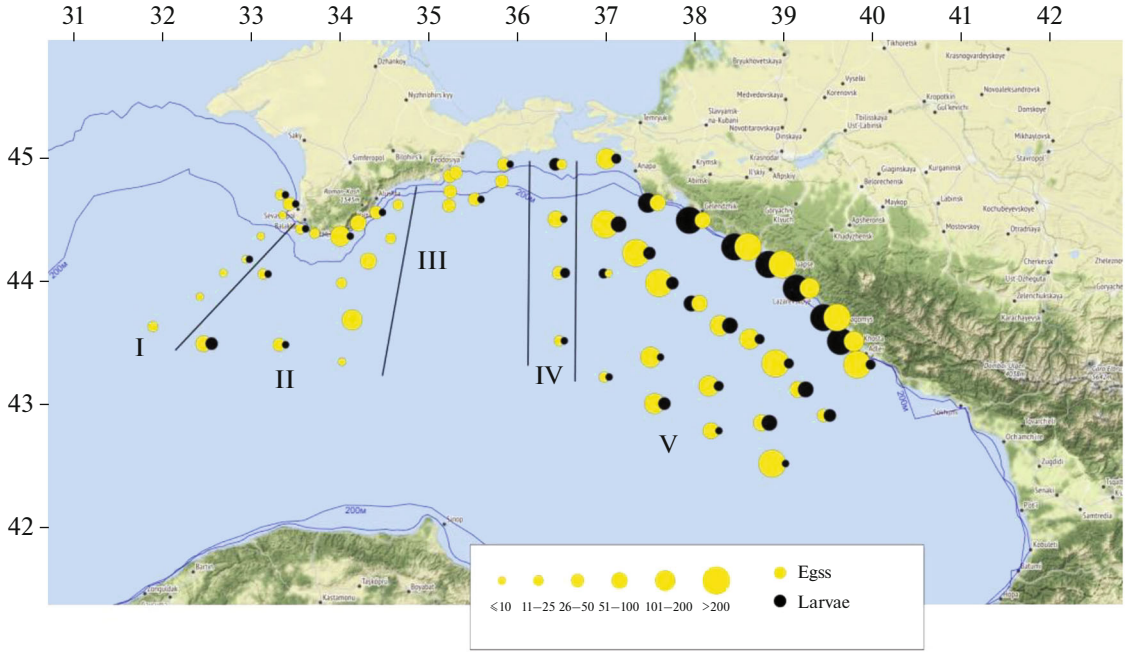


**Fig. 1.** Sketch map of spatial distribution of fish eggs and larvae on cruise 117 of R/V *Professor Vodyanitsky*. I, Southwestern sector; II, South coast sector; III, Eastern sector; IV, Kerch sector; V, Caucasus sector.

August 9 in sectors off the coast of the Caucasus and in the near Kerch Strait zone (Fig. 1).

The first stage of the survey was carried out in the initial phase of the summer hydrological season. It was preceded by a moderately warm winter hydrological season with an SST variability ranging from 10–11°C in early January, with minimum values from 8.0–8.5°C in February and gradually increasing to 11–12°C at the end of April. The spring hydrological season began only in early May and lasted until the middle of the last ten days of June with an increase in SST to 20–21°C. From the beginning of June to the middle of the last ten days, an increase in cyclonic activity was observed over the Black Sea, which slowed the formation of summer-type thermal stratification [3, 15].

By the beginning of the survey, most of the sea area had warmed up to 23–24°C. Minimum SST values (19–21°C) corresponded to the narrow coastal zone from Cape Fiolent to Feodosia Bay, as a result of transformed coastal upwelling, and the maximum (up to 24–25°C), shelf and open waters within the south coast sector (Fig. 2a).

The predominance of cloudy weather during the entire survey stage practically did not change the pattern of spatial changes in SST, only expanding the zone of maximum heating to the Feodosia Gulf (Fig. 2b).

The alternation of short periods of active radiative heating of the upper layer of the sea with periods of increased wind waves in June slowed the formation of the thermal structure of summer-type waters. During the survey, the thickness of the mixed layer was 6–9 m, and the SST had a weakly gradient structure with a lower boundary of up to 17–20 m. In the coastal upwelling zone, a layer of maximum vertical temperature gradients was observed from the surface to the bottom. After a long period since the last update of the cold intermediate layer in the winter of 2016–2017. [14], the minimum temperature values in the water column throughout the study area were noted in the range of 8.4–8.7°C at horizons from 40 to 47 m.

The salinity of surface waters varied from minimum values of 17.8–17.9‰ in the area of Feodosia Gulf to 18.2–18.4‰ in the Rim Current zone and 18.4–18.6‰ in the central regions of the sea.

Winter-type surface circulation observed until the first ten days of June was significantly transformed during the month into a system of individual dynamic structures without a pronounced Rim Current jet with the absence of coastal-shelf quasi-stationary AEs characteristic of this time of the year and was characterized by weak and unstable currents with speeds of up to 10–15 cm/s [1, 11, 15]. The most significant element of the dynamic structure of waters was the cyclonic meander of the Rim Current south of Feodosia Gulf (Figs. 2c, 2d).

In the middle of the first ten days of July, weather conditions were complicated by the emergence of another active cyclone in the Black Sea. Its subsequent deepening and localization in the northeastern part of the sea led to an increase in northerly and northeasterly winds up to 12–15 m/s and a sea state up to 4. The influence of this slow-moving cyclone in the study area was observed until July 9 [15]. The second stage of the survey was carried out from July 30 to August 9 in

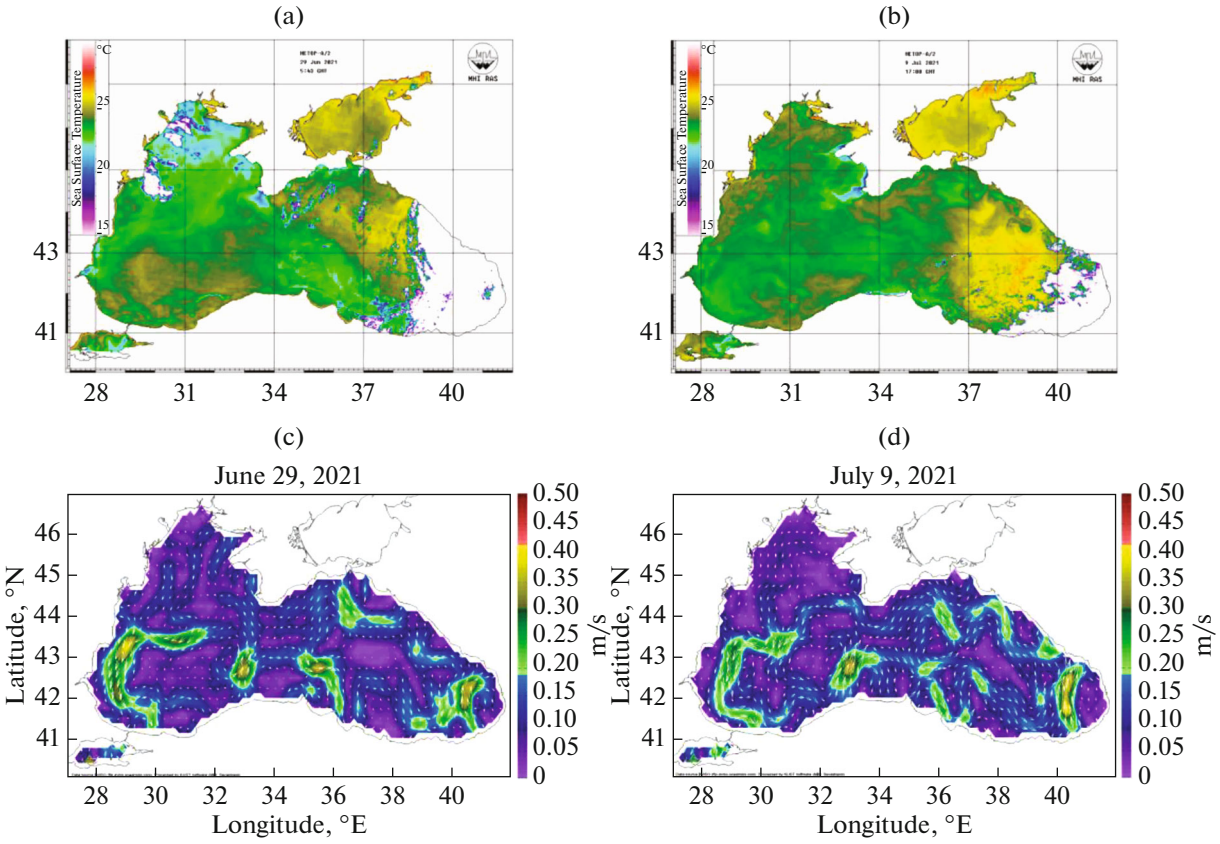


**Fig. 2.** Satellite maps of SST distribution (June 29, 2021 (a), July 9, 2021 (b)) and calculation schemes of geostrophic currents (June 29, 2021 (c), July 9, 2021 (d)) during first stage of survey [15].

the coastal shelf zone and in the deep sea along the coast of the Caucasus from the Kerch Strait to the border of the Russian economic zone in conditions of summer-type vertical thermal stratification with maximum heating of the upper layer of the sea. It should be noted that during July, the passing of another active cyclone (July 21–22) and an atmospheric front (July 26) was observed over the Black Sea [15].

The predominance of partly cloudy weather during the study period resulted in intense heating of surface waters from 25–27°C at the beginning of the survey to 28–29°C at the end. The highest SST values corresponded to the Rim Current jet and deep-sea areas in the southeastern part of the study area (Figs. 3a, 3b).

The thickness of the mixed layer varied from 7–11 m in deep-water areas to 12–14 m in the Rim Current jet and up to 16–17 m in the coastal shelf zone. The minimum temperature values in the core of the transformed cold intermediate layer were 8.6–8.8°C at a depth of 40–45 m in deep-sea areas to 85–90 m above the continental slope.

The salinity of surface waters varied widely from 18.6–18.85‰ in deep-sea areas to less than 18‰ in the narrow coastal zone with minimum values of 17.7–17.8‰ south of Gelendzhik in the discharge zones of mountain rivers.

By the beginning of the survey off the coast of the Caucasus, the structure of surface currents was characterized by the absence of a pronounced Rim Current jet, and of the synoptic and quasi-stationary thermodynamic formations, only the Caucasian AE appeared in the area of its typical location for this period of the year [11, 24] (Fig. 3c). By August 3, the Rim Current had already sharply intensified and turned into a continuous jet up to 40 km wide with speeds up to 30–35 m/s, oriented along the continental slope and in some places penetrating into the shelf zone of the Caucasus. By the end of the first ten days of August, the closed cyclonic core of the Rim Current had formed in the eastern part of the sea. The cyclonic meander of the Rim Current, previously observed south of Feodosia Gulf, "eroded" against the background of intensification of the Rim Current jet, which extended its influence to the coastal-shelf zone south of the Kerch Strait, and the Caucasian AE was deformed and localized in a narrow coastal zone in the southeast of the studied water area (Fig. 3d). The most likely reason for the transformation of the Rim Current into a pronounced flow atypical for this time of year was the inertial reaction of the water column to intraseasonal wind pumping during the period of intensified cyclonic activity over the eastern part of the sea in June–July [9, 10].

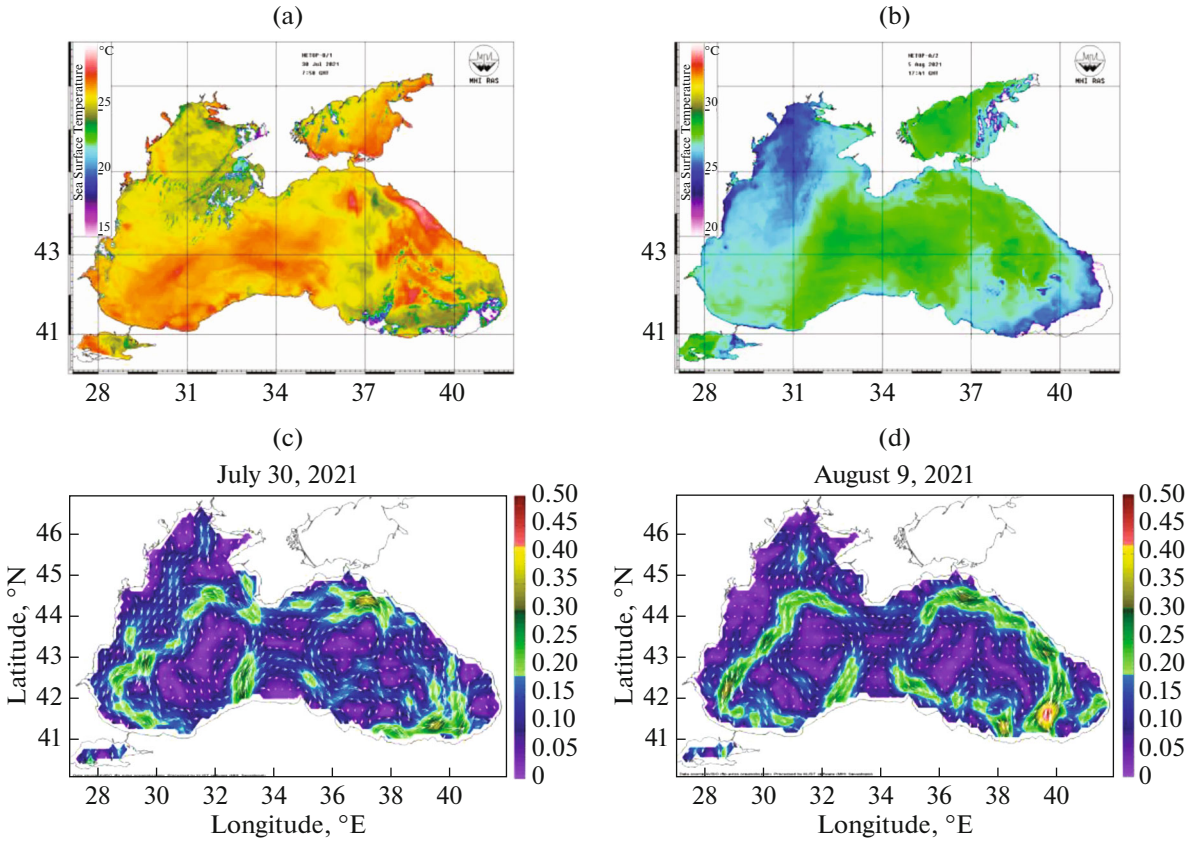


**Fig. 3.** Satellite maps of SST distribution (July 30, 2021 (a), August 5, 2021 (b)) and calculation schemes of geostrophic currents (July 30, 2021 (c), August 9, 2021 (d)) during second stage of survey [15].

Studies in the Kerch sector were complicated by an active slow-moving cyclone in the eastern Black Sea, which determined the weather conditions in this area from August 7 to 16 [15].

**Ichthyoplankton studies.** In total, eggs and larvae of 23 fish species from 15 families were identified during the study period, of which 19 were warm-water, and 4, temperate-water. The average number of eggs was 87.8, and larvae, 74.4 ind./m$^2$.

The first stage of the ichthyoplankton survey began from the southwestern sector at SST 19–21°C and a sea state of 1–2 (Figs. 1, 2a). Eggs and larvae of eight fish species (six warm-water and two temperate-water) were identified in ichthyoplankton. Spawning of warm-water fish species was just beginning: the average number of eggs was 12.1, and larvae, 0.9 ind./m$^2$. The samples were dominated by eggs of four species of pelagophilic fish (*Engraulis encrasicolus*, *Trachurus mediterraneus*, *Diplodus annularis*, and *Arnoglossus kessleri*). Their share in the total number of eggs was 78.5%, but spawning was still unsuccessful. The maximum number of eggs (40 ind./m$^2$) was observed in the coastal zone of Sevastopol above a depth of 70 m. Larvae were represented only by single individuals of *Syngnathus schmidti* and *Gobius niger*. Under the thermocline layer, spawning of temperate-water fish species continued, the eggs of were represented by *Merlangius merlangus* and *Sprattus sprattus*; larvae, only by *S. sprattus*.

In the sector of the southern coast of the Crimea, research was carried out when the upper layer of the sea warmed up to 21–25°C with a sea state of 2–3 (Figs. 1, 2b). Here, as in the southwestern sector, eggs and larvae of eight species of fish (five warm-water and three temperate-water) were noted. The average number of ichthyoplankton in the samples increased: eggs to 37.3, and larvae, to 2.5 ind./m$^2$. The maximum number of eggs was 73 ind./m$^2$, and larvae–18 ind./m$^2$ (Fig. 1; Table 1). Four types of eggs of warm-water pelagophilic fish species were noted, among which the eggs of *E. encrasicolus* (63.5%) dominated; the second most abundant was *T. mediterraneus* (over 23%), and eggs of *Pomatomus saltatrix* and *Serranus scriba* were encountered rarely.

Spawning was efficient only in *E. encrasicolus*: the share of its larvae in samples was 88%. Among the larvae of warm-water species, in addition to *E. encrasicolus*, *S. schmidti* was encountered sporadically. Spawning of temperate-water fish species continued, the share of *M. merlangus* and *S. sprattus* eggs in total

**Table 1.** Average abundance (ind./m$^2$) of eggs (numerator) and larvae (denominator) of fish in different study areas off coast of Crimea and Caucasus in summer 2021

| Taxonomic composition | Research sectors near Crimean Peninsula | | | | Caucasian sector 30.07–07.08 2021 |
|---|---|---|---|---|---|
| | Southwestern June 29–30, 2021 | South coast July 3–5, 2021 | Eastern July 6–7, 2021 | Kerch August 7–9, 2021 | |
| **Family: Engraulidae** | | | | | |
| *Engraulis encrasicolus* (Linnaeus, 1758) | 5.0 / 0 | 23.7 / 2.2 | 21.7 / 0 | 36.3 / 7.6 | 154.7 / 143.5 |
| **Family: Clupeidae** | | | | | |
| *Sprattus sprattus* (Linnaeus, 1758) | 0.7 / 0.3 | 0.5 / 0 | | | |
| **Family: Gadidae** | | | | | |
| *Merlangius merlangus* (Linnaeus, 1758) | 1.9 / 0 | 3.5 / 0 | 4.0 / 0 | | 0.8 / 0 |
| *Trisopterus lucus* (Linnaeus 1758) | | 0 / 0.2 | | | |
| *Gadidae* sp. | | | | | 0 / 0.1 |
| **Family**: **Syngnathidae** | | | | | |
| *Syngnathus schmidti* (Popov, 1927) | 0 / 0.3 | 0 / 0.1 | | 0 / 3.1 | 0 / 0.6 |
| **Family: Blenniidae** | | | | | |
| *Parablennius zvonimiri* (Kolombatovic, 1892) | | | | | 0 / 0.1 |
| *Blennius* sp. | | | | | 0 / 0.1 |
| **Family: Scorpaenidae** | | | | | |
| *Scorpaena porcus* (Linnaeus, 1758) | | | | | 0 / 0.3 |
| **Family: Callionymidae** | | | | | |
| *Callionymus* sp. | | | 0 / 0.5 | | 0.1 / 0 |
| **Family: Gobiidae** | | | | | |
| *Gobius niger* (Linnaeus, 1758) | 0 / 0.3 | | 0 / 0.7 | 0 / 1.3 | 0 / 1.2 |
| *Pomatoschistus marmoratus* (Risso, 1810) | | | 0 / 0.3 | | 0 / 1.7 |
| *P. minutus* (Pallas, 1770) | | | | | 0 / 0.3 |
| *P. pictus* (Malm, 1865) | | | | | 0 / 0.7 |
| *Gobius* sp. | | | | | 0 / 0.1 |
| **Family**: **Carangidae** | | | | | |
| *Trachurus mediterraneus* (Steindachner, 1868) | 1.6 / 0 | 8.7 / 0 | 5.7 / 0 | 1.3 / 2.5 | 4.6 / 13.9 |
| **Family: Mullidae** | | | | | |
| *Mullus barbatus* (Linnaeus, 1758) | | | | 1.3 / 0 | 0 / 0.4 |
| **Family: Pomatomidae** | | | | | |
| *Pomatomus saltatrix* (Linnaeus, 1766) | | 0.8 / 0 | 0.3 / 0 | | 0.3 / 0 |
| **Family**: **Serranidae** | | | | | |
| *Serranus scriba* (Linnaeus, 1758) | | 0.1 / 0 | | | |
| **Family: Sparidae** | | | | | |
| *Diplodus annularis* (Linnaeus, 1758) | 2.6 / 0 | | | | 0 / 0.7 |
| *Spicara smaris* (Linnaeus, 1758) | | | | | 0 / 0.2 |

**Table 1.** (Contd.)

| Taxonomic composition | Research sectors near Crimean Peninsula | | | | Caucasian sector 30.07–07.08 2021 |
|---|---|---|---|---|---|
| | Southwestern June 29–30, 2021 | South coast July 3–5, 2021 | Eastern July 6–7, 2021 | Kerch August 7–9, 2021 | |
| **Family: Trachinidae**<br>*Trachinus draco* (Linnaeus, 1758) | | | | | 0<br>0.3 |
| **Family: Bothidae**<br>*Arnoglossus kessleri* (Schmidt, 1915) | 0.3<br>0 | | | | 0<br>0.5 |
| **Number of species** | 8 | 8 | 7 | 5 | 20 |
| **Average abundance, ind./m$^2$** | 12.1<br>0.9 | 37.3<br>2.5 | 31.7<br>1.5 | 38.9<br>14.5 | 160.8<br>164.2 |
| **Standard deviation** | 12.2<br>1.3 | 30.3<br>5.0 | 7.97<br>1.88 | 29.09<br>10.23 | 111.7<br>272.3 |

was 11%. The larvae were represented by the Mediterranean invader *Trisopterus luscus*, 8% [31].

Due to the subsequent intensification of the sea state to 4 in the open part of the sea, the work area in the Eastern sector was limited to the coastal shelf zone (Fig. 1). SST varied from 22 to 24°C with an increase in temperature from the narrow coastal zone to the edge of the shelf (Fig. 2b). In ichthyoplankton, seven species of fish eggs and larvae were noted, with an average abundance of 31.7 and 1.5 ind./m$^2$, respectively. Eggs of *E. encrasicolus* (68.4%) and *T. mediterraneus* (18%) predominated; eggs of *P. saltatrix* were encountered singly. The larvae were represented by *Callionymus* sp. and two species of the family Gobiidae. The maximum abundance of eggs (45 ind./m$^2$) was noted above the continental slope, and larvae (5 ind./m$^2$), at a shallow-water station above a depth of 30 m. Of the temperate-water fish species, only eggs of *M. merlangus* (Table 1) were observed.

Along the coast of the Caucasus and in the Kerch sector, ichthyoplankton was collected after the break from July 8 to 29, associated with intensified cyclonic activity over the northeastern part of the sea at the end of the first and third ten days of July.

In the Caucasian sector, the survey was carried out under conditions of summer-type vertical thermal stratification with maximum heating of the upper layer of the sea from 25 to 29°C with a sea state of 1–2 (Figs. 3a, 3b). Here, 20 species of fish eggs and larvae from 14 families were observed (Fig. 1, Table 1). Warm-water fish were represented by 18 species. The average abundance of eggs off the coast of the Caucasus was 160.8; larvae, 164.2 ind./m$^2$. Spawning of 7 out of 9 pelagophilic fish was efficient. The samples were dominated by eggs and larvae of *E. encrasicolus*, amounting to 96.1 and 87.3% respectively. Shares of eggs and larvae *T. mediterraneus* did not exceed 3 and 8%, respectively, and eggs and larvae of other species were found sporadically. The species composition of larvae from demersal eggs expanded to include five species from the families Blenniidae and Gobiidae and *Spicara smaris*. The abundance of larvae of warm-water fish species was evidence of their massive efficient spawning. Temperate water species were represented only by rare eggs of *M. merlangus* and one larva of *Gadidae* sp.

In the Kerch sector, ichthyoplankton was collected from August 7 to 9 against an intensified Rim Current jet with an SST of 26.5–28.0°C and a sea state from 2 to 4 (Figs. 1, 3d; Table 1). Only five species from five families of the warm-water assemblage spawned here. The average number of eggs was 38.9; and larvae, 14.5 ind./m$^2$. The samples were dominated by *E. encrasicolus;* the percentage of its eggs was 93.4; of larvae, 52.4%. At three deep-sea stations, four species of fish eggs and larvae were identified in the ichthyoplankton, the average abundance of which was 45.9 and 10.1 ind./m$^2$ respectively. Only one station was made in shelf waters, where four species of fish eggs and larvae were also noted. However, here the larvae dominated in abundance, amounting to 27.6 ind./m$^2$, and the number of eggs did not exceed 17.6 ind./m$^2$.

**Size and weight characteristics and feeding of fish larvae.** A total of 1022 ind. of *E. encrasicolus* larvae were measured, collected in the first ten days of July in two sectors off the coast of Crimea and at the end of the survey, in the Caucasus and Kerch sectors. Larvae of *T. mediterraneus* in the amount of 111 ind. were collected only off the coast of the Caucasus and in the Kerch sector. Among the larvae of *E. encrasicolus*, both of the Crimean and the Caucasus coasts, larvae with a yolk type of feeding dominated, 87 and 74%, respectively. In the Kerch sector, the samples were dominated by larvae of *E. encrasicolus* on external feeding, amounting to 44%; the share of larvae on the yolk type of feeding did not exceed 33% (Fig. 4).

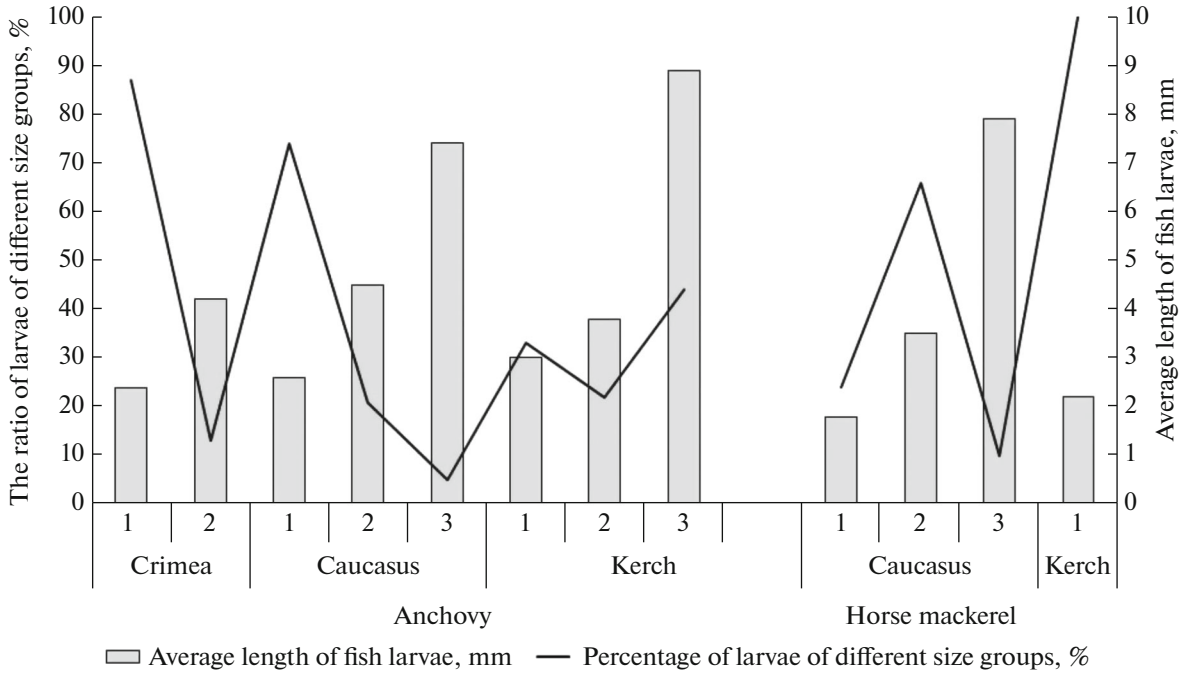


**Fig. 4.** Percentage ratio of larvae of different size groups of *E. encrasicolus* and *T. mediterraneus* (% of total abundance) and average length (mm) of fish larvae by group.

Feeding was studied in 56 larvae of *E. encrasicolus* with a length from 6.1 to 11.4 mm. In 18 larvae, highly digested food objects were found, represented by juvenile stages of copepods (Calanoida). Their number varied from 1 to 4 ind. in gut; length varied from 0.15 to 0.275 mm. In the remaining larvae, only an amorphous mass was found in the guts, which is typical of this species [7, 8].

In the Caucasus region, larvae of *T. mediterraneus* was represented in all size groups. Larvae with a mixed type of feeding dominated, their share amounting to 66% of the total. The share of larvae on the yolk type of feeding was 24%, on external feeding–10%. In addition to larvae, one specimen of juvenile *T. mediterraneus* was caught off the coast of the Caucasus length 18.3 mm and weight 38.5 mg was caught off the coast of the Caucasus. The Kerch sector was dominated by larvae of *T. mediterraneus* with a yolk type of feeding; large larvae were absent in the samples (Fig. 4).

Feeding of *T. mediterraneus* larvae was studied in 58 ind. 2.4–10.2 mm long, collected in the Caucasian sector. In 48 ind. with a mixed type of feeding (length 2.3–5.5 mm), copepods (Calanoida) of juvenile stages were found in the intestines, which accounted for 86% of the total number of consumed organisms, the share of cladocerans was 14%. The intestines were dominated by juvenile stages of copepods (Calanoida), among which *Acartia* predominated (*A. tonsa* + *A. clausi*). The contribution other copepod species—*Paracalanus parvus* and *Pseudocalanus elongatus*—was low, among cladocerans *Penilia avirostris* dominated. The sizes of cladocerans in the guts of larvae varied from 0.2 to 0.5 mm. The number of food objects varied from 1 to 3 ind. per gut. The length of copepods ranged from 0.1 to 0.375 mm, with small copepods no more than 0.2 mm long accounting for up to 70%.

In the guts of ten larvae of *T. mediterraneus* with external feeding, TL 5.8–10.2 mm and a weight of 1.8–8.7 mg, juvenile stages of copepods (Calanoida) dominated, accounting for 62% of the total amount of consumed objects. The length of copepods varied from 0.1 to 1.125 mm; copepodite stages with a length of about 0.4 mm dominated. The percentage of cladocerans in the diet of larvae increased to 38%. The number of food items varied from 1 to 4 ind. per gut.

**Fodder zooplankton.** During the research period, 25 taxa were found in zooplankton, among which fish food organisms predominated. Off the shore of the Crimean Peninsula, the average abundance of fodder zooplankton was 526.78 ind./m$^3$, and the average biomass, 39.45 mg/m$^3$. Copepods dominated, accounting for 91.4% of the total abundance of fodder zooplankton; the percentage of larvae of benthic organisms was 3.1%, while the percentage of cladocerans did not exceed 1.5% (Table 2).

Off the coast of the Caucasus, the average abundance of fodder zooplankton turned out to be 5.6 times higher than off the coast of Crimea, and amounted to 2965.9 ind./m$^3$ (Table 2). The average biomass of fodder zooplankton was 124 mg/m$^3$, which was three times higher than its value off the coast of Crimea. Cladocerans and copepods predominated in zooplank-

**Table 2.** Average abundance, biomass of main groups of zooplankton, and average mass of one ind. in each taxonomic group

| Taxon | Off shore of the Crimean Peninsula, end of June–July | | Off shore of the Caucasus, August | |
|---|---|---|---|---|
| | abundance, ind./m$^3$ | biomass, mg/m$^3$ | abundance, ind./m$^3$ | biomass, mg/m$^3$ |
| Copepods | 481.61 | 30.814 | 1098.93 | 57.289 |
| Average weight, mg/ind. | 0.0640 | | 0.0521 | |
| Cladocerans | 7.64 | 0.210 | 1510.75 | 53.506 |
| Average weight, mg/ind. | 0.0275 | | 0.0354 | |
| *Oikopleura dioica* | 23.48 | 0.017 | 26.53 | 0.017 |
| Average weight, mg/ind. | 0.0007 | | 0.0007 | |
| *Parasagitta setosa* | 6.05 | 8.337 | 105.08 | 12.698 |
| Average weight, mg/ind. | 1.3773 | | 0.1208 | |
| Larvae of benthic animals | 7.99 | 0.067 | 224.64 | 0.676 |
| Average weight, mg/ind. | 0.0084 | | 0.0032 | |
| Fodder zooplankton | 526.78 | 39.445 | 2965.94 | 124.189 |
| Average weight, mg/ind. | 0.0749 | | 0.0419 | |
| Average surface sea temperature, °C | 24.81 | | 27.75 | |

ton samples, accounting for 46 and 43% of the total abundance of all food organisms, respectively.

## DISCUSSION

Spawning of warm-water fish species in the Black Sea usually begins when the water temperature rises above 13°C. The main factor influencing the onset of mass efficient spawning is favorable temperature of the upper layer of the sea (18–26°C) and the formation of summer-type vertical thermal stratification, since warm-water fish species reproduce only in the well-heated mixing layer [6].

The first stage of the ichthyoplankton survey was carried out near the Crimean Peninsula from June 29 to July 7, 2021, in the initial phase of the summer hydrological season. On the shelf of the Crimean Peninsula, eggs and larvae of 13 species from 11 families were noted, and in the deep-sea area, 7 species from 6 families. The spawning intensity of warm-water fish species was still low. At the same time, the spawning of three temperate-water species continued, the share of eggs of which was 12.4%; of larvae, 10%. The average abundance of eggs on the shelf was 32.3 ind./m$^2$, and in deep-sea waters, 28.6 ind./m$^2$. The abundance of larvae on the shelf and in the deep sea were comparable, 3.1 and 3.3 ind./m$^2$ respectively. The ichthyoplankton species similarity index [38] in the shelf and deep-sea study areas was 0.60. In this study area, a comparable number of species in ichthyoplankton was observed in the initial phase of the 2018 summer hydrological season, when in the middle and last ten days of June, 12 species of fish eggs and larvae were noted in ichthyoplankton. However, whereas the abundance of larvae was quite comparable with the data for 2021 and averaged 2.9 ind./m$^2$, the number of eggs was half as much and did not exceed 15 ind./m$^2$ [34].

Although the SST near the Crimean Peninsula at the first stage of the survey in 2021 was favorable for the spawning of warm-water fish species, the activation of atmospheric processes, as well as increased wind and sea waves, led to a slowdown in the formation of thermodynamic conditions favorable for the onset of efficient spawning of warm-water fish species and to an increase in the share of dead eggs in samples [6, 12]. When the sea state increases to 4–5, the mortality rate of eggs in the upper layer of the sea can reach 85% [21]. Near the Crimean Peninsula on June 29–30, 2021, with a sea state of 1–2, share of dead eggs of *E. encrasicolus* was 60%, and in the period from July 1 to 7, when the sea state increased to 3–4, it increased to 77%.

The second stage of the survey was carried out in the coastal–shelf and deep-water zones of the northeastern sea off the coast of the Caucasus in the period from July 30 to August 7, 2021. The hydrological regime already corresponded to the period of the summer hydrological season with an established vertical thermal structure. The number of ichthyoplankton species on the shelf and in the deep-sea zone off the coast of the Caucasus was quite comparable—16 and 14, respectively. Species similarity index [38] was 0.66. The average abundance of eggs at shelf and deep-sea stations was 159.6 and 160.9 ind./m$^2$. The share of dead

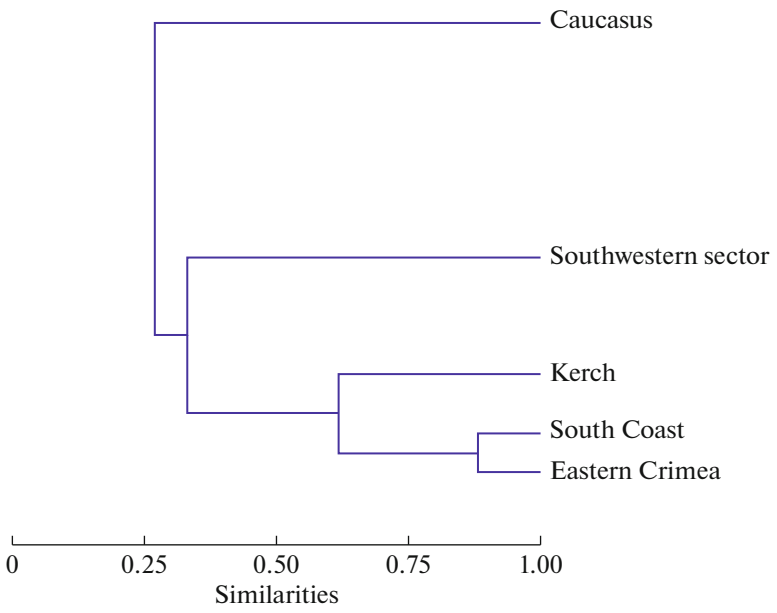


**Fig. 5.** Dendrogram of taxonomic similarity of ichthyoplankton assemblages in five research sectors (UPGMA method, Bray–Curtis similarity index [37]).

eggs in the samples was 58%. At the same time, the average abundance of larvae on the shelf was 452 ind./m$^2$, 4.7 times higher than in the deep-sea zone, and the maximum abundance reached 936 ind./m$^2$. Probably, the larvae were transported to the coastal–shelf zone by the Rim Current jet. The spawning activity of warm-water fish species, both on the shelf and in open waters, was significantly higher than previously observed by studies in this area [33]. Under similar hydrological conditions in the last ten days of July 2019, in the Caucasus region, 14 species of fish were noted in ichthyoplankton, and the average abundance of eggs was 1.8; of larvae, 13.6. This was lower than in August 2021. The maximum abundance of eggs and larvae was observed in the zone of coastal shelf waters with low salinity, 330 and 148 ind./m$^2$, respectively [33].

At the end of the second stage of the survey (August 7–9), ichthyoplankton was collected in the Kerch sector under conditions of an active slow-moving cyclone entering the eastern Black Sea [15] and an increasing sea state up to 4. Despite favorable temperature conditions, spawning activity of warm-water fish species sharply decreased. The average abundance of eggs (38.9 ind./m$^2$) was comparable to that off the coast of Crimea (SCC and Eastern sectors), where the survey was carried out in early July during a period of increased sea state in the open sea. The share of dead eggs dominating in samples of *E. encrasicolus* in the Kerch sector increased to 70%.

To compare the taxonomic similarity of ichthyoplankton assemblages from the five research sectors, cluster analysis was carried out using the unweighted pair group method with arithmetic mean (UPGMA) [37]. The distribution of clusters on the dendogram was determined by the peculiarities of the thermodynamic state of the waters during the survey (Fig. 5).

The maximum level of taxonomic similarity of ichthyoplankton is observed in the South Coast and Eastern sectors due to their regional proximity, correspondence to a single phase of the formation of the thermal structure of waters, as well as the degree of wind waves during the survey. The proximity of the Kerch sector, studied in August, to the South Coast and Eastern sectors, studied in early July, is associated with similar periods of wind-wave water conditions. During the ichthyoplankton survey in these areas, periods of increased sea state in the open part of the sea from 1–2 to 4 were observed as a result of two cyclones entering the Black Sea from July 5 to 9 and from August 7 to 16, which led to an increased sea state.

The inertial transformation of the Rim Current into a pronounced flow off the coast of the Caucasus coincided with mass spawning of warm-water fish species, which led to an increase in species diversity and high abundance of ichthyoplankton (Fig. 5). From a separate group of clusters in the Crimean Peninsula region, the Caucasus cluster is adjacent not to the territorially close Kerch, but to the Southwestern clusters, probably due to minimal sea conditions in these study areas.

The high abundance of fish larvae in the coastal shelf zone off the coast of the Caucasus was accompanied by a high abundance of fodder zooplankton (up to 3000 ind./m$^3$), probably due to their removal from deep-sea areas by the Rim Current jet. As the summer spawning season unfolded, a redistribution of the con-

tribution of the main species of fodder zooplankton occurred. Near the Crimean Peninsula, copepods dominated in abundance and biomass, and in the Caucasus area, the main increase in the abundance of fodder zooplankton occurred owing to cladocerans, the abundance of which was two orders of magnitude higher than off the coast of Crimea. The maximum abundance of cladocerans in the Black Sea usually occurs in August and coincides with the seasonal maximum surface temperature, observed off the coast of the Caucasus. Elevated temperatures also contributed to the active reproduction of benthic organisms, the larvae of which appeared in large numbers in the plankton off the coast of the Caucasus; their percentage in the total abundance of fodder zooplankton was 7.6%.

At the beginning of the ichthyoplankton survey in the Crimea region and at the end of the survey in the Caucasus region, the abundance of food objects in the food bolus of fish larvae varied from 1 to 4 ind. per gut. The larvae *E. encrasicolus* consumed juvenile stages of copepods (Calanoida) which predominanted in the fodder zooplankton. The food spectrum of larvae *T. mediterraneus* was expanded with the contribution of cladocerans, which, like copepods, predominated in the fodder zooplankton. In larvae of *T. mediterraneus* with a mixed type of feeding caught in the Caucasus region, juvenile stages of copepods (Calanoida) dominated in the guts, accounting for 86%; the share of cladocerans was 14% of the total amount of consumed organisms. The length of most consumed organisms did not exceed 0.2 mm. With the transition to external feeding, the share of cladocerans in the food bolus of *T. mediterraneus* larvae increased to 38%; there was an increase in the average length of food objects to 0.4 mm. In August 2021, the share of small cladocerans and copepods in the food bolus of *T. mediterraneus* larvae was significantly higher than in summer 2019 [41]. In the 1990s, during the period of mass development of the ctenophore *Mnemiopsis leidyi*—a predator and competitor in the nutrition of fish larvae and juveniles, with a low abundance of the small-sized fraction of cladocerans and copepods—fish larvae switched to feeding on other available food organisms, including pelagic larvae of benthic hydrobionts [25]. During the 2021 ichthyoplankton survey, pelagic forms of benthic hydrobionts were not found in the guts of fish larvae; apparently, this food is forced and is used in the nutrition of larvae only in the absence of the main food items: copepods and cladocerans.

## CONCLUSIONS

The intensification of atmospheric processes over the eastern half of the Black Sea in June–July 2021 and the alternating periods of active heating of the upper layer of the Black Sea with periods of increased wind waves led to a slowdown in the formation of thermodynamic conditions favorable for the onset of spawning of warm-water fish species. As a result, the beginning of the summer spawning season has shifted to an abnormally late date: the first ten days of July. Off shore of the Crimean Peninsula, 13 species of fish were recorded in the initial phase of the summer hydrological season. The average abundance of eggs was 29.1, and larvae, 2.0 ind./m$^2$. The maximum abundance of eggs and larvae was observed in the South Coast sector: 37.3 and 2.5 ind./m$^2$, respectively. In the Caucasus region, with a stable state of parameters of the summer hydrological season with maximum heating of the upper layer of the sea and the formation of vertical thermal stratification of summer-type waters, 20 species of fish eggs and larvae were noted in ichthyoplankton; their average abundance was 159.6 and 160.9 ind./m$^2$, respectively.

Increased wind waves during research off the Crimean Peninsula led to an increase in the mortality of *E. encrasicoluss*, egss from 60% when sea state was 1–2 and 77% when sea state was 3–4. Off the coast of the Caucasus in a sea state of 1–2, the mortality rate of *E. encrasicolus* eggs on average was 58%, and in the Kerch sector with a sea state of 3–4, it increased to 70%.

Cluster analysis showed that the similarity of the taxonomic composition of ichthyoplankton in different research sectors was governed by the peculiarities of the thermodynamic state of the waters during the survey. Against this background, the maximum proximity of individual clusters, regardless of the area, was determined by the intensity of wind waves during the survey.

Near the Crimean Peninsula, with unsteady circulation of surface waters in the initial phase of formation of the summer-type vertical thermal structure of waters, a quasi-uniform distribution of the abundance of fish eggs and larvae is observed in shelf and deep-sea areas of the sea.

In the area of the Caucasian research sector, wind pumping of the upper layer of the sea during intensifying cyclonic activity in June–July 2021 at the beginning of the first ten days of August led to a significant restructuring of surface water circulation in the studied water area. Transformation of the Rim Current into a continuous flow with speeds up to 30–35 m/s and its displacement to the edge of the shelf along the Caucasian coast up to the Kerch Strait did not affect the spawning activity of mass commercial fish species. The average abundance of eggs on the shelf and in the deep-sea zone was comparable: about 160 ind./m$^2$. At the same time, due to the shift of the Rim Current jet to the coastal shelf zone, the average abundance of fish larvae reached 452 ind./m$^2$, which was almost five times higher than that in the deep-sea zone, and their maximum abundance was 936 ind./m$^2$.

Analysis of the feeding spectrum of fish larvae of different sizes showed that the most favorable feeding conditions were observed off the coast of the Caucasus. In this area, small-sized fractions of copepods and cladocerans predominated, while their abundance and

biomass were significantly higher than in the Crimean Peninsula, which collectively favored the survival of fish larvae.

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## ETHICS APPROVAL AND CONSENT TO PARTICIPATE

All studies were conducted in accordance with the principles of biomedical ethics as set out in the 1964 Declaration of Helsinki and its subsequent amendments. The study was approved by the bioethics commission of the Federal Research Center Kovalevsky Institute of Biology of the Southern Seas, Protocol no. 4/23 of October 26, 2023.

## CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

## REFERENCES

1. V. N. Belokopytov and N. V. Nikolsky, "Stable anticyclonic eddies off the southern and western coasts of Crimea," Ekol. Bezop. Pribrezhn. Shelf. Zon Morya **1**, 47–53 (2015).
2. V. N. Belokopytov, Extended Abstract of Doctoral Dissertation in Geography (Mor. Gidrofiz. Inst., Sevastopol, 2017).
3. A. V. Gavrikov, O. V. Zovina, O. A. Razorenova, et al., "Extreme precipitation in June 2021 over the Black Sea in the context of long-term climate change," Oceanology **62** (3), 303–309 (2022). https://doi.org/10.1134/S0001437022030055
4. A. I. Ginzburg, A. G. Kostyanoy, I. V. Serykh, and S. A. Lebedev, "Climate Change in the Hydrometeorological Parameters of the Black and Azov Seas (1980–2020)," Oceanology **61** (6), 745–756 (2021). https://doi.org/10.1134/S0001437021060060
5. T. V. Dekhnik, *Ichthyoplankton of the Black Sea* (Naukova dumka, Kiev, 1973) [in Russian].
6. T. V. Dekhnik, "Dynamics of abundance, survival and elimination of eggs and larvae of common fish," in *Fundamentals of Biological Productivity of the Black Sea*, Ed. by V. N. Greze (Naukova dumka, Kiev, 1979), pp. 272–279 [in Russian].
7. L. A. Duka, "Nutrition of Black Sea anchovy larvae," Tr. Sevastopol. Biol. St. **14**, 242–256 (1961).
8. L. A. Duka and V. I. Sinyukova, *Guidelines for Studying the Nutrition of Marine Fish Larvae and Fry under Natural and Experimental Conditions* (Naukova dumka, Kiev, 1976) [in Russian].
9. A. G. Zatsepin, V. V. Kremenetsky, V. B. Piotukh, et al., "Formation of the coastal current in the Black Sea caused by spatially inhomogeneous wind forcing upon the upper quasi-homogeneous layer," Oceanology **48** (2), 159–174 (2008).
10. A. G. Zatsepin, D. N. Yolkin, A. O. Korzh, et al., "On the influence of current variability in the deep-water zone of the Black Sea on the dynamics of waters of the narrow North Caucasus shelf," Mor. Gidrofiz. Zh. **3**, 16–25 (2016). https://doi.org/10.22449/0233-7584-2016-3-16-25
11. V. A. Ivanov and V. N. Belokopytov, *Oceanography of the Black Sea* (EKOSI-Gidrofizika, Sevastopol, 2011) [in Russian].
12. B. V. Koshelev, *Ecology of Fish Reproduction* (Nauka, Moscow, 1984) [in Russian].
13. N. V. Markova, V. N. Belokopytov, O. A. Dymova, and N. A. Miklashevskaya, "Assessment of climatic fields of temperature and salinity of the Black Sea waters for the modern period (1991–2020)," Mor. Gidrofiz. Zh. **37** (4), 423–435 (2021).
14. A. N. Morozov and E. V. Mankovskaya, "Cold intermediate layer of the Black Sea according to expeditionary research in 2016–2019," Ekol. Bezop. Pribrezhn. Shelf. Zon Morya **2**, 5–16 (2020).
15. Marine portal. Marine Hydrophysical Institute, Russian Academy of Sciences. http://dvs.net.ru/mp/index_ru.shtml. Accessed June 1, 2022.
16. Odum, E., *Fundamentals of Ecology* (Saunders, Philadelphia, 1953), Vol. 2.
17. *Key to the Fauna of the Black and Azov Seas* (Naukova dumka, Kiev, 1969), Vol. 2 [in Russian].
18. *Key to the Fauna of the Black and Azov Seas* (Naukova dumka, Kiev, 1972), Vol. 3 [in Russian].
19. O. I. Podymov, A. G. Zatsepin, and V. V. Ocherednik, "Increase in salinity and temperature in the active layer of the northeastern part of the Black Sea from 2010 to 2020," Mor. Gidrofiz. Zh. **37** (3), 279–287 (2021). https://doi.org/10.22449/0233-7584-2021-3-279-287
20. A. B. Polonsky and A. N. Serebrennikov, "On the mechanism of a dramatic sea surface temperature drop

in the northwest Black Sea and off the Crimean coast," Meteorol. Gidrol. **2**, 31–40 (2023).

21. N. I. Revina, "On the issue of reproduction and survival of eggs and juveniles of large horse mackerel in the Black Sea," Tr. Azovo-Chernomor. NII mor. Ryb. Khoz. Okeanogr. **7**, 9–10 (1958).
22. V. I. Sinyukova, "Nutrition of Black Sea horse mackerel larvae," Tr. Sevastop. Biol. St. **15**, 302–325 (1964).
23. *Current State of the Ichthyofauna of the Black Sea*, ed. S. M. Konovalov (Ekosi-gidrofizika, Sevastopol, 1995) [in Russian].
24. V. B. Titov, "Characteristics of the Main Black Sea Current and near-shore anticyclonic eddies in the Russian sector of the Black Sea," Oceanology **42** (5), 637–645 (2002).
25. A. V. Tkach, "Nutrition of Black Sea fish larvae," in *Current State of the Ichthyofauna of the Black Sea: Collection of Works of the National Academy of Sciences of Ukraine*, Ed. by S. M. Konovalov (InBYuM, Sevastopol, 1996), pp. 153–168 [in Russian].
26. O. A. Troshchenko and A. A. Subbotin, "Abiotic factors and conditions of hydrobiont habitats in the coastal zone of South-East Crimea. Hydrological features," in Biology of the Black Sea off the Coast of South-Eastern Crimea, Ed. by N. S. Kostenko (ARIAL, Simferopol, 2018), pp. 46–59 [in Russian].
27. O. M. Phillips, *The Dynamics of the Upper Ocean* (Cambridge Univ. Press, 1966).
28. E. G. Arashkevich, A. V. Drits, A. G. Timonin, and V. V. Krementsky, "Variability of spatial zooplankton distribution affected by the water dynamics in the northeastern part of the Black Sea," Oceanology **42** (Suppl. 1), S79–S94 (2002).
29. T. D. Auth, E. A. Daly, R. D. Brodeur, and J. L. Fisher, "Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean," Global Change Biology **24** (11), 259–272 (2017).
30. T. N. Klimova, "Dynamics of species composition and numbers of ichthyoplankton of the Black Sea in the area of the Crimea in the summer periods of 1988–1992," J. Ichthyol. **38** (8), 645–651 (1998).
31. T. Klimova and P. Podrezova, "Seasonal distribution of the Black Sea ichthyoplankton near the Crimean Peninsula," Reg. Stud. Mar. Sci. **24**, 260–269 (2018).
32. T. N. Klimova, A. A. Subbotin, I. V. Vdodovich, et al., "Distribution of ichthyoplankton in relation to specifics of hydrological regime off the Crimean coast (the Black Sea) in the spring–summer season 2017," J. Ichthyology **61** (2), 259–269 (2021).
33. T. N. Klimova, A. A. Subbotin, P. S. Podrezova, and S. V. Kurshakov, "Ichthyoplankton of the Black Sea during the period of mass spawning of warm-water fish species," Oceanology **62** (4), 517–527 (2022).
34. T. N. Klimova, P. S. Podrezova, A. A. Subbotin, et al., "Ichthyoplankton of the Black Sea at the beginning of the summer spawning season 2018," Water Resour. **49** (3), 493–502 (2022).
35. A. A. Kubryakov, S. V. Stanichny, A. G. Zatsepin, and V. V. Kremenetskiy, "Long-term variations of the Black Sea dynamics and their impact on the marine ecosystem," J. Mar. Syst. **163**, 80–94 (2016).
36. T. Oguz, "Controls of Multiple Stressors on the Black Sea Fishery," Front. Mar. Sci. **4**, 1–12 (2017).
37. H. C. Romesburg, *Cluster Analysis for Researchers* (Robert E. Krieger Pub. Co., Florida, 1990).
38. T. Sörensen, "A method of establishing groups of equal amplitude in plant sociology based on similarity of species content," Kongelige Danske Videnskabernes Selskab. Biol. Krifter. **4**, 1–34 (1948).
39. C. Turan, D. Erguden, M. Gürlek, "Climate Change and Biodiversity Effects in Turkish Seas," Nat. Eng. Sci. **1** (2), 15–24 (2016).
40. WoRMS Editorial Board, World register of marine species. Version 02/2022 (2021). https://www.marinespecies.org/index.php.
41. Yu. A. Zagorodnyaya, I. V. Vdodovich, P. S. Pjdrezova, T. N. Klimova, "Species composition and feeding of the fish larvae in the northern part of the Black Sea in July–August 2019," J. Ichthyol. **62** (6), 1042–1052 (2022).